



Limb Morphometrics in Carnivora: Locomotion, Phylogeny and Size

Análisis morfométrico del esqueleto apendicular en Carnivora: Locomoción, filogenia y alometría

Eloy Gálvez López

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PhD Thesis 2014

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Barcelona, Julio 2014

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Locomoción, filogenia y alometría

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Eloy Gálvez López
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“All the colors of the rainbow,
hidden ‘neath my skin.
Hearts have colors, don’t we all know?
Red runs through our veins.

Feel the fire burning up,
inspire me with blood of blue and green.
I have hope,
inside is not a heart,
but a kaleidoscope.”

Kaleidoscope Heart,
Sara Bareilles

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ABSTRACT

The effect of function, phylogeny, and size, on the morphology of the limb bones in Carnivora was studied. First, the locomotor strategy of non-arboreal mammals on narrow supports was determined, and compared to that of arboreal mammals. To do that, kinematic and coordination variables were studied in the cat (scansorial) and the dog (terrestrial). Arboreal, scansorial and terrestrial species used different strategies to increase stability on narrow supports. However, common features were also observed, such as reducing swing phase duration and using a crouched posture. Secondly, the factors influencing limb morphology were explored and quantified using univariate, bivariate, and multivariate approaches. For the univariate and scaling (bivariate) approaches, a set of 43 variables were measured in the limb bones of 435 specimens belonging to 143 species of Carnivora. The multivariate approach consisted in the study of scapula shape using geometric morphometrics methods. For this analysis, 34 3D-landmarks were digitized on 213 scapulas from 101 carnivoran species. In all those studies, limb bone morphology was determined by the complex interaction of size, phylogenetic history, and function. Conformity to either the elastic or the geometric similarity hypotheses was low. Furthermore, differential scaling was detected in most variables, as well as significant differences between the scaling exponents obtained using traditional regression methods and those using phylogenetically independent contrasts. Both phylogeny and adaptation caused significant deviations from the scaling pattern of the whole order. Locomotor adaptations in the scapula shape of extant carnivorans seemed independent of size or shared ancestry and reflected the particular muscular function associated to different locomotor habits. Finally, a medium-sized, forest-dwelling mammal with mixed adaptations for arboreal and terrestrial habits is supported as the hypothetical ancestor for extant Carnivora.

RESUMEN

La morfología del esqueleto apendicular en Carnivora se estudió desde un punto de vista funcional, filogenético y alométrico. En primer lugar se determinó la estrategia locomotora empleada por los mamíferos no arborícolas sobre soportes estrechos, que se comparó con la de los mamíferos arborícolas. Para ello, se estudiaron ciertas variables cinemáticas y de coordinación en el gato (trepador) y el perro (terrestre). Las especies arborícolas, trepadoras y terrestres usan estrategias diferentes para aumentar su estabilidad sobre soportes estrechos. No obstante, también se observaron características comunes, como presentar fases de recuperación más cortas y usar una postura agazapada. En segundo lugar, se exploraron y cuantificaron los factores que determinan la morfología apendicular usando enfoques univariantes, bivariantes y multivariantes. Para los dos primeros se midieron 43 variables en el esqueleto apendicular de 435 especímenes de 143 especies de Carnivora. El enfoque multivariante consistió en un estudio de la forma de la escápula usando morfometría geométrica. Para ello, las coordenadas 3D de 34 puntos homólogos se digitalizaron en 213 escápulas de 101 especies de Carnivora. En todos estos estudios, la morfología del esqueleto apendicular respondía a la compleja interacción del tamaño corporal, el efecto filogenético y la función. La conformidad con las hipótesis de similitud geométrica y elástica del patrón de alometría del esqueleto apendicular fue baja, y se detectó alometría compleja en la mayoría de variables estudiadas. Tanto la filogenia como la adaptación causa-ron desviaciones significativas del patrón alométrico del orden. Además, los exponentes alométricos obtenidos usando regresiones tradicionales y de contrastes independientes fueron significativamente diferentes. Las adaptaciones locomotoras en la forma escapular parecían independientes del tamaño y de un origen común. Por último, se respalda que los carnívoros actuales evolucionaron a partir de un ancestro común de mediano tamaño, con adaptaciones mixtas a hábitos terrestres y arborícolas, y que habitaba zonas boscosas .

General Introduction

INTRODUCTION

Animal locomotion

Animals move to find food, a mate, a suitable place to settle, and to escape predators or a stressful environment (Biewener, 2003). Thus, **animal locomotion**, which is the act of self-propulsion by an animal, is essential to its survival, resulting in selective pressures shaping the locomotor systems and strategies used by moving animals (Alexander, 2002). Several modes of locomotion, or **locomotor habits**, can be distinguished relative to the substrate in which the animal is moving. Swimming in water, digging through soil, climbing inclined supports, flying through the air... all of these habits require particular locomotor strategies depending on the properties of the substrate (i.e. particular modifications to the dynamics, kinematics, and coordination, of locomotion; Alexander, 2002; Biewener, 2003). For instance, aquatic animals are not overly concerned by supporting their weight, since they have developed systems to achieve neutral buoyancy. However, due to the high density and viscosity of water, drag forces represent an impressive hindrance to their movement. On the other hand, in terrestrial locomotion (Box A), gravitational forces are the main factor to overcome, since the low density and viscosity of air impose a small drag. Furthermore, those gravitational forces pose different problems to an animal when moving on the ground or climbing up a branch. In the former case, gravity pulls the body towards the substrate, risking the collapse of the limbs (e.g. Day & Jayne, 2007). In arboreal locomotion, gravitational forces can also cause the animal to roll (rotate around their sagittal axis) and topple from the branch because all their support points are effectively collinear (Cartmill, 1985). Finally, most animals do not always move on the same substrate and thus are able to perform several modes of locomotion. The sum of all the locomotor habits of an animal, as well as the frequency of its use, represents its **locomotor pattern** (or repertoire). For instance, the locomotor pattern of a tiger mainly

Box A. Considerations on the use of the term terrestrial.

WHAT IS A TERRESTRIAL MAMMAL?

Classically, terrestrial mammals are those that live mainly or exclusively on land (e.g. tigers, horses), as opposed to aquatic mammals, which live mainly or exclusively in the water (e.g. seals, whales). However, according to its locomotion, a terrestrial mammal is that which moves on land, as opposed, again, to aquatic mammals (those which move in water) and, also, to flying mammals, which move through air (and would be terrestrial mammals in the first sense). Furthermore, terrestrial locomotion is not restricted to walking and running over ground: some mammals move on the branches high in the forest canopy, while others dig their way through the ground. The former are known as arboreal mammals and the latter as fossorial mammals, and both are usually considered separately from other terrestrial mammals in ecomorphological studies. What is thus a terrestrial mammal?

Subtracting the aforementioned opposites and exceptions, terrestrial mammals would be, in locomotor terms, all the non-aquatic, non-flying, non-arboreal, non-fossorial species, which is a less than adequate description indeed. Furthermore, where do we draw the line between arboreal and terrestrial? Or between fossorial and terrestrial? This is particularly important in studies on the locomotor adaptations of mammals, as this dissertation, since an ambiguous definition could lead to spurious results. Thus, throughout this dissertation the term **terrestrial** is only used to designate mammals that rarely or never climb, swim or fly, and that do not dig regularly for food. Similarly, **overground locomotion** is used to describe animals moving on the ground, as opposed to arboreal locomotion (taking place in trees), fossorial locomotion (under ground), aquatic locomotion (swimming), and aerial locomotion (flying).

consists of walking and running on the ground, with less frequent amounts of climbing and swimming (e.g. Mazák, 1981; Wilson & Mittermeier, 2009).

Locomotion in vertebrates is possible thanks to their particular **musculoskeletal system**, which comprises bones, muscles, tendons, and other connective tissues. Particularly, bones provide a place for muscles to attach and, through movable joints, they also constitute a system of levers upon which muscles act to produce movement. That is, muscles generate the forces required for locomotion, while bone displacements transmit those forces to the external environment to produce movement (Alexander, 2002;

Biewener, 2003). Thus, bone morphology (i.e., its form and structure; Box B) is closely related to the size and position of attached muscles, and also to the magnitude and direction of the forces they exert (e.g. Roberts, 1974; Argot, 2001). This way, the study of bone morphology not only allows the identification of functional adaptations on the bones, but also the use of those adaptations to infer the morphology and force production of associated muscles (e.g. Smith & Savage, 1956; Roberts, 1974; English, 1977; Cartmill, 1985; Hildebrand, 1985*a, b*). Furthermore, by understanding the functional morphology of the bones of extant species, the biology and ecology of extinct species can be reconstructed from their skeletal fossil remains (e.g. Thomason, 1997; Argot, 2001; Spaulding & Flynn, 2009). These kinds of studies belong to the field of **ecomorphology**, or ecological morphology (Bock, 1990; Ricklefs & Miller, 1999).

When studying the adaptations to particular locomotor habits, ecomorphological studies usually follow one of two alternative approaches: categories or continua. In the

MORPHOLOGY, MORPHOMETRICS, FORM AND SHAPE

In biology, **morphology** is the branch devoted to the study of the form and structure of organisms. It has many subbranches, like anatomy, which is concerned with the bodily structure and shape of organisms, and functional morphology, which studies the relationship between the structure and function of form. **Morphometrics**, or morphometry, refers to the quantitative analysis of form (i.e., the study of shape variation and its covariation with other variables; Bookstein, 1991; Zelditch et al., 2004).

Traditionally, morphometrics consisted in the application of statistics to groups of morphological variables, generally linear measurements, ratios and angles. However, this kind of measurements is usually highly correlated with the size of the object, biasing the patterns of shape variation (Bookstein et al., 1985). In an attempt to disengage shape from size, several landmark-based methods (i.e., based on points and their coordinates, not on the linear distances between those points) were developed at the late 20th century (Bookstein, 1991; Zelditch et al., 2004). These methods are known as **geometric morphometrics**, and are considered the fusion of geometry and biology.

This new methodology required a more accurate definition of form. The **shape** of an object consists in its geometric properties that are invariant to changes in translation, rotation and scale (Bookstein, 1991). The term **form** is reserved for the shape and size of an object, that is, all its geometric information except for its position and orientation.

Box B. Definition of morphometrics, shape and form.

first approach, a locomotor category is assigned to each species based either on the main habit of their locomotor pattern (e.g. Van Valkenburgh, 1987; Fabre et al., 2013), or on a combination of locomotor habit and some biomechanical property of their locomotion (e.g. gait: Taylor, 1974; Schutz & Guralnick, 2007). Collectively, these categories are usually known as locomotor behaviors or **locomotor types**. While this approach simplifies the interpretation of the results, it also has some inherent problems that complicate results comparison between studies. One problem lies in the categories themselves, since each author tends to define its own set of locomotor types. Another problem is the subjectivity of the assignment, particularly when categories are defined based on the frequency of use of some locomotor habit (e.g. climbing: terrestrial < scansorial < arboreal).

In the second approach, locomotor types are considered to occur along a continuum. Thus, the degree of adaptation to a particular locomotor habit is described quantitatively in locomotor variables, usually coded as multistate, ordered characters (e.g. Iwaniuk et al., 1999, quantified arboreality from 0 to 4). Then, morphometric variables are regressed against the locomotor variable to assess their relationship with that particular locomotor habit. Although this approach is theoretically more realistic, since most locomotor adaptations are quantitative traits, it also has its problems. First, all species that do not present the locomotor habit measured by a particular locomotor variable receive the same score, regardless of whether they present marked adaptations to another locomotor habit. Thus, if the sampled species are not carefully selected, the added statistical noise could cloud an otherwise significant relation between the morphometric and locomotor variables. Second, as in the previous approach, some degree of subjectivity is involved in quantifying locomotor habit.

Consequently, in this dissertation an intermediate approach is used to study locomotor adaptations. As in the first approach, locomotor patterns are categorized into locomotor types (based on the amount of climbing, swimming, or digging). However, when possible, a continuum of locomotor types was established based on the frequency of use of those locomotor habits, as in the second approach.

Size, scaling and similarity hypothesis

Size matters. As animals grow, or change their size during evolution, the properties of their musculoskeletal system and the parameters defining their locomotion change at different rates (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003). These size-

related changes are known as **scaling** and are usually expressed using the **power equation**, in which the relationship between two such properties or parameters (i.e., variables; x , y) is defined by a coefficient (a) and an allometric exponent (b) (Huxley, 1932):

$$y = a \cdot x^b \quad (1)$$

The allometric exponent determines the rate of change in variable y relative to changes in variable x (Biewener, 2003). When the relationship between two variables remains proportional as size changes, **isometric scaling** occurs. On the other hand, any deviation from isometry is considered **allometric scaling**.

In order to understand the consequences of scaling and thus be able to predict how these musculoskeletal and locomotor variables would be affected by variations in body size, several hypotheses have been proposed. These are known as **similarity hypotheses** and provide theoretical values for the allometric exponent in isometric scaling based on different biomechanical constraints. For instance, the **geometric** similarity hypothesis is grounded on Euclidean geometry and the square-cube law. According to the former, two objects (or organisms) are geometrically similar if their linear dimensions can be made equal by multiplying those of one of them by a constant ($l_1 = k \cdot l_2$). Following the square-cube law, when an organism undergoes a proportional increase in size, its new surface area is proportional to the square of the multiplier ($A_1 = k^2 \cdot A_2$) and its new volume is proportional to the cube of the multiplier ($V_1 = k^3 \cdot V_2$) (Galilei, 1638/1933). Assuming a constant density (ρ), which would be logical if both organisms are made of the same materials, body mass (M_b) would also be proportional to k^3 ($M_b = \rho \cdot V \propto \rho \cdot l^3$). Then, geometrically similar animals made of the same materials should present linear dimensions proportional to body mass^{1/3} (e.g. Hill, 1950; Fig. 1). On the other hand, the **elastic** similarity hypothesis is based on the assumption that organisms have evolved to withstand similarly the effect of gravity (i.e., to resist buckling and bending loads similarly)

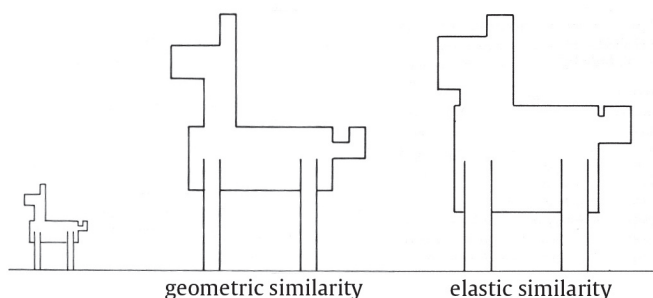


Figure 1. Similarity hypotheses. The large silhouettes represent scaled version of the small animal. In the geometrically scaled animal, all linear dimensions are thrice those of the small animal. In the elastically scaled animal, however, since diameters scale to length^{3/2}, the lengths equal thrice those of the small one, while diameters are $3^{3/2} \cong 5$ times larger. (Modified after Alexander, 1985.)

(McMahon, 1973). Thus, in order to maintain this similar elastic recovery, and again assuming constant density, the lengths (l) of an animal should be proportional to body mass^{1/4}, while its diameters (d) should scale as body mass^{3/8} (Fig. 1). Other similarity hypotheses are based on maintaining constant stresses, either while standing (**static stress** similarity: $l \propto M_b^{1/5}$, $d \propto M_b^{2/5}$; McMahon, 1975) or during locomotion (**dynamic stress** similarity: extends geometric similarity to locomotor variables; Alexander & Jayes, 1983). A final example of similarity hypothesis would be the recently proposed **Garcia-Silva model** for long bone allometry (Garcia & da Silva, 2006), which is based on the premise that bone scaling is related to muscle force scaling (Selker & Carter, 1989). In this model, the resultant muscle force acting on a bone is divided in two components, namely a compressive or axial component (F_{ax}) and a bending or transverse component (F_t), each scaling to body mass with its own allometric exponent (b_{ax} and b_t , respectively). Assuming that bone safety factors and yield stresses are independent of body mass, it can be shown that the axial component is proportional to bone cross-sectional area (S), and thus scales to body mass with an exponent double to the allometric exponent for bone diameters (b_d ; $F_{ax} \propto S \propto d^2$). Similarly, it can be shown that the transverse component is proportional to the second moment of area of the bone divided by bone length times diameter ($F_t \propto I / ld$), which leads to:

$$b_t = 3b_d - b_l, \quad (2)$$

where b_l is the allometric exponent for bone lengths. Then, the theoretical values proposed by this model for the scaling of bone dimensions, namely $b_d \approx 0.37$ and $b_l \approx 0.27$, are derived from experimental results on the scaling of the axial and transverse components of muscle force ($b_{ax} \approx 0.74$; $b_t \approx 0.84$; see Garcia & da Silva, 2006, and references therein). However, this model also contemplates that, in small mammals, the axial and transverse components could scale similarly ($b_{ax} = b_t$), which would result in faster bone length scaling ($b_l = b_d \approx 0.37$).

An interesting property of the power equation is that it becomes a straight line when logarithmized, with the allometric exponent representing the slope of that line (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003):

$$\log y = \log a + b \cdot \log x \quad (3)$$

However, several scaling studies have found a significant curvature in the scatter when plotting logarithmized data (e.g. Economos, 1983; Bertram & Biewener, 1990; Christiansen, 1999; Carrano, 2001). This would suggest that allometric exponents do change with size in those cases, which is known as **differential scaling** (or complex allometry, since multiple

allometric equations should be used to accurately represent the scaling of those variables). Although the causes behind this differential scaling are currently unclear, some authors have suggested that it would be related to large animals developing more robust limb bones (Biewener, 1990; Christiansen, 1999). In turn, this would be a strategy to withstand the higher bone stresses associated to increased size once those stresses cannot be reduced with postural changes (Biewener, 2003; Carrano, 2001).

Carnivora

The order Carnivora is probably the most enthralling mammalian clade. They represent, literally, the nature of the beast. Historically, carnivorans have played a major role in the folklore and mythology of almost every culture. Nowadays, they still have a strong presence in our everyday life: they are on TV, in every toy store, on your neighbor's car, waiting for you at home, or sharing an apartment with you. Similarly, carnivorans have long and often been the subject of scientific studies on morphology, behavior, ecology, and evolution (e.g. Van Valkenburgh, 1987; Gittleman, 1989; Bertram & Biewener, 1990; Iwaniuk et al., 1999; Goswami & Friscia, 2010).

Evolutionarily, carnivoran species can be separated into two major clades: Feliformia and Caniformia. The former groups cats, hyaenas, and the “viverrid-like” taxa (mongooses, civets, genets, linsangs...), while the latter includes dogs, bears, seals, skunks, raccoons, otters, weasels, and the like (Wozencraft, 2005; Wilson & Mittermeier, 2009; Fig. 2). The phylogenetic relationships between and within these clades have received a lot of

NOT JUST MEAT-EATERS

Although Carnivora comes from Latin *caro* / *carnis* (meat) + *vorare* (to eat), the species of this order are not exclusively meat-eaters (i.e., **carnivores**), ranging in diet instead from pure carnivores to fruit and leaves specialists, and including piscivores (fish-eaters), insectivores, and the full spectrum of mixed diets. Thus, in order to separate the ecological concept of meat-eater from the phylogenetic classification, the term **carnivoran** should be used to designate the species of the order Carnivora. Finally, it is worth noting that “carnivore” is a noun, being “**carnivorous**” the adjective. This way, the tiger, for instance, would be a carnivorous carnivoran.

Box C. Clarification on the use of the terms carnivore, carnivoran & carnivorous.

attention in the last decade (see Nyakatura & Bininda-Emonds, 2012, and references therein). This resulted in a major taxonomic revision of the previously defined carnivoran families, going from 11 (e.g. Wozencraft, 1993) to 16 (e.g. Wilson & Mittermeier, 2009). Similarly, recent molecular phylogenetic studies have changed our understanding of mammalian evolution. Previous studies suggested that Carnivora was close to Archonta (Primates, Scandentia, Dermoptera, Chiroptera) (Wozencraft, 1989). However, it is currently accepted that pangolins (Pholidota) are the closest living relatives to carnivorans, and that both orders belong to the superorder Laurasiatheria, which also includes Perissodactyla, Cetartiodactyla, Chiroptera, and Soricomorpha (Murphy et al., 2001; Bininda-Emonds et al., 2007).

With its over 280 extant species, Carnivora is one of the most speciose of mammalian orders (Wozencraft, 2005). Carnivoran species are native of all continents but Australia and Antarctica, and also dwell in all the oceans of the world (Goswami & Friscia, 2010; Wilson & Mittermeier, 2009). Furthermore, this order encompasses a broad range of body size, and dietary and locomotor adaptations. As frequently stated in the literature (e.g. Gittleman, 1989; Goswami & Friscia, 2010), all these characteristics make Carnivora a remarkably interesting group for ecomorphological studies. Some of these characteristics are of particular relevance for this dissertation. First, carnivorans present one of the widest locomotor diversities among mammals, lacking only flying and truly fossorial species (Van Valkenburgh, 1987; Wilson & Mittermeier, 2009). This makes them perfect subjects for the comparative study of the locomotor adaptations of the appendicular skeleton. Secondly, spanning over four orders of magnitude in body mass, ranging from the least weasel ($M_b < 0.1$ kg) to elephant seals ($M_b > 2000$ kg), Carnivora has the greatest range of body mass of any mammalian order. Thus, they provide a good base for scaling studies and enable testing for differential scaling (Bertram & Biewener, 1990). Furthermore, coupled with the wide locomotor diversity, the effect of locomotor specializations in the scaling of limb bones can be studied. Finally, the recent supertree analysis of Nyakatura & Bininda-Emonds (2012) has provided an estimate of the phylogenetic relationships between all extant Carnivora, as well as their estimated divergence times, which allows the previously mentioned studies to be carried out in a phylogenetically comparative framework.

As a final remark, it is worth mentioning that some authors have supported that Carnivora is an evolutionary conservative group regarding locomotor habits and limb morphology, suggesting that most morphological differences between carnivoran species would probably be size-related (e.g. Oxnard, 1968; Bertram & Biewener, 1990; Day &



Figure 2. Carnivora.

Left to right, top to bottom:

Canidae, *Canis lupus*, gray wolf; Mustelidae, *Gulo gulo*, wolverine; Felidae, *Panthera tigris*, tiger; Ailuridae, *Ailurus fulgens*, red panda; Procyonidae, *Procyon lotor*, raccoon; Ursidae, *Ailuropoda melanoleuca*, giant panda; Viverridae, *Genetta genetta*, common genet; Nandiniidae, *Nandinia binotata*, African palm civet; Prionodontidae, *Prionodon linsang*, banded linsang; Herpestidae, *Suricata suricatta*, meerkat; Otariidae, *Zalophus californianus*, California sea lion; Phocidae, *Hydrurga leptonyx*, leopard seal; Eupleridae, *Cryptoprocta ferox*, fossa; Mephitidae, *Mephitis mephitis*, striped skunk; Hyaenidae, *Crocuta crocuta*, spotted hyaena.

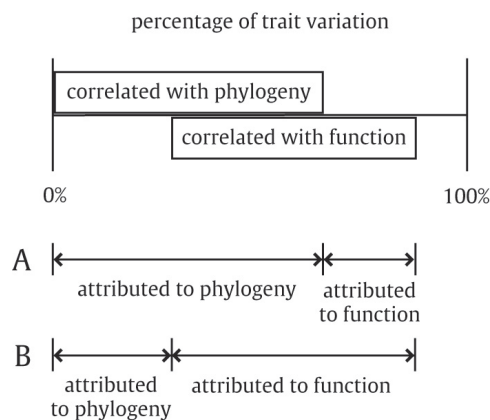
(ARKive, 2014).

Jayne, 2007). This argument has been strongly criticized, however, since both morphological and postural differences have been described between locomotory diverse carnivoran species (e.g. Jenkins & Camazine, 1977; Heinrich & Biknevicius, 1998; Iwaniuk et al., 1999; Schutz & Guralnick, 2007). Ultimately, these conflicting ideas have fueled the present dissertation. Previous studies have shown that both size and phylogeny have a significant effect on the morphology of the appendicular skeleton in Carnivora (e.g. Bertram & Biewener, 1990; Christiansen, 1999; Day & Jayne, 2007). The question is, do these effects constraint bone morphology in Carnivora?

Phylogenetic comparative methods

Most statistical analyses assume that the observations are independent of each other, that is, that they are sampled randomly from the same distribution (Sokal & Rohlf, 1995). Species, however, cannot be considered independent in this sense, since they are part of a hierarchically structured phylogeny (Felsenstein, 1985). This violation of the independence assumption results in an underestimation of the standard error of the estimates, which increases the rate of type I errors (i.e., false positive: incorrect rejection of the null hypothesis) (Martins & Garland, 1991; Rohlf, 2006). Thus, several methods, known as **phylogenetic comparative methods**, have been proposed to incorporate this hierarchical structure into interspecific analyses. One of these methods is **phylogenetic autocorrelation (PA)**, which partitions the variance in a trait into a phylogenetic component and a residual, or adaptive, component (Cheverud et al., 1985). The variance attributed to the effect of phylogeny is then discarded, and the statistical analyses are carried out in the adaptive component of variance. However, as pointed out by Westoby et al. (1995), of the variation of a trait, some portion will be related to phylogeny, some to ecomorphological properties (e.g. locomotion, diet), some to both, and some to neither (Fig. 3). Thus, by removing all variance related to phylogeny, PA also removes some of the adaptive variation of the trait. This extreme prioritization of phylogeny over other factors (ecology, biomechanics...) as a correlate of trait variation in PA is the main reason of the often dire criticism of phylogenetic comparative methods in general (e.g. Westoby et al., 1995). A second category of methods would include **phylogenetic generalized least squares (PGLS)** and related models (e.g. Martins & Hansen, 1997), in which both the phylogenetic structure of the observations and an assumed evolutionary model are

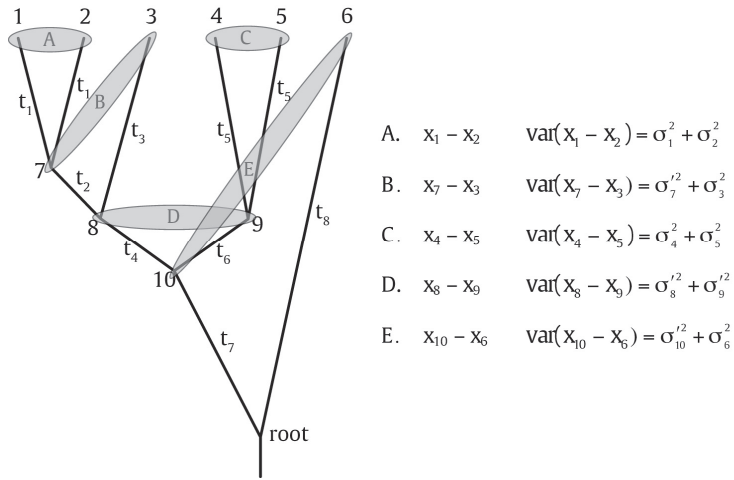
Figure 3. Trait variation. Interspecific variation in a trait (e.g. bone length) can be related, among other factors, with phylogeny and functional adaptations. This can lead to extreme attributions of trait variation (A, B). For instance, extreme A is responsible for most of the criticism on phylogenetic comparative methods. (Modified after Westoby et al., 1995.)



incorporated in the error covariance matrix (Rohlf, 2006). In ordinary least squares methods (OLS; e.g. OLS regression), the residuals (i.e. the error term) are assumed to be independent and normally distributed, with a mean of zero and a variance of s^2 . In PGLS, however, the error term is assumed to follow a multivariate normal distribution with a mean of $\mathbf{0}$ (null vector of length n) and an $n \times n$ covariance matrix (where n is the number of species). The diagonal elements of the covariance matrix are the variances of the n species, which are a function of the distance from the root of the tree to the corresponding species (i.e. a function of the height of each species). The off-diagonal elements correspond to the covariances between each pair of species, which are a function of the height of their most recent ancestor. Most applications of PGLS assume Brownian motion to model character evolution (i.e. constant evolution rate, equal in all branches of the phylogenetic tree), although other evolutionary models can be implemented, such as the Ornstein-Uhlenbeck process (Blomberg et al., 2003). Finally, another set of phylogenetic comparative methods are known as “minimum evolution” methods, like the **squared-change parsimony method** proposed by Maddison (1991). These methods do not deal explicitly with observation nonindependence, and were originally proposed to reconstruct the character states of the internal nodes of a phylogeny. They can be used, however, to generate the probability distribution from which the species are sampled, which in turn can be used to assess the significance of interspecific analyses (Martins & Garland, 1991).

In the present dissertation, the violation of the independence assumption was addressed using **phylogenetically independent contrasts (PIC)** (Felsenstein, 1985), a particular application of PGLS. This methodology assumes Brownian motion and, thus, that trait variance at each node is proportional to branch length (in time). That is, after t units of time, the change in variable x has a variance of s^2t . Since the evolution of a trait by Brownian motion is independent in each lineage, it follows that differences between the values of variable x between adjacent nodes (e.g. $x_1 - x_2$, $x_4 - x_5$; Fig. 4) must be independent. More precisely, both $x_1 - x_2$ and $x_4 - x_5$ depend only of the evolutionary events occurring along their respective pair of branches, and these two sets of events are independent under Brownian motion. Thus, using these differences between node values, or “contrasts”, in statistical analyses instead of species values does not violate the independence assumption. In order to calculate these independent contrasts, a value for variable x must first be estimated for each internal node. The estimated value for a given node k , x_k , is calculated as the weighted mean of its two direct descendants:

Figure 4. Phylogenetically Independent Contrasts. Example phylogeny with six terminal taxa. Each contrasts (A–E) is calculated as the difference in observed values (x_i) between adjacent nodes and has an associated variance (σ_i^2) proportional to branch length (in time; t_i). See Box D for the calculation of internal node values.



$$x_k = \frac{\frac{x_i}{\sigma_i^2} + \frac{x_j}{\sigma_j^2}}{\frac{1}{\sigma_i^2} + \frac{1}{\sigma_j^2}} = \frac{x_i \sigma_j^2 + x_j \sigma_i^2}{\sigma_i^2 + \sigma_j^2}, \quad (4)$$

where x_i, x_j are the values of variable x at the descendant nodes i, j , and σ_i^2, σ_j^2 are their corresponding variances. This weighted mean has an associated variance $\bar{\sigma}_k^2$, which must be added to the variance of x at node k , σ_k^2 , to calculate the effective variance at node k , $\sigma_k'^2$:

$$\sigma_k'^2 = \sigma_k^2 + \bar{\sigma}_k^2, \quad (5)$$

$$\bar{\sigma}_k^2 = \frac{1}{\frac{1}{\sigma_i^2} + \frac{1}{\sigma_j^2}} = \frac{\sigma_i^2 \sigma_j^2}{\sigma_i^2 + \sigma_j^2}. \quad (6)$$

Once these values have been estimated, a contrast can be calculated for the descendants of each internal node (e.g. $x_i - x_j$ for node k). Each contrast has an associated variance, $\text{var}(x_i - x_j)$, that, per the basic properties of variance, equals:

$$\text{var}(x_i - x_j) = \text{var}(x_i) + \text{var}(x_j) - 2 \text{cov}(x_i, x_j), \quad (7)$$

where $\text{cov}(x_i - x_j)$ is the covariance between the values of variable x at nodes i, j . However, as stated above, according to Brownian motion, the evolutionary events occurring along each branch are independent, thus:

$$\text{cov}(x_i, x_j) = 0, \forall (i \neq j). \quad (8)$$

Then, substituting into equation 7, the variance of each contrast equals the sum of the variances of those nodes. Again, at node k :

$$\text{var}(x_i - x_j) = \sigma_i^2 + \sigma_j^2. \quad (9)$$

EXAMPLE: PIC CALCULATION

Observations (i.e. data for terminal taxa):

species values: $X_1, X_2, X_3, X_4, X_5, X_6$
 associated variances: $\sigma_1^2 = \sigma_2^2 = s^2 t_1$; $\sigma_3^2 = s^2 t_3$; $\sigma_4^2 = \sigma_5^2 = s^2 t_5$; $\sigma_6^2 = s^2 t_8$

Internal node estimations:

associated variances: $\sigma_7^2 = s^2 t_2$; $\sigma_8^2 = s^2 t_4$; $\sigma_9^2 = s^2 t_6$; $\sigma_{10}^2 = s^2 t_7$

node 7:

$$X_7 = \frac{X_1 \sigma_2^2 + X_2 \sigma_1^2}{\sigma_1^2 + \sigma_2^2} = \frac{X_1 s^2 t_1 + X_2 s^2 t_1}{s^2 t_1 + s^2 t_1} = \frac{X_1 + X_2}{2}$$

$$\sigma_7'^2 = \sigma_7^2 + \frac{\sigma_1^2 \sigma_2^2}{\sigma_1^2 + \sigma_2^2} = s^2 t_2 + \frac{s^2 t_1 \cdot s^2 t_1}{s^2 t_1 + s^2 t_1} = s^2 \left(t_2 + \frac{t_1}{2} \right)$$

node 8:

$$X_8 = \frac{X_7 \sigma_3^2 + X_3 \sigma_7'^2}{\sigma_7'^2 + \sigma_3^2} = \frac{(X_1 + X_2) t_3 + X_3 (t_1 + 2t_2)}{t_1 + 2t_2 + 2t_3}$$

$$\sigma_8'^2 = \sigma_8^2 + \frac{\sigma_7'^2 \sigma_3^2}{\sigma_7'^2 + \sigma_3^2} = s^2 \left(t_4 + \frac{t_1 t_3 + 2t_2 t_3}{t_1 + 2t_2 + 2t_3} \right)$$

node 9:

$$X_9 = \frac{X_4 \sigma_5^2 + X_5 \sigma_4^2}{\sigma_4^2 + \sigma_5^2} = \frac{X_4 + X_5}{2} \quad \sigma_9'^2 = \sigma_9^2 + \frac{\sigma_4^2 \sigma_5^2}{\sigma_4^2 + \sigma_5^2} = s^2 \left(t_6 + \frac{t_5}{2} \right)$$

node 10:

$$X_{10} = \frac{X_8 \sigma_9'^2 + X_9 \sigma_8'^2}{\sigma_8'^2 + \sigma_9'^2} = \frac{(X_1 + X_2)(t_3 t_5 + 2t_3 t_6) + X_3(t_1 t_5 + 2t_1 t_6 + 2t_2 t_5 + 4t_2 t_6) + (X_4 + X_5)(t_1 t_3 + 2t_1 t_3)}{2t_1 t_3 + 4t_2 t_3 + t_1 t_5 + 2t_1 t_6 + 2t_2 t_5 + 4t_2 t_6 + 2t_3 t_5 + 4t_3 t_6}$$

$$\sigma_{10}'^2 = \sigma_{10}^2 + \frac{\sigma_8'^2 \sigma_9'^2}{\sigma_8'^2 + \sigma_9'^2} = s^2 \left(t_7 + \frac{t_1 t_3 t_5 + 2t_1 t_3 t_6 + 2t_2 t_3 t_5 + 4t_2 t_3 t_6}{2t_1 t_3 + 4t_2 t_3 + t_1 t_5 + 2t_1 t_6 + 2t_2 t_5 + 4t_2 t_6 + 2t_3 t_5 + 4t_3 t_6} \right)$$

Since a fully resolved phylogeny with n terminal taxa (species) has $n - 1$ internal nodes, sample size is reduced by one when using phylogenetically independent contrasts. Figure 4 shows an example phylogeny with its associated contrasts, whose calculation is presented in Box D.

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Box D. Estimation of the internal node values used in Figure 4.

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OBJECTIVES

Main objective

The main aim of this dissertation was to explore and quantify the effect of function, size, and phylogeny, on the morphology of the limbs in Carnivora based on morphometric and biomechanical analyses.

Specific objectives

To achieve this objective, this dissertation has been subdivided into four sections, each representing a different methodological approach to the study of limb morphology.

Section A: Locomotion

Of the different locomotor habits present in Carnivora, the continuum between terrestrial and arboreal habits poses the most difficulties when attempting to distinguish locomotor adaptations in bones. The locomotor kinematics, dynamics, and coordination, of both fully terrestrial species and arboreal specialists are well documented in the literature. Similar studies have dealt with the particularities of locomotion of small non-arboreal specialists in an arboreal substrate. Thus, the objective of this section was to complement this previous information characterizing the locomotion of larger non-arboreal specialists when moving in an arboreal substrate. Secondly, it was also investigated whether a completely terrestrial species would employ a similar locomotor strategy when forced into an arboreal-like situation.

Section B: Interaction

In this section, the individual effect of function, size and phylogeny on a series of skeletal measurements is evaluated separately. Then, the possible interaction of those factors in each particular variable is explored with generalized linear models. The results of this section will allow a more precise interpretation of the results of the following sections.

Section C: Scaling

The scaling pattern of the carnivoran appendicular skeleton is determined in this section. Furthermore, the presence of differential scaling is assessed for all the studied variables. Additionally, chapters III and IV analyze whether the scaling pattern of the main phyletic lines within Carnivora differs from the scaling pattern of the whole order, and also whether particular locomotor habits cause deviations from this ordinal scaling pattern. Finally, Chapter V explores the biomechanical consequences of scaling in the particular case of the felid calcaneus.

Section D: Scapula

The scapula presents the most variable morphology of the whole appendicular skeleton. However, its shape variation has not been studied in Carnivora. This section addresses that and also characterizes several adaptations to particular locomotor habits that can be observed in the shape of the carnivoran scapula. Finally, the evolution of carnivoran scapula shape is reconstructed and the locomotor type of the carnivoran ancestor is inferred.

SUPERVISOR'S REPORT

Dr. Adrià Casinos, supervisor of the PhD thesis entitled "Limb morphometrics in Carnivora: Locomotion, phylogeny and size", certifies that the dissertation presented here has been developed entirely by Eloy Gálvez López, and grants him the right to defend his thesis in front of a scientific committee.

As supervisor, I have contributed in designing, guiding, and correcting the drafts of the chapters and manuscripts written by the PhD candidate. This dissertation consists of six scientific manuscripts, presented as chapters. Each chapter either has been published in, or will be shortly submitted to, a scientific journal covered by the Science Citation Index. The contribution of the PhD candidate to each manuscript, as well as the impact factor of the related scientific journal (according to the Thomson Institute for Scientific Information), is detailed below:

Chapter I

Gálvez-López E, Maes LD, Abourachid A (2011) The search for stability on narrow supports: An experimental study in cats and dogs. *Zoology* **114**, 224–232.

Impact Factor (2012): 1.471

Study design: **EGL**, LDM, AA

Data analysis: **EGL**

Data collection: **EGL**, LDM

Writing: **EGL**, LDM, AA, AC

Chapter II

Gálvez-López E. Quantifying morphological adaptations using direct measurements: The carnivoran appendicular skeleton as a case of study. *Journal of Morphology* (to be submitted)

Impact Factor (2012): 1.602

Chapter III

Gálvez-López E, Casinos A. Scaling pattern of the carnivoran forelimb: Locomotor types and differential scaling. *PLoS ONE* (to be submitted)

Impact Factor (2012): 3.730

Study design: **EGL, AC** Data analysis: **EGL**
Data collection: **EGL, AC** Writing: **EGL, AC**

Chapter IV

Gálvez-López E, Casinos A. Scaling pattern of the carnivoran hind limb: Locomotor types and differential scaling. *Journal of Anatomy* (to be submitted)

Impact Factor (2012): 2.357

Study design: **EGL, AC** Data analysis: **EGL**
Data collection: **EGL, AC** Writing: **EGL, AC**

Chapter V

Gálvez-López E, Casinos A (2012) Scaling and mechanics of the felid calcaneus: Geometric similarity without differential allometric scaling. *Journal of Anatomy* **220**, 555–563. Impact Factor (2012): 2.357

Study design: **EGL, AC** Data analysis: **EGL**
Data collection: **EGL, AC** Writing: **EGL, AC**

Chapter VI

Gálvez-López E, Casinos A. Evolution of scapula size and shape in Carnivora: locomotor adaptations and differential shape scaling. *Evolution* (to be submitted)

Impact Factor (2012): 4.864

Study design: **EGL** Data analysis: **EGL**
Data collection: **EGL** Writing: **EGL, AC**

I also certify that none of the manuscripts included in this PhD thesis has been used as a part of another PhD thesis.

Barcelona, 8th July 2014

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Section A: Locomotion

Journal Reference

Gálvez-López E, Maes LD, Abourachid A (2011) The search for stability on narrow supports: An experimental study in cats and dogs. *Zoology* **114**, 224–232.

The search for stability on narrow supports: An experimental study in cats and dogs



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Abstract

Kinematic and coordination variables were studied in two carnivorans, one with known locomotor capabilities in arboreal substrates (cat), and the other a completely terrestrial species (dog). Two horizontal substrates were used: a flat trackway on the ground (overground locomotion) and an elevated and narrow runway (narrow support locomotion). Despite their different degree of familiarity with the 'arboreal' situation, both species developed a strategy to adapt to narrow supports. The strategy of cats was based on using slower speeds, coupled with modifications to swing phase duration, to keep balance on narrow supports. The strategy of dogs relied on high speeds to gain in dynamic stability, and they increased cycle frequency by reducing swing phase duration. Furthermore, dogs showed a high variability in limb coordination, although a tendency to canter-like coordination was observed, and also avoided whole body aerial phases. In different ways, both strategies suggested a reduction of peak vertical forces, and hence a reduction of the vertical oscillations of the centre of mass. Finally, lateral oscillation was reduced by the use of a crouched posture.

Keywords: anteroposterior sequence; locomotion; narrow supports; stability

Introduction

The gaits employed by animals when walking or running over ground, and their corresponding dynamics and kinematics, have been rigorously studied since the 19th Century (e.g. Marey, 1873; Muybridge, 1899; Manter, 1938; Hildebrand, 1966, 1980, 1985; Demes et al., 1994; Lee et al., 1999; Larson et al., 2000; Cartmill et al., 2002; Fischer et al., 2002; Abourachid, 2003; Hutchinson et al., 2006; Maes et al., 2008). Nevertheless, the ground is not the only support on which animals move; they also move on the branches high in the forest canopy or dig its way through the ground. It is supported that each substrate requires different anatomical, morphological, and mechanical adaptations, as well as modifications to the dynamics and kinematics of locomotion (Biewener, 2003). Locomotion on arboreal substrates has not been so thoroughly studied as overground locomotion, but its main particularities have already been covered (Cartmill, 1974, 1985; Meldrum, 1991; Schmitt, 1999; Schmitt & Lemelin, 2002; Lemelin et al., 2003; Schmitt, 2003*b*; Lammers & Biknevicius, 2004; Schmidt & Fischer, 2010).

The main problem affecting arboreal locomotion is the tendency of animals to roll (rotate around their sagittal axis) and topple from the support because all their support points are effectively collinear, which greatly reduces their support polygon. Several solutions to this problem, each involving different morphological adaptations, have already been described (Cartmill, 1985): 1/ relatively short limbs, as in arboreal viverrids (Taylor, 1970), or the use of a crouched posture (Schmidt & Fischer, 2010), keep the body's centre of mass close to the support and minimize lateral oscillation; 2/ prehensile hands and/or feet allow gripping the branch and thus exerting a torque that resists the toppling moment, as in primates (Rollinson & Martin, 1981; Vilensky & Larson, 1989; Schmitt, 1999), some opossums (Schmitt & Lemelin, 2002; Lemelin et al., 2003), and tupaiids (Sargis, 2001); 3/ the reduced body size of small animals, like squirrels, overcomes the toppling problem by spreading the support points relatively more widely on the surface of the branch; and 4/ foolproof solution to totally avoid toppling is hanging underneath the branch, like sloths do. Another source of locomotor instability during arboreal locomotion is the round section of branches, which increases the potential of slipping off them. Animals with prehensile hands and/or feet avoid this problem by firmly grasping the support; while clawed animals, whose grasping abilities are reduced or absent, change limb placement during arboreal locomotion to reorient substrate reaction forces inwards to the branch, and thus prevent slipping off it (Schmitt, 2003*b*; Lammers & Biknevicius,

2004; Schmidt & Fischer, 2010). Finally, another problem affecting arboreal locomotion are vertical oscillations of the support. Branches, especially the fine ones, tend to deflect under an animal's weight, which not only hinders joint stabilization, but also could eject the animal from the support due to elastic recovery. Schmitt (1999) proposed compliant gaits as a solution to this problem. Compliant gaits are characterized by substantial limb yield, which reduces vertical oscillations of the body (and thus of the support) and encourages long contact times, which in turn allows the reduction of stride frequency (and thus the potential of branch sway). Furthermore, compliant gaits reduce bone and joint stresses associated to flexed-limb gaits (Schmitt, 1999). The use of compliant gaits in primates, marsupials and other arboreal mammals was later confirmed by Larney and Larson (2004). In addition to compliant gaits, the use of a crouched posture has also been proposed as a mechanism to reduce vertical oscillations of the body both in compliant (Schmitt, 1999) and stiff gaits (i.e. when limb yield is low; Bishop et al., 2008). In this latter case, the authors proposed that, if limb protraction and angular excursion remained unaltered, the use of a crouched posture would reduce vertical displacements of the centre of mass by creating a smaller pendulum (and thus reducing potential energy fluctuations; Bishop et al., 2008). Finally, at higher speeds, ambling gaits have also been proposed as a solution to reduce vertical oscillations of the support, since they allow animals to maintain at least one foot in contact with the substrate during a stride, and thus reduce peak vertical forces on the support (Schmitt et al., 2006).

Most studies on arboreal locomotion, though, focus on primates and, to a lesser extent, on some didelphids, since they consider these groups as arboreal specialists, presenting a set of adaptations to moving and foraging in an arboreal setting so marked that make their overground locomotion distinct from that of other animals. These adaptations involve having prehensile extremities, showing more protracted arm postures at touch-down, producing lower peak vertical substrate reaction forces with the forelimbs than with the hindlimbs, and using diagonal-sequence gaits almost exclusively when walking on narrow supports (Hildebrand, 1967; Vilensky & Larson, 1989; Demes et al., 1994; Larson et al., 2000; Schmitt & Lemelin, 2002). Nevertheless, arboreal specialists are not the only animals known to use arboreal substrates. As stated by Lammers and Biknevicius (2004), many small mammals use fallen logs and branches on the forest floor as arboreal runways. Furthermore, many non-arboreal species often climb trees to escape predators or while hunting (MacDonald, 1984; Wilson & Mittermeier, 2009). Since stability in locomotion is directly linked to performance in escaping or hunting behaviours, so directly linked to

fitness, it would be vital for these non-arboreal mammals navigating arboreal substrates (non-arboreal specialists) to adapt their locomotion and increase their stability.

To date, locomotion on arboreal supports in non-arboreal specialists has only been studied in small species: the common marmoset (*Callithrix jacchus*) (Schmitt, 2003a), the gray short-tailed opossum (*Monodelphis domestica*) (Lammers & Biknevicius, 2004), and the rat (*Rattus norvegicus*) (Schmidt & Fischer, 2010). To increase their stability on arboreal supports, these animals reduced peak vertical forces to reduce the vertical oscillation of the centre of mass. Both the common marmoset and the rat used similar speeds and had similar contact times (i.e. duty factor, and thus stance phase duration) in over ground and arboreal locomotion, while the gray short-tailed opossum used lower speeds and had longer contact times during arboreal locomotion. Schmidt and Fischer (2010) proposed that the reduction of speed could only be accomplished if some grasping ability is retained.

In the light of these results, we wonder how a larger non-arboreal specialist (for instance, a ground-dwelling carnivoran pursuing its prey up into the forest canopy) will adapt its kinematics and coordination to the arboreal substrate. Will the larger mammal use the same strategy as the smaller ones? The first aim of this study was thus to determine how a medium-sized non-arboreal specialist adjusts its kinematics and coordination to adapt to an arboreal substrate. For the experimentation, we chose the domestic cat (*Felis silvestris catus*), which is used to move comfortably along branches, rails, and similar narrow, elevated supports. Taking into account the possible solutions to increase stability presented above, cats were expected to increase stance phase duration, and thus decrease stride frequency. Slower speeds on narrow supports than on flat ground, as was found for the grey short-tailed opossum (Lammers & Biknevicius, 2004), were also expected, since cats can use their claws to grip the support. We also expected that they displayed a more crouched posture in the 'arboreal' situation to bring the centre of mass closer to the support.

Secondly, we wondered whether the strategy employed by non-arboreal specialists to adapt to the arboreal situation, if there was any, would be a universal solution for all non-arboreal species. That is, if we encouraged a completely terrestrial species into an arboreal-like situation, would it arrive at the same solution to keep balance and advance on the narrow support? To answer this question, we used a protocol similar to the one used in cats to study the kinematics and coordination of the domestic dog (*Canis lupus familiaris*) when moving along a narrow, elevated support, before comparing both strategies. We

chose the dog because it is a completely terrestrial species whose kinematics and coordination over ground have already been thoroughly studied (Hildebrand, 1968; Lee et al., 1999; Maes et al., 2008).

Materials and methods

All animals were healthy specimens, with no known pathologies that could affect their vision, balance, or locomotion. Due to the different degree of familiarity of the studied species with the arboreal situation, different experimental settings were used for each species. This way, animals could move along the support, but were at the same time forced to search for stability.

Cats

Seven cats (age = 5.9 ± 3.5 years; shoulder height = 0.27 ± 0.02 m; body mass = 4.4 ± 0.7 kg) were filmed on the ground and in an 'arboreal' situation (narrow support locomotion). In overground locomotion the cats moved along an 8 m flat carpet (Fig. I.1A), while the arboreal situation was simulated by a wooden bar ($0.03 \times 0.03 \times 2.50$ m) raised at a height of 0.75 m (Fig. I.1B). The trestles raising the wooden bar also prevented it to deflect under the cats' weight, thus avoiding external perturbations to their stability (e. g. induced vertical oscillations of the centre of mass). Black lines, perpendicular to the axis of locomotion, were painted at 0.05 m intervals both on the carpet and on the wooden bar and used to assess the location of each foot at touch-down (accuracy: 0.02 m). In both cases, the cats were placed at one end of the structure (bar or carpet) and were encouraged to go to the other end of it. A high-speed video camera (BASLER A504K; Highland, IL, USA), placed perpendicular to the trackway, 3.0 m from its centre (field: 1.0 m; resolution: 1280 pixels/m), was used to film the cats at a frequency of 125 Hz.

We are aware that the experimental situation that we use to represent arboreal locomotion is just an approximation, given that we use a narrow square surface to simulate a support that tends to be round in section. Nevertheless, support width was approximately the same as feet width, which would probably affect stability in a similar degree as a round support of approximately half the body width of the animal. Although this last methodology is useful for studies dealing with changes in the orientation of ground reaction forces on arboreal settings (e.g. Lammers & Biknevicius, 2004), the former provides better insight on the effect of collinear limb placement.

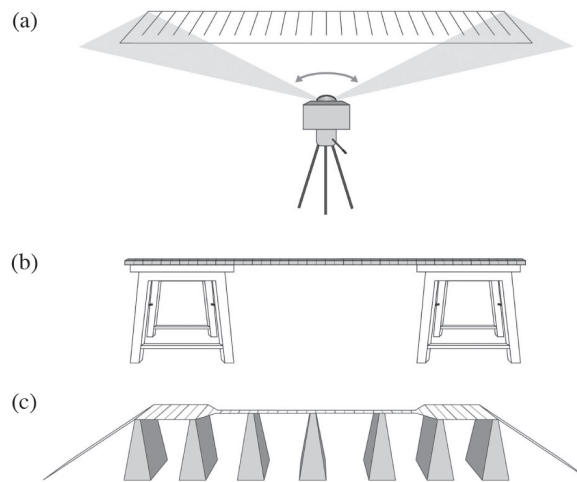


Figure I.1. Experimental situations for the comparison between overground (a) and narrow support locomotion (for cats, b, and dogs, c). See text for details.

Dogs

Five Belgian Shepherd dogs (age = 7.3 ± 1.7 years; shoulder height = 0.61 ± 0.04 m; body mass = 28.0 ± 5.0 kg) were filmed in ‘arboreal’ situation. A 9 m long runway raised at a height of 1.5 m was used in this experimental situation. The elevated runway included a central narrow part (0.15×5.0 m) simulating the arboreal situation, and two wide parts (0.5×2.0 m) allowing the dog to stabilize prior and after the narrow part (Fig. I.1C). The whole structure was reinforced with small beams between the supports to avoid its deflection under the weight of the dogs, which would introduce external perturbations to their stability. Furthermore, since we were interested in the effect of support width, not support slipperiness, the whole surface of the runway was covered with a mix of paint and sand as an anti-slip coat. Black lines, perpendicular to the axis of locomotion, were painted on the runway at 0.10 m intervals and used to assess the location of each foot at touchdown (accuracy: 0.05 m). Since the dogs were trained for *Agility* contests, they moved along the runway when asked by their owners. A high-speed video camera (BASLER A504K; Highland, IL, USA), placed perpendicular to the runway, 10.0 m from its centre and at a height of 2.5 m (field: 2.0 m; resolution: 640 pixels/m), was used to film the dogs at a frequency of 125 Hz.

In the case of dogs, support width was about one and a half feet width, since dogs refused to perform the exercise for support widths narrower than 15 cm. Nevertheless, this situation is comparable to the possible ‘arboreal’ situations that terrestrial mammals could face (e.g. a fallen log traversing a gap...). Finally, given that the aim of this study is to search for possible modifications to kinematic and coordination variables of locomotion

when comparing the 'arboreal' and the usual (overground) situation, we need a minimum degree of regularity, which would be unaffordable if the animals advanced in a truly arboreal substrate.

For overground locomotion, we revisited the data from a previous study that comprised all gaits of Belgian Shepherd dogs, analyzed in the APS framework (Maes et al., 2008). Comparison between our data in the 'arboreal' situation and overground locomotion data from Maes et al. (2008) is possible because we used the same dog breed (Belgian Shepherds), and because the experimental procedure is based on the same processes.

Video analysis and data processing

All locomotor analysis in this study were carried out in the framework of the anteroposterior sequence (APS) approach, since it allows the study of all kinds of interlimb coordination – symmetrical or asymmetrical gaits and unsteady locomotion – with the same set of variables (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). APS methodology has already been described elsewhere (Maes et al., 2008: p. 140), and will only be briefly summarized here. The records were analysed using Virtual Dub (version 1.6.12; <http://www.virtualdub.org/>). The timing of touch-down (when the foot makes contact with the ground) and lift-off (when the last toe leaves the ground) of each limb were noted using frame number. A maximal error of one frame (i.e. 8.0 ms) was estimated for touch-down and lift-off timings. The positions of the feet on each touch-down were determined using the black lines marked on all experimental supports. The data were visualised using classical gait diagrams (Marey, 1873) and track diagrams (Abourachid et al., 2007), which allowed us to spot APSs and to manually identify gaits.

After video analysis, the following kinematic variables were calculated in each APS for the first forelimb to contact the ground (referred to hereafter as reference limb): cycle duration (**D**; seconds), corresponding to the time comprised between consecutive footfalls of the same foot; cycle frequency (**F** = $1/\mathbf{D}$; Hz); stance (**St**; s) and swing (**Sw**; s) phase duration (the time that the foot is in contact with the ground, and the time that it is lifted, respectively, each cycle); and stride length (**L**; m), that is, the distance between consecutive footprints of the same foot. Speed (**u**; m/s) was calculated using stride length and cycle duration (**u** = \mathbf{L}/\mathbf{D} ; m/s).

We also calculated the following temporal coordination variables: fore lag (**FL**; %) and hind lag (**HL**;%), corresponding to the time between the footfalls of both limbs of a pair, fore and hind respectively, in relation to the cycle duration of the reference limb; and pair

lag (**PL**; %), corresponding to the time between footfalls of the first limb of each pair to contact the ground, in relation to the cycle duration of the reference limb. Complementarily, we calculated the following spatial coordination variables: fore gap (**FG**; %) and hind gap (**HG**; %), corresponding to the distance between the footfalls of both limbs of a pair, fore and hind respectively, relative to the stride length of the reference limb; and pair gap (**PG**; %), corresponding to the distance between footfalls of the first limb of each pair to contact the ground, as a percentage of the stride length of the reference limb (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). Positive **PG** values indicate that the hindfoot is placed on the support beyond the forefoot, while negative **PG** values correspond to the hindfoot being placed behind the forefoot. Finally, to assess regularity in limb coordination during locomotion, we compared **PL** values between successive sequences, thus defining the irregularity index as the absolute value of the difference between **PL** of sequence n and **PL** of sequence n-1 ($Irl_n = |PL_n - PL_{n-1}|$).

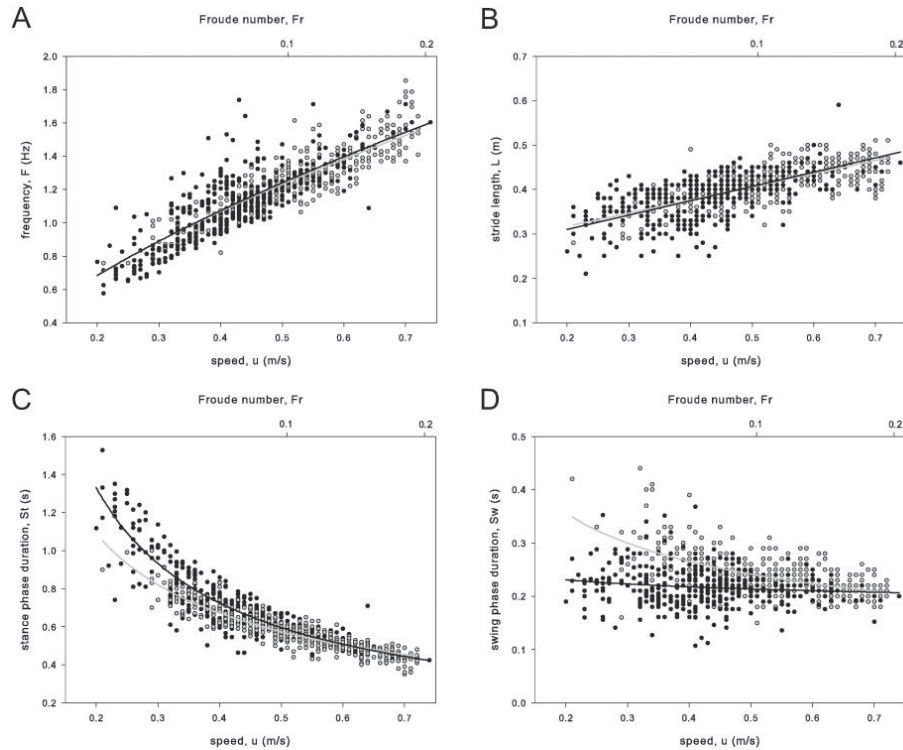
To test for differences in mean values of both kinematic and coordination variables between overground and narrow support locomotion, Mann-Whitney non-parametric tests were performed using SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), since not all the data were normally distributed and homoscedasticity was not always observed. Values of $p < 0.05$ were considered statistically significant.

Regarding the relationship between each variable and speed, we used either the power equation or a linear model of regression considering the best fit. All equations were calculated using model I of regression (least squares) (Sokal and Rohlf, 1995). Possible differences between the regression slopes of over ground and narrow support locomotion were accounted for using an F-test with a significance level of 0.05.

Results

A total of 425 APSs were obtained for cats in overground locomotion, while 403 sequences were filmed in the narrow support situation. Cats did not show great difficulties in performing the exercise. On the contrary, they sometimes even performed a couple of locomotor sequences along the wooden bar, then turned around with no effort, and returned to the starting point. Speed values for cats ranged from 0.21 to 0.72 m/s. For dogs, only 134 APSs could be obtained in narrow support locomotion, since they showed greater difficulties in performing the exercise. Even though they were used to *Agility* training, they sometimes fell or jumped off the runway. Their speed ranged from 1.54 to 4.19 m/s. Since

Figure I.2. Relationship between speed and cycle frequency (A), stride length (B), stance phase duration (C), and swing phase duration (D), in cats. Gray dots represent overground locomotion data, and black dots represent data from narrow support locomotion.



data from Maes et al. (2008) for overground locomotion comprised a much wider range of speeds (from 0.4 to 10.0 m/s), the dataset was reduced to 232 APSs that matched our speed range.

Cats

As expected, cats used significantly slower speeds in narrow support than in overground locomotion (mean \pm standard deviation (s.d.): 0.42 ± 0.10 vs. 0.53 ± 0.11 m/s, respectively; $p < 0.001$). Regarding the slopes of either frequency or stride length, there were no significant differences between both situations (Table I.1; Fig. I.2A, B). Nevertheless, the relative contribution of stance and swing phases differed in both situations. In narrow support locomotion stance phase duration decreased with increasing speed significantly faster than in overground locomotion (Table I.1). Thus, although mean stance phase duration was higher in narrow support locomotion at low speeds, these differences disappeared at higher speeds (Fig. I.2C). Regarding swing phase duration, while it decreased with speed in overground locomotion, it was independent of speed in narrow support locomotion (Table I.1; Fig. I.2D), and also showed lower mean values (mean \pm s.d.: 0.24 ± 0.04 vs. 0.22 ± 0.04 s, respectively; $p < 0.001$).

In both situations, cats used the lateral walk exclusively as their preferred gait. The values of temporal coordination variables (lags) were always close to the theoretical values defined by Abourachid (2003), although their variability slightly exceeded the classically accepted 5% (Hildebrand, 1966; Maes et al., 2008), especially for the hindlimbs (mean \pm s.d.: **HL** = $51.1 \pm 6.4\%$, and $49.3 \pm 6.9\%$, for overground and narrow support locomotion respectively; Table I.2, Fig. I.3A, B). Temporal coordination between sequences was highly regular in both situations, since **PL** variation between consecutive APSs was on average less than 5% (**Irl** < 5%, Table I.2). Pair lag values decreased from a mean of 83% to 75% as speed increased in both over ground and narrow support locomotion. Regarding significant differences in coordination variables between overground and narrow support locomotion, **FL** values were significantly higher and **HL** and **PL** were significantly lower when cats moved along the wooden bar compared to overground locomotion. Finally, regarding spatial coordination, **PG** values were significantly lower in narrow support locomotion (Table I.2). In fact, when walking over ground, cats usually placed each hindfoot beyond its corresponding forefoot (**PG** > 0%), while they placed the hindfeet behind the forefeet when moving along the wooden bar (**PG** < 0%). Together with some differences found in kinematic variables, this finding suggests the use of a different locomotor strategy in each situation.

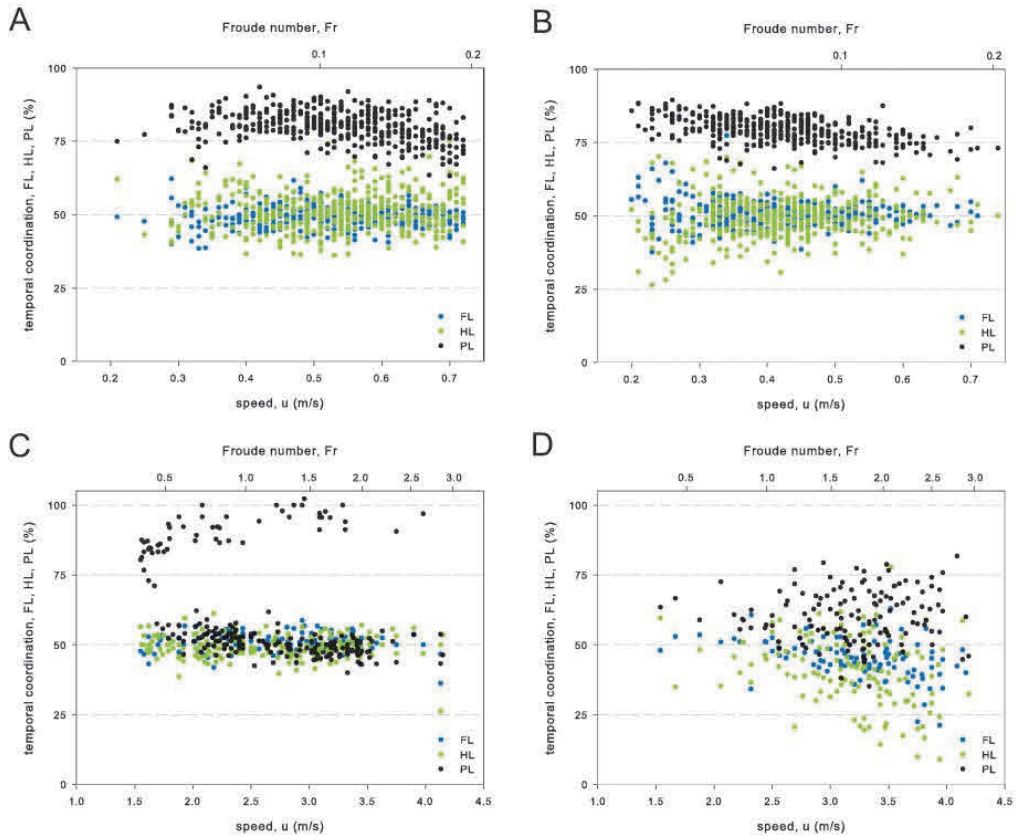
	Overground				Narrow support				p value		
	a	b	CI _a	CI _b	R ²	a	b	CI _a		CI _b	
Cats											
F	1.898	0.628	1.859 – 1.937	0.598 – 0.658	0.799	1.930	0.646	1.853 – 2.009	0.602 – 0.689	0.677	> 0.05
St	0.347	-0.720	0.340 – 0.356	-0.754 – -0.687	0.810	0.332	-0.813	0.326 – 0.355	-0.859 – -0.767	0.749	< 0.01
Sw	0.183	-0.391	0.176 – 0.189	-0.445 – -0.337	0.325	<i>0.201</i>	<i>-0.071</i>	<i>0.190 – 0.213</i>	<i>-0.133 – -0.009</i>	<i>0.012</i>	-
L	0.258	0.296	0.244 – 0.272	0.270 – 0.322	0.548	0.246	0.322	0.229 – 0.262	0.284 – 0.360	0.409	> 0.05
Dogs											
F	1.433	0.395	1.390 – 1.477	0.363 – 0.426	0.722	1.365	0.592	1.187 – 1.569	0.471 – 0.711	0.413	< 0.01
St	0.509	-0.928	0.488 – 0.530	-0.970 – -0.884	0.887	0.608	-1.082	0.518 – 0.715	-1.221 – -0.943	0.639	< 0.05
Sw	<i>0.250</i>	<i>0.061</i>	<i>0.237 – 0.262</i>	<i>0.009 – 0.112</i>	<i>0.023</i>	<i>0.216</i>	<i>-0.094</i>	<i>0.183 – 0.255</i>	<i>-0.236 – 0.048</i>	<i>0.013</i>	-
L	0.480	0.292	0.440 – 0.520	0.277 – 0.306	0.866	0.639	0.171	0.474 – 0.805	0.119 – 0.221	0.245	< 0.01

Table I.1. Regressions on speed for overground and arboreal situation in cats and dogs. Power equation ($y = ax^b$) was used for all regressions except for L, in which a linear model of regression ($y = a + bx$) was used. *Values in grey italics denote nonsignificant regressions.*

Abbreviations: CI_a, 95% confidence interval for a; CI_b, 95% confidence interval for b; F, cycle frequency (Hz); L, stride length (m); p value, significance of the comparison of slopes between overground and narrow support locomotion (“-” denotes that no comparison could be made due to nonsignificant regressions); R², determination coefficient; St, stance phase duration (s); Sw, swing phase duration (s).

Figure I.3. Temporal coordination in cats (A, B) and dogs (C, D).

Graphs on the left correspond to overground locomotion (A, C), while those on the right represent narrow support locomotion (B, D). Blue dots represent fore lag (FL), green dots represent hind lag (HL), and black dots represent pair lag (PL).



	Cats					Dogs			
	Overground		Narrow support		p value	Overground		Narrow support	
	n = 425		n = 403			n = 232		n = 134	
	mean	s. d.	mean	s. d.		mean	s. d.	mean	s. d.
FL	49.5	3.3	50.9	4.0	< 0.001	50.5	2.9	45.7	6.8
HL	51.1	6.4	49.3	6.9	< 0.001	49.5	3.9	40.5	12.6
PL	80.2	5.1	79.5	4.2	< 0.001	60.8	18.2	60.7	9.3
FG	50.3	4.1	50.5	5.1	0.875	50.1	2.9	45.5	6.7
HG	50.7	5.1	50.3	5.9	0.265	50.3	4.0	40.6	11.7
PG	6.8	7.3	-5.7	9.0	< 0.001	11.1	17.8	5.7	11.0
Irl	3.5	2.8	2.6	2.2	0.091	3.3	3.2	6.6	4.6

Table I.2. Comparison between coordination variables in overground and narrow support locomotion in both cats and dogs.

Abbreviations: FG, fore gap (%); FL, fore lag (%); HG, hind gap (%); HL, hind lag (%); Irl, irregularity index (%); n, sample size; p value, significance of the comparison of mean values between overground and arboreal situations in cats (since the coordination patterns were unsteady in narrow support locomotion compared to the steady gaits of the overground locomotion, significant differences in mean values for coordination variables could not be tested for in dogs); PG, pair gap (%); PL, pair lag (%); s. d., standard deviation.

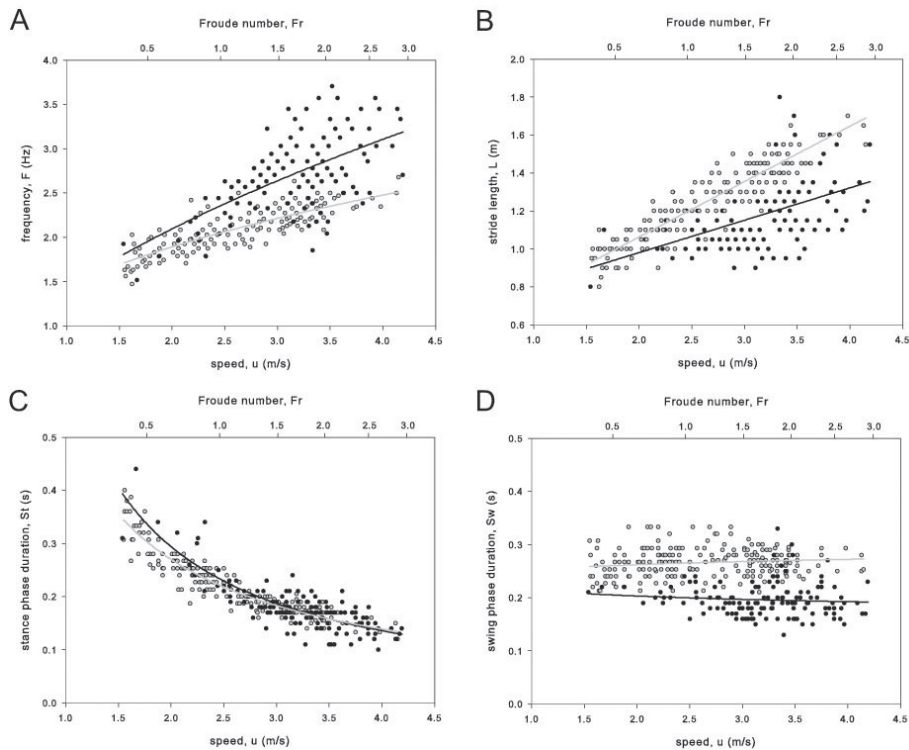


Figure I.4. Relationship between speed and cycle frequency (A), stride length (B), stance phase duration (C), and swing phase duration (D), in dogs. Gray dots represent overground locomotion data, and black dots represent data from narrow support locomotion.

Dogs

Dogs tended to perform the exercise at high speeds: the mean speed for narrow support locomotion was 3.20 ± 0.52 m/s, a value close to the top speeds found for symmetrical gaits in the study of Maes et al. (2008). Regarding the rest of kinematic variables, cycle frequency increased significantly faster in narrow support locomotion, since the slope obtained for the ‘arboreal’ situation was almost 1.5 times the slope obtained for overground locomotion (Table I.1; Fig. I.4A), which suggests the use of different locomotor strategies in each situation. On the other hand, the slope of stride length was significantly lower in narrow support locomotion (Table I.1; Fig. I.4B), probably relating to a consistent reduction of whole body aerial phases, or even lack thereof, in narrow support locomotion. Only 24.6 % of narrow support APs included a whole body aerial phase, whose duration was on average only 4.7 ± 3.1 % of cycle duration (mean \pm s.d.). Stance phase duration decreased significantly faster in narrow support locomotion (Table I.1; Fig. I.4C). Swing phase duration was independent of speed in both situations (Table I.1; Fig. I.4D), and, as observed in cats, it was significantly shorter when dogs moved on the catwalk (mean \pm s.d.: 0.27 ± 0.03 vs. 0.20 ± 0.03 s, for overground and narrow support locomotion respectively; $p < 0.001$).

Even though we considered the same range of speeds, the coordination patterns employed in overground and narrow support locomotion were different. When moving overground, dogs used almost exclusively symmetrical gaits ($\mathbf{FL} = \mathbf{HL} = 50 \pm 5\%$), of which the trot was their preferred gait: of the 232 APSs analyzed for overground locomotion, 30 (12.9%) corresponded to lateral walk, 30 (12.9%) to pace, 1 (0.4%) to transverse gallop, and 171 (73.7%) to trot. On the other hand, in narrow support locomotion dogs preferred asymmetrical coordination patterns ($\mathbf{FL} \neq 50 \pm 5\%$ and/or $\mathbf{HL} \neq 50 \pm 5\%$), since only 28 out of 134 APSs (20.9%) were strictly symmetrical. Temporal coordination between sequences in overground locomotion was highly regular ($\mathbf{Irl} = 3.3 \pm 3.2\%$ (mean \pm s.d.); Table I.2), contrary to what was found in narrow support locomotion, since \mathbf{Irl} exceeded on average the 5% threshold ($\mathbf{Irl} = 6.6 \pm 4.6\%$ (mean \pm s.d.); Table I.2). Given that these high \mathbf{Irl} values, together with the high standard deviation of coordination variables in narrow support locomotion (6.8 and 12.6 for \mathbf{FL} and \mathbf{HL} , respectively; Table I.2), make the correspondence to gaits difficult, we prefer thus to speak about “coordination pattern” instead of “gait”. Only about 92 of the 134 ‘arboreal’ sequences (68.7%) appeared like gaits classically defined in locomotion studies: we found 12 (9.0%) sequences of gallop-like coordination, 45 (33.6%) corresponding to canter-like coordination, and 35 (26.1%) to trot-like coordination. Since the coordination patterns were unsteady in the narrow support locomotion compared to the steady gaits of the overground situation, significant differences in mean values for coordination variables could not be tested for in dogs (Table I.2; Fig. I.3C, D).

Discussion

A common strategy for non-arboreal specialists

The main strategy for cats to adapt to the arboreal situation was to use slower speeds (with the corresponding adjustment of all speed-related variables, e.g. longer stance phase duration), which is generally associated with lower peak vertical forces (Demes et al., 1994; Schmitt & Lemelin, 2002). Similar results were obtained by Lammers and Biknevicius (2004) when studying the dynamics of arboreal locomotion in the grey short-tailed opossum (*Monodelphis domestica*), a smaller non-arboreal specialist with limited grasping abilities that nevertheless navigates frequently on arboreal substrates. Furthermore, these authors also reported an increase in duty factor in an arboreal situation, and significantly steeper slopes when comparing stance phase duration *versus*

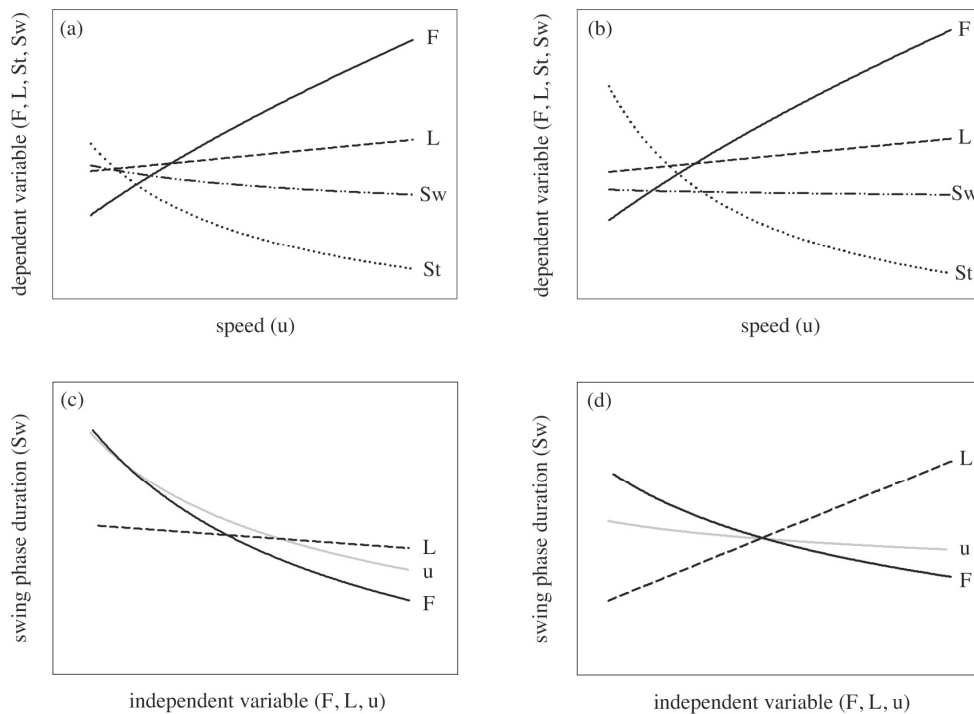


Figure I.5. Relationship between speed and several kinematic variables (A, B), and between swing phase duration and cycle frequency, stride length, and speed (C, D) in cats. Plots on the left (A, D) represent overground locomotion data, while those on the right (B, D) correspond to narrow support locomotion. Abbreviations: F, cycle frequency (Hz); L, stride length (m); St, stance phase duration (s); Sw, swing phase duration (s); u, speed (m/s).

speed in the arboreal trials with those obtained for overground trials, as observed in the present study (Table I.1; Fig. I.2C). This way, in accordance to our prediction, it seems that there is a common strategy for small and medium-sized non-arboreal specialists to increase their stability when in an arboreal support.

Swing phase duration was the only variable that was modified during cat narrow support locomotion in a way not predicted by speed: it decreased significantly with speed when cats moved over ground, but its variation was independent of speed in narrow support locomotion (Fig. I.5A, B). Given that speed is directly related to changes in cycle frequency (**F**) and/or stride length (**L**), we studied the relationship between these variables and swing phase duration (**Sw**) (Fig. I.5C, D). Cycle frequency is inversely related to swing phase duration ($F = [St + Sw]^{-1}$), while in each cycle stride length determination occurs during the swing phase. Therefore, **Sw** should decrease with increasing **F**, and it should also be related to **L** in some way. As expected, as cycle frequency increased, swing phase duration decreased in both the arboreal and flat ground situations (Fig. I.5C, D). Swing phase duration and stride length were not significantly related in overground locomotion in cats ($Sw = 0.280 - 0.099 \cdot L$; $R^2 = 0.014$; Fig. I.5C), suggesting the existence of factors other than swing phase duration to explain the increase in stride length with speed in this situation (e.g. greater angular velocities of the limb during the swing phase). On the other

hand, longer strides were directly related to an increase in swing phase duration in narrow support locomotion ($\mathbf{Sw} = 0.114 + 0.270 \cdot \mathbf{L}$; $R^2 = 0.163$; Fig. I.5D). During film analysis, it was frequently observed that, when cats got out of balance, they quickly leaned their feet on the bar, shortening considerably swing phase duration and thus reducing stride length. It was also observed that, when there were no balance issues, cats usually made tentative steps before definitely placing their forefeet on the bar, allowing them for a steadier grip, but in turn increasing swing phase duration. These observations support the relationship between swing phase duration and stride length, but they also suggest that variations in swing phase duration would be more related to balance than to speed. In summary, during undisturbed overground locomotion in the cat, the relationship between swing phase duration and speed mirrors the relationship between cycle frequency and speed (Fig. I.5C). On the other hand, during 'arboreal' locomotion, a significant relationship appears between swing phase duration and stride length, probably related to the search of stability. This way, there is a direct relationship between \mathbf{Sw} and \mathbf{L} , and an inverse relationship between \mathbf{Sw} and \mathbf{F} . This conflicting compromise between increasing speed and maintaining balance probably renders non-significant the relationship between swing phase duration and speed (since $\mathbf{u} = \mathbf{L} \cdot \mathbf{F}$) (Fig. I.5D).

A possible explanation for the lower pair gap values found in narrow support locomotion could be the crouched posture adopted by most cats and several dogs when moving along the elevated support, which is characteristic for mammals moving on narrow supports (Cartmill, 1985; Schmitt & Lemelin, 2002; Lammers & Biknevicius, 2004; Schmidt & Fischer, 2010). The use of a crouched posture increases stability by approaching the centre of mass to the support, but it also hampers limb protraction, thus causing that the hindlimbs touch the ground not so far as typically observed, and so reducing pair gap values. As suggested by Lepicard et al. (2006), for mice under potentially dangerous environmental conditions, the reduction of swing phase duration and the use a crouched posture are a function of the animals' risk assessment of the environment.

Finally, during film analysis, it was observed that cats placed their feet obliquely to the support. That is, during locomotion on narrow supports the lower arm was kept in an adducted position during the stance phase. These observations agree with previous results on primate arboreal locomotion (Schmitt, 2003*b*). When comparing mediolateral applied forces and joint angles during overground and arboreal locomotion in Primates, Schmitt (2003*b*) found that most of his animals showed a higher degree of adduction on the arboreal support. Lower arm adduction in the cat is probably accomplished thanks to the

angle of the olecranon fossa relative to the long axis of the humerus, which has been previously related to living in densely structured habitats (Gonyea, 1978). In the case of domestic cats, this angle is about 9° , at an intermediate position between the cheetah, *Acinonyx jubatus* (3° ; highly cursorial, open terrain dweller), and the arboreal margay cat, *Leopardus wiedii* (13°). The oblique placement of the feet allows a larger support polygon, since the feet are no longer collinear, thus increasing stability. Furthermore, it probably reorients ground support forces inwards to the support, which prevents slipping off it and reduces lateral oscillations of the centre of mass (Schmitt, 2003*b*; Lammers & Biknevičius, 2004; Schmidt & Fischer, 2010). This finding thus further validates the use of a narrow, square bar to simulate arboreal supports.

Dynamic stability over balance in completely terrestrial species

As shown above, dogs tended to perform the 'arboreal' exercise at high speeds, probably relying on dynamic stability rather than on balance. To increase their speed, dogs reduced cycle duration significantly by shortening the swing phase, which recalls the strategy used by cats when out of balance. This behaviour seems thus characteristic of locomotion on narrow supports in both cats and dogs. It has been demonstrated that increased angular velocities during limb retraction in the swing phase prior to touch-down is a simple strategy to increase the stability of spring-mass running (Seyfarth et al., 2003). These increased angular velocities could account for the observed reduction of swing phase duration during 'arboreal' locomotion in dogs.

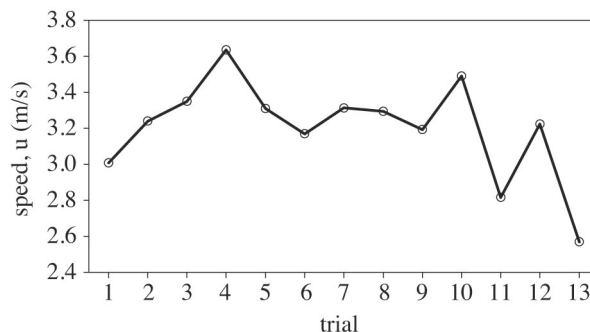
The strategy of dogs during 'arboreal' locomotion involved other striking features, namely the reduction, or even loss, of whole body aerial phases, and important changes in coordination. This way, it seems that completely terrestrial mammals (dogs) use a different strategy to gain stability on narrow supports than non-arboreal specialists. Considering the overlapping speed range (1.54 to 4.19 m/s), 72.3% of the sequences performed over ground included a whole body aerial phase (83.1% when excluding lateral walk), while only 26.3% included an aerial phase on the narrow support. The reduction of whole body aerial phases probably was a strategy to achieve lower peak vertical forces, which reduces vertical oscillation of the centre of mass and of the support, increasing stability. This strategy has also been reported for overground locomotion in elephants (Hutchinson et al., 2006), and for arboreal ambling and canter in Primates, for which it has also been described as a strategy to maintain a secure grip on the branch, thus increasing the importance of this strategy in arboreal locomotion (Schmitt, 1999; Schmitt et al.,

2006).

Regarding coordination, while dogs favoured symmetrical gaits, especially the trot, when moving over ground at the specific speed range considered in this study (1.54 to 4.19 m/s), they used mainly asymmetrical coordination patterns when moving along the elevated narrow support. Although 48% of the APSs of narrow support locomotion could not be classified into any classically defined gait, 34% could be attributed to canter-like coordination, and 9% each to transverse gallop-like and trot-like coordination. In canter only one of the synchronized limb couplets characterizing the trot is retained, thus, by using canter-like coordination, dogs gain an additional functional step per sequence, which grants them another chance to modify their kinematics and coordination (in opposition to just two functional steps in trot; Lee et al., 1999). Furthermore, coupled with whole body aerial phase reduction, canter-like coordination allows dogs to lean on three feet during part of the cycle, and thus reduces bipedality (only two feet on the ground at the same time), which in turn enhances stability when moving forward (Hildebrand, 1980; Cartmill et al., 2002). Both canter-like and trot-like coordination are characterized by periods of diagonal bipedality, which provides mechanical stability during running, given that touch-down synchronization of diagonal limbs opposes the forces that tend to rotate the body in both its transverse (pitch) and sagittal (roll) axis (Hildebrand, 1985; Lee et al., 1999; Cartmill et al., 2002). This would also explain why a pace-like coordination, less stable since it maximizes unilateral bipedality (Cartmill et al., 2002), was never observed in narrow support locomotion while dogs used the pace over ground (Maes et al., 2008).

These results agree with the work of Schmitt et al. (2006) in primates, whose preferred gait in asymmetrical running was the canter when moving either along a horizontal pole or over ground. In the same study, Schmitt et al. (2006) stated that both ambling gaits and canter allow animals to maintain at least one foot in contact with the support during the stride, that is, to eliminate whole body aerial phases. This loss of whole body aerial phases

Figure I.6. Mean speed values of dogs for each successive trial of narrow support locomotion.



cannot be accomplished at high speed trotting (e.g. in our data for dogs in narrow support locomotion, 45.7% of the trot-like sequences included a whole body aerial phase, whereas only 11.1% of the canter-like sequences did it). They also noted that both canter and ambling gaits account for reduced periods of bipedality. According to the authors, these properties of ambling gaits and canter increase the animal's stability by lowering peak vertical forces, thus reducing vertical displacements of the centre of mass and vertical oscillation of the support. It would be interesting to study of substrate reaction force patterns in cats and dogs, as already done on primates and opossums (Schmitt, 1999; Schmitt & Lemelin, 2002; Lammers & Biknevicius, 2004; Schmidt & Fischer, 2010), to assess this decrease in peak vertical forces when these animals advance in an arboreal situation.

Finally, it could be argued that the preference of dogs for high speeds on narrow support locomotion could be a consequence of their *Agility* training. Although it probably influenced their first trials traversing the elevated runway, since the highest observed speed values correspond to the first trials, there might have been a learning process during the subsequent trials, in which dogs progressively decreased their speed on the runway (Fig. I.6). Nevertheless, due to the low sample size (only 3 dogs performed more than 10 trials), no significant correlation could be found between speed and trial number ($p = 0.399$).

Conclusions

Our study of kinematics and coordination in the cat points out the existence of a global strategy for medium-sized (cats) and small (opossums) non-arboreal specialists when moving on narrow, elevated supports. This strategy consists in the use of low speeds, probably to reduce peak vertical forces, hence to reduce the oscillations of the centre of mass and those of the support. No change in gaits is needed to maintain balance.

On the contrary, the completely terrestrial dogs, showed greater difficulties to adapt to narrow support locomotion. They moved at high speeds, to gain in dynamic stability, using unsteady asymmetrical coordination patterns, suggesting constant readjustments in limb coordination. The reduction of whole body aerial phases limited vertical oscillation of the centre of mass.

The only universal strategy observed was the maximization of contact time between the animal and the support by reducing swing phase duration and also by the use of a crouched posture, which probably reduces oscillation of the centre of mass.

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Section B: Interaction

Journal Reference

Manuscript to be submitted to the *Journal of Morphology*.

Quantifying morphological adaptations using direct measurements: The carnivoran appendicular skeleton as a case of study



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Abstract

The effect of several factors (size, phylogeny, locomotion) on limb bone morphology was studied using a set of 43 variables measured in the scapula, long bones (humerus, radius, ulna, femur, tibia), third metacarpal, and calcaneus, of 435 specimens belonging to 143 species of Carnivora. Size was the main factor affecting carnivoran limb morphology, and the allometric effect created several artifactual differences among several locomotion-related categories, while also masking several actual differences among those groups. After removing the allometric effect from the data using regression residuals of each variable on body mass, the effect of locomotion and phylogeny was further explored. Locomotor type was used to represent locomotor specialization, and preferred habitat as an indicator of the ability to perform different modes of locomotion (running, swimming, climbing, digging) and thus maximize resource exploitation by being able to navigate all substrates available in their preferred habitat. Locomotor type produced slightly better results than preferred habitat, suggesting that carnivorans favor locomotor specialization. In agreement with previous studies on carnivoran limb morphology, a significant phylogenetic effect was found on the studied sample. Contrary to some of those studies, however, the phylogenetic effect did not usually mask differences between locomotor types. Finally, the present results support the hypothesis of a “viverrid-like”, forest-dwelling carnivoran ancestor, either arboreal or terrestrial.

Keywords: limb bones; adaptation; size; locomotor type; habitat; Carnivora

Introduction

From the early descriptive studies of H. F. Osborn's students (Dublin, 1903; Osburn, 1903; Shimer, 1903; Lull, 1904), the last century has seen a large amount of studies on the adaptations of mammalian limb bones to different locomotor types. Most of these studies either describe anatomical characteristics typical to some locomotor type (Smith & Savage, 1956; English, 1977; Cartmill, 1985; Hildebrand, 1985*a, b*), or compare the scaling of those characteristics either in a particular locomotor type (mainly terrestrial mammals; e.g. Bertram & Biewener, 1992; Christiansen, 1999) or between different locomotor types (e.g. Bou et al., 1987; Cubo et al., 2006). Few are the studies that compare limb bone measurements (bone lengths or diameters, or indexes with functional significance) between locomotor types using a univariate approach (i.e. that compare raw measurements instead of allometric coefficients or deviations from a general scaling pattern). This is probably due to expected size differences among mammals with different locomotor types (Cartmill, 1974; Eisenberg, 1981; Cartmill, 1985; Wolff & Guthrie, 1985; Van Valkenburgh, 1987) and to the significant effect of size on most limb bone measurements (Alexander et al., 1979; Bou et al., 1987; Bertram & Biewener, 1990, 1992; Christiansen, 1999; Gálvez-López & Casinos, 2012). Most studies comparing limb bone measurements using a univariate approach focus on adaptations either to fossoriality, especially in Rodentia (Lehmann, 1963; Elissamburu & Vizcaíno, 2004), or to arboreality (Gonyea, 1976; Iwaniuk et al., 1999; Argot, 2001). Only a few studies included both arboreal and fossorial species (Van Valkenburgh, 1987; Casinos, 1994). Furthermore, none of these studies tested the effect of phylogenetic relatedness on limb bone morphology.

In order to test the influence of locomotor type, preferred habitat, size, and phylogenetic relatedness on limb bone morphology, a widely-distributed, monophyletic clade whose species spanned a wide size range and presented highly diverse locomotor capabilities was needed. Carnivora is such a widely-distributed monophyletic group (Wilson & Mittermeier, 2009; Nyakatura & Bininda-Emonds, 2012), since carnivorans span a size range of four orders of magnitude (from less than 0.1 kg in the least weasel (*Mustela nivalis*) to well over two tonnes in elephant seals (*Mirounga sp.*)) and present one of the widest locomotor diversities among mammals, lacking only gliding and truly fossorial species (Van Valkenburgh, 1987; Bertram & Biewener, 1990; Wilson & Mittermeier, 2009).

The main aims of the present study are, thus, (1) to assess whether locomotor adaptations can be detected on the limb bones using a univariate approach, (2) to

determine whether the size differences observed among animals with different locomotor types allow of this kind of approach, and (3) to test the effect of phylogenetic relatedness, since the existence of phylogenetic constraints might obscure differences among locomotor types.

Previous studies have suggested that Carnivora is an evolutionarily conservative group regarding locomotor type and limb morphology (Alexander et al., 1979; Flynn et al., 1988; Bertram & Biewener, 1990; Day & Jayne, 2007). Furthermore, Bertram & Biewener (1990) stated that, due to the aforementioned conservative design of carnivoran limbs, morphological differences among terrestrial, scansorial, and arboreal carnivorans are mostly caused by size differences among these groups, whereas adaptations to swimming and digging should be independent of size. However, Iwaniuk and colleagues (Iwaniuk et al., 1999, 2000) have found a significant correlation between several functional indexes and the degree of arboreality, suggesting that size is not the only determinant factor behind differences in limb bone morphology among terrestrial, scansorial, and arboreal mammals.

Thus, regarding the aims introduced above, a significant allometric effect is expected on limb bone measurements, but it is also expected for both semifossorial and aquatic mammals to be significantly different from the rest of locomotor types, and that, at least for some of the variables studied, a gradation related to the degree of arboreality exists. Finally, the carnivoran appendicular skeleton is expected to be optimized for a particular locomotor type, instead of presenting a less specialized morphology in order to perform several locomotor modes (i.e., better results are expected using locomotor type than using preferred habitat), since previous studies have shown that the capability of performing several modes of locomotion comes at the expense of increased costs of locomotion in those locomotor modes (e.g. semiaquatic mammals: Williams, 1983*a, b*, 1989; Williams et al., 2002).

Material and Methods

The sample consisted of 435 specimens from 143 species of Carnivora (Table II.1). For each specimen, measurements were taken on the scapula, humerus, radius, ulna, third metacarpal, femur, tibia, and calcaneus, as described in the Appendix. Although anatomically the scapula is an element of the shoulder girdle, previous studies have shown that, functionally, it acts as the main propulsive segment of the forelimb, being analogous

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Canidae									
<i>Alopex lagopus</i>	3	terr	op	1	<i>Lycalopex culpaeus</i>	3	terr	va	1
<i>Canis adustus</i>	4	terr	mo	1	<i>Lycalopex gymnocercus</i>	4	terr	op	1
<i>Canis aureus</i>	6	terr	va	1	<i>Lycaon pictus</i>	3	terr	mo	1
<i>Canis latrans</i>	3	terr	va	1	<i>Nyctereutes procyonoides</i>	3	terr	fo	1
<i>Canis lupus</i>	5	terr	va	2, 3	<i>Otocyon megalotis</i>	1	terr	op	1
<i>Canis mesomelas</i>	7	terr	op	1	<i>Speothos venaticus</i>	6	terr	fo	1
<i>Cerdocyon thous</i>	2	terr	mo	1	<i>Urocyon cinereoargenteus</i>	1	terr	mo	1
<i>Chrysocyon brachyurus</i>	6	terr	op	4	<i>Vulpes chama</i>	1	terr	op	1
<i>Cuon alpinus</i>	3	terr	fo	1	<i>Vulpes vulpes</i>	12	terr	va	6
<i>Dusicyon australis</i>	1	terr	op	5	<i>Vulpes zerda</i>	2	terr	de	1
Mustelidae									
<i>Aonyx cinereus</i>	2	saq	fw	1	<i>Martes foina</i>	23	scan	mo	9
<i>Arctonyx collaris</i>	1	sfos	fo	1	<i>Martes martes</i>	8	sarb	fo	9
<i>Eira barbara</i>	2	sarb	fo	1	<i>Martes zibellina</i>	1	scan	fo	1
<i>Enhydra lutris</i>	1	aq	ma	1	<i>Meles meles</i>	5	sfos	mo	10
<i>Galictis cuja</i>	2	terr	va	1	<i>Mellivora capensis</i>	2	sfos	va	1
<i>Galictis vittata</i>	2	terr	mo	1	<i>Melogale moschata</i>	1	terr	mo	1
<i>Gulo gulo</i>	2	scan	mo	1	<i>Melogale orientalis</i>	1	terr	mo	1
<i>Ictonyx lybicus</i>	2	terr	de	1	<i>Mustela erminea</i>	8	terr	mo	9
<i>Ictonyx striatus</i>	1	terr	va	1	<i>Mustela eversmannii</i>	1	terr	op	1
<i>Lontra felina</i>	3	saq	ma	1	<i>Mustela lutreola</i>	1	saq	fw	1
<i>Lontra longicaudis</i>	2	saq	fw	1	<i>Mustela nivalis</i>	5	terr	va	9
<i>Lontra provocax</i>	1	saq	fw	7	<i>Mustela nudipes</i>	2	terr	fo	1
<i>Lutra lutra</i>	5	saq	fw	8	<i>Mustela putorius</i>	6	terr	mo	1
<i>Lutrogale perspicillata</i>	1	saq	fw	1	<i>Mustela vison</i>	2	saq	fw	1
<i>Lyncodon patagonicus</i>	2	terr	op	1	<i>Pteronura brasiliensis</i>	2	saq	fw	1
<i>Martes americana</i>	1	sarb	fo	1	<i>Vormela peregusna</i>	3	sfos	va	1
Mephitidae									
<i>Conepatus chinga</i>	2	sfos	op	1	<i>Spilogale gracilis</i>	2	terr	mo	1
<i>Conepatus humboldti</i>	1	sfos	va	1					
Otariidae									
<i>Arctocephalus australis</i>	1	aq	ma	11	<i>Otaria flavescens</i>	2	aq	ma	12
<i>Arctocephalus gazella</i>	1	aq	ma	11	<i>Zalophus californianus</i>	2	aq	ma	12
Phocidae									
<i>Hydrurga leptonyx</i>	1	aq	ma	12	<i>Phoca vitulina</i>	2	aq	ma	13
<i>Mirounga leonina</i>	1	aq	ma	13					
Ailuridae									
<i>Ailurus fulgens</i>	7	scan	fo	14					
Procyonidae									
<i>Bassaricyon gabbii</i>	1	arb	fo	1	<i>Potos flavus</i>	4	arb	fo	1
<i>Bassariscus astutus</i>	1	scan	mo	1	<i>Procyon cancrivorus</i>	3	scan	fw	1
<i>Nasua narica</i>	4	scan	fo	15	<i>Procyon lotor</i>	5	scan	fw	1
<i>Nasua nasua</i>	6	scan	mo	16					

Table II.1. Measured species. See legend on next page.

Table II.1. Measured species. (cont.) See legend on next page.

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Ursidae									
<i>Ailuropoda melanoleuca</i>	2	scan	fo	1	<i>Ursus americanus</i>	2	scan	mo	1
<i>Helarctos malayanus</i>	1	scan	fo	1	<i>Ursus arctos</i>	6	scan	va	1
<i>Melursus ursinus</i>	1	scan	mo	1	<i>Ursus maritimus</i>	4	terr	ma	1
<i>Tremarctos ornatus</i>	2	scan	mo	1					
Viverridae									
<i>Arctictis binturong</i>	4	arb	fo	1	<i>Genetta tigrina</i>	1	sarb	mo	1
<i>Arctogalidia trivirgata</i>	2	arb	fo	1	<i>Hemigalus derbyanus</i>	4	sarb	fo	1
<i>Civettictis civetta</i>	4	terr	mo	21	<i>Paradoxurus hermaphroditus</i>	2	arb	fo	1
<i>Cynogale benettii</i>	1	saq	fw	1	<i>Poiana richardsoni</i>	1	sarb	fo	1
<i>Genetta felina</i>	5	scan	mo	1	<i>Viverra tangalunga</i>	4	terr	fo	1
<i>Genetta genetta</i>	7	scan	mo	1	<i>Viverra zibetha</i>	2	terr	fo	1
<i>Genetta maculata</i>	3	sarb	mo	1	<i>Viverricula indica</i>	4	scan	mo	1
Herpestidae									
<i>Atilax paludinosus</i>	2	saq	fw	1	<i>Herpestes brachyurus</i>	1	terr	fo	1
<i>Crossarchus obscurus</i>	2	terr	fo	9	<i>Herpestes edwardsii</i>	2	terr	mo	1
<i>Cynictis penicillata</i>	4	terr	op	1	<i>Herpestes ichneumon</i>	4	terr	op	1
<i>Galerella pulverulenta</i>	4	terr	fo	1	<i>Herpestes javanicus</i>	1	terr	mo	1
<i>Galerella sanguinea</i>	1	terr	mo	1	<i>Ichneumia albicauda</i>	2	terr	mo	1
<i>Helogale parvula</i>	2	terr	mo	1	<i>Suricata suricatta</i>	4	sfos	op	1
Eupleridae									
<i>Cryptoprocta ferox</i>	2	sarb	fo	1	<i>Mungotictis decemlineata</i>	1	scan	fo	1
<i>Fossa fossa</i>	2	terr	fo	1	<i>Salanoia concolor</i>	2	scan	fo	1
<i>Galidia elegans</i>	4	scan	fo	1					
Hyaenidae									
<i>Crocuta crocuta</i>	2	terr	mo	9	<i>Parahyaena brunnea</i>	1	terr	va	1
<i>Hyaena hyaena</i>	3	terr	va	1	<i>Proteles cristatus</i>	2	terr	op	9
Felidae									
<i>Acinonyx jubatus</i>	3	scan	mo	1	<i>Neofelis nebulosa</i>	1	sarb	fo	18
<i>Caracal caracal</i>	5	scan	mo	1	<i>Otocolobus manul</i>	2	scan	op	1
<i>Felis chaus</i>	1	scan	va	1	<i>Panthera leo</i>	7	scan	op	1
<i>Felis nigripes</i>	2	scan	mo	17	<i>Panthera onca</i>	2	scan	fo	1
<i>Felis silvestris</i>	15	scan	mo	1	<i>Panthera pardus</i>	8	scan	va	13
<i>Leopardus colocolo</i>	2	scan	va	1	<i>Panthera tigris</i>	9	scan	mo	19
<i>Leopardus geoffroyi</i>	2	scan	mo	1	<i>Panthera uncia</i>	4	scan	op	20
<i>Leopardus pardalis</i>	2	scan	fo	1	<i>Pardofelis marmorata</i>	1	arb	fo	1
<i>Leopardus tigrinus</i>	2	scan	fo	1	<i>Prionailurus bengalensis</i>	1	scan	mo	1
<i>Leopardus wiedii</i>	1	arb	fo	1	<i>Prionailurus planiceps</i>	1	scan	fw	1
<i>Leptailurus serval</i>	6	scan	mo	13	<i>Prionailurus viverrinus</i>	1	scan	fw	1
<i>Lynx canadensis</i>	1	scan	mo	1	<i>Profelis aurata</i>	1	scan	fo	1
<i>Lynx lynx</i>	3	scan	mo	1	<i>Puma concolor</i>	5	scan	va	1
<i>Lynx pardinus</i>	4	scan	mo	13	<i>Puma yaguaroundi</i>	3	scan	mo	1
<i>Lynx rufus</i>	1	scan	va	1					
Prionodontidae					Nandiniidae				
<i>Prionodon linsang</i>	1	arb	fo	1	<i>Nandinia binotata</i>	5	sarb	fo	1

Table II.1. Measured species. (cont.) For each species, the table shows the number of measured specimens, the assigned category for both locomotor type and preferred habitat, and the references from which the mean body mass value for that species was taken (M_b). Abbreviations: aq, aquatic; arb, arboreal; de, desert; fo, forest; fw, freshwater; loctyp, locomotor type; ma, marine; mo, mosaic; n, measured specimens; op, open; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial; va, variable. See Table II.3 for a description of locomotor type and preferred habitat categories. References: 1. Wilson & Mittermeier, 2009; 2. Blanco et al., 2002; 3. Mech, 2006; 4. Dietz, 1984; 5. Brook & Bowman, 2004; 6. Cavallini, 1995; 7. Reyes-Küppers, 2007; 8. Yom-Tov et al., 2006; 9. Grzimek, 1988; 10. Virgós et al., 2011; 11. Perrin et al., 2002; 12. MacDonald, 2001; 13. Silva & Downing, 1995; 14. Roberts & Gittleman, 1984; 15. Gompper, 1995; 16. Gompper & Decker, 1998; 17. Sliwa, 2004; 18. Sunquist & Sunquist, 2002; 19. Mazák, 1981; 20. IUCN Cat Specialist Group, 2011; 21. Ray, 1995.

to the femur in the hind limb (Boczek-Funcke et al., 1996; Fischer et al., 2002; Fischer & Blickhan, 2006). Thus, in the present study the scapula is considered the most proximal segment of the forelimb. Table II.2 lists the 43 variables analyzed in this study.

Specimens studied are housed in the collections of the Phylogenetisches Museum (Jena, Germany), the Museum für Naturkunde (Berlin, Germany), the Museu de Ciències Naturals de la Ciutadella (Barcelona, Spain), the Muséum National d'Histoire Naturelle (Paris, France), the Museo Nacional de Ciencias Naturales (Madrid, Spain), the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina), the Museo de La Plata (La Plata, Argentina), and the Naturhistorisches Museum Basel (Basel, Switzerland). Only adult specimens (judged by epiphyseal fusion) were sampled and, where possible, only the limb elements of the left side were measured.

Since body mass values were missing from most specimens, mean values for each species were obtained from the literature (taking into account the sex of the specimen when available, as described in the Appendix) (Table II.1). Taxonomy follows Wilson & Mittermeier (2009), except for a few species for which the synonyms in Wozencraft (2005) were preferred. Locomotor adaptations were studied using two separate sets of categories: locomotor type and preferred habitat (Table II.3). Locomotor type categories represent locomotor specialization, i.e. the main locomotor habit of each species. On the other hand, preferred habitat was used as a broader ecological correlate, representing the ability to use several modes of locomotion besides that defined by its locomotor type in order to exploit all available resources in its home range (e.g. a semiaquatic carnivoran could also dig proficiently). This way, carnivorans inhabiting more complex habitats are considered more likely to use several modes of locomotion (e.g. while desert-dwelling carnivorans are only likely to run or dig, forest-dwelling carnivorans should be able to run, climb, dig, and even swim). Each species was thus assigned a locomotor type category and a preferred habitat

Table II.2. Variable names and abbreviations.

Abbr.	Name	Abbr.	Name
M_b	Body mass	IFA	Indicator of Fossorial Ability
L_s	Scapular length	L_m	Third metacarpal functional length
S	Maximum width of supraspinous fossa	d_{sm}	Third metacarpal sagittal diameter
I	Maximum width of infraspinous fossa	d_{tm}	Third metacarpal transverse diameter
A	Maximum scapular width	MR	Third metacarpal robusticity
H_s	Scapular spine height	L_f	Femur functional length
L_h	Humerus functional length	N	Neck–head length
d_{sh}	Humerus sagittal diameter	d_{sf}	Femur sagittal diameter
d_{th}	Humerus transverse diameter	d_{tf}	Femur transverse diameter
T	Projected height of greater tubercle	FR	Femur robusticity
HR	Humerus robusticity	L_t	Tibia functional length
L_r	Radius functional length	d_{st}	Tibia sagittal diameter
d_{sr}	Radius sagittal diameter	d_{tt}	Tibia transverse diameter
d_{tr}	Radius transverse diameter	TR	Tibia robusticity
P	Styloid process length	L_c	Calcaneus length
RR	Radius robusticity	r	Ankle extensors moment arm
L_u	Ulna functional length	d_{sc}	Calcaneus sagittal diameter
d_{su}	Ulna sagittal diameter	d_{tc}	Calcaneus transverse diameter
d_{tu}	Ulna transverse diameter	%_{prox}	Relative length of the proximal segment of the forelimb
O	Olecranon process length	%_{prox}	Relative length of the proximal segment of the forelimb
α	Olecranon angle	%_{mid}	Relative length of the middle segment of the forelimb
θ	Olecranon abduction angle		
UR	Ulna robusticity		

category based on the literature (Dietz, 1984; Roberts & Gittleman, 1984; Grzimek, 1988; Frandsen, 1993; Gompper, 1995; Ray, 1995; Gompper & Decker, 1998; MacDonald, 2001; Perrin et al., 2002; Sliwa, 2004; Reyes-Küppers, 2007; Wilson & Mittermeier, 2009).

In order to analyse the possible influence of each factor separately on limb bone morphology, a set of one-way fixed-factor analyses of variance (ANOVA) was performed on each variable to determine whether significant differences existed among the mean values of the different locomotor types, preferred habitats, or taxonomic groups (phylogeny). To determine at which taxonomic level most of the phylogenetic effect (if any) occurred, and would thus be most appropriate to test for significant differences among taxonomic groups, percentage variance components at the family, genus, and species level were calculated from a nested ANOVA (Gittleman & Luh, 1992; Smith, 1994).

While ANOVA is robust against violations of the normality assumption (Kirk, 1995), violations of the homoscedasticity assumption can cause serious problem with type I error, especially in unbalanced designs, as is the present study. Consequently, when significant

Locomotor type	Description
arboreal	species that spend most of their life in trees (over 75%), rarely descending to the ground
semiarboreal	species that spend a large amount of their time in the trees (between 50% and 75%), both foraging and resting, but also on ground surface
scansorial	species that, although mostly terrestrial (over half their time is spent on the ground), can climb well and will readily do so to chase arboreal prey or escape, and might nest in trees for protection against terrestrial predators
terrestrial	species that rarely or never climb or swim, and that might dig to modify a burrow but not regularly for food
semifossorial	species that dig regularly for both food and shelter, but that still show considerable ability to move around on the surface
semiaquatic	species that forage regularly underwater and usually plunge into the water to escape, but must spend time ashore to groom,...
aquatic	species that carry out most of their life cycle in water, although some part of this cycle can be confined to land (parturition, mating, rearing the young)
Preferred habitat	Description
desert	open habitats with an extremely low amount of precipitation; they are separated from other open habitats due to the additional adaptations required to live in these harsh conditions. Carnivorans inhabiting deserts should rarely perform any other locomotor habit other than ground locomotion.
open	areas with low to nonexistent tree cover (e.g. grasslands, steppes, tundra,...). Carnivorans inhabiting open habitats could probably be good diggers, maybe also capable swimmers, but should lack climbing skills.
mosaic	this category was created for species that either live in forested areas with scarce tree cover (e.g. savannah), or require the presence of both forested and open areas within their home range, thus, they are expected to be good climbers, while also could be capable diggers or swimmers.
forest	areas with a high density of trees (e.g. rain forest, taiga, deciduous forest,...). Carnivorans inhabiting forested areas should probably be adept climbers, even though not completely arboreal, to be able to chase prey that flee to the canopy. They can also be capable swimmers and diggers.
freshwater	this category was created for species that dwell in or near freshwater systems (e.g. rivers, lakes, swamps,...). Carnivorans inhabiting freshwater habitats are expected to be capable swimmers, while also can present some ability to climb or dig.
marine	saltwater systems and their coastal regions. Marine carnivorans are expected to be very good swimmers, rarely dig, and possess an almost nonexistent ability to climb.
variable	this category includes all species that appear indistinctly in two or more of the other categories and thus probably contains species with highly variable locomotor skills.

Table II.3. Description of locomotor type and preferred habitat categories. Locomotor type categories were adapted from previous works on the relationship between locomotor behavior and forelimb morphology (Eisenberg, 1981; Van Valkenburgh, 1985, 1987).

heteroscedasticity was found for a particular variable, the Welch procedure was used instead of the F statistic to test for significant differences between groups (Cohen, 2001). Since robust analysis cannot be performed if the sample contains groups with only one individual, monotypic families (Ailuridae, Nandiniidae, Prionodontidae) were not included in any of the ANOVAs. In parallel, in the ANOVAs for calcaneal variables, aquatic and desert-dwelling carnivorans were not included because only one specimen was measured for each group. However, the values of all these groups for each variable are presented in their corresponding tables for comparison's sake. Additionally, *post hoc* tests were carried out to search for significant differences between the mean values of each pair of groups. Since sample sizes were unequal among groups, Hochberg's GT2 method (Hochberg, 1974;

Sokal & Rohlf, 1995) was used when the assumption of homoscedasticity was met, and Games-Howell's test in any other case. The *post hoc* tests results were also used to define homogeneous subgroups according to each factor.

Since, by definition, relative segment lengths are interdependent, differences between taxonomic groups, locomotor types, and preferred habitat, were assessed in all relative segment lengths at once using Multivariate Analysis of Variance (MANOVA), which reduces possible type I error inflation when calculating separate ANOVAs for each percentage (Sokal & Rohlf, 1995; Pike & Alexander, 2002).

Finally, General Linear Models (GLMs) were used to assess the possible interactions of size, phylogenetic relatedness, and similar locomotor type and/or preferred habitat. The full model included taxonomic group (at the level determined by the nested ANOVA, see above), locomotor type and preferred habitat as fixed effects, whereas the allometric effect was accounted for including body mass (M_b) as a covariate. Starting with the default full factorial model (i.e. intercept plus all factors, the covariate, and all possible interactions), non-significant effects were successively removed one at a time until only significant effects remained in the final model. The criterion for effect removal was based both on effect significance (p-value) and on effect size (partial eta squared, h^2).

All analyses were carried out using SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA).

Results

Locomotor type

Table II.4 shows mean values and standard deviations by locomotor type for each variable. The assumption of homoscedasticity only held for θ , IFA, MR, TR, d_{tc} , and $\%_{prox}$, so robust tests were used on all other variables. Significant differences between locomotor types were found for all variables but d_{tc} (Fig. II.1). Body mass differences were only significant between scansorial carnivorans and semiarboreal, arboreal, and semifossorial ones. *Post hoc* tests revealed that 23 of the studied variables presented significantly different homogeneous subgroups (Fig. II.2), but only in the case of IFA, $\%_{prox}$, and $\%_{mid}$, were these homogeneous subgroups different from the ones obtained for M_b (aquatic > rest).

The MANOVAs for functional relative segment lengths also recovered significant differences between locomotor types in each segment (Wilks' λ : p-value < 0.001, partial h^2 = 0.489).

	M_b (g)	L_s (mm)	S (mm)	I (mm)	A (mm)	H_s (mm)	L_n (mm)	d_{sn} (mm)	d_{fn} (mm)
terrestrial	14837 ± 47726	71.41 ± 49.51	21.06 ± 13.92	28.65 ± 22.48	50.78 ± 36.83	11.11 ± 7.91	94.64 ± 64.02	9.94 ± 7.42	7.52 ± 5.23
scansorial	30786 ± 51624	99.45 ± 56.10	34.13 ± 20.00	45.31 ± 28.97	80.12 ± 49.45	15.60 ± 10.31	141.08 ± 74.32	15.08 ± 9.69	11.72 ± 7.71
semiarboreal	3295 ± 3756	53.40 ± 17.38	19.16 ± 6.83	22.70 ± 7.77	42.26 ± 14.29	7.01 ± 3.41	82.03 ± 24.57	8.28 ± 3.87	6.12 ± 2.51
arboreal	4056 ± 3803	49.72 ± 13.80	20.13 ± 6.69	28.52 ± 8.48	47.42 ± 14.02	7.18 ± 2.38	89.67 ± 24.64	9.37 ± 2.80	7.07 ± 1.85
semifossorial	4776 ± 4665	50.32 ± 21.61	16.48 ± 8.85	18.67 ± 8.91	36.32 ± 18.15	7.50 ± 6.26	65.06 ± 26.26	7.66 ± 3.16	5.84 ± 2.44
semiaquatic	7373 ± 7274	56.82 ± 16.94	23.84 ± 8.92	20.89 ± 8.22	45.73 ± 16.82	8.00 ± 3.02	75.93 ± 17.98	11.04 ± 4.37	6.45 ± 1.65
aquatic	199753 ± 160956	171.69 ± 46.00	104.15 ± 42.22	87.97 ± 38.70	197.00 ± 62.71	12.96 ± 5.21	144.70 ± 27.44	33.89 ± 13.57	26.98 ± 9.65
	T (mm)	HR	L_r (mm)	d_{sr} (mm)	d_{rr} (mm)	P (mm)	RR	L_u (mm)	
terrestrial	2.70 ± 3.65	0.103 ± 0.018	90.02 ± 65.93	5.36 ± 3.43	6.81 ± 5.45	4.35 ± 4.15	0.067 ± 0.018	94.53 ± 70.38	
scansorial	1.73 ± 2.46	0.102 ± 0.018	123.74 ± 63.74	6.85 ± 4.16	9.76 ± 6.57	6.82 ± 5.00	0.055 ± 0.012	131.14 ± 67.83	
semiarboreal	0.07 ± 0.96	0.098 ± 0.016	65.59 ± 17.98	3.90 ± 0.91	4.76 ± 2.25	3.09 ± 1.54	0.059 ± 0.006	69.95 ± 20.04	
arboreal	0.12 ± 0.70	0.104 ± 0.011	69.24 ± 20.38	4.14 ± 1.31	5.52 ± 1.70	3.20 ± 1.47	0.061 ± 0.011	73.37 ± 22.16	
semifossorial	0.68 ± 0.92	0.116 ± 0.010	54.76 ± 22.12	4.16 ± 1.75	4.38 ± 1.92	2.95 ± 1.02	0.076 ± 0.010	57.69 ± 23.37	
semiaquatic	0.01 ± 0.69	0.142 ± 0.038	56.23 ± 14.81	5.00 ± 1.83	4.86 ± 1.50	3.27 ± 1.12	0.089 ± 0.019	61.03 ± 15.68	
aquatic	12.77 ± 9.12	0.233 ± 0.070	153.68 ± 43.48	14.24 ± 5.84	34.73 ± 15.14	13.18 ± 4.69	0.090 ± 0.020	155.76 ± 38.72	
	d_{su} (mm)	d_{mu} (mm)	O (mm)	θ (°)	α (°)	UR	IFA	L_m (mm)	d_{sm} (mm)
terrestrial	5.43 ± 3.97	5.22 ± 4.07	17.69 ± 12.33	5.24 ± 4.06	22.09 ± 8.82	0.067 ± 0.024	0.202 ± 0.038	37.70 ± 27.26	3.52 ± 2.15
scansorial	9.95 ± 6.42	7.31 ± 5.51	25.18 ± 15.34	5.82 ± 3.16	17.73 ± 7.97	0.073 ± 0.019	0.186 ± 0.030	44.63 ± 23.18	4.94 ± 2.81
semiarboreal	5.48 ± 1.77	3.92 ± 1.36	12.84 ± 5.55	7.40 ± 4.75	12.52 ± 5.24	0.078 ± 0.010	0.178 ± 0.029	23.48 ± 7.63	2.70 ± 1.10
arboreal	6.23 ± 2.40	4.02 ± 1.03	14.48 ± 5.06	3.62 ± 1.61	7.95 ± 3.19	0.084 ± 0.010	0.196 ± 0.028	22.46 ± 6.54	2.67 ± 0.76
semifossorial	5.61 ± 2.71	3.47 ± 1.68	15.41 ± 7.62	7.43 ± 4.71	15.75 ± 6.71	0.097 ± 0.018	0.263 ± 0.053	18.74 ± 7.07	2.87 ± 1.14
semiaquatic	6.22 ± 2.11	4.57 ± 1.33	16.39 ± 5.76	9.48 ± 3.41	17.93 ± 7.80	0.101 ± 0.020	0.266 ± 0.049	25.89 ± 6.94	3.58 ± 1.28
aquatic	21.42 ± 7.48	14.29 ± 5.02	52.94 ± 18.26	7.76 ± 4.63	35.08 ± 13.06	0.136 ± 0.025	0.334 ± 0.056	57.66 ± 23.77	9.57 ± 3.76

Table II.4. Descriptive statistics by locomotor type. For each variable, mean values ± standard deviations are given. All angles are given in degrees for ease of interpretation, but radians were used for all analysis. Variable names are listed in Table II.2.

Table II.4. Descriptive statistics by locomotor type. (Cont.)

	d_{lm} (mm)	MR	L_r (mm)	N (mm)	d_{sf} (mm)	d_{lr} (mm)	FR	L_t (mm)	d_{st} (mm)
terrestrial	3.91 ± 2.52	0.107 ± 0.028	105.77 ± 71.13	13.13 ± 9.51	8.03 ± 5.20	8.34 ± 5.36	0.079 ± 0.012	105.39 ± 62.43	8.53 ± 5.80
scansorial	5.24 ± 3.09	0.111 ± 0.024	157.38 ± 84.51	19.39 ± 12.94	12.01 ± 6.87	13.38 ± 8.26	0.076 ± 0.008	145.81 ± 63.70	13.17 ± 8.09
semiarboreal	2.82 ± 1.18	0.116 ± 0.024	91.17 ± 29.21	10.14 ± 3.39	6.98 ± 2.62	7.29 ± 2.58	0.075 ± 0.011	91.00 ± 23.00	7.26 ± 3.15
arboreal	2.84 ± 0.79	0.120 ± 0.022	94.15 ± 22.48	11.25 ± 4.11	7.61 ± 2.19	8.25 ± 2.45	0.080 ± 0.008	92.58 ± 21.34	7.69 ± 2.16
semifossorial	3.16 ± 1.48	0.153 ± 0.021	69.29 ± 27.09	11.10 ± 4.79	6.31 ± 2.21	6.82 ± 2.51	0.094 ± 0.008	66.76 ± 19.44	6.96 ± 2.89
semiaquatic	3.47 ± 1.28	0.137 ± 0.021	74.11 ± 17.11	11.71 ± 3.46	7.33 ± 2.05	8.45 ± 2.73	0.098 ± 0.013	82.49 ± 20.22	7.98 ± 2.66
aquatic	9.77 ± 3.43	0.168 ± 0.019	98.31 ± 14.31	22.80 ± 5.91	18.67 ± 7.37	30.88 ± 14.02	0.188 ± 0.069	214.60 ± 51.70	17.90 ± 5.78
	d_{tt} (mm)	TR	L_c (mm)	r (mm)	d_{sc} (mm)	d_{tc} (mm)	% _{prox}	% _{mid}	% _{dist}
terrestrial	7.39 ± 4.63	0.082 ± 0.015	29.50 ± 17.02	22.42 ± 13.99	10.69 ± 7.55	5.22 ± 3.40	27.77 ± 1.75	38.60 ± 2.58	33.63 ± 2.95
scansorial	10.94 ± 6.52	0.085 ± 0.019	41.84 ± 20.93	31.90 ± 16.88	15.45 ± 8.54	7.32 ± 3.90	26.96 ± 1.49	38.87 ± 1.45	34.16 ± 1.84
semiarboreal	5.65 ± 1.87	0.078 ± 0.015	22.39 ± 6.46	16.74 ± 4.90	8.34 ± 2.59	3.71 ± 1.13	26.39 ± 1.44	40.81 ± 1.14	32.80 ± 0.87
arboreal	6.03 ± 1.73	0.084 ± 0.011	23.68 ± 6.71	17.78 ± 5.48	8.06 ± 2.01	4.04 ± 1.19	23.81 ± 2.15	43.09 ± 1.61	33.10 ± 1.46
semifossorial	4.82 ± 1.93	0.101 ± 0.015	21.56 ± 9.51	16.64 ± 8.28	8.23 ± 3.79	4.56 ± 2.15	29.44 ± 1.66	38.40 ± 1.26	32.16 ± 1.70
semiaquatic	6.33 ± 2.00	0.095 ± 0.014	21.17 ± 7.02	16.60 ± 5.43	8.57 ± 2.89	3.96 ± 1.20	29.77 ± 1.74	40.47 ± 1.60	29.76 ± 1.99
aquatic	21.20 ± 8.89	0.085 ± 0.022	66.12	56.95	25.94	21.08	36.31 ± 1.49	31.25 ± 2.60	32.44 ± 2.29

Preferred habitat

Table II.5 shows mean values and standard deviations by preferred habitat for each variable. The assumption of homoscedasticity only held for θ , **UR**, **N**, and **TR**, so robust tests were used on all other variables. Significant differences between habitats were found for all variables but H_s , L_h , **RR**, θ , L_m , **TR**, L_c , r , d_{sc} , d_{tc} , and %_{dist} (Fig. II.3). Body mass differences were only significant between desert-dwelling carnivorans and species inhabiting freshwater, marine, and mosaic habitats. *Post hoc* tests revealed that 23 of the studied variables presented significantly different homogenous subgroups (Fig. II.2), but only for %_{mid} were those homogenous subgroups different from the ones obtained for body mass (%_{mid}: marine < rest; M_b : marine > rest).

The MANOVAs for functional relative segment lengths also recovered significant differences between preferred habitats in each segment (Wilks' I: p-value < 0.001, partial h^2 = 0.259). However, these results must be regarded cautiously, since the assumption of equality of covariance matrixes was violated (Box's test: p-value < 0.001).

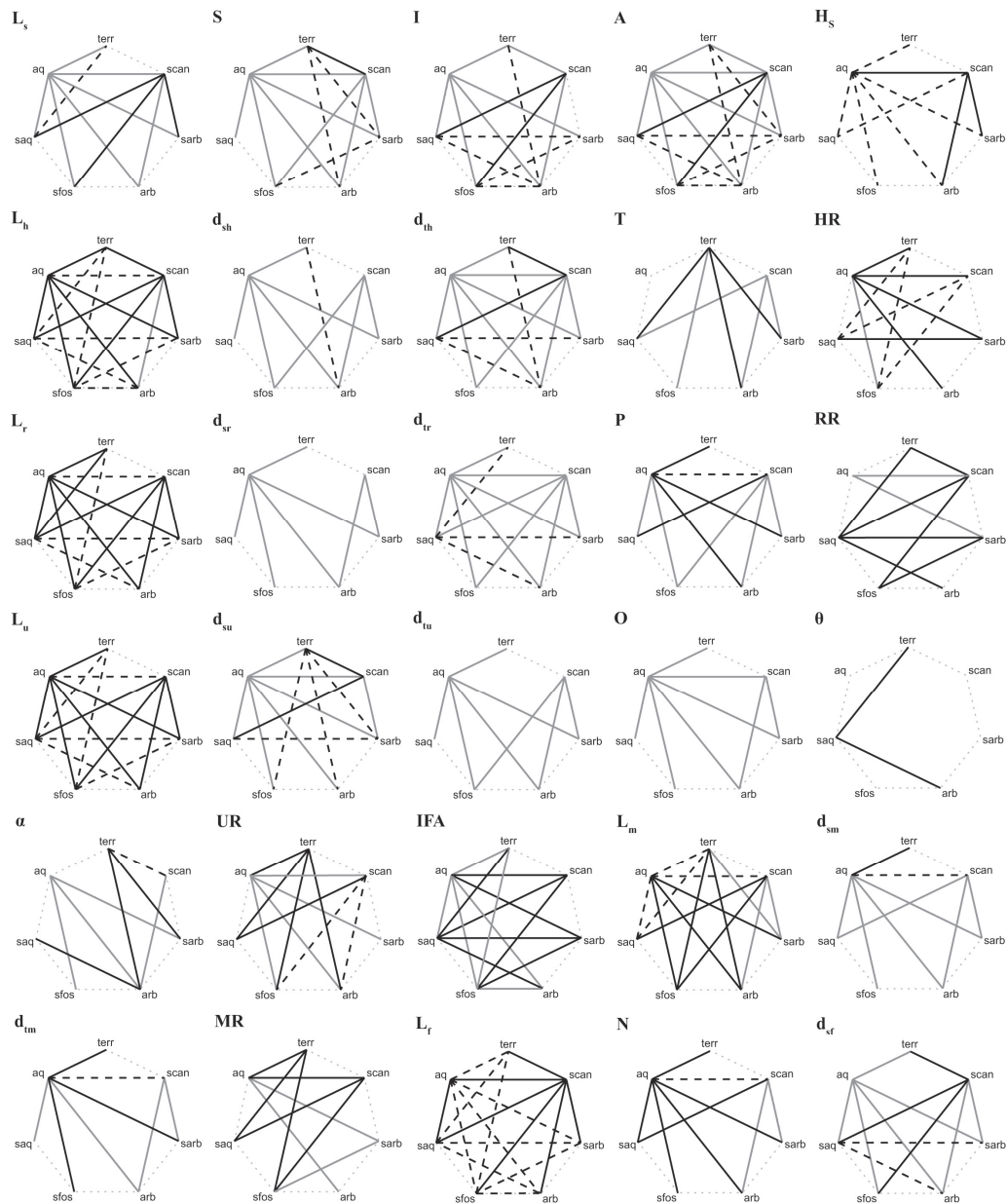
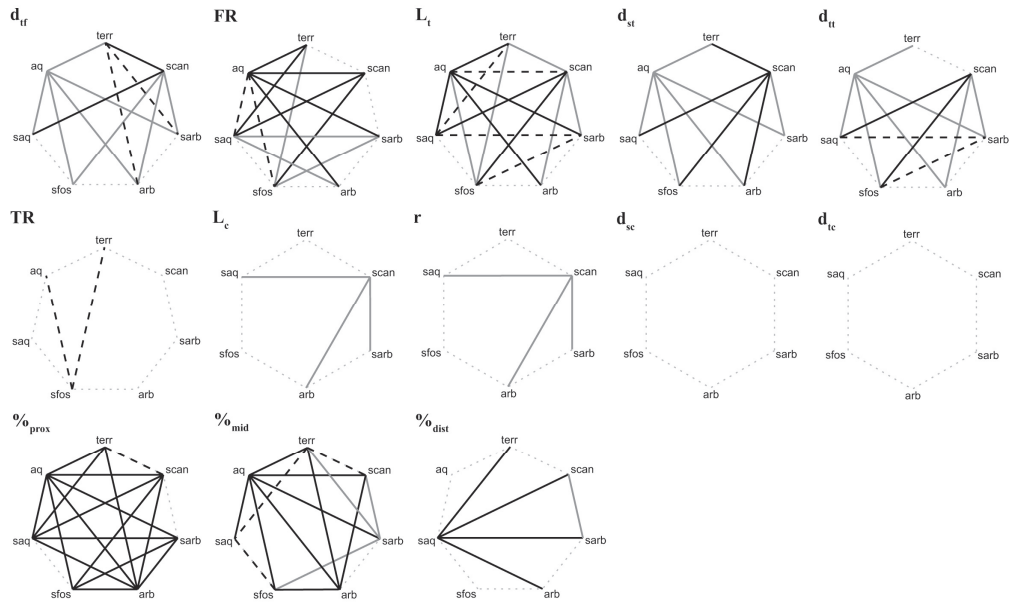


Figure II.1. Significant differences between locomotor types. Grey continuous lines denote significant differences between locomotor types in the uncorrected ANOVAs, black continuous lines represent significant differences recovered both in the uncorrected and the size-corrected ANOVAs, and black dashed lines correspond to significant differences that were revealed after correcting for allometric effects. Abbreviations: aq, aquatic; arb, arboreal; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial. All other abbreviations as in Table II.2.

Figure II.1. Significant differences between locomotor types. (Cont.)



Phylogeny

Table II.6 shows percentage variance components for each variable, but results must be considered cautiously, since the mean number of species measured for each genus is 1.55 (mode = 1, representing 73.9% of sampled genera). For most of the variables, over half the variance was found at the family level (mean \pm s.d.: 57.06% \pm 12.73%), which was thus henceforth used to represent the phylogenetic effect on all subsequent analyses.

Table II.7 shows mean values and standard deviations by family for each variable. The assumption of homoscedasticity only held for α , and **IFA**, so robust tests were used on all other variables. Significant differences between families were found for all variables (Fig. II.4). Body mass differences were only significant between Canidae and Mephitidae, probably due to the large size variation in most families. *Post hoc* tests revealed that 23 of the studied variables presented significantly different homogenous subgroups (Fig. II.2). However, these homogenous subgroups always mirrored to a certain degree the ones obtained for **M_b** (Pho > {Urs, Ota} > rest), that is, for most variables the significantly different subgroups consisted in a combination of one or more of the families with large mean body mass (Pho, Urs, Ota) displaying higher values than the other families (which in turn were represented by a variable number of overlapping subgroups).

The MANOVAs for functional relative segment lengths also recovered significant differences between families in each segment (Wilks' I: p-value < 0.001, partial h^2 = 0.489). Nevertheless, these results must be regarded cautiously, since the assumption of equality

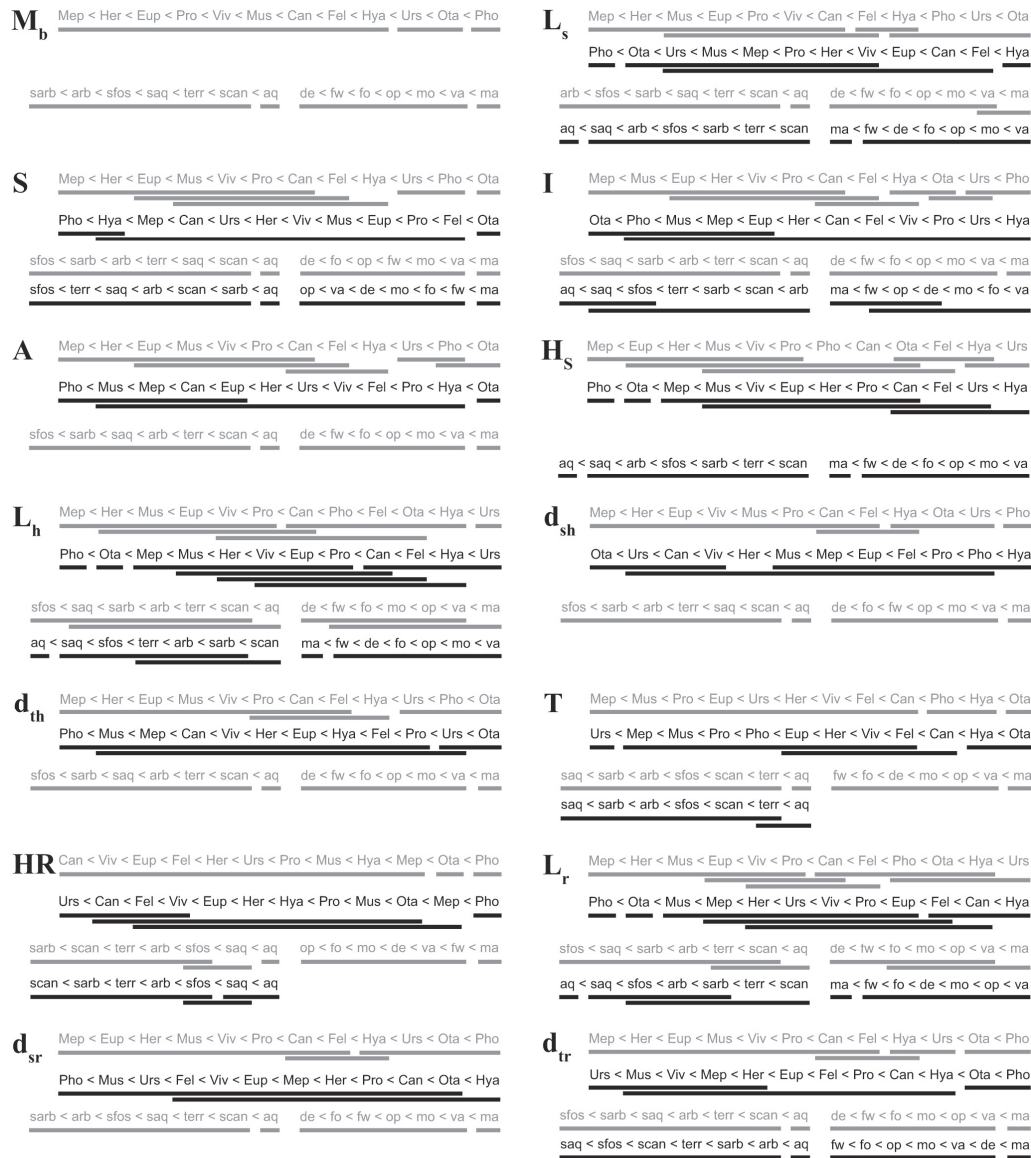


Figure II.2. Homogeneous subgroups. For each variable, categories are listed from lowest to highest mean values, while the lines underneath represent homogeneous subgroups. Results for both the uncorrected ANOVAs (in grey) and the size-corrected ANOVAs (in black) are given. If all categories were included in a single homogeneous subgroup, results are not shown for that particular analysis for that variable. Abbreviations: aq, aquatic; arb, arboreal; Can, Canidae; de, desert; Eup, Eupleridae; Fel, Felidae; fo, forest; fw, freshwater; Her, Herpestidae; Hya, Hyaenidae; ma, marine; Mep, Mephitidae; mo, mosaic; Mus, Mustelidae; Ota, Otariidae; Pho, Phocidae; Pro, Procyonidae; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial; Urs, Ursidae; va, variable; Viv, Viverridae. All other abbreviations as in Table II.2.

Figure II.2. (Cont.)
Homogeneous
subgroups.

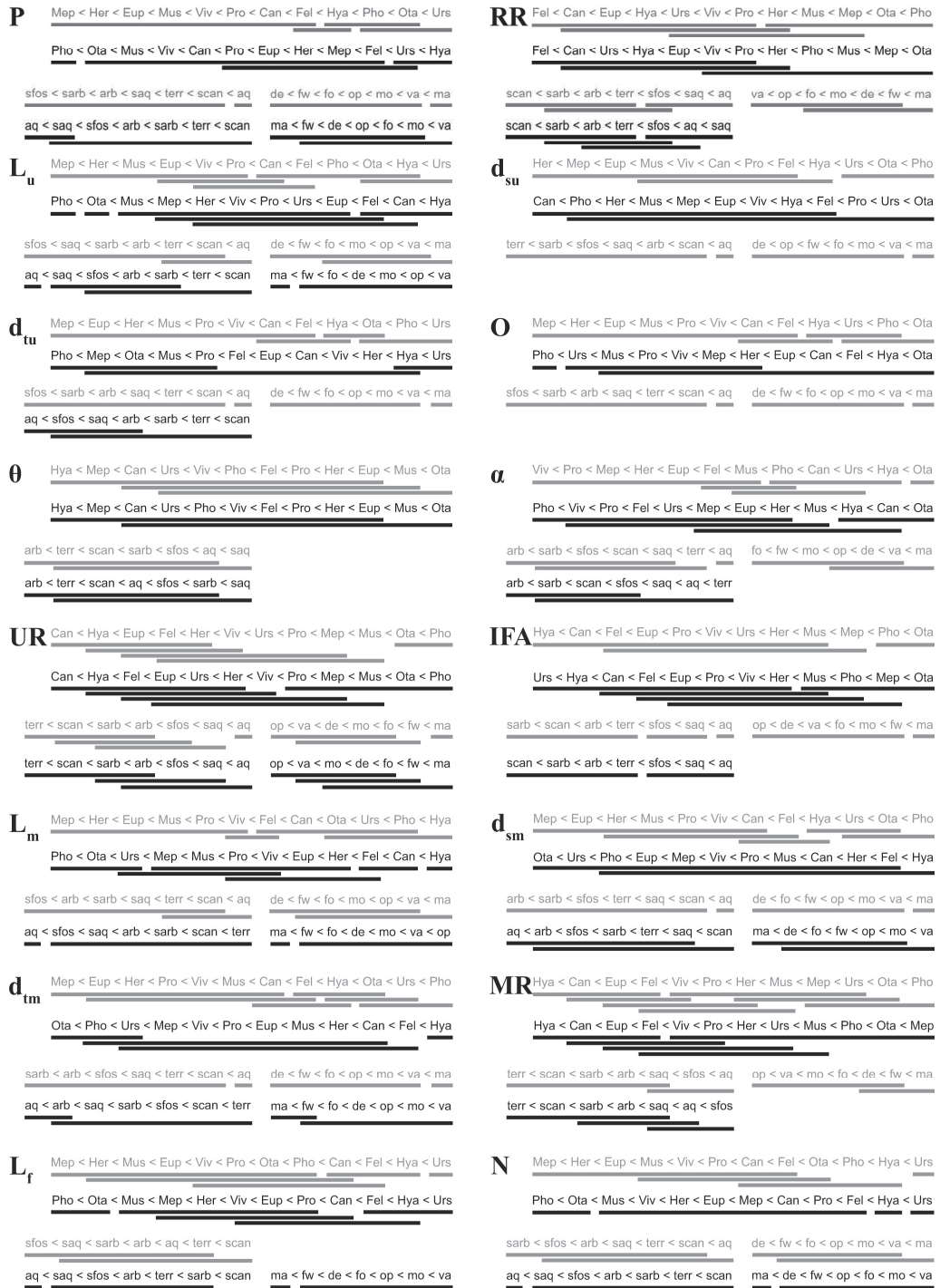




Figure II.2. (Cont.) Homogeneous subgroups.

of covariance matrixes was violated (Box's test: p-value < 0.001), probably due to the large sample size differences among groups.

GLMs

A total of 22 different models summarized the effect of locomotor type, preferred habitat, phylogenetic relatedness, body size, and their interactions, on the observed variability of the 43 variables studied (Table II.8). No effect was common to all models, but

Table II.5. Descriptive statistics by habitat. For each variable, mean values \pm standard deviations are given. All angles are given in degrees for ease of interpretation, but radians were used for all analysis. Variable names are listed in Table II.2.

	M_b (g)	L_s (mm)	S (mm)	I (mm)	A (mm)	H_s (mm)	L_h (mm)	d_{sh} (mm)	d_{th} (mm)
open	18241 \pm 36809	80.83 \pm 55.04	23.15 \pm 15.66	31.42 \pm 22.08	55.22 \pm 37.99	11.24 \pm 8.55	112.95 \pm 73.90	10.85 \pm 8.29	8.30 \pm 5.88
mosaic	18901 \pm 37237	81.53 \pm 54.83	26.84 \pm 18.18	34.87 \pm 25.91	62.59 \pm 44.61	12.40 \pm 9.88	112.86 \pm 71.32	11.94 \pm 8.71	9.32 \pm 6.92
forest	9395 \pm 18927	63.43 \pm 33.85	22.61 \pm 13.09	29.38 \pm 19.83	52.45 \pm 33.15	9.39 \pm 6.42	94.16 \pm 47.35	9.97 \pm 6.06	7.69 \pm 4.74
desert	868 \pm 661	32.46 \pm 17.25	10.36 \pm 3.95	13.30 \pm 10.83	24.53 \pm 14.11	4.25 \pm 3.00	49.63 \pm 30.33	4.54 \pm 1.18	4.05 \pm 1.73
freshwater	7222 \pm 6585	58.92 \pm 15.59	23.53 \pm 8.40	23.26 \pm 8.64	47.55 \pm 16.13	8.20 \pm 3.04	80.91 \pm 18.31	10.82 \pm 4.18	6.59 \pm 1.72
marine	194003 \pm 162657	165.02 \pm 60.48	94.30 \pm 45.29	84.13 \pm 42.96	182.67 \pm 74.63	14.71 \pm 9.37	156.13 \pm 73.49	32.35 \pm 14.12	25.28 \pm 10.87
variable	26273 \pm 69491	96.47 \pm 56.27	29.44 \pm 17.78	40.94 \pm 28.66	71.46 \pm 46.41	14.47 \pm 9.97	129.73 \pm 71.28	14.04 \pm 9.06	10.41 \pm 6.75
	T (mm)	HR	L_r (mm)	d_{sr} (mm)	P (mm)	RR	L_u (mm)		
open	2.71 \pm 2.74	0.095 \pm 0.018	105.60 \pm 73.42	5.76 \pm 3.60	4.91 \pm 4.29	0.061 \pm 0.021	111.61 \pm 78.10		
mosaic	1.86 \pm 3.21	0.105 \pm 0.017	100.36 \pm 67.25	5.84 \pm 3.80	5.16 \pm 4.20	0.064 \pm 0.016	105.28 \pm 71.33		
forest	0.90 \pm 1.65	0.102 \pm 0.017	77.61 \pm 37.56	4.83 \pm 2.60	4.04 \pm 2.95	0.063 \pm 0.013	82.59 \pm 41.20		
desert	0.90 \pm 0.95	0.105 \pm 0.035	45.03 \pm 32.70	2.44 \pm 1.07	3.59 \pm 1.37	0.065 \pm 0.021	47.36 \pm 34.11		
freshwater	0.05 \pm 0.70	0.131 \pm 0.034	64.08 \pm 19.40	4.99 \pm 1.77	5.13 \pm 1.53	0.081 \pm 0.024	68.82 \pm 19.94		
marine	10.29 \pm 9.59	0.217 \pm 0.072	154.91 \pm 65.60	13.60 \pm 6.17	30.89 \pm 16.51	0.087 \pm 0.020	159.85 \pm 68.10		
variable	3.36 \pm 4.18	0.105 \pm 0.015	121.85 \pm 69.69	6.69 \pm 3.90	6.38 \pm 5.10	0.060 \pm 0.016	128.92 \pm 73.11		
	d_{su} (mm)	d_{tu} (mm)	O (mm)	θ ($^\circ$)	α ($^\circ$)	UR	IFA	L_m (mm)	d_{sm} (mm)
open	6.19 \pm 4.85	5.44 \pm 4.22	20.31 \pm 14.73	4.86 \pm 4.33	21.04 \pm 9.20	0.059 \pm 0.022	0.193 \pm 0.047	44.13 \pm 31.02	3.97 \pm 2.47
mosaic	7.55 \pm 5.53	5.96 \pm 4.93	20.45 \pm 14.42	5.88 \pm 4.11	17.51 \pm 8.72	0.075 \pm 0.020	0.200 \pm 0.033	38.07 \pm 25.13	4.07 \pm 2.61
forest	6.67 \pm 4.43	4.92 \pm 3.16	16.77 \pm 9.84	5.98 \pm 3.65	15.19 \pm 7.22	0.079 \pm 0.020	0.199 \pm 0.041	28.41 \pm 13.07	3.33 \pm 1.78
desert	2.58 \pm 0.19	2.61 \pm 1.44	8.05 \pm 3.49	3.67 \pm 1.51	21.65 \pm 0.57	0.075 \pm 0.050	0.195 \pm 0.064	17.82 \pm 12.79	1.68 \pm 0.08
freshwater	6.34 \pm 2.10	4.46 \pm 1.30	16.25 \pm 5.38	8.85 \pm 3.40	17.29 \pm 7.48	0.093 \pm 0.023	0.242 \pm 0.061	26.78 \pm 6.31	3.49 \pm 1.21
marine	20.22 \pm 8.33	14.47 \pm 6.75	50.41 \pm 20.68	7.71 \pm 4.25	32.67 \pm 13.15	0.129 \pm 0.028	0.318 \pm 0.061	57.17 \pm 26.18	9.07 \pm 3.87
variable	8.13 \pm 5.66	6.58 \pm 4.36	23.68 \pm 12.77	5.41 \pm 3.47	24.10 \pm 8.97	0.070 \pm 0.023	0.196 \pm 0.042	47.84 \pm 28.46	4.71 \pm 2.69

both the phylogenetic effect (Fam) and its interaction with size (Fam* M_b) were included in most of the models (18 and 17 models, respectively). It is also interesting to note that preferred habitat seemed to have a more significant effect than locomotor type on carnivoran limb morphology, since habitat was included in more terms and in more models. However, in most cases, the effect of habitat was only significant in its interaction with body size, while the opposite was true in the case of locomotor type. Thus, GLM results must be regarded cautiously.

Size correction

Since the strong allometric effect found in the GLMs for most of the variables could be masking the effect of locomotor type, preferred habitat and phylogeny, all analyses were repeated on the regression residuals of each variable on M_b using ordinary least squares. The power regression ($y = a \cdot x^b$) was used for all variables but **T**, **θ** , **IFA**, and bone robusticities (**HR**, **RR**, **UR**, **MR**, **FR**, **TR**), for which linear regression was used ($y = a + bx$). In the size-corrected ANOVA by locomotor type, significant differences between groups were found for all variables but d_{sr} , d_{tu} , **O**, L_c , **r**, d_{sc}

	d_{tm} (mm)	MR	L_r (mm)	N (mm)	d_{sr} (mm)	d_{tr} (mm)	FR	L_t (mm)	d_{st} (mm)
open	4.32 ± 2.87	0.103 ± 0.028	120.90 ± 82.52	14.49 ± 9.70	8.88 ± 5.91	9.37 ± 6.37	0.076 ± 0.011	124.53 ± 77.26	9.60 ± 6.67
mosaic	4.35 ± 2.87	0.112 ± 0.023	128.49 ± 82.95	15.71 ± 11.56	9.83 ± 6.38	10.64 ± 7.51	0.079 ± 0.011	121.73 ± 66.95	10.90 ± 7.67
forest	3.55 ± 2.02	0.117 ± 0.026	102.11 ± 48.67	12.78 ± 8.60	8.13 ± 4.10	8.94 ± 5.22	0.080 ± 0.009	97.85 ± 36.62	8.43 ± 4.39
desert	1.99 ± 0.66	0.130 ± 0.099	50.00 ± 32.96	6.07 ± 2.27	3.88 ± 1.55	4.10 ± 1.58	0.085 ± 0.021	58.20 ± 38.79	4.22 ± 1.64
freshwater	3.45 ± 1.17	0.130 ± 0.022	82.11 ± 20.66	12.03 ± 3.41	7.63 ± 2.04	8.63 ± 2.62	0.093 ± 0.014	89.54 ± 21.44	8.11 ± 2.55
marine	9.33 ± 3.78	0.162 ± 0.023	122.66 ± 92.16	24.87 ± 12.58	18.73 ± 8.74	28.73 ± 14.37	0.169 ± 0.073	206.98 ± 69.96	18.49 ± 8.55
variable	5.20 ± 2.91	0.109 ± 0.031	142.25 ± 81.79	17.79 ± 10.79	10.67 ± 6.21	11.42 ± 7.00	0.078 ± 0.013	135.08 ± 66.60	11.54 ± 7.02
	d_{tt} (mm)	TR	L_c (mm)	r (mm)	d_{sc} (mm)	d_{tc} (mm)	% _{prox}	% _{mid}	% _{dist}
open	8.38 ± 5.57	0.079 ± 0.015	35.83 ± 22.90	27.29 ± 17.74	12.84 ± 9.11	6.13 ± 4.32	27.16 ± 1.99	38.27 ± 1.60	34.57 ± 2.84
mosaic	8.89 ± 6.00	0.087 ± 0.018	34.36 ± 18.50	25.98 ± 14.52	12.56 ± 7.43	5.92 ± 3.12	27.60 ± 1.66	39.02 ± 1.99	33.38 ± 2.23
forest	7.04 ± 4.10	0.084 ± 0.015	28.10 ± 13.36	21.64 ± 11.27	10.24 ± 5.12	5.08 ± 2.82	26.72 ± 2.39	40.16 ± 2.49	33.12 ± 1.65
desert	3.63 ± 2.15	0.080 ± 0.028	17.24	13.16	6.06	3.17	26.55 ± 3.19	39.36 ± 1.00	34.10 ± 4.20
freshwater	6.48 ± 1.90	0.090 ± 0.016	23.85 ± 8.09	18.09 ± 5.69	9.15 ± 2.87	4.56 ± 1.50	28.86 ± 2.35	40.00 ± 1.78	31.14 ± 3.24
marine	19.99 ± 9.41	0.089 ± 0.022	59.39 ± 36.11	49.75 ± 30.39	25.81 ± 16.95	14.92 ± 9.63	34.77 ± 3.57	33.06 ± 4.45	32.17 ± 2.21
variable	9.82 ± 5.85	0.085 ± 0.016	38.92 ± 20.32	30.33 ± 16.41	13.89 ± 8.42	6.57 ± 3.53	27.71 ± 1.40	38.12 ± 2.52	34.16 ± 3.00

Table II.5. Descriptive statistics by habitat. (Cont.)

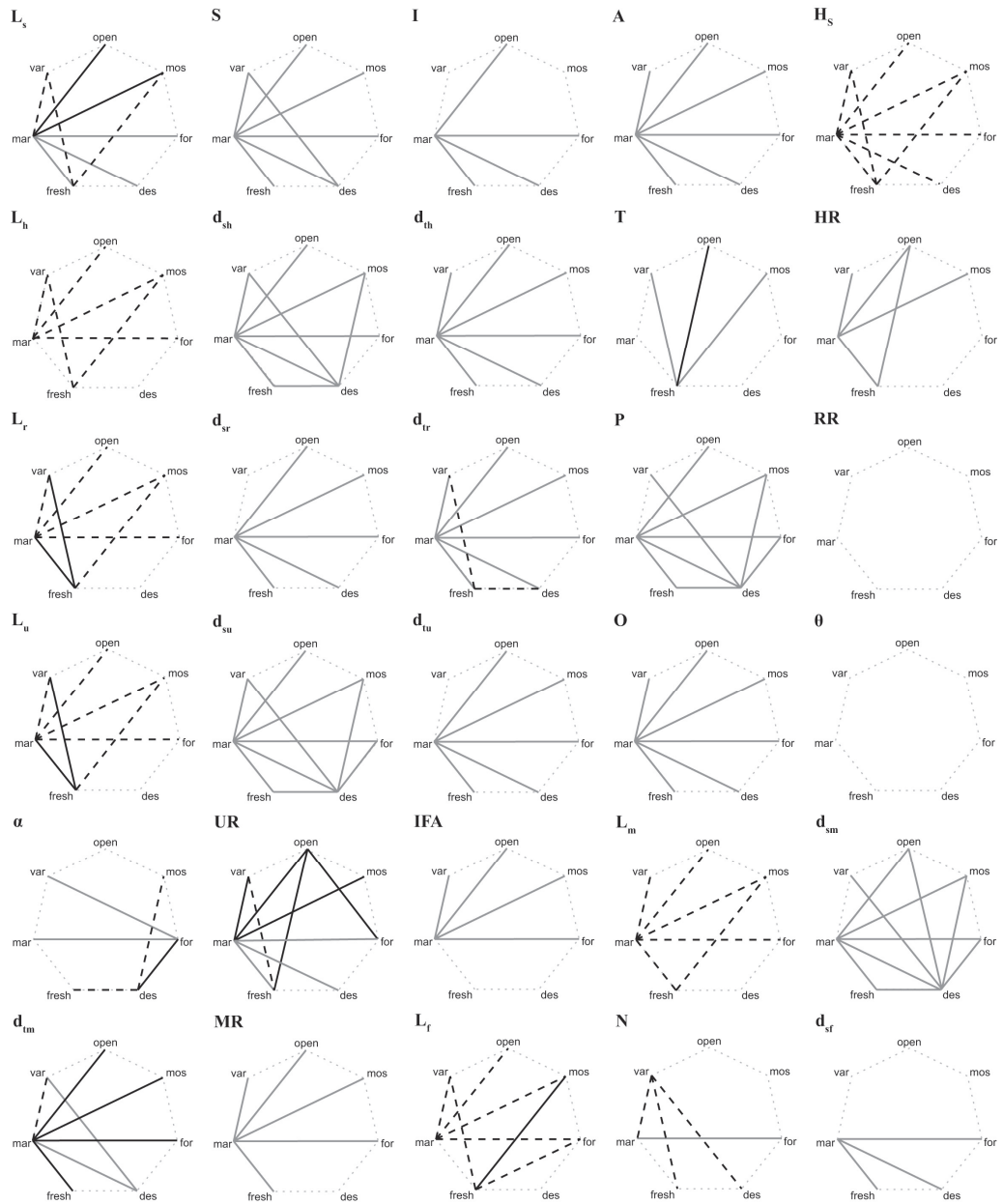


Figure II.3. Significant differences between preferred habitats. Grey continuous lines denote significant differences between preferred habitats in the uncorrected ANOVAs, black continuous lines represent significant differences recovered both in the uncorrected and the size-corrected ANOVAs, and black dashed lines correspond to significant differences that were revealed after correcting for allometric effects. Abbreviations: des, desert; for, forest; fresh, freshwater; mar, marine; mos, mosaic; var, variable. All other abbreviations as in Table II.2.

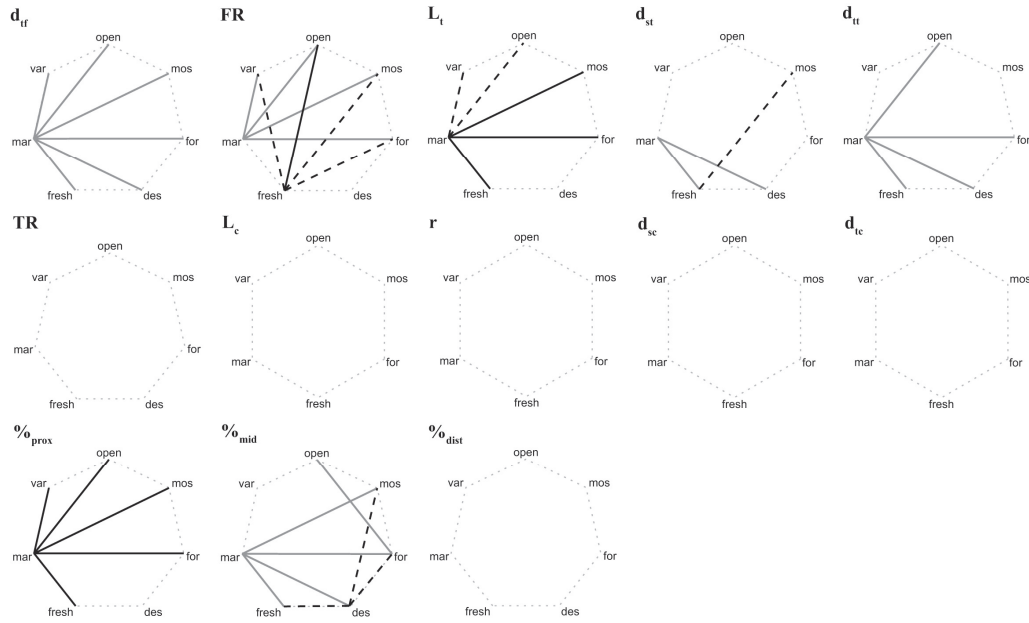


Figure II.2. Significant differences between habitats. (Cont.)

	M_b	L_s	S	I	A	H_s	L_h	d_{sh}	d_{th}	T	HR
Family	60.15 %	59.94 %	81.37 %	69.42 %	76.22 %	53.40 %	56.42 %	57.53 %	72.00 %	75.11 %	64.29 %
Genus	21.56 %	27.42 %	12.36 %	20.46 %	15.20 %	31.04 %	27.44 %	30.83 %	21.40 %	19.63 %	26.48 %
Species	18.29 %	12.64 %	6.27 %	10.12 %	8.58 %	15.54 %	16.14 %	11.64 %	6.60 %	5.26 %	9.22 %
	L_r	d_{sr}	d_{tr}	P	RR	L_u	d_{su}	d_{tu}	O	θ	α
Family	58.70 %	57.07 %	75.74 %	64.76 %	53.08 %	58.62 %	64.94 %	62.30 %	59.81 %	24.26 %	61.11 %
Genus	27.06 %	33.05 %	18.63 %	21.25 %	30.97 %	26.92 %	25.20 %	20.58 %	24.63 %	-	15.85 %
Species	14.23 %	9.88 %	5.63 %	14.00 %	15.95 %	14.45 %	9.86 %	17.13 %	15.56 %	75.74 %	23.05 %
	UR	IFA	L_m	d_{sm}	d_{tm}	MR	L_f	N	d_{sf}	d_{tf}	FR
Family	63.64 %	50.46 %	52.92 %	58.06 %	54.77 %	55.65 %	54.18 %	59.64 %	51.93 %	67.96 %	73.92 %
Genus	19.02 %	36.15 %	29.83 %	28.87 %	30.97 %	15.02 %	29.61 %	28.26 %	36.47 %	26.04 %	22.34 %
Species	17.34 %	13.40 %	17.25 %	13.08 %	14.26 %	29.33 %	16.21 %	12.10 %	11.60 %	6.01 %	3.74 %
	L_t	d_{st}	d_{tt}	TR	L_c	r	d_{sc}	d_{tc}	$\%_{prox}$	$\%_{mid}$	
Family	58.09 %	47.13 %	63.65 %	34.34 %	32.24 %	32.44 %	31.15 %	42.70 %	53.78 %	63.93 %	
Genus	26.89 %	39.33 %	25.27 %	44.48 %	37.41 %	36.60 %	35.83 %	31.09 %	40.47 %	29.71 %	
Species	15.02 %	13.54 %	11.08 %	21.17 %	30.35 %	30.97 %	33.03 %	26.21 %	5.66 %	6.37 %	
	$\%_{dist}$	mean \pm s.d.	min	max							
Family	41.94 %	57.06 % \pm 12.73 %	24.26 %	81.37 %							
Genus	40.48 %	27.00 % \pm 8.58 %	-	44.48 %							
Species	17.57 %	15.93 % \pm 11.66 %	3.74 %	75.74 %							

Table II.6. Percentage variance components. For each variable, the percentage of the variance at each phylogenetic level is given. The last three columns report mean variance \pm standard deviation (s.d.), and minimum (min) and maximum (max) percentage variance values, at each phylogenetic level. Variable names are listed in Table II.2.

Table II.7. Descriptive statistics by family.

For each variable, mean values \pm standard deviations are given. All angles are given in degrees for ease of interpretation, but radians were used for all analysis.

Abbreviations: Ail, Ailuroidae; Nan, Nandiniidae; Pdn, Prionodontidae. All other abbreviations as in Figure II.4. Variable names are listed in Table II.2.

	M_b (g)	L_s (mm)	S (mm)	I (mm)	A (mm)	H_s (mm)
Can	11768 \pm 12290	92.46 \pm 32.60	25.46 \pm 8.66	36.90 \pm 11.89	63.23 \pm 20.93	13.04 \pm 5.05
Mus	5229 \pm 6960	46.29 \pm 22.48	19.01 \pm 9.90	16.15 \pm 9.80	35.97 \pm 19.67	6.37 \pm 4.00
Mep	1174 \pm 565	33.63 \pm 6.98	9.03 \pm 1.57	13.41 \pm 1.56	23.18 \pm 2.35	1.14 \pm 0.11
Ota	166188 \pm 67605	185.58 \pm 42.96	136.76 \pm 25.38	81.75 \pm 34.32	225.20 \pm 49.85	14.11 \pm 5.20
Pho	301675 \pm 226442	176.38 \pm 42.39	80.63 \pm 22.89	113.19 \pm 33.95	198.37 \pm 40.02	11.55 \pm 6.77
Ail	5036	64.31	23.29	32.73	56.10	9.10
Pro	3773 \pm 2104	53.10 \pm 14.24	20.15 \pm 4.30	28.18 \pm 4.82	47.98 \pm 9.75	8.45 \pm 3.01
Urs	149589 \pm 102618	184.79 \pm 33.72	71.02 \pm 9.95	101.30 \pm 13.71	173.76 \pm 22.29	32.91 \pm 5.02
Fel	25278 \pm 40607	107.01 \pm 49.13	34.70 \pm 15.89	44.91 \pm 21.53	80.46 \pm 38.04	16.31 \pm 8.46
Her	1569 \pm 1206	41.70 \pm 10.52	13.03 \pm 3.20	17.72 \pm 4.66	31.54 \pm 7.71	6.06 \pm 1.38
Eup	2080 \pm 2482	46.50 \pm 15.29	15.25 \pm 5.56	17.45 \pm 7.96	33.25 \pm 12.69	5.75 \pm 2.17
Hya	32729 \pm 18123	154.56 \pm 43.32	37.14 \pm 9.20	61.99 \pm 19.60	103.07 \pm 30.91	23.68 \pm 5.79
Viv	4409 \pm 4090	57.85 \pm 15.60	19.52 \pm 5.59	27.08 \pm 7.55	46.25 \pm 12.60	7.59 \pm 2.77
Nan	2100	46.35	16.64	22.88	39.59	6.55
Pnd	800	41.32	14.43	17.54	32.80	5.02

	L_h (mm)	d_{sh} (mm)	d_{th} (mm)	T (mm)	HR	L_r (mm)
Can	128.79 \pm 43.35	11.67 \pm 4.22	9.28 \pm 3.16	3.50 \pm 1.61	0.090 \pm 0.013	125.77 \pm 49.17
Mus	65.37 \pm 26.68	8.31 \pm 4.95	5.46 \pm 2.40	-0.07 \pm 0.82	0.122 \pm 0.034	49.51 \pm 22.20
Mep	44.53 \pm 6.91	5.82 \pm 1.03	4.13 \pm 0.88	-0.36 \pm 0.31	0.127 \pm 0.006	36.86 \pm 6.98
Ota	154.86 \pm 25.51	29.56 \pm 7.26	29.68 \pm 7.97	17.70 \pm 3.06	0.190 \pm 0.016	164.04 \pm 26.82
Pho	143.09 \pm 28.42	43.40 \pm 18.15	28.69 \pm 9.21	11.40 \pm 10.18	0.297 \pm 0.081	162.32 \pm 54.26
Ail	108.77	10.76	8.21	-0.12	0.100	85.88
Pro	83.76 \pm 13.89	9.98 \pm 2.50	7.07 \pm 1.33	0.05 \pm 0.63	0.117 \pm 0.016	72.11 \pm 17.39
Urs	267.65 \pm 44.25	30.43 \pm 5.97	26.36 \pm 3.51	0.26 \pm 2.14	0.114 \pm 0.005	220.57 \pm 37.55
Fel	149.11 \pm 60.51	15.77 \pm 9.07	11.59 \pm 5.91	2.93 \pm 2.43	0.101 \pm 0.017	133.95 \pm 53.56
Her	57.28 \pm 13.91	5.92 \pm 1.42	4.59 \pm 0.88	0.95 \pm 0.54	0.103 \pm 0.014	47.98 \pm 14.14
Eup	66.33 \pm 23.81	6.82 \pm 3.64	5.20 \pm 2.50	0.24 \pm 1.40	0.098 \pm 0.019	59.93 \pm 16.08
Hya	180.13 \pm 36.73	22.62 \pm 7.97	14.37 \pm 4.97	12.59 \pm 4.58	0.123 \pm 0.024	193.42 \pm 40.35
Viv	83.17 \pm 20.53	8.23 \pm 2.75	6.43 \pm 2.04	1.11 \pm 1.34	0.098 \pm 0.013	69.04 \pm 17.46
Nan	74.58	8.20	6.07	0.22	0.110	57.28
Pnd	60.40	5.50	4.73	-0.66	0.090	48.72

and **d_{tc}** (Fig. II.1). Due to heteroscedasticity, robust tests had to be used on all variables but **P**, **θ** , **d_{sm}**, **d_{tm}**, **MR**, **FR**, **TR**, **L_c**, **r**, **d_{sc}**, **d_{tc}**, **%_{prox}**, and **%_{mid}**. After removing the allometric effect, only six of the variables for which significantly different homogeneous subgroups had been previously found retained this differentiation: aquatic carnivorans still had the highest values for **S**, **d_{tr}**, **IFA**, **FR**, and **%_{prox}**, and the lowest for **%_{mid}** (Fig. II.2). Furthermore, *post hoc* tests recovered the lowest **%_{prox}** values for arboreal carnivorans. Besides artifactually separating aquatic carnivorans from the rest of groups in most variables, the

	d_{sr} (mm)	d_{tr} (mm)	P (mm)	RR	L_u (mm)	d_{su} (mm)
Can	6.59 ± 2.34	9.19 ± 3.45	4.85 ± 1.73	0.053 ± 0.013	133.66 ± 53.25	5.73 ± 2.05
Mus	4.00 ± 1.84	4.12 ± 2.22	2.71 ± 1.31	0.082 ± 0.015	53.54 ± 23.75	5.15 ± 2.52
Mep	3.11 ± 0.35	3.02 ± 1.30	2.35 ± 0.84	0.083 ± 0.012	38.63 ± 6.50	3.62 ± 0.83
Ota	15.41 ± 5.61	34.85 ± 7.71	14.49 ± 3.96	0.093 ± 0.022	170.31 ± 27.93	22.56 ± 6.33
Pho	15.73 ± 4.95	42.33 ± 18.89	14.12 ± 4.05	0.097 ± 0.012	156.37 ± 43.06	23.56 ± 8.12
Ail	6.54	6.10	3.51	0.080	91.47	7.38
Pro	4.51 ± 0.90	5.71 ± 1.41	3.25 ± 0.79	0.064 ± 0.005	75.39 ± 17.95	6.92 ± 2.29
Urs	13.65 ± 2.69	20.38 ± 4.87	16.36 ± 4.63	0.061 ± 0.007	236.57 ± 41.19	21.16 ± 3.53
Fel	6.78 ± 3.92	10.34 ± 5.78	7.15 ± 3.97	0.048 ± 0.011	142.11 ± 56.50	9.84 ± 5.37
Her	3.41 ± 0.86	3.30 ± 0.84	2.42 ± 0.76	0.074 ± 0.014	50.26 ± 14.43	3.62 ± 1.07
Eup	3.34 ± 1.09	4.09 ± 1.95	2.51 ± 1.36	0.056 ± 0.005	62.04 ± 16.82	4.17 ± 2.01
Hya	10.82 ± 3.16	15.47 ± 3.90	11.01 ± 4.33	0.058 ± 0.005	201.11 ± 41.67	11.41 ± 3.83
Viv	4.31 ± 1.34	4.78 ± 1.76	3.09 ± 1.19	0.062 ± 0.007	72.61 ± 18.42	5.52 ± 1.97
Nan	3.29	5.40	1.84	0.060	60.37	5.58
Pnd	2.98	3.79	1.29	0.060	50.78	4.83
	d_{cu} (mm)	O (mm)	θ (°)	α (°)	UR	IFA
Can	6.23 ± 2.04	22.76 ± 7.75	3.64 ± 2.28	29.00 ± 6.52	0.044 ± 0.012	0.176 ± 0.035
Mus	3.62 ± 1.70	12.93 ± 6.72	9.74 ± 4.64	18.11 ± 5.60	0.097 ± 0.018	0.239 ± 0.052
Mep	2.01 ± 0.43	9.88 ± 2.76	3.10 ± 2.40	13.03 ± 6.78	0.093 ± 0.006	0.253 ± 0.031
Ota	15.02 ± 3.64	61.39 ± 15.18	10.34 ± 3.59	45.90 ± 3.39	0.130 ± 0.014	0.358 ± 0.039
Pho	16.35 ± 4.46	52.31 ± 12.97	4.76 ± 5.29	27.17 ± 7.75	0.153 ± 0.032	0.340 ± 0.030
Ail	5.10	15.68	6.47	11.99	0.080	0.170
Pro	3.87 ± 0.75	14.02 ± 3.96	5.62 ± 2.39	11.66 ± 4.73	0.093 ± 0.025	0.189 ± 0.037
Urs	18.17 ± 4.52	46.91 ± 9.06	4.15 ± 1.51	29.01 ± 7.50	0.089 ± 0.011	0.199 ± 0.022
Fel	6.99 ± 4.58	27.51 ± 14.98	5.10 ± 2.70	17.28 ± 6.94	0.067 ± 0.015	0.186 ± 0.033
Her	3.34 ± 0.98	10.60 ± 2.78	5.91 ± 3.38	13.55 ± 4.25	0.073 ± 0.015	0.213 ± 0.029
Eup	3.23 ± 1.27	11.82 ± 5.02	7.75 ± 3.37	13.76 ± 4.89	0.066 ± 0.015	0.186 ± 0.029
Hya	9.89 ± 2.71	35.29 ± 11.61	2.41 ± 2.12	32.91 ± 3.21	0.058 ± 0.013	0.173 ± 0.033
Viv	4.39 ± 1.36	14.41 ± 4.88	4.60 ± 1.60	10.65 ± 4.89	0.074 ± 0.010	0.196 ± 0.028
Nan	3.30	13.50	2.96	5.53	0.090	0.220
Pnd	2.67	8.36	3.35	8.67	0.100	0.160

Table II.7. Descriptive statistics by family. (Cont.)

allometric effect also masked differences between subgroups in 10 variables, for which the size-corrected ANOVAs detected significantly lower values for aquatic carnivorans (Fig. II.2). Finally, the size-corrected MANOVA for the functional relative segment lengths still resulted in significant differences between locomotor types in each segment after removing the allometric effect. However, these results must be regarded cautiously, since the assumption of equality of covariance matrixes was violated (Box's test: p-value < 0.001).

Table II.7. Descriptive statistics by family.
(Cont.)

	L_m (mm)	d_{sm} (mm)	d_{tm} (mm)	MR	L_t (mm)	N (mm)	d_{st} (mm)
Can	54.15 ± 21.25	4.43 ± 1.60	4.81 ± 1.64	0.084 ± 0.015	138.47 ± 47.12	15.63 ± 4.99	9.56 ± 3.08
Mus	21.17 ± 8.70	2.77 ± 1.31	2.97 ± 1.45	0.132 ± 0.028	65.93 ± 25.97	9.88 ± 4.84	6.07 ± 2.84
Mep	12.33 ± 1.13	1.78 ± 0.49	1.90 ± 0.49	0.143 ± 0.032	50.30 ± 8.75	7.89 ± 2.14	4.48 ± 1.28
Ota	57.63 ± 12.62	9.42 ± 2.37	9.03 ± 2.07	0.163 ± 0.013	96.84 ± 18.56	20.45 ± 5.62	15.25 ± 4.20
Pho	68.64 ± 31.92	11.64 ± 4.34	12.10 ± 4.17	0.177 ± 0.029	99.81 ± 13.85	26.60 ± 6.34	24.47 ± 9.12
Ail	27.46	3.98	3.67	0.150	109.49	13.03	8.51
Pro	22.78 ± 4.34	2.80 ± 0.62	2.86 ± 0.45	0.123 ± 0.018	92.08 ± 17.95	11.75 ± 3.00	7.75 ± 1.70
Urs	62.84 ± 15.17	9.00 ± 1.19	9.56 ± 1.49	0.147 ± 0.017	295.03 ± 61.37	45.81 ± 6.92	23.87 ± 5.16
Fel	52.81 ± 22.75	5.31 ± 2.56	5.68 ± 2.95	0.101 ± 0.014	168.85 ± 69.48	18.35 ± 9.26	12.42 ± 5.80
Her	20.10 ± 6.17	2.45 ± 0.54	2.58 ± 0.58	0.126 ± 0.017	62.94 ± 16.30	8.24 ± 2.30	5.54 ± 1.40
Eup	20.95 ± 4.49	1.97 ± 0.85	2.29 ± 0.93	0.090 ± 0.020	75.54 ± 29.68	8.59 ± 3.92	6.41 ± 3.17
Hya	85.51 ± 13.47	6.77 ± 2.01	8.35 ± 2.83	0.078 ± 0.013	195.08 ± 46.25	27.21 ± 8.26	14.48 ± 4.45
Viv	23.57 ± 7.45	2.81 ± 0.86	2.90 ± 0.84	0.121 ± 0.016	90.81 ± 20.12	10.73 ± 3.62	7.23 ± 2.20
Nan	19.69	2.21	2.32	0.110	83.70	9.29	6.91
Pnd	16.05	2.28	2.06	0.140	67.46	7.25	5.43
	d_{tf} (mm)	FR	L_t (mm)	d_{st} (mm)	d_{tt} (mm)	TR	
Can	9.81 ± 3.06	0.069 ± 0.007	145.46 ± 49.16	9.99 ± 3.21	9.49 ± 3.19	0.069 ± 0.010	
Mus	6.64 ± 3.48	0.092 ± 0.018	69.75 ± 27.51	6.58 ± 3.29	5.06 ± 2.36	0.092 ± 0.015	
Mep	4.77 ± 1.34	0.090 ± 0.010	52.73 ± 10.50	4.75 ± 0.91	3.12 ± 0.53	0.090 ± 0.000	
Ota	26.06 ± 7.40	0.155 ± 0.017	205.44 ± 27.91	18.81 ± 7.91	17.55 ± 4.67	0.090 ± 0.024	
Pho	41.85 ± 16.91	0.243 ± 0.095	255.00 ± 44.65	17.80 ± 3.99	29.63 ± 7.33	0.070 ± 0.010	
Ail	9.44	0.080	105.78	8.65	6.84	0.080	
Pro	8.40 ± 1.69	0.086 ± 0.005	92.29 ± 16.98	7.70 ± 1.48	6.03 ± 1.46	0.084 ± 0.008	
Urs	28.59 ± 4.55	0.081 ± 0.004	223.03 ± 44.92	26.72 ± 6.73	20.71 ± 4.01	0.119 ± 0.012	
Fel	13.23 ± 6.43	0.073 ± 0.007	162.79 ± 56.52	13.70 ± 6.92	11.69 ± 5.80	0.082 ± 0.015	
Her	6.00 ± 1.38	0.087 ± 0.010	65.92 ± 17.37	5.88 ± 1.28	4.92 ± 1.13	0.091 ± 0.010	
Eup	6.79 ± 2.42	0.084 ± 0.011	79.96 ± 25.00	6.47 ± 3.04	5.19 ± 1.92	0.078 ± 0.015	
Hya	15.26 ± 4.91	0.073 ± 0.005	170.36 ± 25.24	16.49 ± 4.66	13.11 ± 2.95	0.095 ± 0.013	
Viv	7.90 ± 2.28	0.078 ± 0.007	91.22 ± 16.56	7.41 ± 2.01	6.05 ± 1.73	0.080 ± 0.010	
Nan	6.78	0.080	81.63	7.01	5.43	0.090	
Pnd	5.59	0.080	69.09	4.07	4.79	0.060	

In the case of preferred habitat, after the size correction significant differences between habitats were only found for L_s , H_s , L_h , T , L_r , d_{tr} , L_u , α , **UR**, L_m , d_{tm} , L_f , **N**, **FR**, L_t , d_{st} , $\%_{prox}$, and $\%_{mid}$ (Fig. II.3). Due to heteroscedasticity, robust tests had to be used on all variables but θ , **UR**, d_{tm} , **TR**, d_{tc} , and $\%_{prox}$. As in the analysis by locomotor type, the removal of the allometric effect revealed that, for most of the variables, the significantly higher values for marine carnivorans were a size-related artifact. In this case, only for **S**, d_{tr} , and $\%_{prox}$ were the values of marine carnivorans still significantly the highest. Furthermore, also in

	L_c (mm)	r (mm)	d_{sc} (mm)	d_{tc} (mm)	$\%_{prox}$	$\%_{mid}$	$\%_{dist}$
Can	32.52 ± 11.25	25.09 ± 9.24	10.96 ± 4.69	5.57 ± 1.82	26.64 ± 1.84	37.36 ± 1.16	36.00 ± 1.92
Mus	18.54 ± 8.23	14.46 ± 6.59	7.40 ± 3.33	3.48 ± 1.52	28.32 ± 2.46	41.05 ± 1.73	30.63 ± 1.83
Mep	9.87	8.23	3.95	1.89	29.15 ± 0.91	38.84 ± 1.47	32.01 ± 0.61
Ota					36.50 ± 1.73	30.82 ± 0.95	32.69 ± 0.86
Pho	66.12	56.95	25.94	21.08	36.72 ± 0.99	30.03 ± 2.29	33.25 ± 3.22
Ail	25.06	19.26	9.37	3.82	24.83	42.01	33.16
Pro	23.94 ± 2.78	18.24 ± 2.18	8.82 ± 1.34	4.48 ± 0.77	25.19 ± 2.74	40.48 ± 2.70	34.33 ± 1.64
Urs	68.59 ± 16.16	56.32 ± 13.82	30.41 ± 8.55	13.03 ± 4.87	27.32 ± 0.55	39.84 ± 1.05	32.84 ± 0.69
Fel	47.25 ± 19.83	35.30 ± 16.05	16.49 ± 7.90	8.16 ± 3.74	27.13 ± 1.52	38.37 ± 1.10	34.50 ± 1.90
Her	21.88 ± 6.65	16.38 ± 5.24	8.04 ± 2.38	3.61 ± 0.96	28.46 ± 1.33	39.14 ± 1.34	32.51 ± 2.09
Eup	20.28 ± 8.16	15.30 ± 6.20	7.76 ± 2.68	3.49 ± 0.99	26.80 ± 1.06	38.13 ± 2.55	35.08 ± 2.30
Hya	31.69	23.63	12.48	4.12	28.98 ± 1.79	34.28 ± 1.16	36.74 ± 1.32
Viv	23.26 ± 6.62	17.59 ± 5.49	8.60 ± 2.48	4.22 ± 1.32	27.46 ± 2.69	39.71 ± 2.61	32.83 ± 1.19
Nan	20.66	15.92	7.56	3.35	26.00	41.86	32.15
Pnd					27.46	40.15	32.39

Table II.7. Descriptive statistics by family. (Cont.)

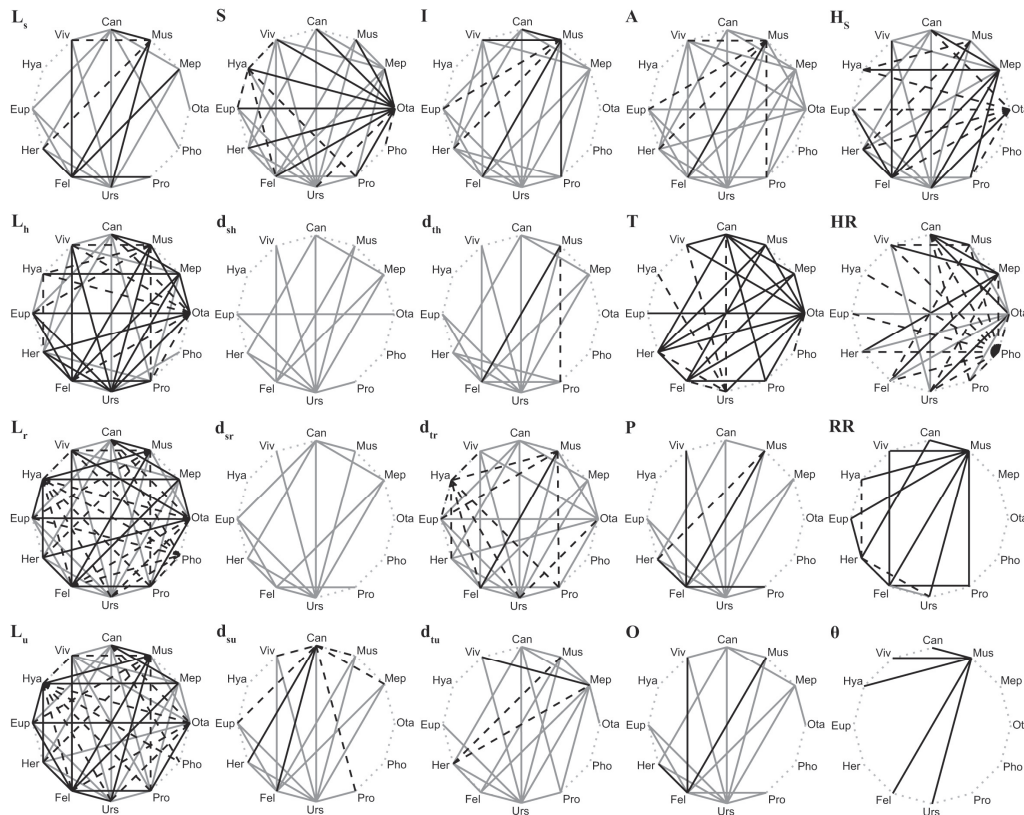


Figure II.4. Significant differences between families. Legend next page.

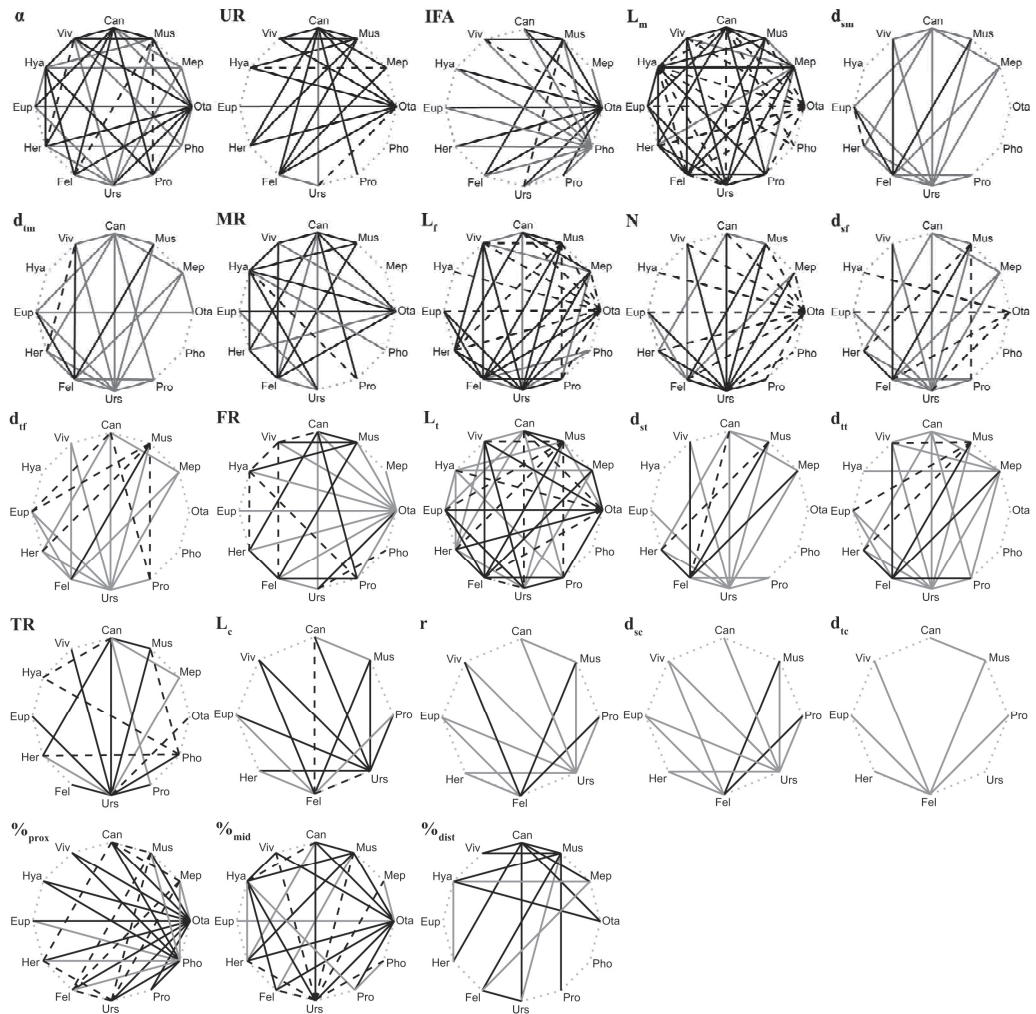


Figure II.4. Significant differences between carnivoran families. Grey continuous lines denote significant differences between carnivoran families in the uncorrected ANOVAs, black continuous lines represent significant differences recovered both in the uncorrected and the size-corrected ANOVAs, and black dashed lines correspond to significant differences that were revealed after correcting for allometric effects. Abbreviations: Can, Canidae; Eup, Eupleridae; Fel, Felidae; Her, Herpestidae; Hya, Hyaenidae; Mep, Mephitidae; Mus, Mustelidae; Ota, Otariidae; Pho, Phocidae; Pro, Procyonidae; Urs, Ursidae; Viv, Viverridae. All other abbreviations as in Table II.2.

agreement with the results by locomotor type, *post hoc* tests showed that 11 variables have had their differentiation in subgroups masked by the allometric effect, and again all of them presented significantly lower values for marine carnivorans (Fig. II.2). Again, the size-corrected MANOVA by preferred habitat produced the same results as the uncorrected one, but also violating the assumption of equality of covariance matrixes (Box's test:

Model	Variables
(1) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + \varepsilon$	S, I, A, L_{th}, d_{th}, L_r, d_{sr}, d_{su}, L_m, L_t, r
(2) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \mathbf{M}_b + \varepsilon$	d_{tt}
(3) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	d_{tm}, d_{sf}
(4) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + a_5 \cdot \text{habitat} + a_6 \cdot \text{Fam} * \text{habitat} + \varepsilon$	d_{tu}
(5) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} + \varepsilon$	O
(6) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \mathbf{M}_b + a_4 \cdot \text{habitat} * \mathbf{M}_b + a_5 \cdot \text{Fam} * \text{habitat} + a_6 \cdot \text{habitat} + \varepsilon$	P, d_{tc}[†]
(7) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	H_s, L_f, N, d_{st}, d_{tt}
(8) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	d_{sm}
(9) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} + \varepsilon$	RR, %_{dist}
(10) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} + a_5 \cdot \text{loctyp} * \mathbf{M}_b + \varepsilon$	%_{prox}
(11) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{loctyp} * \text{habitat} * \mathbf{M}_b + \varepsilon$	L_s, d_{sh}
(12) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{loctyp} + a_4 \cdot \text{Fam} * \text{loctyp} + \varepsilon$	%_{mid}
(13) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \mathbf{M}_b + a_3 \cdot \text{loctyp} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{loctyp} + \varepsilon$	FR[†]
(14) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{loctyp} * \text{habitat} * \mathbf{M}_b + a_3 \cdot \text{Fam} * \text{habitat} + \varepsilon$	T[†]
(15) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	d_{tr}, L_c[†], d_{sc}[†]
(16) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + a_3 \cdot \text{Fam} * \text{loctyp} + \varepsilon$	UR, TR
(17) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{loctyp} * \mathbf{M}_b + \varepsilon$	L_u
(18) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{loctyp} + a_3 \cdot \text{habitat} * \mathbf{M}_b + \varepsilon$	MR
(19) $y = a_0 + a_1 \cdot \text{Fam} * \mathbf{M}_b + a_2 \cdot \text{habitat} + a_3 \cdot \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	θ[†]
(20) $y = a_0 + a_1 \cdot \text{Fam} * \mathbf{M}_b + a_2 \cdot \text{Fam} * \text{habitat} + a_3 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + \varepsilon$	α
(21) $y = a_0 + a_1 \cdot \text{Fam} * \mathbf{M}_b + a_2 \cdot \text{Fam} * \text{habitat} + a_3 \cdot \text{Fam} * \text{habitat} * \mathbf{M}_b + a_4 \cdot \text{habitat} * \mathbf{M}_b + a_5 \cdot \text{loctyp} + \varepsilon$	IFA
(22) $y = a_0 + a_1 \cdot \text{Fam} * \mathbf{M}_b + a_2 \cdot \text{loctyp} + \varepsilon$	HR

†: intercept (a_0) was not significant in this case

p-value < 0.001).

In the size-corrected ANOVA by phylogeny, significant differences between families were found for all variables but **d_{sh}**, **d_{sr}**, **d_{sc}**, and **d_{tc}** (Fig. II.4). Due to heteroscedasticity, robust tests had to be used on all variables but **TR** and **L_c**. *Post hoc* tests revealed that the different homogeneous subgroups obtained for **d_{sh}**, **d_{th}**, **d_{su}**, **α**, **UR**, **IFA**, **r**, **d_{sc}**, and **d_{tc}** were a size-related artifact (Fig. II.2). For most variables, however, after removing the allometric effect the relationships found between homogeneous subgroups were reversed. This way,

Table II.8. General Linear Models. The different models show which factors (family, habitat, locomotor type, size) are significantly related to the variability of a particular variable, and whether there are significant interactions among these factors. Abbreviations: Fam, family; loctyp, locomotor type. Variable names are listed in Table II.2.

Table II.9. Size-corrected General Linear Models.

The different models show which factors (family, habitat, locomotor type, size) are significantly related to the variability of a particular variable, and whether there are significant interactions among these factors. Abbreviations: Fam, family; loctyp, locomotor type. Variable names are listed in Table II.2.

Model	Variables
(1) $y = a_0 + a_1 \cdot \text{Fam} + \varepsilon$	$L_s^\dagger, S, P^\dagger, A^\dagger, H_s, d_{sh}^\dagger, d_{th}^\dagger, L_r^\dagger, d_{sr}^\dagger, d_{tr}^\dagger, P^\dagger, L_u^\dagger, d_{su}^\dagger, d_{tu}^\dagger, \alpha^\dagger, \theta^\dagger, d_{sm}^\dagger, d_{tm}^\dagger, L_f^\dagger, N^\dagger, d_{sf}^\dagger, d_{tf}, L_t^\dagger, d_{st}^\dagger, d_{tt}^\dagger, L_c, r$
(2) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{loctyp} + \varepsilon$	L_h, IFA^\dagger, L_m
(3) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{loctyp} + a_3 \cdot \text{Fam} * \text{loctyp} + \varepsilon$	$\%_{mid}^\dagger$
(4) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{loctyp} + a_3 \cdot \text{Fam} * \text{habitat} + \varepsilon$	$\%_{prox}^\dagger$
(5) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{loctyp} + a_3 \cdot \text{habitat} + a_4 \cdot \text{Fam} * \text{habitat} + \varepsilon$	T^\dagger, FR^\dagger
(6) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{loctyp} + \varepsilon$	$TR^\dagger, \%_{dist}^\dagger$
(7) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{loctyp} + a_3 \cdot \text{habitat} + \varepsilon$	HR^\dagger, UR^\dagger
(8) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{habitat} + \varepsilon$	RR^\dagger
(9) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{loctyp} + a_3 \cdot \text{Fam} * \text{habitat} + \varepsilon$	MR^\dagger
(10) $y = a_0 + a_1 \cdot \text{Fam} + a_2 \cdot \text{Fam} * \text{habitat} + a_3 \cdot \text{habitat} + \varepsilon$	O^\dagger
(11) $y = a_0 + a_1 \cdot \text{Fam} * \text{habitat} + \varepsilon$	d_{tc}^\dagger
(12) $y = a_0 + a_1 \cdot \text{loctyp} * \text{habitat} + \varepsilon$	d_{sc}^\dagger

†: intercept (a_0) was not significant in this case

Phocidae presented the lowest values for L_s , P , and O ; Otariidae for d_{sf} and d_{tc} ; Pinnipedia for H_s , L_h , L_r , L_u , L_t , N , and d_{st} ; and Ursidae for T , FR , and L_c . Furthermore, as in the other size-corrected ANOVAs, significantly different homogeneous subgroups that had been masked by the allometric effect were detected (e.g. Hyaenidae presented the highest values for L_s , L_m , and d_{tm}). The size-corrected MANOVA for functional relative segment lengths produced the same results as the uncorrected MANOVA.

Finally, GLMs were fitted to the regression residuals to reassess the effect of locomotor type, preferred habitat, phylogenetic relatedness, and their interactions, on the studied variables once the allometric effect have been removed. A total of 12 different models were obtained (Table II.9). As in the GLMs including the allometric effect, phylogenetic relatedness (Fam) was the main factor explaining the observed residual variability, since it was included in the final model for all variables but d_{sc} and d_{tc} (Table II.9). As expected, once the allometric effect was removed, the effect of locomotor type on carnivoran limb morphology was similar to that of habitat, since the number of model terms in which habitat was included was severely reduced.

Discussion

Size differences or locomotor adaptations?

In all the variables studied, size was the main factor determining limb bone morphology, since for most variables differences among locomotor types, preferred habitats, and taxonomic groups, tended to separate the groups with the largest mean body mass from the rest (Figs. II.1, II.3, II.4). Furthermore, the homogeneous subgroups obtained for most of the variables mirrored those obtained for body mass (M_b) (Fig. II.2). Finally, all the models summarizing the observed variability of the studied variables included M_b in their factorization, mostly as a significant interaction with another factor (Table II.8).

As would be expected, the use of regression residuals revealed that most of these group differences were size-related artifacts, since they either were not recovered, or changed their polarity, after removing the allometric effect, especially in the analyses by preferred habitat (Figs. II.1–II.4). All subsequent discussion of group differences and descriptions of particular groups are thus based on the size-corrected analyses.

Contrary to the expectations of Bertram & Biewener (1990), differences between terrestrial, scansorial, and arboreal carnivorans were not mainly caused by size differences among those groups. In fact, most of the significant differences between those groups in the uncorrected analyses proved to be size-related artifacts (Fig. II.1). On the other hand, after removing the allometric effect, the amount of significant differences between terrestrial, scansorial and arboreal carnivorans increased, especially between terrestrial and arboreal carnivorans (Fig. II.1). Furthermore, while Bertram & Biewener (1990) expected adaptations to swimming to be independent of size, the present study proves that size created a huge number of artifactual differences between aquatic carnivorans and the other locomotor types. It must be pointed out, however, that adaptations in both aquatic carnivorans (generally large) and semiaquatic carnivorans (generally small) were quite similar after removing the allometric effect (see below).

In a study on the scaling of relative functional segment lengths in primates and other mammals, Schmidt (2008) obtained a fairly constant set of forelimb proportions for the carnivoran species that she studied, namely 26% – 40% – 34 % for the proximal – middle – distal segments (i.e. scapula – humerus – radius). Furthermore, these proportions seemed size-independent in Carnivora. Overall, the results of the present study partially support those findings, since functional segment proportions only deviated considerably from

those values in Canidae (27% – 37% – 36%), Hyaenidae (29% – 34% – 37%) and Pinnipedia (37% – 30% – 33%); in arboreal, aquatic, and semiaquatic carnivorans (respectively: 24% – 43% – 33%; 36% – 31% – 33%; 30% – 40% – 30%), and in marine species (35% – 33% – 32%). Furthermore, this deviation was only significant in Pinnipedia and aquatic/marine carnivorans. Similar deviations for Canidae and Hyaenidae have also been reported by Schmidt & Fischer (2009). However, different sets of significant differences and homogeneous subgroups were obtained prior and after the size-correction, especially in the middle segment (Figs. II.1–II.4). Thus, the size-independence of functional limb proportions proposed by Schmidt (2008) is not supported in the present study. Similar results were obtained by Schmidt & Fischer (2009), who reported a significant allometric effect in the relative length of the scapula in Felidae and in the relative length of the humerus in “Carnivora” (mainly Felidae + Mustelidae). Unfortunately, segment proportions in Pike & Alexander (2002) were calculated using different measurements for limb bone lengths, preventing the comparison of their results and those of the present study. Finally, according to Fischer & Blickhan (2006), functional relative segment lengths of about 33% – 33% – 33% increase the self-stability of crouched limbs, which are characteristic of small mammals (Jenkins, 1971; Fischer et al., 2002). On the other hand, a more extended limb posture requires “asymmetrical limb segment proportions” for self-stability (Seyfarth et al., 2001). This way, large carnivorans would have been expected to present highly asymmetrical functional relative segment lengths and small carnivorans to approach symmetrical proportions. However, this was never the case, as all carnivorans present asymmetrical limb segment proportions (Tables II.4, II.5, II.7). In fact, the closest values to symmetric proportions belong to the larger carnivorans: aquatic/marine carnivorans and pinnipeds. Thus, either small carnivorans do not present a crouched posture, which is probably not the case (Horner & Biknevicius, 2010), or more likely small mammals retain the limb segment proportions of an ancestor with more extended limbs, which supports the morphological conservativeness of carnivoran limbs (see below for further evidence).

Finally, regarding the use of ratios to avoid size-related issues in interspecific comparisons, in the present study the same differences prior and after correcting for size were only obtained for %_{prox} between preferred habitats. In all other cases, different results were obtained in the uncorrected and size-corrected analyses. As pointed out by Aiello (1981), a ratio between two variables will only be independent of size if both variables scale to body mass with the same exponent. These results, plus the artifactual differences detected among locomotor and habitat categories, suggest not using limb bone

measurements, be it distances or ratios, to infer behavioral traits of extinct taxa using univariate methods, at least not without previously employing some sort of size correction. For instance, in a sample including species with unknown behavioral traits, some variable could be used to estimate body mass (and then left out to avoid circularity), and then the regression residuals of each other variable on the estimated body mass could be used to infer the unknown behavioral traits.

Locomotor specialization or resource maximization?

Overall, using either locomotor type or preferred habitat to define morphologically different groups within Carnivora produced similar results, both in the ANOVAs and the GLMs. This is probably caused by the similar species composition of some locomotor type and habitat groups, particularly aquatic/marine carnivorans and semiaquatic/freshwater carnivorans. Some overlapping between locomotor type and preferred habitat groups is to be expected because, for instance, specialization to swimming can only occur in watery environments and truly arboreal animals cannot be found outside zones with dense tree cover. However, in the present study marine carnivorans include all aquatic carnivorans plus one semiaquatic (*Lontra felina*) and one terrestrial carnivoran (*Ursus maritimus*), while freshwater carnivorans include all other semiaquatic species plus four scansorial carnivorans that live near watercourses. Thus, each pair of categories is almost interchangeable and thus similar results are to be expected. That being said, more significant differences were found in the analyses by locomotor type than in those by preferred habitat (Figs. II.1, II.3), indicating that locomotor type is a better criterion to define morphologically different groups within Carnivora using univariate analyses. Therefore, since locomotor type was used to represent locomotor specialization and preferred habitat as an indicator of the ability to perform different modes of locomotion (running, swimming, climbing, digging), these results suggest that carnivorans favor optimizing the performance of a specific mode of locomotion rather than maximizing resource exploitation by being able to navigate all substrates available in their preferred habitat. This finding is probably related to the higher costs of locomotion of mammals adapted to perform conflicting modes of locomotion, as demonstrated by the work of Williams and colleagues on the energetics of locomotion in semiaquatic mustelids (Williams, 1983*a, b*, 1989; Williams et al., 2002). This way, the general trend for carnivorans would be to specialize in one locomotor mode and hence minimize the cost of locomotion, probably related to the low catch success rate of most carnivoran species

(Wilson & Mittermeier, 2009). However, when coping with the increased costs of locomotion of several locomotor modes is possible thanks to a significant increase in prey availability, optimal performance of multiple locomotor modes would be preferred (as in the North American mink; Williams, 1983*a, b*).

Morphological adaptations to the different locomotor types

In agreement with previous anatomical studies (Osburn, 1903; Smith & Savage, 1956; English, 1977), aquatic carnivorans are characterized by having the shortest and more robust limb bones, and the lowest scapular spines. As pointed out by English (1977), short limbs both reduce the resistance arms of drag forces (increasing streamlining) and increase the ability of limb muscles to produce forward thrust. Furthermore, their limb bones are transversely flattened to increase the surface of the flippers (i.e., fin-like limbs): aquatic carnivorans studied present both the largest transverse diameters and the smallest sagittal diameters for the humerus, radius, ulna, and femur (actually, by definition, largest sagittal diameter and smallest transverse diameter in the case of the ulna). Aquatic carnivorans also present the highest values of the indicator of fossorial ability (**IFA**), which indicates an enlarged olecranon process relative to ulna length. In this case, however, it obviously does not correlate with frequency of digging, just indicates very powerful elbow extensors, which could be related to supporting their heavy body on land. Furthermore, in otariids, as pectoral oscillators (see below), those muscles must exert powerful forces to retract the forelimb and produce forward thrust to propel the body while swimming, since water is denser and more viscous than air (Williams et al., 2002; Pierce et al., 2011). Aquatic carnivorans also present the widest supraspinous fossae and the narrowest infraspinous fossae (that combine in the widest scapulas), and the largest projected height of the greater humeral tubercle (**T**), while the adduction angle of the olecranon (**θ**) is only larger in semiaquatic carnivorans. All these adaptations (but large **θ** values), were already observed by English (1977), who related them to the particular swimming style of otariids. The enlarged fossa supraspinata provides larger insertion area for the serratus ventralis and supraspinatus muscles, while the brachiocephalicus, supraspinatus and infraspinatus insert in the robust greater tubercle. All these muscles play an important role in protracting and abducting the forelimb during the recovery phase of the forelimb cycle while swimming, while supraspinatus and infraspinatus also contribute as shoulders stabilizers (English, 1977). Otariids are pectoral oscillators, that is, they swim propelling themselves forward with thrust produced by the enlarged foreflippers, while phocids

swim by pelvic oscillation, generating thrust with horizontal undulations of the spine combined with hindflipper paddling (Pierce et al., 2011). This way, all these adaptations would be of little use for phocids, and indeed, if we look at the size-corrected results by Family (Fig. II.4), phocids present the narrowest supraspinous fossae (hence the narrowest scapulas), and just intermediate values for **T** and **θ**. According to Fujiwara (2009), the highly medially oriented olecrana would suggest that the forearm is generally kept at an adducted position, which would bring it close to and under the body, which in turn would help increase streamlining. This also explains why phocids have intermediate **θ** values, since they short forelimbs usually are kept close to, but parallel, to the body while swimming. Finally, regarding limb segment composition, aquatic carnivorans have the largest proximal segments and the smallest middle and distal segments, which could also be related to the development of flippers: since the proximal segment does not protrude from the body like the middle and distal segments, its shortening is less pronounced, which results in a longer relative length of the scapula relative to the humerus and the radius. Similar results were also reported by English (1977).

Most of the adaptations described for aquatic carnivorans, namely wider supraspinous fossa than infraspinous fossa, high bone robusticities, large **IFA**, highly adducted olecrana, short limb bones, and relatively longer proximal than middle and distal segments, can also be found in semiaquatic carnivorans (which present similar mean residual values to aquatic carnivorans, although not so extreme). Contrary to aquatic carnivorans, however, semiaquatic carnivorans present the narrowest scapulas, have the lowest values of **T**, and their proximal limb bones are not flattened. The first two characters, narrow scapula and a greater tubercle of the humerus not protruding from the humeral head, were also observed in phocids (pelvic oscillators), which suggest a similar swimming style for semiaquatic carnivorans. However, semiaquatic carnivorans propel themselves underwater either with alternate, cyclic thrusts involving all four limbs, or using a combination of hind-paw strokes and dorso-ventral body undulations, depending on their commitment to swimming (Williams, 1983*a, b*; Williams et al., 2002). Thus, the similarity with phocids is probably caused by the abundance of highly committed swimmers (otters) in the semiaquatic sample. The lack of limb bone flattening would be explained by the even larger increase of the cost of locomotion in land that semiaquatic carnivorans would incur into by acquiring flippers (Williams et al., 2002).

Semifossorial carnivorans present the most robust metacarpals and tibiae and, as fossorial rodents (Lehmann, 1963), the longest olecrana. Furthermore, in agreement with

studies on fossoriality in mammals (Lehmann, 1963; Van Valkenburgh, 1987; Elissamburu & Vizcaíno, 2004), **IFA** is large, although smaller than in aquatic and semiaquatic carnivorans. By having long moment arms (i.e., olecrana), the triceps can produce the large forces at the manus required for digging with the forelimbs (Hildebrand, 1985a; Van Valkenburgh, 1987). Similarly to aquatic and semiaquatic carnivorans, semifossorial carnivorans have relatively longer scapulas (high %_{prox} values) and remarkably robust and short limb bones (including the scapula), which provide a twofold advantage: they are mechanically optimized to resist the bending stresses placed on the bones while digging (Hildebrand, 1985a), and they also provide an advantage for moving through narrow tunnels while chasing prey (Shimer, 1903; Gambaryan, 1974). These findings agree with previous studies on fossoriality in rodents, which did not include aquatic species and thus concluded that fossorial species had the shortest limb bones (Lehmann, 1963; Bou et al., 1987; Casinos, 1994) and the more robust forelimb bones (Elissamburu & Vizcaíno, 2004). However, the higher values of aquatic and semiaquatic carnivorans could also be attributed to the lack of truly fossorial species in the sample. Finally, also like semiaquatic carnivorans, the scapulas of semifossorial carnivorans are narrow, contrary to what would be expected according to Smith & Savage (1956).

Regarding adaptations to arboreality, as suggested by Bertram & Biewener (1990), significant differences between the various locomotor categories related to the degree of arboreality were scarce (Fig. II.1). However, in agreement with previous studies on arboreality (Van Valkenburgh, 1987; Iwaniuk et al., 1999, 2000; Argot, 2001), an association between several variables and arboreality was observed. As the degree of arboreality increased, so did scapular width (**A**), ulnar and metacarpal robusticity (**UR**, **MR**; contrary to the results of Iwaniuk et al., 1999), and relative length of the humerus segment (%_{mid}). On the other hand, projected height of the greater tubercle (**T**), olecranon orientation (α ; in agreement with the results of Van Valkenburgh, 1987), and length of the third metacarpal (**L_m**), among others, decreased with increasing arboreality. Both the decrease in **T** values and the increase in **A** values reflect the compromise between the benefit of having a large mobility at the shoulder in the three-dimensional environment of the canopy (a low greater tubercle of the humerus allows a wider range of forelimb abduction) and the need of prevent shoulder dislocation (a wider scapula allows for the development of larger shoulder stabilizer muscles; Smith & Savage, 1956). As discussed elsewhere (Van Valkenburgh, 1987; Fujiwara, 2009), the orientation of the olecranon relative to the ulnar shaft (α) determines the forelimb position in which the triceps muscle

has its greatest leverage. A cranially bent or straight olecranon (low α values) maximizes triceps leverage in a crouched position, which is generally used in clawed arboreal mammals, like carnivorans (Cartmill, 1974). On the other hand, a caudally bent olecranon (high α values) provides maximum triceps leverage when the limb is extended, as in most terrestrial carnivorans specialized in running (Howell, 1944; Day & Jayne, 2007). Another adaptation to running in terrestrial mammals is the elongation of the distal segments (Lull, 1904; Hildebrand, 1985*b*; Iwaniuk et al., 1999), which would explain the increase in L_m as arboreality decreases. The observed increase in robusticity of the distal forelimb elements (ulna, third metacarpal) as the degree of arboreality increased probably relates to the development of more powerful muscles of the forearm and manus (pronators, supinators, deep digital flexors), as already described for rodents with increasing degree of fossoriality (Hildebrand, 1985*a*; Elissamburu & Vizcaíno, 2004). In the present study, no association between arboreality and **IFA** was found, contrary to the results of Iwaniuk and colleagues (Iwaniuk et al., 1999), which seems to confirm their hesitations about their results being an artifact caused by the predominance of digging and swimming species in their non-arboreal sample. Finally, in some of the studied variables an increase from arboreal and semiarboreal species to terrestrial species and then to scansorial species was observed, so its relationship with arboreality was unclear. These variables included the lengths of the scapula, radius and ulna, the height of the scapular spine, and the lengths of the olecranon, styloid process of the radius, and neck of the femur. Some of these variables, namely radius and ulna length, did increase from forest species, to species of mosaic habitats, to species dwelling in open habitats, as also did tibia and metacarpus length, which agrees with the results of Gonyea (1976) in large felids and with the expectations of Cartmill (1985) for arboreal adaptations in Carnivora.

Phylogenetic signal in limb morphology

In agreement with previous studies on carnivoran limb morphology (Flynn et al., 1988; Bertram & Biewener, 1990; Day & Jayne, 2007), the present study has shown that phylogenetic relatedness has a significant effect on the morphology of the carnivoran appendicular skeleton. Even after correcting for size differences between families, significant differences between families were found for almost all variables studied (Figs. II.2, II.4). Furthermore, a significant phylogenetic effect was included in almost all GLMs modelling factor interactions on the different variables after the size-correction (Table II.9).

As stated above, aquatic and marine carnivorans are composed by roughly the same

species, which in turn mainly belong to the same monophyletic clade, Pinnipedia (Arnason et al., 2006). It could be argued, then, that the adaptations described above for aquatic/marine carnivorans only represent the particular response of Pinnipedia to the requirements of an aquatic lifestyle, and not a general trend for aquatic/marine carnivorans. However, this is unlikely because, not only non-pinniped species in those categories present similar (residual) values to pinniped species, but similar adaptations have also been found in semiaquatic carnivorans, which are only distantly related to pinnipeds. Furthermore, results of the ANOVAs by locomotor type and preferred habitat were not completely replicated in the ANOVAs by family. For instance, while aquatic carnivorans as a whole presented the largest values for most variables related to scapular width (**A**, **S**), Phocidae presented the lowest values for these variables, while aquatic carnivorans presented the shortest olecrana (**O**) and Otariidae the longest.

Thoughts on the carnivoran ancestor

Habitat mean residual values were closest to zero in forest-dwelling carnivorans, while the same was true for Viverridae, Herpestidae, and Eupleridae, in the case of family mean residual values (Fig. II.5). Furthermore, differences between these families were only significant in a few cases (less than 5% of possible differences were significant; Fig. II.4), supporting the similar limb morphology of these families. Thus, the results of the present study suggest a forest-dwelling “viverrid-like” ancestor for Carnivora, which agrees with the placement of “miacids” at the branch leading to extant Carnivora (Wesley-Hunt & Flynn, 2005). In the case of locomotor-type mean residual values, both terrestrial and arboreal carnivorans had the values closest to zero, so it is unclear whether that forest-dwelling “viverrid-like” ancestor spent most of its time on the canopy or on the ground. However, this ambiguous result also agrees with a “miacid” ancestor of Carnivora, since recent studies have described a mixed set of adaptations to arboreality and high-speed running for these fossil species (Spaulding & Flynn, 2009).

The more limb morphology deviates from the “viverrid-like” pattern, the higher mean residual values become. For instance, procyonids have similar limb morphology than viverrids, herpestids and euplerids, as evidenced by no significant difference with these families and mean residual values close to zero. However, mustelids present a rather different limb morphology from the “viverrid-like” pattern, having more extreme mean residual values (Fig. II.5c) and showing significant differences with “viverrid-like” families (Viverridae, Herpestidae, Eupleridae) in most variables (Fig. II.4). Interestingly, the linsang

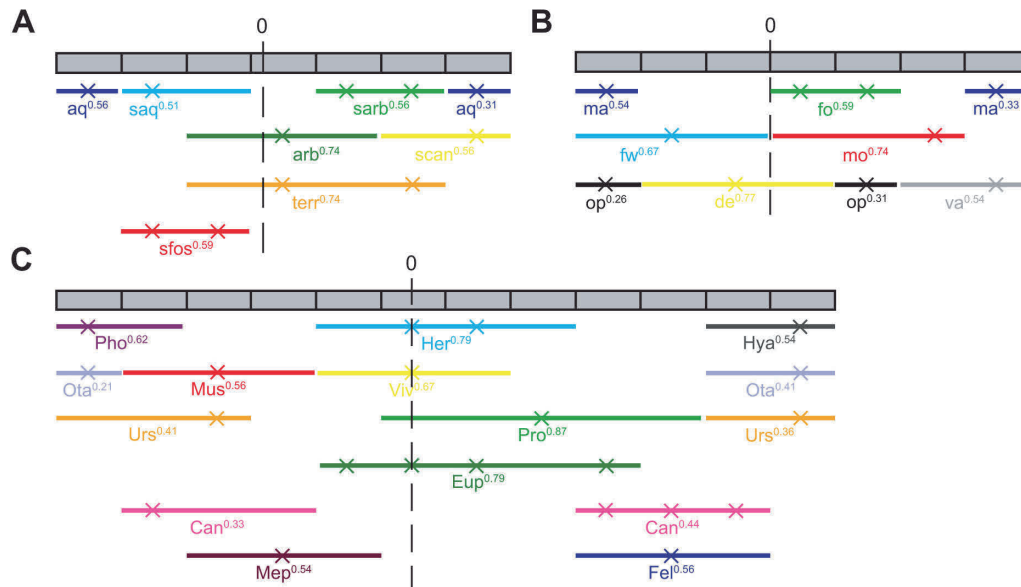


Figure II.5. Mean residual values distribution. The distribution of mean residual values among the studied variables is presented for locomotor type (A), preferred habitat (B), and family (C). Calcaneal variables were excluded because no data exists for various species. The dashed zero line (0) represents the position of zero relative to the values of all categories in each factor, since in most cases residuals were slightly skewed to the right. For each category, each segment indicates where were concentrated the residual values, relative to zero, for most of the studied variables. The superindex on a category name represents the proportion of the studied variables whose residual values occupy that segment for that category. For example, among locomotor types (A), over half of the variables presented the lowest residual values for aquatic carnivorans, hence a segment $aq^{0.56}$ is placed on the first relative position to the left. Finally, on segments spanning several relative positions, a cross marks the relative position with the highest proportion of studied variables. All abbreviations as in Figure II.2.

(*Prionodon linsang*) would occupy an intermediate position between felids and “viverrid-like” carnivorans (Fig. II.5c), probably retaining a similar limb morphology to the ancestor that diverged from the main “viverrid-like” stem to eventually lead to the Felidae + Prionodontidae clade about 33 million years ago (Gaubert & Veron, 2003).

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Appendix – Database

The main database consisted of 435 specimens from 143 species of Carnivora (Table II.1). Specimens are housed in the collections of the Phylogenetisches Museum (Jena, Germany), the Museum für Naturkunde (Berlin, Germany), the Museu de Ciències Naturals de la Ciutadella (Barcelona, Spain), the Muséum National d'Histoire Naturelle (Paris, France), the Museo Nacional de Ciencias Naturales (Madrid, Spain), the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina), the Museo de La Plata (La Plata, Argentina), and the Naturhistorisches Museum Basel (Basilea, Suiza).

For each specimen, measurements were taken on the scapula, humerus, radius, ulna, third metacarpal, femur, tibia, and calcaneus. In a few cases, some bones were missing, hence the different sample sizes of the analyses. The adult status of the skeletal specimens was judged on the basis of the fusion of the epiphyses of the long bones.

For each bone, the three-dimensional coordinates of several landmarks were acquired using a MicroScribe 3D digitizer (Figs. II.A1 – II.A6; Tables II.A1 – II.A8). From these sets of landmarks, several distances and angles were calculated. A total of 59 variables were calculated for each specimen (see Table II.A9 for a preliminary list of variable names and abbreviations).

Since body mass values were missing from most specimens, average body masses were obtained from the literature. When the gender of the specimen was known, separate male and female average body masses were assigned accordingly, while specimens of unknown gender were assigned an average species value (averaged male and female values). Average body mass of each species was thus weighted by the number and gender of the individual specimens measured (Table II.1).

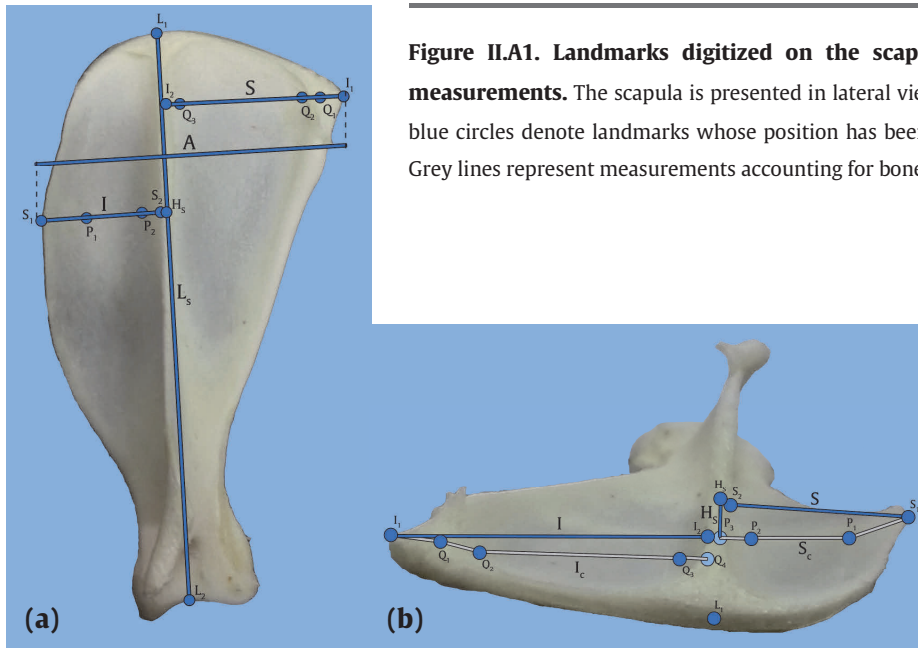


Figure II.A1. Landmarks digitized on the scapula and corresponding linear measurements. The scapula is presented in lateral view (a) and in dorsal view (b). Light blue circles denote landmarks whose position has been calculated to be inside the bone. Grey lines represent measurements accounting for bone curvature.

Scapula

Over 12 landmarks were measured on the scapula (Fig. II.A1; Table II.A1), and the following measurements were calculated (Table II.A9):

$$L_s = d(L_1, L_2) , \text{ where } L_s \text{ is scapular length}$$

$$S = d(S_1, S_2) , \text{ where } S \text{ is the maximum projected width of supraspinous fossa}$$

$$S_c = d(S_1, P_1) + \sum_{i=1}^{n-1} d(P_i, P_{i+1}) , \text{ where } S_c \text{ is the maximum real width of supraspinous fossa}$$

$$I = d(I_1, I_2) , \text{ where } I \text{ is the maximum projected width of infraspinous fossa}$$

$$I_c = d(I_1, Q_1) + \sum_{j=1}^{m-1} d(Q_j, Q_{j+1}) , \text{ where } I_c \text{ is the maximum real width of infraspinous fossa}$$

$$A = \left| \overline{I_1 S_1} \right| \cdot \left(\widehat{I_1 S_1} \cdot \widehat{I_1 I_2} \right) , \text{ where } A \text{ is maximum projected scapular width, } \left| \overline{I_1 S_1} \right| = d(I_1, S_1)$$

and $\widehat{I_1 S_1} \cdot \widehat{I_1 I_2}$ is the dot product between the unit vectors

$$\widehat{I_1 S_1} = \left(\frac{x_{I_1} - x_{S_1}}{d(I_1, S_1)}, \frac{y_{I_1} - y_{S_1}}{d(I_1, S_1)}, \frac{z_{I_1} - z_{S_1}}{d(I_1, S_1)} \right) \text{ and } \widehat{I_1 I_2} = \left(\frac{x_{I_1} - x_{I_2}}{d(I_1, I_2)}, \frac{y_{I_1} - y_{I_2}}{d(I_1, I_2)}, \frac{z_{I_1} - z_{I_2}}{d(I_1, I_2)} \right)$$

$$A_c = S_c + I_c , \text{ where } A_c \text{ is maximum scapular width accounting for scapular blade curvature}$$

$$H_s = d(H_s, P_n) , \text{ where } H_s \text{ is scapular spine height at the point of maximum supraspinous fossa width}$$

Table II.A1. Landmark definitions for the scapula.

Landmark	Definition
L ₁	Intersection between scapular spine and vertebral border.
L ₂	Point of maximum curvature of glenoid cavity on the plane of scapular spine.
S ₁	Cranialmost point of cranial border.
S ₂	Projection of S ₁ onto scapular spine.
I ₁	Caudalmost point of caudal border.
I ₂	Projection of I ₁ onto scapular spine.
H _s	Lateralmost point of scapular spine on S projection line.
P ₁ to P _n	Points of maximum curvature along supraspinous fossa on the S projection line.
Q ₁ to Q _m	Points of maximum curvature along infraspinous fossa on the I projection line.

Humerus

Seven landmarks were measured on the humerus (Fig. II.A2a; Table II.A2), and the following measurements were calculated (Table II.A9):

$$L_h = d(L_{H1}, L_{H2}), \text{ where } L_h \text{ is humerus functional length}$$

$$L'_h = d(L_{H2}, L_{H3}), \text{ where } L'_h \text{ is humerus maximum anatomical length}$$

$$d_{sh} = d(s_{H1}, s_{H2}), \text{ where } d_{sh} \text{ is humerus sagittal diameter}$$

$$d_{th} = d(t_{H1}, t_{H2}), \text{ where } d_{th} \text{ is humerus transverse diameter}$$

$$HR = d_{sh} / L_h, \text{ where } HR \text{ is humerus robusticity}$$

Let $\vec{s} = \vec{s}_{H1} + \lambda \vec{u}$ be the line containing s_{H1} and s_{H2} , and let $\vec{t} = \vec{t}_{H1} + \mu \vec{v}$ be the line containing t_{H1} and t_{H2} , we define the point I_H as the intersection between both lines. Then we can use I_H to calculate bone length approximating for the curvature of the midshaft:

$$L_{ch} = d(L_{H1}, I_H) + d(I_H, L_{H2}), \text{ where } L_{ch} \text{ is humerus functional length accounting bone curvature}$$

$$L'_{ch} = d(L_{H2}, I_H) + d(I_H, L_{H3}), \text{ where } L'_{ch} \text{ is humerus maximum anatomical length accounting bone curvature}$$

$$T = d(I_H, L_{H2}) - \left| \overrightarrow{I_H L_{H1}} \right| \cdot \left(\widehat{I_H L_{H1}} \cdot \widehat{I_H L_{H2}} \right), \text{ where } T \text{ is the projected height of greater tubercle above the humeral head, } \left| \overrightarrow{I_H L_{H1}} \right| = d(I_H, L_{H1}), \text{ and } \widehat{I_H L_{H1}} \cdot \widehat{I_H L_{H2}} \text{ is the dot product between the unit vectors } \widehat{I_H L_{H1}} = \left(\frac{x_{L_{H1}} - x_{I_H}}{d(I_H, L_{H1})}, \frac{y_{L_{H1}} - y_{I_H}}{d(I_H, L_{H1})}, \frac{z_{L_{H1}} - z_{I_H}}{d(I_H, L_{H1})} \right)$$

$$\text{and } \widehat{I_H L_{H1}} = \left(\frac{x_{L_{H1}} - x_{I_H}}{d(I_H, L_{H1})}, \frac{y_{L_{H1}} - y_{I_H}}{d(I_H, L_{H1})}, \frac{z_{L_{H1}} - z_{I_H}}{d(I_H, L_{H1})} \right)$$

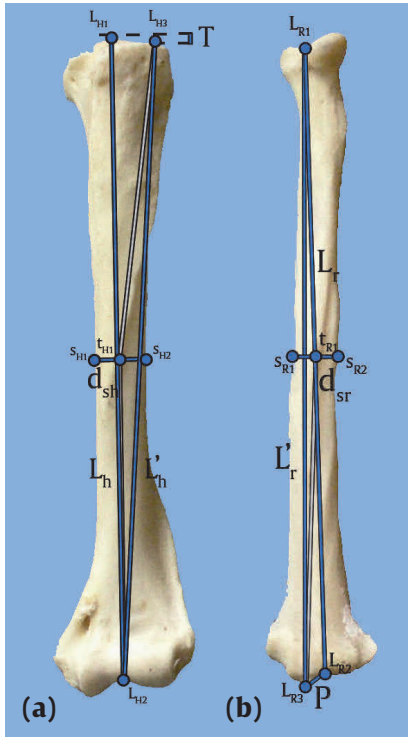


Figure II.A2. Landmarks digitized on the humerus (a) and radius (b), and corresponding linear measurements. Grey lines represent measurements accounting for bone curvature.

Landmark	Definition
L _{H1}	Point of maxi. curvature of humeral head.
L _{H2}	Proximalmost point of greater tubercle.
L _{H3}	Point of maximum curvature of trochlea.
S _{H1}	Cranialmost point of humeral midshaft.
S _{H2}	Caudalmost point of humeral midshaft.
t _{H1}	Medialmost point of humeral midshaft.
t _{H2}	Lateralmost point of humeral midshaft.

Landmark	Definition
L _{R1}	Point of maximum curvature of radial head.
L _{R2}	Base of styloid process.
L _{R3}	Tip of styloid process.
S _{R1}	Cranialmost point of radial midshaft.
S _{R2}	Caudalmost point of radial midshaft.
t _{R1}	Medialmost point of radial midshaft.
t _{R2}	Lateralmost point of radial midshaft.

Table II.A2. Landmark definitions for the humerus.

Table II.A3. Landmark definitions for the radius.

Radius

Seven landmarks were measured on the radius (Fig. II.A2b; Table II.A3), and the following measurements were calculated (Table II.A9):

$$L_r = d(L_{R1}, L_{R2}), \text{ where } L_r \text{ is radius functional length}$$

$$L'_r = d(L_{R1}, L_{R3}), \text{ where } L'_r \text{ is radius maximum anatomical length}$$

$$d_{sr} = d(s_{R1}, s_{R2}), \text{ where } d_{sr} \text{ is radius sagittal diameter}$$

$$d_{tr} = d(t_{R1}, t_{R2}), \text{ where } d_{tr} \text{ is radius transverse diameter}$$

$$P = d(L_{R2}, L_{R3}), \text{ where } P \text{ is styloid process length}$$

$$RR = d_{sr} / L_r, \text{ where } RR \text{ is radius robusticity}$$

Let $\vec{s} = \vec{s}_{R1} + \lambda \vec{u}$ be the line containing S_{R1} and S_{R2} , and let $\vec{t} = \vec{t}_{R1} + \mu \vec{v}$ be the line containing t_{R1} and t_{R2} , we define the point I_R as the intersection between both lines. Then we can use I_R to calculate bone length approximating for the curvature of the midshaft:

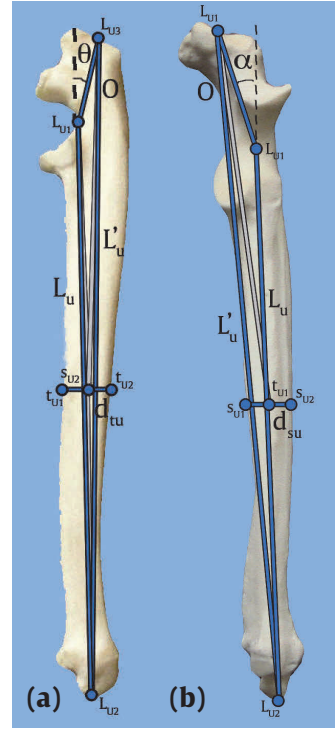
$$L_{cr} = d(L_{R1}, I_R) + d(I_R, L_{R2}), \text{ where } L_{cr} \text{ is radius functional length accounting bone curvature}$$

$$L'_{cr} = d(L_{R1}, I_R) + d(I_R, L_{R3}), \text{ where } L'_{cr} \text{ is radius maximum anatomical length accounting bone curvature}$$

Figure II.A3. Landmarks digitized on the ulna and corresponding linear measurements.

The ulna is presented in lateral view (a) and dorsal view (b). Grey lines represent measurements accounting for bone curvature.

Landmark	Definition
L_{U1}	Point of maximum curvature of semilunar notch.
L_{U2}	Tip of olecranon process.
L_{U3}	Tip of styloid process.
S_{U1}	Cranialmost point of ulnar midshaft.
S_{U2}	Caudalmost point of ulnar midshaft.
t_{U1}	Medialmost point of ulnar midshaft.
t_{U2}	Lateralmost point of ulnar midshaft.


Table II.A4. Landmark definitions for the ulna.

Ulna

Seven landmarks were measured on the ulna (Fig. II.A3; Table II.A4), and the following measurements were calculated (Table II.A9):

$$L_u = d(L_{U1}, L_{U3}), \text{ where } L_u \text{ is ulna functional length}$$

$$L'_u = d(L_{U2}, L_{U3}), \text{ where } L'_u \text{ is ulna maximum anatomical length}$$

$$d_{su} = d(s_{U1}, s_{U2}), \text{ where } d_{su} \text{ is ulna sagittal diameter}$$

$$d_{tu} = d(t_{U1}, t_{U2}), \text{ where } d_{tu} \text{ is ulna transverse diameter}$$

$$O = d(L_{U1}, L_{U2}), \text{ where } O \text{ is olecranon process length}$$

$$UR = d_{su} / L_u, \text{ where } UR \text{ is ulna robusticity}$$

$$IFA = O / L_u, \text{ where } IFA \text{ is short for Indicator of Fossorial Ability}$$

Let $\vec{s} = s_{U1} + \lambda \vec{u}$ be the line containing s_{U1} and s_{U2} , and let $\vec{t} = t_{U1} + \mu \vec{v}$ be the line containing t_{U1} and t_{U2} , we define the point I_U as the intersection between both lines. Then we can use I_U to calculate bone length approximating for the curvature of the midshaft:

$$L_{cu} = d(L_{U1}, I_U) + d(I_U, L_{U3}), \text{ where } L_{cu} \text{ is ulna functional length accounting bone curvature}$$

$$L'_{cu} = d(L_{U2}, I_U) + d(I_U, L_{U3}), \text{ where } L'_{cu} \text{ is ulna maximum anatomical length accounting bone curvature}$$

$$\alpha = \pi - \arccos\left(\widehat{L_{U1}I_U} \cdot \widehat{L_{U1}L_{U2}}\right), \text{ where } \alpha \text{ is olecranon angle and } \widehat{L_{U1}I_U} \cdot \widehat{L_{U1}L_{U2}} \text{ is the dot}$$

product between the unit vectors $\widehat{L_{U1}I_U} = \left(\frac{X_{L_{U1}} - X_{I_U}}{d(L_{U1}, I_U)}, \frac{Y_{L_{U1}} - Y_{I_U}}{d(L_{U1}, I_U)}, \frac{Z_{L_{U1}} - Z_{I_U}}{d(L_{U1}, I_U)} \right)$

and $\widehat{L_{U1}L_{U2}} = \left(\frac{X_{L_{U1}} - X_{L_{U2}}}{d(L_{U1}, L_{U2})}, \frac{Y_{L_{U1}} - Y_{L_{U2}}}{d(L_{U1}, L_{U2})}, \frac{Z_{L_{U1}} - Z_{L_{U2}}}{d(L_{U1}, L_{U2})} \right)$

θ : Let $\Pi : \vec{n} \cdot (\vec{s} - \vec{L_{U1}}) = 0$ be the plane containing the point L_{U1} and the line $\vec{s} = \vec{s_{U1}} + \lambda \vec{u}$, we define $\vec{n} = (X, Y, Z)$, with norm $\|\vec{n}\| = \sqrt{X^2 + Y^2 + Z^2}$, as a normal vector to Π ,

where $X = (y_{s_{U2}} - y_{L_{U1}})(z_{s_{U1}} - z_{L_{U1}}) - (z_{s_{U2}} - z_{L_{U1}})(y_{s_{U1}} - y_{L_{U1}})$,

$Y = (z_{s_{U2}} - z_{L_{U1}})(x_{s_{U1}} - x_{L_{U1}}) - (x_{s_{U2}} - x_{L_{U1}})(z_{s_{U1}} - z_{L_{U1}})$, and

$Z = (x_{s_{U2}} - x_{L_{U1}})(y_{s_{U1}} - y_{L_{U1}}) - (y_{s_{U2}} - y_{L_{U1}})(x_{s_{U1}} - x_{L_{U1}})$. We can then define

$\theta = \arcsin(\widehat{\vec{n}} \cdot \widehat{L_{U1}L_{U2}})$, where θ is the olecranon abduction angle, and $\widehat{\vec{n}} \cdot \widehat{L_{U1}L_{U2}}$ is

the dot product between the unit vectors $\widehat{\vec{n}} = \frac{\vec{n}}{\|\vec{n}\|}$ and $\widehat{L_{U1}L_{U2}}$ (see above).

Third metacarpal

Six landmarks were measured on the third metacarpal (Fig. II.A4; Table II.A5), and the following measurements were calculated (Table II.A9):

$L_m = d(L_{M1}, L_{M2})$, where L_m is third metacarpal functional length

$d_{sm} = d(s_{M1}, s_{M2})$, where d_{sm} is third metacarpal sagittal diameter

$d_{tm} = d(t_{M1}, t_{M2})$, where d_{tm} is third metacarpal transverse diameter

$MR = d_{sm} / L_m$, where MR is third metacarpal robusticity

Let $\vec{s} = \vec{s_{M1}} + \lambda \vec{u}$ be the line containing s_{M1} and s_{M2} , and let $\vec{t} = \vec{t_{M1}} + \mu \vec{v}$ be the line containing t_{M1} and t_{M2} , we define the point I_M as the intersection between both lines. Then we can use I_M to calculate bone length approximating for the curvature of the midshaft:

$L_{cm} = d(L_{M1}, I_M) + d(I_M, L_{M2})$, where L_{cm} is third metacarpal functional length accounting bone curvature

Forelimb segments relative lengths

Relative lengths were calculated for the functional segments of the forelimb (i.e., not considering the length of the autopod, since it barely contributes to forelimb progression; Schmidt & Fischer, 2009) (Table II.A9):

$\%_{prox} = L_s / (L_s + L_h + L_r) \cdot 100\%$, where $\%_{prox}$ is relative length of the proximal segment

$\%_{mid} = L_h / (L_s + L_h + L_r) \cdot 100\%$, where $\%_{mid}$ is relative length of the middle segment

$\%_{dist} = L_r / (L_s + L_h + L_r) \cdot 100\%$, where $\%_{rad}$ is relative length of the distal segment

Figure II.A4. Landmarks digitized on the third metacarpal and corresponding linear measurements. Grey lines represent measurements accounting for bone curvature.

Landmark	Definition
L_{M1}	Proximalmost point of third metacarpal.
L_{M2}	Distalmost point of third metacarpal.
S_{M1}	Cranialmost point of metacarpal midshaft.
S_{M2}	Caudalmost point of metacarpal midshaft.
t_{M1}	Medialmost point of metacarpal midshaft.
t_{M2}	Lateralmost point of metacarpal midshaft.

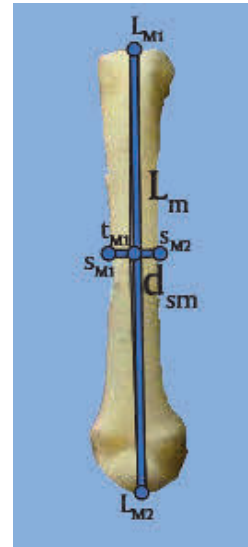


Table II.A5. Landmark definitions for the third metacarpal.

Femur

Seven landmarks were measured on the femur (Fig. II.A5a; Table II.A6), and the following measurements were calculated (Table II.A9):

$$L_f = d(L_{F1}, L_{F3}), \text{ where } L_f \text{ is femur functional length}$$

$$L'_f = d(L_{F2}, L_{F3}), \text{ where } L'_f \text{ is femur maximum anatomical length}$$

$$d_{sf} = d(s_{F1}, s_{F2}), \text{ where } d_{sf} \text{ is femur sagittal diameter}$$

$$d_{tf} = d(t_{F1}, t_{F2}), \text{ where } d_{tf} \text{ is femur transverse diameter}$$

$$N = d(L_{F1}, L_{F2}), \text{ where } N \text{ is neck-head length}$$

$$FR = d_{sf} / L_f, \text{ where } FR \text{ is femur robusticity}$$

Let $\vec{s} = s_{F1} + \lambda \vec{u}$ be the line containing s_{F1} and s_{F2} , and let $\vec{t} = t_{F1} + \mu \vec{v}$ be the line containing t_{F1} and t_{F2} , we define the point I_f as the intersection between both lines. Then we can use I_f to calculate bone length approximating for the curvature of the midshaft:

$$L_{cf} = d(L_{F1}, I_f) + d(I_f, L_{F2}), \text{ where } L_{cf} \text{ is femur functional length accounting bone curvature}$$

Tibia

Six landmarks were measured on the tibia (Fig. II.A5b; Table II.A7), and the following measurements were calculated (Table II.A9):

$$L_t = d(L_{T1}, L_{T2}), \text{ where } L_t \text{ is tibia functional length}$$

$$d_{st} = d(s_{T1}, s_{T2}), \text{ where } d_{st} \text{ is tibia sagittal diameter}$$

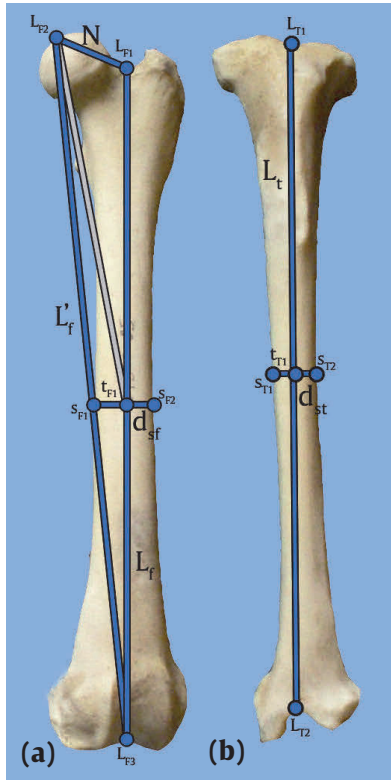


Figure II.A5. Landmarks digitized on the femur (a) and tibia (b), and corresponding linear measurements. Grey lines represent measurements accounting for bone curvature.

Landmark	Definition
L_{F1}	Point of maximum curvature of femoral neck near greater trochanter.
L_{F2}	Point of maximum curvature of femoral head.
L_{F3}	Point of maximum curvature between medial and lateral condyles.
S_{F1}	Cranialmost point of femoral midshaft.
S_{F2}	Caudalmost point of femoral midshaft.
t_{F1}	Medialmost point of femoral midshaft.
t_{F2}	Lateralmost point of femoral midshaft.

Table II.A6. Landmark definitions for the femur.

Landmark	Definition
L_{T1}	Point of maximum curvature between medial and lateral intercondylar tubercles.
L_{T2}	Point of maximum curvature of inferior articular surface near medial malleolus.
S_{T1}	Cranialmost point of tibial midshaft.
S_{T2}	Caudalmost point of tibial midshaft.
t_{T1}	Medialmost point of tibial midshaft.
t_{T2}	Lateralmost point of tibial midshaft.

Table II.A7. Landmark definitions for the tibia.

$$d_{st} = d(t_{T1}, t_{T2}), \text{ where } d_{st} \text{ is tibia transverse diameter}$$

$$TR = d_{st} / L_t, \text{ where } TR \text{ is tibia robusticity}$$

Let $\vec{s} = \vec{s}_{T1} + \lambda \vec{u}$ be the line containing s_{T1} and s_{T2} , and let $\vec{t} = \vec{t}_{T1} + \mu \vec{v}$ be the line containing t_{T1} and t_{T2} , we define the point I_T as the intersection between both lines. Then we can use I_T to calculate bone length approximating for the curvature of the midshaft:

$$L_{ct} = d(L_{T1}, I_T) + d(I_T, L_{T2}), \text{ where } L_{ct} \text{ is tibia functional length accounting bone curvature}$$

Calcaneus

Seven landmarks were measured on the calcaneus (Fig. II.A6; Table II.A8), and the following measurements were calculated (Table II.A9):

$$L_{calc} = d(L_{c1}, L_{c2}), \text{ where } L_c \text{ is calcaneus length}$$

$$r = d(L_{c2}, L_{c3}), \text{ where } r \text{ is ankle extensors moment arm}$$

$$d_{sc} = d(s_{c1}, s_{c2}), \text{ where } d_{sc} \text{ is calcaneus sagittal diameter}$$

$$d_{tc} = d(t_{c1}, t_{c2}), \text{ where } d_{tc} \text{ is calcaneus transverse diameter}$$

Figure II.A6. Landmarks digitized on the calcaneus and corresponding linear measurements. Grey lines represent measurements accounting for bone curvature, while the grey landmark is behind the image.

Landmark	Definition
L _{C1}	Point of maximum curvature of cuboid bone articular surface.
L _{C2}	Posteriormost point of tuber calcanei.
L _{C3}	Point of max. curvature of posterior articular surface.
S _{C1}	Dorsalmost point of tuber calcanei.
S _{C2}	Ventralmost point of tuber calcanei.
t _{C1}	Medialmost point of ulnar midshaft.
t _{C2}	Lateralmost point of ulnar midshaft.

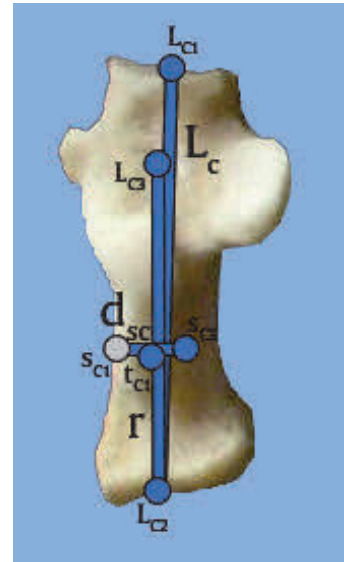


Table II.A8. Landmark definitions for the calcaneus.

Preliminary data exploration

Measurement error

Measurement error can be defined as the variability of repeated measurements of a particular variable taken on the same individual, relative to its variability among the individuals studied. To quantify the amount of measurement error present in the variables measured, percent measurement error (%ME) was calculated following Bailey & Byrnes (1990):

$$\%ME = \frac{s_{within}^2}{s_{within}^2 + s_{among}^2} \cdot 100\%$$

where s_{within}^2 is the within-individual component of variance, and s_{among}^2 is the among-individuals component of variance.

Both s_{within}^2 and s_{among}^2 can be estimated from the mean sums of squares (MS) of an ANOVA:

$$s_{within}^2 = MS_{within}, \text{ and } s_{among}^2 = \frac{MS_{among} - MS_{within}}{n},$$

where MS_{among} is the MS among individuals, MS_{within} is the MS within individuals, and n is the number of measurements per individual.

To estimate %ME, six individuals from different carnivoran species (*Acinonyx jubatus*, *Hyaena hyaena*, *Martes foina*, *Procyon lotor*, *Puma concolor*, *Vulpes vulpes*) were measured five times each (n = 5).

Overall, measurement error was negligible in the studied variables, since %ME was lower than 1% in all variables (ranging from 0.03% in **L_s** and **I** to 0.56% in **S**).

Abbr.	Name	Abbr.	Name
M_b	Body mass	d_{tu}	Ulna transverse diameter
L_s	Scapular length	O	Olecranon process length
S	Maximum projected width of supraspinous fossa	α	Olecranon angle
S_c	Maximum width of supraspinous fossa (accounting bone curvature)	θ	Olecranon abduction angle
I	Maximum projected width of infraspinous fossa	UR	Ulna robusticity
I_c	Maximum width of infraspinous fossa (accounting bone curvature)	IFA	Indicator of Fossorial Ability
A	Maximum projected scapular width	L_m	Third metacarpal functional length
A_c	Maximum scapular width (accounting scapular blade curvature)	L_{cm}	Third metacarpal functional length (accounting bone curvature)
H_s	Scapular spine height at point of maximum supraspinous fossa width	d_{sm}	Third metacarpal sagittal diameter
L_h	Humerus functional length	d_{tm}	Third metacarpal transverse diameter
L'_h	Humerus maximum anatomical length	MR	Third metacarpal robusticity
L_{ch}	Humerus functional length (accounting bone curvature)	L_f	Femur functional length
L'_{ch}	Humerus maximum anatomical length (accounting bone curvature)	L'_f	Femur maximum anatomical length
d_{sh}	Humerus sagittal diameter	L_{cf}	Femur functional length (accounting bone curvature)
d_{th}	Humerus transverse diameter	d_{sf}	Femur sagittal diameter
T	Projected height of greater tubercle	d_{tf}	Femur transverse diameter
HR	Humerus robusticity	N	Neck–head length
L_r	Radius functional length	FR	Femur robusticity
L'_r	Radius maximum anatomical length	L_t	Tibia functional length
L_{cr}	Radius functional length (accounting bone curvature)	L_{ct}	Tibia functional length (accounting bone curvature)
L'_{cr}	Radius maximum anatomical length (accounting bone curvature)	d_{st}	Tibia sagittal diameter
d_{sr}	Radius sagittal diameter	d_{tt}	Tibia transverse diameter
d_{tr}	Radius transverse diameter	TR	Tibia robusticity
P	Styloid process length	L_c	Calcaneus length
RR	Radius robusticity	r	Ankle extensors moment arm
L_u	Ulna functional length	d_{sc}	Calcaneus sagittal diameter
L'_u	Ulna maximum anatomical length	d_{tc}	Calcaneus transverse diameter
L_{cu}	Ulna functional length (accounting bone curvature)	%_{prox}	Relative length of the proximal segment of the forelimb
L'_{cu}	Ulna maximum anatomical length (accounting bone curvature)	%_{mid}	Relative length of the middle segment of the forelimb
d_{su}	Ulna sagittal diameter	%_{dist}	Relative length of the distal segment of the forelimb

Table II.A9. Measured variables.

Alternative variables

Some osteological characters were measured according to slightly different definitions in order to explore the relative importance of factors such as bone curvature or maximum anatomical length.

The comparison between such sets of alternative variables was carried out using two ANOVAs:

- one-way ANOVA: to test for differences between measurement definitions.
- two-way ANOVA: to study the possible interaction between measurement definition and broad phylogenetic relationships (at the family level). It was also considered whether differences between measurement definitions could be found at the family level (i.e. whether in a given family, there were differences between measurement definitions).

Curvature of the scapular fossae

The maximum width of the scapular fossae was measured as an orthogonal projection of the most external point of the border of the scapular blade to the scapular spine (**S**, **I**), and also approximately following its curvature (**S_c**, **I_c**). Likewise, maximum scapular width was defined as the distance, orthogonally projected to the plane of the scapular spine, between the most external points of the cranial and caudal borders (**A**), and as the sum of the fossae widths accounting scapular blade curvature (**A_c**).

No significant differences between measurement definitions were found for any pair of alternative variables (Table II.A10). Furthermore, the interaction between phylogeny and measurement definition was never significant (Table II.A10). This lack of significant differences, coupled with the lower %ME for the variables not accounting scapular blade curvature (e.g. **I**: 0.03% vs. **I_c**: 0.12%), suggests the use of projected distances over distances accounting curvature to quantify fossae widths. Furthermore, projected widths require fewer landmarks for its calculation (i.e. fewer measurement error sources).

Long bone curvature and anatomical vs. functional length

Long bone length was measured between articular surfaces for all bones (**L**, functional length), and also as maximum anatomical length (**L'**) for humerus, radius, ulna, and femur. Furthermore, an alternative measurement passing through the approximate centre of the midshaft was taken for each of these lengths (**L_c**, **L'_c**) except femur maximum anatomical length (**L'_f**).

	one-way	two-way
S vs. S_c	0.775	1
I vs. I_c	0.462	1
A vs. A_c	0.462	1
L_h vs. L_{ch} vs. L'_h vs. L'_{ch}	0.987	1
L_r vs. L_{cr} vs. L'_r vs. L'_{cr}	0.860	1
L_u vs. L_{cu} vs. L'_u vs. L'_{cu}	< 0.001	0.996
L_m vs. L_{cm}	0.969	1
L_f vs. L_{cf} vs. L'_f	0.822	1
L_t vs. L_{ct}	0.917	1

Table II.A10. Results of the ANOVAs comparing sets of alternative variables. P-values lower than 0.05 indicate significant differences between the alternative measurements.

Significant differences between functional and anatomical lengths were only found for the ulna (Table II.A10), since the olecranon process' length adds a relatively large contribution to ulna maximum anatomical length. Regarding bone curvature, no significant differences were found between any length and its corresponding measurement accounting bone curvature. Finally, the interaction between measurement definition and phylogeny was never significant (Table II.A10), although the differences between functional and anatomical lengths of the ulna were also significant within some families (Canidae, Otariidae, Ursidae, and Felidae), again probably due to a large contribution of the olecranon process.

Thus, given the lack of significant differences between long bone length measurement definitions, functional lengths only were further analyzed, since their mechanical importance is higher. Further variables, such as olecranon process length (**O**) and femur neck-head length (**N**), were analyzed separately.

Final database

Following the results of the preliminary data exploration, 16 variables were dropped, and thus the final database consisted of 43 variables (see Table II.2 for the definitive list of variable names and abbreviations).

References

Bailey RC, Byrnes J (1990) A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst Zool* **39**, 124–130.

Section C: Scaling

Journal Reference

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Scaling pattern of the carnivoran forelimb: Locomotor types and differential scaling



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Abstract

The scaling pattern of the forelimb in Carnivora was determined using a sample of 30 variables measured on the scapula, humerus, radius, ulna, and third metacarpal, of 429 specimens belonging to 137 species of Carnivora. Standardized major axis regressions on body mass were calculated for all variables, using both traditional regression methods and phylogenetically independent contrasts (PIC). In agreement with previous studies on the scaling of the appendicular skeleton, conformity to either the geometric similarity hypothesis or the elastic similarity hypothesis was low. The scaling pattern of several phyletic lines and locomotor types within Carnivora was also determined, and significant deviations from the scaling pattern of the order were found in some of these subsamples. Furthermore, significant evidence for differential scaling was found for several variables, both in the whole sample and in various phylogenetic and locomotor subsamples. Contrary to previous studies, significant differences were found between the allometric exponents obtained with traditional and PIC regression methods, emphasizing the need to take into account phylogenetic relatedness in scaling studies. In light of these and previous results, we conclude that similarity hypotheses are too simplistic to describe scaling patterns in the carnivoran appendicular skeleton, and thus we propose that scaling hypotheses should be built from similarities in the scaling patterns of phylogenetically narrow samples of species with similar locomotor requirements. The present work is a first step in the study of those samples.

Keywords: biomechanics; Carnivora; differential scaling; forelimb; habitat; locomotor type; phylogenetically independent contrasts; scaling

Introduction

Size is one of the most important factors affecting the shape and function of the elements of the musculoskeletal system of animals, as well as the parameters defining their locomotor dynamics (e.g. duty factor) (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003). Thus, several hypotheses have been proposed to predict how these musculoskeletal elements and locomotor parameters would be affected by variations in body size (i.e. scaling). The most widespread of these similarity hypotheses are the geometric similarity hypothesis (already supported by Hill (1950)) and the elastic similarity hypothesis (proposed by McMahon (1973)). The former states that all linear measurements of an organism are proportional to its body mass^{0.33}, while according to the latter, lengths scale to body mass^{0.25} and diameters to body mass^{0.375}.

In the case of skeletal measurements, early studies suggested that geometric similarity explained their scaling in mammals (e.g. Alexander et al., 1979), while elastic similarity was only found in Bovidae (McMahon, 1975*a*; Alexander, 1977). However, as the number of studies in this subject increased, empirical evidence showed that conformity to either hypotheses was low in mammals (Bou et al., 1987; Bertram & Biewener, 1990; Christiansen, 1999*a,b*; Carrano, 2001; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012). Furthermore, in some cases it has been found that the same skeletal measurement scaled geometrically in small species and elastically in large species (Economos, 1983; Bertram & Biewener, 1990; Silva, 1998; Christiansen, 1999*a,b*; Carrano, 2001). This differential scaling (also known as complex allometry) suggests that general allometric calculations would thus not be applicable to a large range of variations in body size.

Despite the large number of studies on the scaling of the mammalian appendicular skeleton, little to no consideration has been given to the scaling of skeletal measurements other than the length and diameters of the humerus, radius/ulna, femur and tibia. In fact, only the study of Lilje et al. (2003) on Ruminantia and that of Schmidt & Fischer (2009) on Mammalia have paid any attention to the scaling of the scapula, which has been shown to be the main propulsive element of the forelimb (Lilje & Fischer, 2001; Fischer et al., 2002). Furthermore, although several studies have dealt with the scaling of particular orders within Mammalia, their sample sizes are usually too low to perform interfamilial comparisons. Finally, no work so far has studied how locomotor specializations affect the scaling pattern of the appendicular skeleton in a comparative framework. It has been suggested that similarity hypotheses imply adaptive neutrality, or at least independence of

the locomotor type of the species that are compared (Bou et al., 1987). Therefore, samples including extreme locomotor patterns should deviate markedly from the predictions of similarity hypotheses.

The order Carnivora is one of the few groups of mammals that allows an allometric study of the appendicular in such a multifaceted approach, since: 1) carnivorans span a size range of four orders of magnitude (from less than 0.1 kg in the least weasel (*Mustela nivalis*) to well over two tonnes in elephant seals (*Mirounga sp.*)), which enables not only classic allometric studies but also to test for differential scaling; 2) they constitute a monophyletic group with several well-represented families, granting interfamilial scaling comparisons; and 3) they present one of the widest locomotor diversities among mammals, which allows to study the effect of locomotor specializations in the scaling of the limb bones (Van Valkenburgh, 1987; Bertram & Biewener, 1990; Wilson & Mittermeier, 2009; Nyakatura & Bininda-Emonds, 2012).

Thus, the first aim of this study was to determine the scaling pattern of the carnivoran appendicular skeleton, with emphasis on the scapula and several morphofunctional dimensions of the appendicular skeleton, and to assess whether differential scaling could be found in this pattern. Previous studies on the scaling of the appendicular skeleton in Carnivora have shown low conformity to either similarity hypothesis when long bone lengths are regressed against diameters (Bertram & Biewener, 1990). However, when regressed against body mass, bone lengths tend to scale geometrically and least circumference elastically (Christiansen, 1999a). More recently, two studies on the scaling of relative segment lengths in Mammalia have also presented separate results for the carnivoran species in their sample. However, while first Schmidt (2008) suggested that limb proportions are size-independent in Carnivora, significant size-related variation in those variables was later found by the same author (Schmidt & Fischer, 2009). Finally, regarding differential scaling, Bertram & Biewener (1990) found evidence for complex allometry in the length and diameters of the carnivoran humerus, radius, femur and tibia.

Once this scaling pattern for the whole order was determined, the second aim of this study was to analyze whether the main phyletic lines (families) within Carnivora deviated from it, and if so, then how. To date, few scaling studies have been carried out on the appendicular skeleton of any particular family within Carnivora. When regressing long bone lengths and diameters to femur length in Canidae, Wayne (1986) found significant deviations from isometric scaling, which suggested low conformity with either geometric or elastic similarity in the appendicular skeleton of canids. However, in a study with over

sixty dog breeds, Casinos et al. (1986) found that the scaling of humerus, radius and tibia conformed to geometric similarity but not that of the femur, which could explain the lack of conformity in Wayne's study. Heinrich & Biknevicius (1998) showed that, in Martinae (Mustelidae), long bone dimensions tended to scale elastically, but conformity was also low. Finally, recent studies suggest geometric scaling with no differential scaling in Felidae (Day & Jayne, 2007; Gálvez-López & Casinos, 2012).

The last objective of the present study was to test whether particular locomotor habits within Carnivora cause deviations from the general scaling pattern for the order. To our knowledge, only the study of Bou et al. (1987) has pursued a similar approach, but then in rodents and other small mammals. In the case of Carnivora, this lack of studies could be related to the general belief that their appendicular skeleton is highly conservative in terms of bone morphology and locomotor style (Flynn et al., 1988; Bertram & Biewener, 1990; Day & Jayne, 2007; but see Heinrich & Biknevicius, 1998; Chapter II).

Material and Methods

The sample consisted of 429 specimens from 137 species of Carnivora (Table III.1), representing about 48% of extant species (Wozencraft, 2005). For each specimen, measurements were taken on the scapula, humerus, radius, ulna, and third metacarpal. The specimens and variables have already been described in Chapter II, as were the locomotor type and preferred habitat categories used to build the subsamples (Table III.2). As in the previous study (Chapter II), locomotor type was used to represent locomotor specialization, and preferred habitat as an indicator of the ability to perform different modes of locomotion (running, swimming, climbing, digging) and thus maximize resource exploitation by being able to navigate all substrates available in their preferred habitat. As described in Appendix 1, taxonomy follows Wilson & Mittermeier (2009), except for a few species for which the synonyms in Wozencraft (2005) were preferred.

The 30 studied variables included 19 linear measurements, one projected distance (**T**), 8 ratios, and 2 angles (**θ**, **α**), and are summarized in Table III.3. The linear measurements could be subdivided into bone lengths (represented as L_x , where x indicates each particular bone, e.g. L_s for scapula length), bone diameters (d_{sx} , d_{dx}), and other measurements (e.g. **P**, **O**), while the ratios calculated were the indicator of fossorial ability (**IFA**), several bone robusticities ($XR = d_{sx} / L_x$), and relative segment lengths ($\%_{prox}$, $\%_{mid}$, $\%_{dist}$). As stated in the introduction, the scapula has been shown to be the main propulsive element of the

Table III.1. Measured species. See legend on next page.

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Canidae									
<i>Alopex lagopus</i>	3	terr	op	1	<i>Lycalopex culpaeus</i>	3	terr	va	1
<i>Canis adustus</i>	4	terr	mo	1	<i>Lycalopex gymnocercus</i>	4	terr	op	1
<i>Canis aureus</i>	6	terr	va	1	<i>Lycaon pictus</i>	3	terr	mo	1
<i>Canis latrans</i>	3	terr	va	1	<i>Nyctereutes procyonoides</i>	3	terr	fo	1
<i>Canis lupus</i>	5	terr	va	2, 3	<i>Speothos venaticus</i>	6	terr	fo	1
<i>Canis mesomelas</i>	7	terr	op	1	<i>Vulpes chama</i>	1	terr	op	1
<i>Cerdocyon thous</i>	2	terr	mo	1	<i>Vulpes vulpes</i>	12	terr	va	5
<i>Chrysocyon brachyurus</i>	6	terr	op	4	<i>Vulpes zerda</i>	2	terr	op	1
<i>Cuon alpinus</i>	3	terr	fo	1					
Mustelidae									
<i>Aonyx cinereus</i>	2	saq	fw	1	<i>Martes foina</i>	23	scan	mo	8
<i>Arctonyx collaris</i>	1	sfos	fo	1	<i>Martes martes</i>	8	sarb	fo	8
<i>Eira barbara</i>	2	sarb	fo	1	<i>Martes zibellina</i>	1	scan	fo	1
<i>Enhydra lutris</i>	1	aq	ma	1	<i>Meles meles</i>	5	sfos	mo	9
<i>Galictis cuja</i>	2	terr	va	1	<i>Mellivora capensis</i>	2	sfos	va	1
<i>Galictis vittata</i>	2	terr	mo	1	<i>Melogale moschata</i>	1	terr	mo	1
<i>Gulo gulo</i>	2	scan	mo	1	<i>Melogale orientalis</i>	1	terr	mo	1
<i>Ictonyx lybicus</i>	2	terr	op	1	<i>Mustela erminea</i>	8	terr	mo	8
<i>Ictonyx striatus</i>	1	terr	va	1	<i>Mustela eversmannii</i>	1	terr	op	1
<i>Lontra felina</i>	3	saq	ma	1	<i>Mustela lutreola</i>	1	saq	fw	1
<i>Lontra longicaudis</i>	2	saq	fw	1	<i>Mustela nivalis</i>	5	terr	va	8
<i>Lontra provocax</i>	1	saq	fw	6	<i>Mustela nudipes</i>	2	terr	fo	1
<i>Lutra lutra</i>	5	saq	fw	7	<i>Mustela putorius</i>	6	terr	mo	1
<i>Lutrogale perspicillata</i>	1	saq	fw	1	<i>Mustela vison</i>	2	saq	fw	1
<i>Lyncodon patagonicus</i>	2	terr	op	1	<i>Pteronura brasiliensis</i>	2	saq	fw	1
<i>Martes americana</i>	1	sarb	fo	1	<i>Vormela peregusna</i>	3	sfos	va	1
Mephitidae									
<i>Conepatus chinga</i>	2	sfos	op	1	<i>Spilogale gracilis</i>	2	terr	mo	1
<i>Conepatus humboldti</i>	1	sfos	va	1					
Otariidae									
<i>Arctocephalus australis</i>	1	aq	ma	10	<i>Otaria flavescens</i>	2	aq	ma	11
<i>Arctocephalus gazella</i>	1	aq	ma	10	<i>Zalophus californianus</i>	2	aq	ma	11
Phocidae									
<i>Hydrurga leptonyx</i>	1	aq	ma	11	<i>Phoca vitulina</i>	2	aq	ma	12
<i>Mirounga leonina</i>	1	aq	ma	12					
Ailuridae									
<i>Ailurus fulgens</i>	7	scan	fo	13					
Procyonidae									
<i>Bassaricyon gabbii</i>	1	arb	fo	1	<i>Potos flavus</i>	4	arb	fo	1
<i>Bassariscus astutus</i>	1	scan	mo	1	<i>Procyon cancrivorus</i>	3	scan	fw	1
<i>Nasua narica</i>	4	scan	fo	14	<i>Procyon lotor</i>	5	scan	fw	1
<i>Nasua nasua</i>	6	scan	mo	15					
Ursidae									
<i>Ailuropoda melanoleuca</i>	2	scan	fo	1	<i>Ursus americanus</i>	2	scan	mo	1
<i>Helarctos malayanus</i>	1	scan	fo	1	<i>Ursus arctos</i>	6	scan	va	1
<i>Melursus ursinus</i>	1	scan	mo	1	<i>Ursus maritimus</i>	4	terr	ma	1
<i>Tremarctos ornatus</i>	2	scan	mo	1					

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Viverridae									
<i>Arctictis binturong</i>	4	arb	fo	1	<i>Genetta tigrina</i>	1	sarb	mo	1
<i>Arctogalidia trivirgata</i>	2	arb	fo	1	<i>Hemigalus derbyanus</i>	4	sarb	fo	1
<i>Civettictis civetta</i>	4	terr	mo	20	<i>Paradoxurus hermaphroditus</i>	2	arb	fo	1
<i>Cynogale benettii</i>	1	saq	fw	1	<i>Poiana richardsoni</i>	1	sarb	fo	1
<i>Genetta felina</i>	5	scan	mo	1	<i>Viverra tangalunga</i>	4	terr	fo	1
<i>Genetta genetta</i>	7	scan	mo	1	<i>Viverra zibetha</i>	2	terr	fo	1
<i>Genetta maculata</i>	3	sarb	mo	1	<i>Viverricula indica</i>	4	scan	mo	1
Herpestidae									
<i>Atilax paludinosus</i>	2	saq	fw	1	<i>Herpestes brachyurus</i>	1	terr	fo	1
<i>Crossarchus obscurus</i>	2	terr	fo	8	<i>Herpestes edwardsii</i>	2	terr	mo	1
<i>Cynictis penicillata</i>	4	terr	op	1	<i>Herpestes ichneumon</i>	4	terr	op	1
<i>Galerella pulverulenta</i>	4	terr	fo	1	<i>Herpestes javanicus</i>	1	terr	mo	1
<i>Galerella sanguinea</i>	1	terr	mo	1	<i>Ichneumia albicauda</i>	2	terr	mo	1
<i>Helogale parvula</i>	2	terr	mo	1	<i>Suricata suricatta</i>	4	sfos	op	1
Eupleridae									
<i>Cryptoprocta ferox</i>	2	sarb	fo	1	<i>Mungotictis decemlineata</i>	1	scan	fo	1
<i>Fossa fossa</i>	2	terr	fo	1	<i>Salanoia concolor</i>	2	scan	fo	1
<i>Galidia elegans</i>	4	scan	fo	1					
Hyaenidae									
<i>Crocuta crocuta</i>	2	terr	mo	8	<i>Parahyaena brunnea</i>	1	terr	va	1
<i>Hyaena hyaena</i>	3	terr	va	1	<i>Proteles cristatus</i>	2	terr	op	8
Felidae									
<i>Acinonyx jubatus</i>	3	scan	mo	1	<i>Neofelis nebulosa</i>	1	sarb	fo	17
<i>Caracal caracal</i>	5	scan	mo	1	<i>Otocolobus manul</i>	2	scan	op	1
<i>Felis chaus</i>	1	scan	va	1	<i>Panthera leo</i>	7	scan	op	1
<i>Felis nigripes</i>	2	scan	mo	16	<i>Panthera onca</i>	2	scan	fo	1
<i>Felis silvestris</i>	15	scan	mo	1	<i>Panthera pardus</i>	8	scan	va	12
<i>Leopardus colocolo</i>	2	scan	va	1	<i>Panthera tigris</i>	9	scan	mo	18
<i>Leopardus geoffroyi</i>	2	scan	mo	1	<i>Panthera uncia</i>	4	scan	op	19
<i>Leopardus pardalis</i>	2	scan	fo	1	<i>Pardofelis marmorata</i>	1	arb	fo	1
<i>Leopardus tigrinus</i>	2	scan	fo	1	<i>Prionailurus bengalensis</i>	1	scan	mo	1
<i>Leptailurus serval</i>	6	scan	mo	12	<i>Prionailurus planiceps</i>	1	scan	fw	1
<i>Lynx lynx</i>	3	scan	mo	1	<i>Profelis aurata</i>	1	scan	fo	1
<i>Lynx pardinus</i>	4	scan	mo	12	<i>Puma concolor</i>	5	scan	va	1
<i>Lynx rufus</i>	1	scan	va	1	<i>Puma yaguaroundi</i>	3	scan	mo	1
Prionodontidae					Nandiniidae				
<i>Prionodon linsang</i>	1	arb	fo	1	<i>Nandinia binotata</i>	5	sarb	fo	1

Table III.1. Measured species. For each species, the table shows the number of measured specimens, the assigned category for both locomotor type and preferred habitat, and the references from which the mean body mass value for that species was taken (M_b). Abbreviations: aq, aquatic; arb, arboreal; fo, forest; fw, freshwater; loctyp, locomotor type; ma, marine; mo, mosaic; n, measured specimens; op, open; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial; va, variable. See Table II.3 for a description of locomotor type and preferred habitat categories. References: 1. Wilson & Mittermeier, 2009; 2. Blanco et al., 2002; 3. Mech, 2006; 4. Dietz, 1984; 5. Cavallini, 1995; 6. Reyes-Küppers, 2007; 7. Yom-Tov et al., 2006; 8. Grzimek, 1988; 9. Virgós et al., 2011; 10. Perrin et al., 2002; 11. MacDonald, 2001; 12. Silva & Downing, 1995; 13. Roberts & Gittleman, 1984; 14. Gompper, 1995; 15. Gompper & Decker, 1998; 16. Sliwa, 2004; 17. Sunquist & Sunquist, 2002; 18. Mazák, 1981; 19. IUCN Cat Specialist Group, 2011; 20. Ray, 1995.

Table III.2. Description of locomotor type and preferred habitat categories. Locomotor type categories were adapted from previous works on the relationship between locomotor behavior and forelimb morphology (Eisenberg, 1981; Van Valkenburgh, 1985, 1987).

Locomotor type	Description
arboreal	species that spend most of their life in trees (over 75%), rarely descending to the ground
semiarboreal	species that spend a large amount of their time in the trees (between 50% and 75%), both foraging and resting, but also on ground surface
scansorial	species that, although mostly terrestrial (over half their time is spent on the ground), can climb well and will readily do so to chase arboreal prey or escape, and might nest in trees for protection against terrestrial predators
terrestrial	species that rarely or never climb or swim, and that might dig to modify a burrow but not regularly for food
semifossorial	species that dig regularly for both food and shelter, but that still show considerable ability to move around on the surface
semiaquatic	species that forage regularly underwater and usually plunge into the water to escape, but must spend time ashore to groom,...
aquatic	species that carry out most of their life cycle in water, although some part of this cycle can be confined to land (parturition, mating, rearing the young)
Preferred habitat	Description
open	areas with low to nonexistent tree cover (e.g. grasslands, steppes, tundra,...). Carnivorans inhabiting open habitats could probably be good diggers, maybe also capable swimmers, but should lack climbing skills.
mosaic	this category was created for species that either live in forested areas with scarce tree cover (e.g. savannah), or require the presence of both forested and open areas within their home range, thus, they are expected to be good climbers, while also could be capable diggers or swimmers.
forest	areas with a high density of trees (e.g. rain forest, taiga, deciduous forest,...). Carnivorans inhabiting forested areas should probably be adept climbers, even though not completely arboreal, to be able to chase prey that flee to the canopy. They can also be capable swimmers and diggers.
freshwater	this category was created for species that dwell in or near freshwater systems (e.g. rivers, lakes, swamps,...). Carnivorans inhabiting freshwater habitats are expected to be capable swimmers, while also can present some ability to climb or dig.
marine	saltwater systems and their coastal regions. Marine carnivorans are expected to be very good swimmers, rarely dig, and possess an almost nonexistent ability to climb.
variable	this category includes all species that appear indistinctly in two or more of the other categories and thus probably contains species with highly variable locomotor skills.

forelimb (Fischer et al., 2002; Lilje & Fischer, 2001), and is thus considered here the most proximal segment of the forelimb.

Regression methods were used to relate each variable to body mass (M_b). All regressions were calculated with the standardised major axis method (SMA), since regression slopes were the primary interest of this study, and ordinary least squares regression methods (OLS) tend to underestimate the slope of the line-of-best-fit because its calculation involves fitting the predicted y-values as closely as possible to the observed y-values (Warton et al., 2006). The power equation ($y = a \cdot x^b$; Eq. 1) was assumed for all variables but T and θ , for which the linear model of regression was used ($y = a + b \cdot x$; Eq. 2), and 95% confidence intervals were calculated for both the coefficient (a) and the allometric exponent (b_{rad}). All regressions were calculated using PAST (Hammer et al., 2001). In order to compare the present results with those previously published using OLS regressions,

SMA slopes were calculated for those studies prior to the comparison by dividing their OLS slopes by the corresponding correlation coefficient (Sokal & Rohlf, 1995).

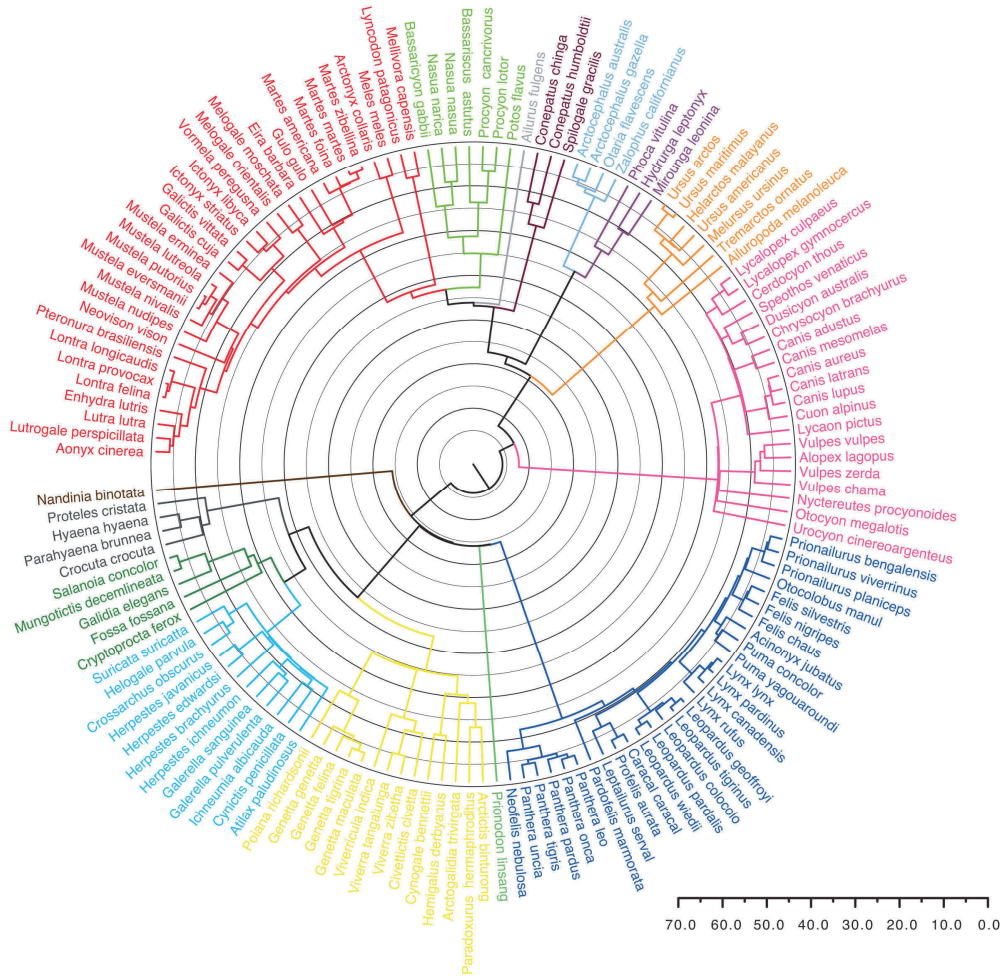
Furthermore, all the SMA regression slopes were also calculated using phylogenetically independent contrasts (PIC; Felsenstein, 1985). This methodology takes into account the phylogenetic signal inherent to interspecific data and thus accounts for the potential correlation of the error terms that could arise due to the lack of independence among species, since they can be arranged in a hierarchical sequence (i.e. a phylogenetic tree; Felsenstein, 1985; Grafen, 1989; Harvey & Pagel, 1991; Christiansen, 2002*a*, *b*). PIC regression slopes (b_{PIC}) were calculated using the PDAP: PDTREE module of Mesquite (Maddison & Maddison, 2010; Midford et al., 2010). The structure of the phylogenetic tree used in the present study is

discussed and detailed in Appendix 1 and is presented in Figure III.1. When necessary, branch lengths were transformed in order to obtain a low and non-significant correlation between the standardized value of the PIC contrasts and their corresponding standard deviation. This process has proven to be a good solution against possible violations of the assumptions implied by PIC methodology (Felsenstein, 1985; Grafen, 1989; Díaz-Urriarte & Garland, 1996, 1998).

Abbr.	Name	Appendix 2
M_b	Body mass	
L_s	Scapular length	III.A1
S	Maximum width of supraspinous fossa	III.A2
I	Maximum width of infraspinous fossa	III.A3
A	Maximum scapular width	III.A4
H_s	Scapular spine height	III.A5
L_h	Humerus functional length	III.A6
d_{sh}	Humerus sagittal diameter	III.A7
d_{th}	Humerus transverse diameter	III.A8
T	Projected height of greater tubercle	III.A9
HR	Humerus robusticity	III.A10
L_r	Radius functional length	III.A11
d_{sr}	Radius sagittal diameter	III.A12
d_{tr}	Radius transverse diameter	III.A13
P	Styloid process length	III.A14
RR	Radius robusticity	III.A15
L_u	Ulna functional length	III.A16
d_{su}	Ulna sagittal diameter	III.A17
d_{tu}	Ulna transverse diameter	III.A18
O	Olecranon length	III.A19
α	Olecranon angle	III.A20
θ	Olecranon abduction angle	III.A21
UR	Ulna robusticity	III.A22
IFA	Indicator of Fossorial Ability	III.A23
L_m	Third metacarpal functional length	III.A24
d_{sm}	Third metacarpal sagittal diameter	III.A25
d_{tm}	Third metacarpal transverse diameter	III.A26
MR	Third metacarpal robusticity	III.A27
%_{prox}	Relative length of the proximal segment of the forelimb	III.A28
%_{mid}	Relative length of the middle segment of the forelimb	III.A29
%_{dist}	Relative length of the distal segment of the forelimb	III.A30

Table III.3. Variable names and abbreviations. For each variable, it is also indicated in which table of Appendix 2 its regression results are shown.

Figure III.1. Phylogenetic relationships among the species of Carnivora used in this study. The time-scale represents divergence times in millions of years. The phylogeny shown was modified after Nyakatura & Bininda-Emonds (2012), as described in Appendix 1.



For each variable and methodology (traditional and PIC), separate regressions were calculated for the whole sample, for a subsample excluding Pinnipedia (i.e. a fissiped subsample, since pinnipeds showed atypical values for their body mass in most of the scatter plots), and also for several subsamples by family, locomotor type, and preferred habitat. Regressions were not calculated for any subsample with a sample size lower than 5, which was the case for Hyaenidae, Mephitidae, Phocidae, Otariidae, the monotypic families (Ailuridae, Nandiniidae, Prionodontidae), and Eupleridae when using PIC regression.

Allometric exponents were considered to deviate significantly from the predictions of either similarity hypothesis when their 95%CI did not include the corresponding theoretical value. As stated in the introduction, according to the geometric similarity hypothesis, all linear dimensions should be proportional to $M_b^{0.33}$. Thus, all ratios, including

relative lengths and bone robusticities, should present an allometric exponent not different from 0. On the other hand, the elastic similarity hypothesis proposes that lengths are proportional to $M_b^{0.25}$ and diameters to $M_b^{0.375}$, which derives into bone robusticities scaling with a theoretical exponent of 0.125 while ratios other than bone robusticities should present an allometric exponent not different from 0. Finally, angles, when measured in radians, can be considered lengths, and thus they should scale to $M_b^{0.33}$ or $M_b^{0.25}$, according to the geometric or the elastic similarity hypotheses, respectively.

For each variable, allometric exponents were then compared between the whole sample and the fissiped subsample, and between the different family, locomotor type, and preferred habitat subsamples. Furthermore, the PIC slopes (b_{PIC}) were compared to those obtained by traditional regression analysis (b_{trad}) with an F-test ($p < 0.05$) to assess whether the phylogenetic signal had any effect on the results.

Finally, also for each variable and each subsample, the presence of differential scaling was also evaluated using the model proposed by Jolicoeur (1989):

$$\ln y = \ln A - C \cdot (\ln x_{max} - \ln x)^D, \quad (\text{Eq. 3})$$

where A is a constant (corresponding to a in Eq. 1), C is the coefficient of allometry, x_{max} is the maximum observed value of the independent variable (i.e., body mass, M_b), and D is the exponent of complex allometry, a time-scale factor. In our case, $D > 1$ indicated faster relative growth in small carnivorans, and $D < 1$ that relative growth increased with size. The complex allometry hypothesis was thus accepted when D was significantly different from 1 ($p < 0.05$). Equation 3 was fitted with SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), and 95% confidence intervals were calculated for all parameters.

Results

Tables III.A1 through III.A30 in Appendix 2 show the regression results for each variable. As observed in previous studies comparing traditional and PIC regressions (Christiansen, 2002*a,b*; Gálvez-López & Casinos, 2012), the correlation coefficients (R) from the PIC analyses were lower than those from traditional regressions in most cases, which sometimes resulted in regressions no longer being significant (e.g. Table III.A30). Some authors have attributed this phenomenon to a higher risk of type I errors (i.e., indicating a significant correlation between two variables when there was none) when the effect of phylogeny is neglected in correlation analyses (Grafen, 1989; Christiansen, 2002*a*). In some cases, however, R actually increased after taking into account the effect of phylogeny,

which could result in regressions becoming significant (e.g. Table III.A28).

Figures III.2 through III.4 illustrate the allometric exponents' comparison between Families (Fig. III.2), locomotor types (Fig. III.3), and preferred habitats (Fig. III.4). Branch lengths ought to be transformed in most cases before performing the PIC regressions (Table III.S1).

Whole sample vs. Fissiped subsample

No significant relation with body mass was found for the olecranon abduction angle (θ), or the robusticity of the ulna (**UR**) or the third metacarpal (**MR**). Neither was significant the regression of radial robusticity (**RR**) in the whole sample (b_{trad}), nor those of **IFA** (b_{trad}), **T** (b_{PIC}), $\%_{prox}(b_{trad})$, and $\%_{dist}$ (both), after removing Pinnipedia (i.e. in the fissiped subsample).

Overall, removal of Pinnipedia from the sample caused a generalized increase of the allometric exponents when using traditional regression methods, although this increase was only significant for **L_h**, **L_r**, **L_u**, and $\%_{mid}$. The exception to this general trend were **S**, **A**, **d_{th}**, **HR**, and **d_{tr}**, for which a reduction in the allometric exponent was observed (although it was only significant for **S**; Table III.A2). These differences were not recovered by the PIC regressions, which produced fairly similar allometric exponents for the whole sample and the fissiped subsample. In fact, only for **d_{tu}** was the allometric exponent of the fissiped subsample significantly different from that obtained for the whole sample.

Contrary to previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012), significant differences between the allometric exponents obtained with each method were observed in the present study. In the case of **S**, **I**, **A**, and **d_{tr}** for both samples, and **L_s**, **L_h**, **d_{th}**, **L_r**, and **L_u** for the fissiped subsample, the allometric exponents obtained using traditional regression methods were significantly higher than PIC slopes (Tables III.A1–III.A4, III.A6, III.A8, III.A11, III.A13, III.A16). On the other hand, in **HR** and α for both samples, **d_{tm}** for the whole sample, and **RR** and **d_{tu}** for the fissiped subsample, the PIC slopes were significantly higher than those obtained with traditional regression methods (Tables III.A10, III.A15, III.A18, III.A21, III.A26).

Regarding conformity with the similarity hypotheses, Table III.4 presents the percentage of linear measurements that conform to each similarity hypothesis in both the whole sample and the fissiped subsample, and also using either traditional regression methods or PIC. As indicated by the low percentages, the scaling pattern of the forelimb in Carnivora conformed poorly to either similarity hypothesis, no matter whether Pinnipedia

		traditional	PIC		traditional	PIC
whole sample	G	7/19 (36.8%)	9/19 (47.4%)	scansorial	G	9/19 (47.4%)
	E	4/19 (21.1%)	5/19 (26.3%)		E	5/19 (26.3%)
fissipeds	G	2/19 (10.5%)	9/19 (47.4%)	terrestrial	G	5/19 (26.3%)
	E	4/19 (21.1%)	5/19 (26.3%)		E	6/19 (31.6%)
Canidae	G	11/19 (57.9%)	10/19 (52.6%)	semifossorial	G	18/18 (100%)
	E	7/19 (36.8%)	7/19 (36.8%)		E	17/18 (94.4%)
Mustelidae	G	14/19 (73.7%)	17/19 (89.5%)	semiaquatic	G	18/19 (94.7%)
	E	6/19 (31.6%)	8/19 (42.1%)		E	14/19 (73.7%)
Procyonidae	G	18/18 (100%)	7/7 (100%)	aquatic	G	12/17 (70.6%)
	E	17/18 (94.4%)	7/7 (100%)		E	11/17 (64.7%)
Ursidae	G	8/18 (44.4%)	6/8 (75.0%)	forest	G	8/19 (42.1%)
	E	14/18 (77.8%)	8/8 (100%)		E	7/19 (36.8%)
Felidae	G	9/19 (47.4%)	14/19 (73.7%)	mosaic	G	5/19 (26.3%)
	E	9/19 (47.4%)	7/19 (36.8%)		E	5/19 (26.3%)
Herpestidae	G	18/19 (94.7%)	18/19 (94.7%)	open	G	13/19 (68.4%)
	E	9/19 (47.4%)	11/19 (57.9%)		E	8/19 (42.1%)
Eupleridae	G	18/19 (94.7%)	–	freshwater	G	18/19 (94.7%)
	E	16/19 (84.2%)	–		E	14/19 (73.7%)
Viverridae	G	16/19 (84.2%)	17/17 (100%)	marine	G	17/18 (94.4%)
	E	15/19 (78.9%)	14/17 (82.4%)		E	11/18 (61.1%)
arboreal	G	18/18 (100%)	13/17 (76.5%)	variable	G	8/19 (42.1%)
	E	15/18 (83.3%)	6/17 (35.3%)		E	7/19 (36.8%)
semiarboreal	G	13/19 (68.4%)	16/19 (84.2%)			
	E	14/19 (73.7%)	17/19 (89.5%)			

Table III.4. Conformity to the similarity hypotheses summary. For each subsample, the number of linear measurements conforming to geometric (G) or elastic similarity (E) is given, as is the percentage of the significant regressions for that subsample that they represent. Values in grey indicate that the number of variables conforming to a particular similarity hypothesis is either less than half the number of variables, or over 20% lower than the number of variables conforming to the other similarity hypothesis.

was included in the sample. The decrease of most allometric exponents after taking into account phylogenetic relatedness resulted in about half the variables including 0.33 in their 95% CI_b, improving thus conformity to the geometric similarity (see Table III.4, PIC results). Again, results were the same with or without Pinnipedia.

Although **IFA** and the relative segment lengths were supposed to be independent of body mass according to both similarity hypotheses, this was not the case (Tables III.A23, III.A28–III.A30). In the case of **T** a significant but minimal allometric effect was detected (Tables III.A9). The olecranon angle (α) scaled with an exponent not significantly different from 0.33 in most cases (Tables III.A21). Finally, regarding bone robusticities, regressions were only significant for **HR** and **RR**. Traditional regression provided conflicting results between the whole sample and the fissiped subsample in each bone robusticity. On the other hand, using PIC regression both bone robusticities in both subsamples scaled with positive allometry to body mass, no matter which similarity hypotheses was used (Tables III.A10, III.A15).

Family subsamples

No significant differences were found between the allometric exponents obtained with each method (Tables III.A1–III.A30), which agrees with previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012).

Whereas the scaling pattern of some families conformed clearly better to the geometric similarity hypothesis (Mustelidae, Herpestidae) or the elastic similarity hypothesis (Ursidae), for others the 95% CI_b were wide enough to include the theoretic value for both hypotheses in most of the variables and no similarity hypothesis could be ruled out (Procyonidae, Eupleridae, Viverridae) (Table III.4). In Canidae, conformity to the geometric similarity hypothesis was low (under 60%), but clearly better than to elastic similarity (under 40%, just diameters conformed to elastic similarity). In the case of Felidae, conformity to either similarity hypotheses was low when considering traditional regression results, since many of the narrow 95% CI_b excluded the theoretical values proposed by both hypotheses. Considering the PIC regression results, however, the felid scaling pattern clearly conformed to the geometric similarity hypothesis (Table III.4).

As observed for the whole sample and the fissiped subsample, when significant, **IFA** scaled positively to body mass (except for Eupleridae; Table III.A23), and **T** presented a significant but minimal allometric exponent (except for Mustelidae; Table III.A9). In the case of relative segment lengths (Tables III.A28–III.A30), regressions were significant only in a few cases, but $\%_{prox}$ always increased with body mass ($b > 0$), while $\%_{mid}$ always decreased with increasing body mass ($b < 0$). Regarding the angles, regressions for θ were only significant for Herpestidae (b_{trad}) and Canidae (b_{PIC}), in both cases presenting allometric exponents very close to zero (Table III.A20). On the other hand, the 95% CI_b for α included both 0.25 and 0.33 in all significant traditional regressions. However, after correcting for phylogeny, only the regression for Felidae remained significant (and scaled geometrically; Table III.A21). Finally, regressions of bone robusticities on body mass were not significant in most cases, but when they were significant, their allometric exponents conformed better to the predictions of the hypothesis of elastic similarity, since they were in every case different from 0 (Tables III.A10, III.A15, III.A22, III.A27).

Figure III.2 shows comparisons of the allometric exponents between different families for each variable, which are summarized in Table III.5. No significant differences between families were found for **HR**, θ , α , **UR**, **IFA**, **MR**, $\%_{prox}$, $\%_{mid}$, or $\%_{dist}$. Overall, Canidae scaled faster than all other families in each case where significant differences between allometric

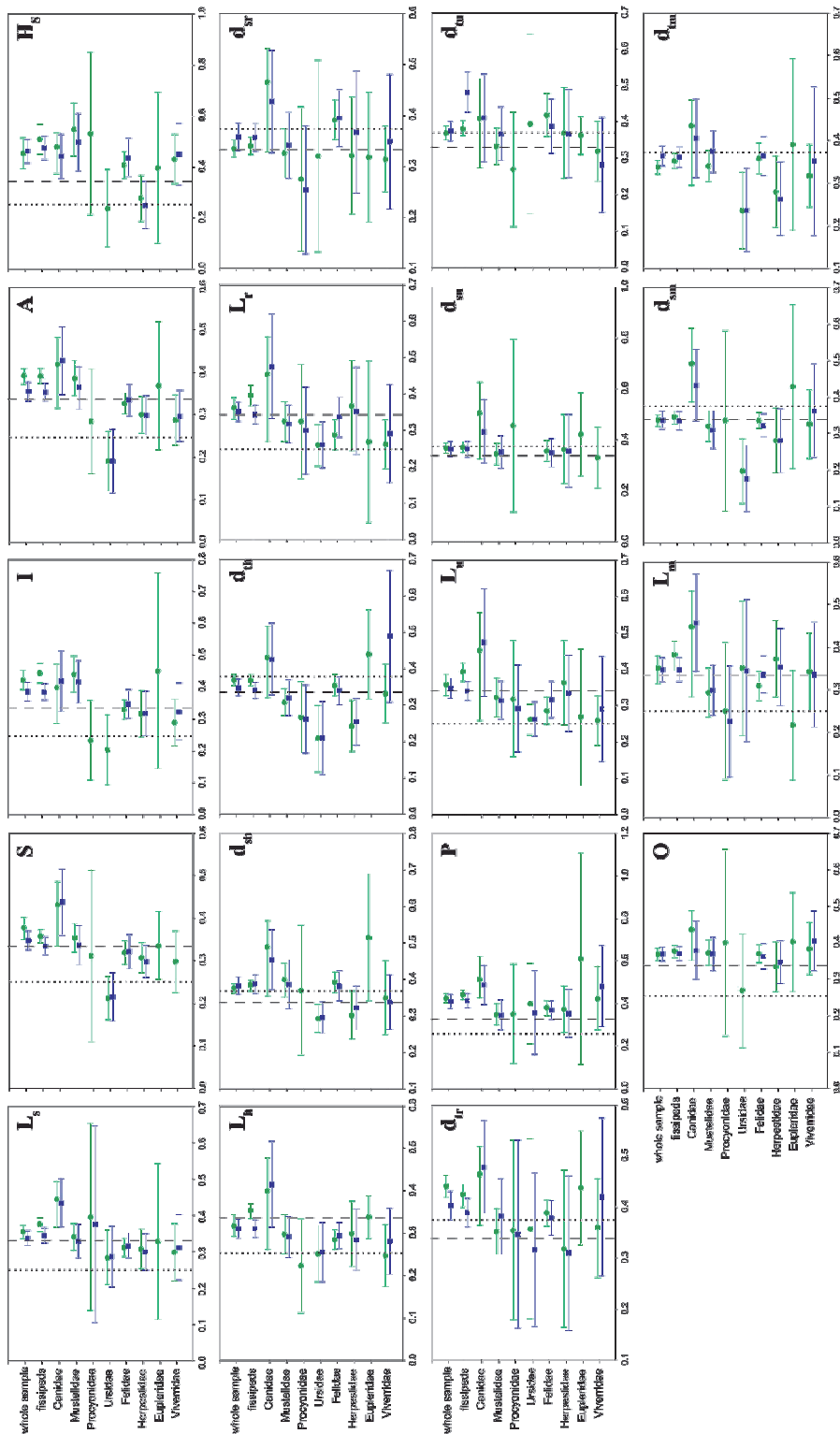


Figure III.2. Allometric exponents by family. For each subsample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissiped subsample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dotted line corresponds to that proposed by the elastic similarity hypothesis. Variable names are listed in Table III.3.

exponents were found (especially when considering PIC regression results), while the relationships among the rest of the families varied among the variables studied.

Locomotor type subsamples

Contrary to previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012), significant differences between the allometric exponents obtained with each method were observed for some locomotor type categories. Most of these significant differences occurred in terrestrial carnivorans, where PIC slopes were generally lower than those obtained using traditional regression methods (**L_s, I, A, L_h, L_r, d_{tr}, P, L_u, L_m**; Tables III.A1,

	< Can	< Mus	< Fel	< Her	< Eup	< Viv
Can <	-	-	-	trad: T	-	PIC: T
Mus <	both: L_s, d_{th}, d_{tr}, P, d_{sm} trad.: d_{sr} PIC: L_h, T, L_r, L_u, L_m	-	trad.: d_{th}, d_{sr}, d_{tu} PIC: T	-	trad.: d_{th}	PIC: T
Pro <	both: d_{th}, d_{sr}, L_m trad.: I, A, L_h, d_{tm} PIC: L_r, L_u	trad.: I	PIC: d_{sr}	-	trad.: L_h, d_{th}	PIC: d_{sh}
Urs <	both: L_s, S, A, d_{sh}, d_{th}, L_r, d_{sm}, d_{tm} trad.: I, H_s, d_{sur}, O PIC: L_h, d_{tr}, L_u	both: S, A, d_{sh}, d_{th}, L_u, d_{sm}, d_{tm} trad.: I, H_s, L_r	both: S, A, d_{sh}, d_{th}, d_{sm}, d_{tm} trad.: I, H_s PIC: L_r, L_u	both: S, A trad.: I PIC: d_{sm}	trad.: S, A, L_h, d_{sh}, d_{th}, d_{sm}	both: A, d_{th}, d_{sm} trad.: S, H_s
Fel <	both: L_s, S, T, P, d_{sm} PIC: A, L_h, d_{tr}, L_u, L_m	both: I trad.: S, A, H_s	-	trad: T	trad.: L_h	both: T
Her <	both: L_s, S, A, H_s, d_{sh}, d_{th}, P, d_{sm}, d_{tm} trad.: d_{sr}, O PIC: I, L_h, d_{tr}	both: I, A, H_s trad.: S, d_{sh} PIC: d_{tm}	both: H_s, d_{sh}, d_{th} PIC: d_{tm}	-	trad.: d_{sh}, d_{th}	both: H_s, d_{th}
Eup <	trad.: d_{sr}, L_m	-	-	trad.: L_m	-	-
Viv <	both: L_s, A, L_h, d_{sh}, L_r trad.: S, d_{sr}, d_{tr}, d_{sm} PIC: I, L_h, L_u	both: I, A trad.: H_s	trad.: d_{sr}, RR, d_{tu}	-	trad.: L_h	-

Table III.5. Differences in the allometric exponents between families. In each cell, row indicates the family with an allometric exponent (*b*) significantly lower than the column family for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; Can, Canidae; Eup, Eupleridae; Fel, Felidae; Her, Herpestidae; Mus, Mustelidae; PIC, regression using phylogenetically independent contrasts; Pro, Procyonidae; trad., traditional regression methods; Urs, Ursidae; Viv, Viverridae. Variable names are listed in Table III.3.

III.A3, III.A4, III.A6, III.A11, III.A13, III.A14, III.A16, III.A24). However, significantly lower PIC slopes were also found for scansorial carnivorans (d_{th} ; Table III.A8). Finally, PIC slopes were significantly higher for $\%_{mid}$ in terrestrial carnivorans (Table III.A29).

The scaling pattern of scansorial and semiaquatic carnivorans conformed better to the geometric similarity hypothesis (Table III.4). In the case of semiarboreal, semifossorial, and aquatic carnivorans, however, the 95% CI_b were wide enough to include the theoretic value for both hypotheses in most of the variables and thus no similarity hypothesis could be ruled out. In the case of arboreal carnivorans, conformity to both similarity hypotheses was high when considering traditional regression results. On the other hand, for terrestrial carnivorans, the scaling pattern obtained using traditional regression methods did not conform to any similarity hypothesis. Considering the PIC regression results, however, the scaling pattern of both locomotor types clearly conformed to the geometric similarity hypothesis (Table III.4).

Regarding ratios and angles, the results were similar to those obtained for the whole sample, the fissiped subsamples and the family subsamples. First, when significant, **IFA** scaled positively to body mass (except for arboreal and terrestrial carnivorans, b_{PIC} and b_{trad} respectively; Table III.A23), and **T** presented a significant but minimal allometric exponent (Table III.A9). And second, in the case of relative segment lengths (Tables III.A28–III.A30), $\%_{prox}$ always increased with body mass ($b > 0$), while $\%_{mid}$ generally decreased with increasing body mass ($b < 0$; except for arboreal and semiaquatic carnivorans, b_{PIC} both). On the other hand, $\%_{dist}$ either increased (terrestrial, aquatic) or decreased (semiarboreal, semiaquatic) with body mass. Regarding the angles, again regressions for θ were only significant in two cases, in both cases presenting allometric exponents very close to zero: semifossorial (b_{trad} , $b > 0$) and arboreal (b_{PIC} , $b < 0$) (Table III.A20). The scaling of the olecranon angle (α) conformed either to elastic similarity (scansorial, b_{trad}), to geometric similarity (scansorial, b_{PIC}), or to both (terrestrial, b_{trad}) (Table III.A21). Finally, although the allometric exponents for bone robusticities were positive and conforming to the elastic similarity hypothesis for most locomotor types (Tables III.A10, III.A22, III.A27), contrary to the results for the previous subsamples, the allometric exponents were negative in the radius, ulna, and third metacarpal, of terrestrial carnivorans (b_{trad} in all cases), indicating that bone robusticity decreased with increasing body mass values (Tables III.A15, III.A22, III.A27).

Figure III.3 shows comparisons of the allometric exponents between different locomotor types for each variable, which are summarized in Table III.6.

Preferred habitat subsamples

As observed for the locomotor type subsamples, significant differences between the allometric exponents obtained using traditional and PIC regression methods were observed for some preferred habitat categories, which opposes previous studies comparing both methodologies (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012). Significantly lower PIC slopes for all bone lengths and the width of the infrapinuous fossa (**I**) were found for carnivorans with no habitat preference (i.e., our variable habitat category; Tables III.A1, III.A3, III.A6, III.A11, III.A16, III.A24), while the same was true for a different set of variables in carnivorans inhabiting mosaic habitats (**L_s**, **S**, **I**, **A**, **L_h**, **d_{tr}**; Tables III.A1–III.A4, III.A6, III.A13) and for scapular spine height (**H_s**; Table III.A5) in those inhabiting open habitats (Tables III.A1–III.A30). Furthermore, significantly higher PIC slopes were found for forest-dwelling carnivorans (**HR**, **UR**; Tables III.A10, III.A22).

	< arb	< sarb	< scan	< terr	< sfos	< saq	< aq
arb <	–	PIC: IFA	PIC: L _s , d _{tu}	trad: I PIC: L _s , d _{tu} , T	PIC: L _s , d _{tu}	PIC: L _s , IFA	both: d _{tu} trad: d _{tr} PIC: IFA
sarb <	PIC: A	–	both: A, L _r , d _{sr} , L _u , d _{tu} trad: d _{su} PIC: I	both: A, L _r , d _{sr} , L _u trad: L _s , I, L _h , % _{dist}	–	both: d _{sr} PIC: A	both: d _{tu} , L _m trad: d _{sr} , d _{tr} , d _{sm} , % _{dist}
scan <	PIC: % _{mid}	–	–	trad: L _s , I, A, H _s , L _h , L _r , d _{tr} , L _u , L _m PIC: T	trad: T	PIC: % _{mid}	both: d _{sm} trad: IFA, L _m
terr <	PIC: % _{mid}	trad: IFA	trad: d _{su} , UR, IFA, MR PIC: P	–	–	trad: IFA, MR PIC: % _{mid}	both: d _{sm} trad: IFA
sfos <	–	trad: P	trad: P	trad: P	–	–	both: d _{sm} trad: d _{tr} , P, L _m
saq <	trad: N PIC: UR	trad: d _{th}	trad: d _{th} , d _{tr}	both: L _r , L _u trad: L _h , d _{th} , d _{tr} , L _m	–	–	both: L _m trad: d _{tr} , d _{tu} , d _{sm}
aq <	PIC: % _{mid}	–	PIC: % _{mid}	both: % _{mid} trad: L _h	–	–	–

Table III.6. Differences in the allometric exponents between locomotor types. In each cell, row indicates the locomotor type with an allometric exponent (*b*) significantly lower than the locomotor type of that column for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; PIC, regression using phylogenetically independent contrasts; trad., traditional regression methods. Other abbreviations as in Table III.1. Variable names are listed in Table III.3.

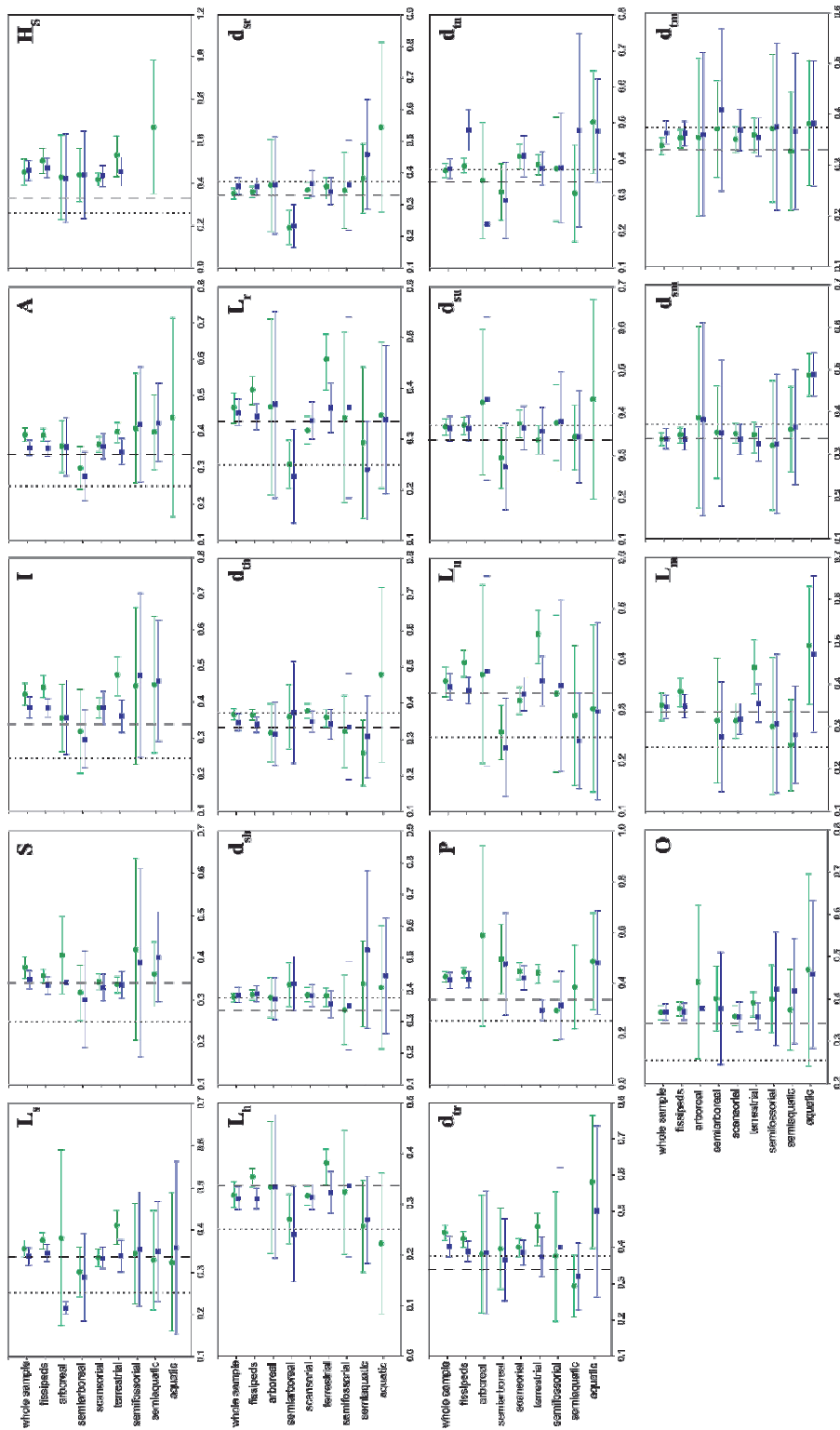


Figure III.3. Allometric exponents by locomotor type. For each subsample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissiped subsample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dotted line corresponds to that proposed by the elastic similarity hypothesis. See Table III.2 for a description of locomotor type categories. Variable names are listed in Table III.3.

Overall, the scaling pattern of most habitat subsamples conformed better to the geometric similarity hypotheses (Table III.4). However, in the forest and mosaic habitat subsamples, when considering the results from the traditional regressions, conformity to either similarity hypothesis was low. On the other hand, when using PIC regressions, the scaling pattern of both subsamples conformed clearly better to the geometric similarity hypothesis. For marine carnivorans, PIC regressions produced lower allometric exponents, which resulted in the 95% CI_b including both 0.25 and 0.33, so their scaling pattern conformed to both hypotheses when considering that methodology. Finally, the scaling pattern of the variable habitat category conformed poorly to either similarity hypothesis.

Again, as observed for the whole sample and most subsamples, when significant, **IFA** scaled positively to body mass, $\%_{prox}$ increased with body mass ($b > 0$), and $\%_{mid}$ decreased with increasing body mass ($b < 0$) (Tables III.A23, III.A28, III.A29). The results for the rest of ratios and angles mirrored to some extent the results of the regressions by locomotor type. $\%_{dist}$ either increased (mosaic, variable) or decreased (forest) with body mass (Table III.A30). Regressions for θ were again only significant in two cases, in both cases presenting allometric exponents very close to zero: marine habitats ($b > 0$) and open habitats ($b < 0$) (Table III.A20). The scaling of the olecranon angle (α) generally conformed to the geometric similarity hypothesis, although the PIC slopes for open and variable habitats conformed to elastic similarity (in the latter case excluding geometric scaling; Table III.A21). Using traditional regression methods, the scaling pattern of bone robusticities generally conformed to the elastic similarity hypothesis (Tables III.A10, III.A22, III.A27). However, after accounting for phylogenetic relatedness, bone robusticities tended to scale faster than predicted by elastic similarity (Tables III.A10, III.A22). As found for terrestrial carnivorans, **RR** and **MR** decreased with increasing body mass values in carnivorans inhabiting, respectively, mosaic and open habitats (also b_{rad} in both cases; Tables III.A15, III.A27). Finally, the habitat subsamples were the only set in which the 95% CI_b for **T** included zero in a significant regression, and then only using traditional regression methods (Table III.A9). Significant PIC regressions for **T** followed the previous pattern of significant but minimal allometric exponents (Table III.A9).

Figure III.4 shows comparisons of the allometric exponents between different preferred habitats for each variable, which are summarized in Table III.7. The habitat subsamples were the set in which the least number of differences between categories was found.

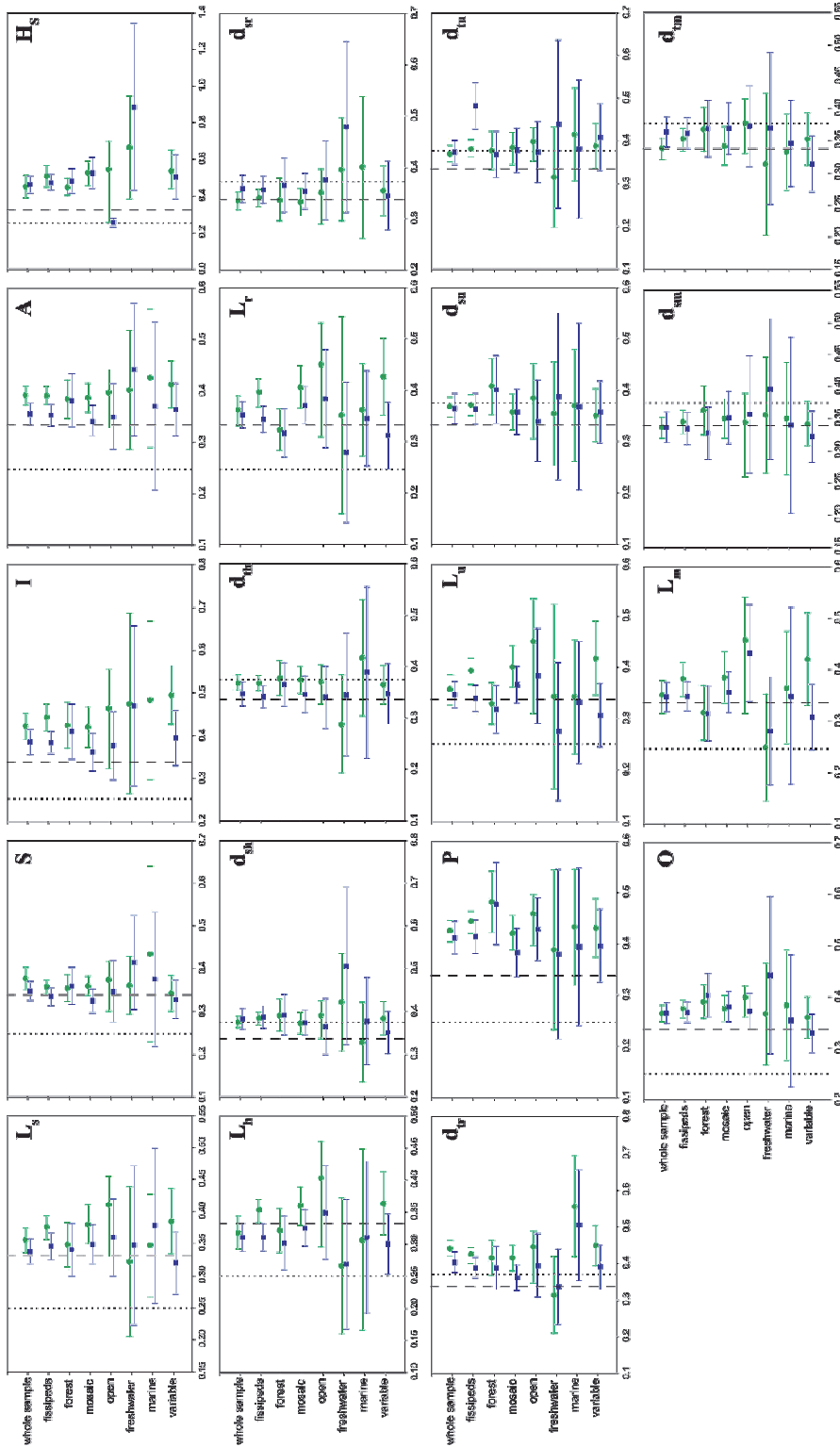


Figure III.4. Allometric exponents by preferred habitat. For each subsample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissipid subsample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dotted line corresponds to that proposed by the elastic similarity hypothesis. See Table III.2 for a description of preferred habitat categories. Variable names are listed in Table III.3.

Complex allometry

Results for the test for complex allometry are shown in Supplementary Tables III.S2 through III.S30. Since **T** presented negative values, Equation 3 could not be fit, which made impossible testing for complex allometry with this method.

In the whole sample, evidence for complex allometry was found in almost half of the variables. In the case of **L_s, I, H_s, L_h, L_r, L_u, O, L_m**, and **%_{dist}**, *D* was significantly higher than 1, indicating that these variables scale faster in small species; while in **HR, IFA, %_{prox}**, and **%_{mid}**, *D* was significantly lower than 1, suggesting that these variables scale faster in large species. However, in all cases where *D* < 1, the 95% CI_{*D*} included 0, which would result in $(\ln \mathbf{x}_{max} - \ln \mathbf{x})^D = 1$, and hence $\ln \mathbf{y} = \ln A - C$, which indicates independence from the dependent variable **x** (here body mass).

After removing Pinnipedia from the sample (i.e. in the fissiped subsample), evidence for complex allometry was not recovered in most cases. Only for **H_s, O, L_m**, and **%_{dist}**, was *D* still significantly different from 1 (*D* > 1 in all cases). Furthermore, significant evidence for complex allometry was also found for **d_{tu}**, which presented *D* < 1.

Overall, significant evidence for complex allometry was scarce in the family subsamples. In Procyonidae, Ursidae and Felidae no variable presented complex allometry, while in Canidae and Eupleridae only one variable presented complex allometry in each

	< forest	< mosaic	< open	< freshwater	< marine	< variable
forest <	-	both: L_r, L_u trad: H_s, L_h, L_m PIC: %_{dist}	PIC: L_m	-	trad: d_{tr}	trad: I, L_r, L_u, L_m
mosaic <	both: P	-	PIC: %_{mid}	-	trad: d_{tr}	trad: I
open <	trad: MR PIC: H_s, T	PIC: H_s, T	-	trad: MR PIC: H_s	PIC: θ	PIC: H_s
freshwater <	PIC: HR	trad: L_m	both: L_m trad: L_h, d_{tr}	-	both: d_{tr} trad: d_{th}, L_m	trad: d_{tr}, L_m
marine <	PIC: T	PIC: T	-	-	-	-
variable <	trad: d_{su} PIC: HR, P, O, α, d_{tm}	PIC: O, α, L_m	PIC: O, α, L_m	PIC: HR	-	-

Table III.7. Differences in the allometric exponents between preferred habitats. In each cell, row indicates the preferred habitat with an allometric exponent (*b*) significantly lower than the preferred habitat of that column for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; PIC, regression using phylogenetically independent contrasts; trad., traditional regression methods. Variable names are listed in Table III.3.

subsample (respectively, **P** and **d_{sh}**; $D > 1$ in both cases). On the other hand, some variables presented significant evidence for complex allometry in Mustelidae (**HR**, **d_{tr}**, **%_{prox}**, **%_{mid}**), Herpestidae (**L_s**, **H_s**, **P**), and Viverridae (**I**, **L_h**, **L_r**, **d_{sr}**, **d_{tr}**, **L_u**), with $D < 1$ in all cases. However, as observed for the whole sample when $D < 1$, in some cases the 95% CI_D also included 0, indicating independence from body mass. This was the case for **HR**, **%_{prox}** and **%_{mid}** in Mustelidae, **H_s** and **P** in Herpestidae, and **L_h** in Viverridae.

In the locomotor type subsamples, significant evidence for complex allometry was even less frequent than in the family subsamples. Thus, evidence for complex allometry was only found for **A**, **L_h**, **d_{tr}** and **L_u** in semiarborescens carnivorans, for **H_s**, **L_h**, **P**, **O**, **L_m** and **d_{sm}** in scansorial carnivorans, and for **d_{su}** in terrestrial carnivorans. In terrestrial and semiarborescens carnivorans, when complex allometry was detected, it indicated that large carnivorans scaled faster than small species (i.e. $D < 1$), while the opposite was true for scansorial carnivorans (i.e. $D > 1$). No 95% CI_D included 0.

Finally, although evidence for complex allometry was found in all preferred habitat subsamples but open, it was only for a few variables each subsample. Large carnivorans scaled significantly faster than small species ($D < 1$) in forest (**d_{tu}**), mosaic (**d_{tu}**), freshwater (**d_{tm}**), and marine (**d_{sh}**) habitats; while the opposite was true for **O** in species of the variable category and for **H_s** in species inhabiting mosaic habitats. However, the 95% CI_D for **d_{tm}** also included 0.

Discussion

Considerations on the scaling pattern of the carnivoran forelimb

The present study is currently the largest and most thorough work on skeletal allometry in Carnivora, regarding both the number of species sampled and the skeletal elements considered. In fact, even when considering all previous allometric studies on Mammalia, only that of Christiansen (1999a) on long-bone allometry and that of Silva (1998) on the scaling of body length include a larger amount of species.

Regarding the scaling of the appendicular skeleton in Carnivora, similarly to previous studies on the subject in this and other groups (Bou et al., 1987; Bertram & Biewener, 1990; Christiansen, 1999a,b; Carrano, 2001; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012), conformity to either the geometric similarity hypothesis or the elastic similarity hypothesis was low. It could be argued that geometric similarity provided a better explanation than elastic similarity (Table III.4), but that was only because no length

scaled elastically. Also in agreement with previous studies (Economos, 1983; Bertram & Biewener, 1990; Silva, 1998; Christiansen, 1999*a,b*; Carrano, 2001), significant evidence for complex allometry was found in several of the studied variables. Finally, contrary to previous studies comparing traditional regression methods and phylogenetically independent contrasts (PIC) (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012), significant differences between the allometric exponents of both methodologies were found, especially in the fissiped subsample. Thus, in order to avoid any possible artefacts caused by the phylogenetic relatedness of the species in our sample, only the PIC results will be further discussed.

One of the predicted consequences of increasing size is enduring higher peak stresses (especially during locomotion), which could lead to mechanical failure (Alexander, 2002). Thus, as mammals get larger, they must either develop more robust bones to resist these higher stresses, or change their limb posture to reduce the magnitude of these stresses (Biewener, 2003; Carrano, 2001). Based on previous results, it has been proposed that limb posture changes might be the preferred strategy to cope with the size-related increase of peak stresses, but that at body masses over 200kg more robust bones must be developed, since limbs cannot be further straightened (Christiansen, 1999*a*; Carrano, 2001). The change in bone scaling required to develop more robust bones in large mammals has commonly been considered the cause of differential scaling in bone dimensions (Biewener, 1990; Christiansen, 1999*b*). In Carnivora, only a handful of non-aquatic species attain such large body sizes, suggesting that peak stresses should be reduced in this group by limb straightening, not by changing limb bone scaling. In the present study, two arguments were found against this assumption. First, significant evidence for differential scaling was found in several variables, indicating that the scaling of the forelimb does change with size in Carnivora. However, since the amount of variables showing complex allometry severely decreased after removing Pinnipedia, most of these scaling changes are probably related to the locomotor specialization of that group (swimming) and not to reducing peak stresses. Second, limb bones seemed to scale elastically in Ursidae, which includes most of the largest non-aquatic carnivorans. Since the elastic scaling of limb bones in Bovidae (which includes most of the largest non-aquatic mammals) was one of the main arguments supporting that large mammals develop more robust bones to cope with increased peak stresses (Economos, 1983; Christiansen, 1999*a*), the present results for Ursidae would point to a similar conclusion. However, the elastic scaling of Ursidae could be an artefact caused by the combination of their overall lower allometric exponents than other families

(i.e. both in lengths and diameters) and their wide 95%CI_b (Figure III.2). Furthermore, although the regressions for bone robusticities are not significant in Ursidae, their allometric exponents are not higher than those of other carnivoran families. In fact, they were lower than in most other families, especially for the humerus (**HR**; Table III.A10). Thus, the results of the present study support that, in large non-aquatic carnivorans, mechanical failure is mainly avoided by limb posture changes instead of by modifying limb bone scaling. Further evidences for this conclusion are the lack of differential scaling in the “large” families (Canidae, Felidae, Ursidae; Tables III.S2–III.S30) and the significant increase with size of the olecranon angle (α ; Table III.A21), especially in the fissiped subsample. This angle determines the position in which the triceps muscle has the greatest leverage, being a flexed elbow when α is small (straight or cranially bent olecranon) or an extended limb when it is large (caudally bent olecranon) (Van Valkenburgh, 1987). Thus, an allometric increase of α suggests that large carnivorans have increasingly straighter forelimbs (but see Day & Jayne, 2007).

Several authors have suggested that proximal limb segments are more conservative in lengthening with increasing body mass than distal ones (McMahon, 1975*a*; Lilje et al., 2003; Schmidt & Fischer, 2009). According to this, when regressing bone length to body mass, proximal bones should produce higher correlation coefficients, and, when comparing allometric exponents, significant differences between subsamples should be scarce for proximal segments. While this might be the case for Artiodactyla (McMahon, 1975*a*; Lilje et al., 2003), the results of the present study suggest that, while it might also apply for Carnivora as a whole, the more conservative nature of proximal limb segments is not evident in several carnivoran subsamples. For instance, the highest correlation coefficients correspond to the radius and ulna in Procyonidae and Ursidae, and to the third metacarpal in aquatic carnivorans. Furthermore, when comparing the allometric exponents obtained for bone lengths, significant differences were found for all forelimb bones in all subsample sets (i.e. by family, by locomotor type, and by preferred habitat).

Previous studies had reported differences in the scaling of the various forelimb bones (Wayne, 1986; Bertram & Biewener, 1990; Christiansen, 1999*a*; Lilje et al., 2003). In those studies, the lengths of the middle segment (i.e. humerus) tended to scale slower than the rest of the forelimb segments. The scaling of the proximal element (i.e., scapula) was seldom described, but it presented intermediate values between the humerus and the distal elements in Canidae (Wayne, 1986) and the fastest scaling in Ruminantia (Lilje et al., 2003). In the present study the humerus presented the lowest allometric exponent in

almost all subsamples, but no significant differences were found among the other forelimb bones. Only in arboreal, semiarboreal and semifossorial carnivorans the humerus scaled faster than other segments consistently (scapula, radius/ulna and third metacarpal, respectively). Together with previous results, this suggests that the slow scaling of the humerus relative to the other forelimb segments could be a common trend in Mammalia, with groups with particular locomotor adaptations (such as climbing or digging) deviating from this pattern. Furthermore, the slow scaling of the humerus relative to other forelimb segments would explain the negative allometry found for its relative length ($\%_{\text{mia}}$) both here and in the study of Schmidt & Fischer (2009). Regarding bone diameters, few studies have obtained confidence intervals narrow enough to describe differences in the scaling of different bones: Cubo & Casinos (1998) reported a faster scaling of the transverse diameter of the radius (\mathbf{d}_{tr}) relative to the sagittal diameter of the radius and both humerus diameters in Mammalia. On the other hand, while comparing the same bones, Heinrich & Biknevičius (1998) and Llorens et al. (2001) found higher allometric exponents for the sagittal diameter of the humerus (\mathbf{d}_{sh}) than for other bone diameters in Martiniinae and Platyrrhina, respectively. The results of the present study in Carnivora showed that the sagittal diameter of the third metacarpal (\mathbf{d}_{sm}) scaled significantly slower than most other bone diameters, and the transverse diameters of both radius and ulna (\mathbf{d}_{tr} , \mathbf{d}_{tu}) and the sagittal diameter of the humerus (\mathbf{d}_{sh}) scaled significantly faster than most other bone diameters. In the case of \mathbf{d}_{sh} , our results suggest that the conflicting results found in previous studies could be related to whether the deltoid tuberosity was included in its measurement, since it was included within \mathbf{d}_{sh} in the present study, and only in Viverridae, whose species do not present a particularly developed deltoid tuberosity, scaled \mathbf{d}_{sh} significantly slower than \mathbf{d}_{th} (Tables III.A7, III.A8). Finally, regarding the fast scaling of \mathbf{d}_{tr} and \mathbf{d}_{tu} , it could be related to a greater development of the muscles originating in the shaft on the radius and ulna (pronators and supinators of the hand, some wrist flexors and extensors). These increased forearm muscles would provide a stronger grip to large climbing species (e.g. bears) and also to species relying in the forelimb for prey capture (e.g. felids), but would also cause larger mediolateral stresses on those bones, hence the need of increased transverse diameters. In agreement to this, significant evidence for differential scaling was found for \mathbf{d}_{tr} in fissipeds and in semiarboreal carnivorans, in both cases with larger species scaling faster than small species.

Aiello (1981) stated that the use of ratios is only correct when both variables comprising it scale isometrically between them. In agreement with this, due to differences

in scaling among bone lengths, the allometric exponents found for the relative length of the proximal and middle segment ($\%_{\text{prox}}$, $\%_{\text{mid}}$; Tables III.A28, III.A29) and the indicator of fossorial ability (**IFA**; Table III.A23) were significantly different from zero, the value predicted by both similarity hypotheses. Furthermore, the present results on the scaling of relative segment lengths of the forelimb in Carnivora mirrored those obtained previously for Schmidt & Fischer (2009) in both Carnivora and Artiodactyla: relative humerus length scales negatively to body mass, while the relative scapula length does it positively. Finally, it has been proposed that group-specific differences in limb kinematics are characteristic of large mammals, since small mammals are relatively similar in limb kinematics regardless of locomotor habit and phylogenetic position (Fischer et al., 2002; Schmidt & Fischer, 2009). Furthermore, small mammals present crouched limbs and large mammals extended limbs, each requiring different sets of limb-segment proportions for self-stability (Seyfarth et al., 2001). Thus, since Carnivora includes both small and large species, differential scaling would be expected for their relative segment lengths, as it has been found in the present study (Tables III.S28–III.S30).

Phylogenetic deviations to the scaling of the carnivoran forelimb

Overall, the scaling patterns found in the different carnivoran families for the forelimb were similar to the pattern found in the whole order. However, several families deviated significantly from it (Fig. III.2). In the case of Canidae, scapula and humerus length (L_s , L_h), as well as the maximum width of the supraspinous fossa (S), scaled faster than in the rest of Carnivora. Furthermore, when comparing the allometric exponents obtained for each variable between families, Canidae scaled faster than all other families in each case. This agrees with the expectations of Wayne (1986), who suggested that size selection is likely one of the most predominant forces in canid evolution because size differences help mitigate interspecific competition. On the other hand, several variables scaled significantly slower in Ursidae and in Herpertiae than in the whole sample (Fig. III.2). Finally, it should be noted that the wide confidence intervals (95%CI_b) obtained for some families could be obscuring further significant deviations from the ordinal scaling pattern (e.g. Procyonidae, Eupleridae, Viverridae).

The lack of significant differences between the allometric exponents calculated using traditional and PIC regression methods agrees with a previous study stating that most morphological variability of the appendicular skeleton in Carnivora occurs at the family level (Chapter II).

Regarding conformity to the similarity hypotheses, the present results agree with those of Bertram & Biewener (1990) in that 1) Ursidae tended to conform better to the elastic similarity hypothesis; 2) mustelids scaled geometrically; and 3) conformity to either similarity hypotheses was low in Canidae, but slightly better to geometric similarity. However, contrary to the results of Bertram & Biewener (1990) but in agreement with those of Day & Jayne (2007) and Gálvez-López & Casinos (2012), felids conformed well to the geometric similarity hypothesis. The wide 95%CI_b obtained for Procyonidae in both studies made both similarity hypotheses equally (un)likely.

Finally, an interesting pattern was found among the families of Caniformia: for most linear measurements, the allometric exponents consistently increased from Ursidae to Procyonidae, to Mustelidae, and then to Canidae (Fig. III.2). Neither body mass nor phylogenetic relatedness could explain this pattern, since Canidae and Ursidae represent both the largest caniforms, and the first phyletic lines to diverge from the caniform stem, and are placed in opposite extremes of this pattern. A possible explanation to this pattern could be an increasing degree of adaptation to overground locomotion, or a decrease in arboreal activity. Of all bears studied, only the polar bear (*Ursus maritimus*) is not an adept climber, since young brown bears (*Ursus arctos*) do climb (Gambaryan, 1974; Wilson & Mittermeier, 2009). Procyonids stand in a similar position, which could explain why they present lower allometric exponents than bears for some variables. Several mustelid lineages have diverged from the scansorial life-style (e.g. Lutrinae, Mustelinae), and thus Mustelidae presents intermediate values between ursids/procyonids and Canidae, which are fully adapted to a fully terrestrial life-style (understanding here the word “terrestrial” as defined in Table III.2, i.e. with no specific climbing, digging, or swimming capabilities). In agreement with this, the four studied families within Feliformia, all of which but Herpestidae included species with a varied degree of climbing skills, presented similar allometric exponents in most variables (Fig. III.2). In fact, only the terrestrial Herpestidae presented, in a few cases, allometric exponents significantly different from the rest of feliform families (Table III.5). Another possible explanation could be a different degree of size selection within each caniform family. Both the present study and that of Wayne (1986) suggest size selection as a major force in canid evolution. However, nothing is known on the importance of size selection in the rest of caniform families.

Locomotor habit and the scaling pattern of the carnivoran forelimb

Significant deviations from the ordinal scaling pattern were found for several

locomotor type subsamples (Fig. III.3), but not for the preferred habitat subsamples (Fig. III.4). Furthermore, more significant differences between allometric exponents were found among locomotor types than among preferred habitats (Tables III.6, III.7). Thus, locomotor type is a better criterion than preferred habitat to identify adaptive deviations from the general scaling pattern of the forelimb in Carnivora. Similar results were obtained in a univariate study comparing the linear dimensions used to calculate the allometric exponents compared in the present study (Chapter II). Since in both studies locomotor type was used to represent locomotor specialization, and preferred habitat as an indicator of the ability to perform different modes of locomotion (running, swimming, climbing, digging), these results suggest that carnivorans favor optimizing the performance of a specific mode of locomotion rather than maximizing resource exploitation by being able to navigate all substrates available in their preferred habitat. As suggested in the previous study, this optimizing strategy is probably related to the higher locomotor costs associated to performing conflicting modes of locomotion (e.g. overground locomotion vs. swimming: Williams, 1983*a,b*, 1989; Williams et al., 2002), and to the high commitment of most carnivoran species to specific prey capture strategies in order to increase their usually low catch success rates (Wilson & Mittermeier, 2009).

Lilje et al. (2003) suggested that the scaling of limb bone lengths is more heavily influenced by phylogenetic relatedness than by habitat preference, at least in Artiodactyla. The present results suggest that this might also be the case for Carnivora, since the comparison of allometric exponents for bone lengths obtained using traditional regression methods produced more significant differences than the comparison of PIC slopes for the same variables, both among locomotor types and among preferred habitats. In fact, this was true for all the studied variables, not just bone lengths.

Regarding the particular deviations associated to each locomotor type, in arboreal carnivorans scapular length (L_s) and ulna transverse diameter (d_{tu}) increased with body mass with significantly lower exponents than those obtained for Carnivora as a whole and the fissiped subsample (Fig. III.3). However, the narrow 95%CI_b and high R for these regressions were unexpected given the low sample size of the arboreal subsample, suggesting that these results should be regarded cautiously (Tables III.A1, III.A18). Thus, the deviations observed for semiarboreal carnivorans probably represent a more accurate description of the scaling pattern associated to species spending most of their time in the canopy. In this subsample, significantly lower allometric exponents than those obtained for Carnivora were obtained for the functional length of the radius and the ulna (L_r , L_u), the

sagittal diameter of the radius (d_{sr}), and most scapular widths (**A, I**) (Fig. III.3; Table III.6). Similar deviations were found for the other functional bone lengths (L_s , L_h , L_m) and the width of the supraspinous fossa (**S**), although they were not significant (Fig. III.3). Furthermore, in all these cases, the allometric exponents for semiarboreal carnivorans were lower than those for scansorial and terrestrial species (Fig. III.3), often significantly (Table III.6). Thus, with increasing size, semiarboreal carnivorans will present shorter limbs and narrower scapulas than similar-sized scansorial and terrestrial species. According to Cartmill (1985), the first would be a strategy to increase stability during arboreal locomotion for claw-climbing mammals, like carnivorans, since relatively shorter limbs enable to maintain their center of mass close to the support, and thus reduce lateral oscillations of the center of mass. Carnivorans less adapted to arboreal locomotions, such as scansorial species, should then resort to postural changes and other strategies in order to gain in stability when navigating arboreal supports, as demonstrated for the domestic cat by Gálvez-López et al. (2011). Continuing with adaptations to arboreality, in a study on forelimb morphology in North American carnivorans, Iwaniuk et al. (1999) found that the degree of arboreality was positively correlated with long-bone robusticities (calculated as L_x/d_{sx}). Thus, they stated that, with increasing arboreality, forelimb bones became wider, more robust, to better withstand the multidimensional loads resulting from arboreal locomotion. However, from the definition of their ratios, their results seemed to indicate just the opposite, that is, that arboreal carnivorans presented less robust forelimb bones (i.e. relatively longer or more slender bones). In the present study, the regressions of bone robusticities onto body mass tended to produce higher allometric exponents in the subsamples with the most arboreal species (e.g. **HR**: allometric exponents for semiarboreal carnivorans were higher than for scansorial and terrestrial carnivorans; Table III.A10). Since in the present study bone robusticity was the inverse of the definition of Iwaniuk et al. (1999) (i.e. d_{sx}/L_x), these higher allometric exponents did indeed suggest that forelimb bones become sturdier (i.e. relatively wider or shorter) with increasing arboreality in Carnivora. Finally, regarding the pattern of increasing allometric exponents with decreasing arboreality found in Caniformia, it was not recovered in most cases in the locomotor type or preferred habitat subsamples (Figs. III.3, III.4), which could be explained by feliform species making up around 70% of the arboreal, semiarboreal and scansorial subsamples.

Although all mammals run (i.e. present gaits, either symmetrical or asymmetrical, in which their limbs spend less than half a cycle on the ground; Alexander, 2002; Biewener,

2003), some of them have developed certain morphological adaptations to increase step length (and thus speed) and to minimize energy costs while running (e.g. Gambaryan, 1974; Hildebrand, 1985). These mammals better adapted to running are often referred to as “cursorial mammals” (Smith & Savage, 1956; Gambaryan, 1974; Hildebrand, 1985). However, as pointed out by Stein & Casinos (1997), the works of Jenkins and other authors (Jenkins, 1971; Jenkins & Camazine, 1977; Alexander & Jayes, 1983) introduced ambiguity into the concept of “cursorial” so it no longer meant “specialized runner”. Thus, the term “cursorial” will not be used in the present work, and instead “efficient runner” will be used to designate those mammals that have developed morphological adaptations to run efficiently. It has been described that presenting long limbs is an adaptation to effective running, since it allows for longer steps and thus higher speeds (Lull, 1904; Gambaryan, 1974; Hildebrand, 1985; Van Valkenburgh, 1987). However, limb elongation is mainly effected through the distal segments (Hildebrand, 1985; Van Valkenburgh, 1987), and thus, the radius, ulna and metacarpals of running species should scale faster than the humerus. In the present study, there was not a specific subsample grouping “efficient runners”, but three subsamples included a fair amount of those species: Canidae, terrestrial carnivorans, and those inhabiting open habitats. Thus, bone lengths were expected to scale faster in these subsamples than in other subsample. Additionally, L_r , L_u and L_m were expected to scale faster than L_h . Both assumptions were supported by the results of the present study (Figs. III.2–III.4; Tables III.5–III.7). Another adaptation to effective running was proposed by Smith & Savage (1956), who described larger infraspinous fossae than supraspinous fossae in mammals adapted to running. Thus, it was expected that I scaled faster than S in Canidae, terrestrial carnivorans, and those inhabiting open habitats. However, the present results suggest that a faster scaling of the infraspinous fossa is a common trend in Carnivora, not a particular adaptation to running efficiently. Oddly enough, Canidae was one of the subsamples deviating from this general trend. Thus, it might be concluded that previously described adaptations to effective running other than limb elongation are present in the scaling of most carnivoran subsamples (not just “effective runners”), which suggests that they are more related to the biomechanical consequences of increasing size than to effective running.

The effect of adaptations to digging and swimming to the scaling pattern of the carnivoran forelimb were hard to ascertain, since 95%CI_b were usually too wide in semifossorial, semiaquatic and aquatic carnivorans. In the case of semifossorial carnivorans, they presented high allometric exponents for scapular widths (S , I , A) and

olecranon length (**O**), but they were not significantly different from any other subsample due to high 95%CI_b (Fig. III.3; Table III.6). Regarding adaptations to swimming, both semiaquatic and aquatic carnivorans tended to present high allometric exponents for scapular widths (**S, I, A**), olecranon length (both absolute, **O**, and relative, **IFA**), and several bone diameters (**d_{sh}**, **d_{sr}**, **d_{tu}**) and bone robusticities (**HR, RR, UR**) (Fig. III.3; Table III.6). Furthermore, in semiaquatic carnivorans bone lengths scaled slower than in most carnivorans (significantly in the middle segment: **L_r**, **L_u**), while in aquatic carnivorans the third metacarpal scaled faster than in the rest of Carnivora, in both sagittal diameter and length (Fig. III.3; Table III.6). Most of these adaptations had already been suggested by previous anatomical and morphometrical analyses (Osburn, 1903; Smith & Savage, 1956; English, 1977; Chapter II), and were recovered here as characteristic deviations of the aquatic/semiaquatic scaling pattern: shorter and more robust limb bones, larger olecrana (both **O** and **IFA**), and wider scapulas (although not in semiaquatic carnivorans).

Differential scaling, phylogeny and locomotor habit

According to Bertram & Biewener (1990), differential scaling might not be evident within the individual carnivoran families due to their narrow body size ranges. Furthermore, they also stated that differences in scaling explained by differences in locomotor habit would probably be overridden by phylogenetic differences in scaling. Those concerns proved irrelevant in the present study, since not only did more significant cases of complex allometry were found in Viverridae (**M_b**, range: 0.54kg – 13.25kg) than in other families with wider body mass ranges (Canidae, Felidae, Mustelidae), but also in several locomotor type and preferred habitat categories were detected significant cases of complex allometry (again, no matter their body mass range).

Previous studies in our group have suggested that differential scaling could be a consequence of mixing species with different locomotor specializations (Castiella & Casinos, 1990; Gálvez-López & Casinos, 2012). The results of the present study provide arguments both in favour and against this hypothesis. On one hand, significant evidence for complex allometry was found in almost half the variables in the whole sample. Furthermore, several variables presented differential scaling in Mustelidae and Viverridae, both including species with several locomotor types, and the latter also presenting a narrow body mass range. On the other hand, after removing the large, swimming, pinniped species, significant evidence for complex allometry was rarely found. Furthermore, differential scaling was found in some locomotor type categories.

On the viability of similarity hypotheses and scaling studies

The present and previous results on the scaling of limb bone morphology have made clear that no similarity hypothesis alone can explain the scaling patterns existing in mammalian limb bones (Bou et al., 1987; Bertram & Biewener, 1990; Christiansen, 1999*a,b*; Carrano, 2001; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012). In our understanding, the main problem with any similarity hypothesis is their extremely simplistic approach: each similarity hypothesis chooses one of the many factors determining how limb bone morphology changes with increasing size and defines allometric exponents based on it (geometric similarity: isometric growth; elastic similarity: deformation under gravity; static stress: constant stresses while standing still; dynamic stress: constant stresses during locomotion; McMahon, 1973, 1975*b*; Alexander & Jayes, 1983; Alexander, 2002). Thus, since no such single determining factor exists, all similarity hypotheses are doomed to fail. However, their inability to produce an accurate theoretical allometric exponent is instead excused by stating that variability around that “universal” trend is clouding the results, and thus the observed allometric exponents deviate from the predicted ones.

A further problem is that large and small mammals have different locomotor requirements (Lilje & Fischer, 2001; Seyfarth et al., 2001; Fischer et al., 2002; Schmidt & Fischer, 2009). This results in differential scaling and its oversimplification by establishing a threshold body mass value with which separate those small and large mammals, and thus be able to ascribe them separately to some similarity hypothesis (or a similarity hypothesis with different allometric exponents for small and large mammals; Garcia & da Silva, 2006). But see also Kokshenev (2003, 2007) for a criticism of Garcia-Silva’s model. The thing with differential scaling is that it is indeed differential. As observed in any plot representing complex allometry (Fig. III.5), the allometric exponent changes gradually

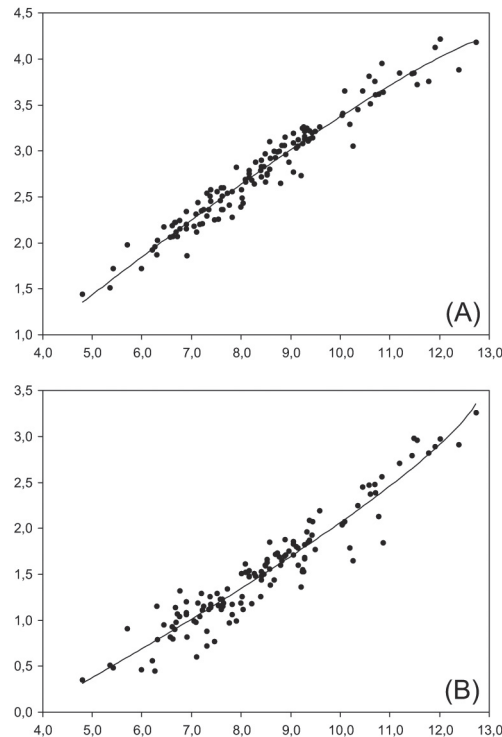


Figure III.5. Differential scaling. Complex allometry plots for olecranon length (A) and ulna transverse diameter (B) in the fissiped subsample. As indicated by the curvature of the plot, olecranon length scales faster in small carnivorans than in large carnivorans (i.e., $D > 1$), while the opposite is true for ulna transverse diameter (i.e., $D < 1$).

along a wide spectrum of body masses, and no real threshold exists, no matter how beautifully justifiable it is (e.g. the 20 kg threshold in Carnivora, which is related to prey size changes; Carbone et al., 1999).

Another source of variability is the adaptation to performing different modes of locomotion besides walking and running (climbing, swimming, digging). As stated in the introduction, Bou et al. (1987) suggested that similarity hypothesis imply adaptive neutrality, which is not the case, since the present study has proved that adaptations to different locomotor habits do indeed result in different scaling patterns. Furthermore, differences in locomotor habit within the same sample has been proposed as another possible explanation for differential scaling (Castiella & Casinos, 1990; Gálvez-López & Casinos, 2012).

Finally, at least in Carnivora, phylogenetic relatedness also plays an important role in limb bone scaling, as suggested by the different allometric exponents obtained with traditional and PIC regression methods in the present study (contrary to previous studies comparing both methodologies in this and other mammal groups; Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012).

In conclusion, thus, we propose that either an overcomplicated model should be constructed including all these factors (and the ones we are probably missing), or we finally drop the “universal scaling” searching and focus on solving little problems one at a time, and from the sum of them formulate a generalization (if possible). For instance, how does limb bone morphology change with size in arboreal carnivorans? What about in arboreal didelphids and so on? Can we generalize all those scaling patterns into one scaling pattern for arboreal mammals? We consider that the present study constitutes a first step in that direction.

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Appendix 1 – Phylogeny

Comparative studies require the phylogeny of the studied species to test their hypotheses in an evolutionary context, but nowadays most mammalian orders lack a well-established phylogeny. In the case of Carnivora, for over two decades the sole study including a complete phylogeny for all carnivoran species was that of Bininda-Emonds et al. (1999), which was widely used in comparative studies on this order since its publication (e.g. Carbone et al., 1999; Iwaniuk et al., 2000; Webster et al., 2004; Christiansen & Adolfssen, 2005; Finarelli & Flynn, 2006; Goswami, 2006; Friscia et al., 2007; Schutz & Guralnick, 2007; Meloro et al., 2008; Meloro, 2011). This phylogeny was constructed using supertree techniques, which combine many smaller phylogenies to provide a consensus

estimate of the phylogeny of all taxa present in the smaller phylogenies. Recent molecular phylogenetic studies, however, have rendered Bininda-Emonds' et al. (1999) hypothesis obsolete (e.g. Dragoo & Honeycutt, 1997; Gaubert & Veron, 2003; Yoder et al., 2003). Three recent studies have used different approaches to provide an updated phylogeny for the order Carnivora:

- Flynn et al. (2005) chose character sampling over taxon sampling. Their study combined nuclear and mitochondrial genes (ntDNA + mtDNA) to provide a well-resolved tree for 26% of carnivoran species. The resulting phylogeny recovered the monophyly of all carnivoran families and the main relationships between them. However, in a conservative approach, the authors established polytomies where interfamilial relationships were unclear, namely basal feliform relationships (*Nandinia* + (Felidae + Viverridae + (Hyaenidae + (Herpestidae + Eupleridae)))) and relationships within Musteloidea *s.l.* (*Ailurus* + Mephitidae + (Mustelidae + Procyonidae)). These polytomies, together with low taxon sampling, make this phylogeny not conflicting with more recent phylogenies for the different families within Carnivora.
- Agnarsson et al. (2010) advocated that dense taxon sampling increases phylogenetic accuracy, building a phylogeny for 82% of carnivoran species based solely in cytochrome *b* sequences. Monophyly was recovered for all families but Procyonidae, since *Potos* was placed at the base of all Musteloidea *s.l.* Most interfamilial relationships were also recovered, like monophyletic Pinnipedia, *Nandinia* at the base of Feliformia, and the clade ((Eupleridae + Herpestidae) + Hyaenidae). However, this study failed to retrieve some highly supported groups from prior studies: monophyletic *Canis s.l.* (*Canis* + *Cuon* + *Lycaon*; Bardeleben et al., 2005), lineages within Felidae (Johnson et al., 2006), sociality in mongooses (Veron et al., 2004), and monophyletic Lutrinae (Koepfli et al., 2008) among others. Furthermore, the authors also proposed new and controversial relationships for other groups: *Ailurus* as sister to Canidae in the base of Caniformia instead of within Musteloidea *s.l.*, Pinnipedia as sister to Ursidae instead of to Musteloidea *s.l.*, Procyonidae as sister to Mephitidae instead of to Mustelidae, and Prionodontidae as sister to the clade ((Eupleridae + Herpestidae) + Hyaenidae) instead of to Felidae (cf. Gaubert & Veron, 2003; Flynn et al., 2005; Fulton & Strobeck, 2006; Arnason et al., 2007). All these inconsistencies with previous analysis were probably caused by the use of cytochrome *b* data as the only source of phylogenetic signal, since Koepfli et al.

(2006) shown that this gene is unlikely to contain robust phylogenetic signal for all levels of a phylogeny.

- Nyakatura & Bininda-Emonds (2012) provided an updated version of the carnivoran supertree of Bininda-Emond et al. (1999). This updated phylogeny not only reflected the increased number of carnivoran species, but also included additional data sources (mainly DNA sequence data, but also new phenotypic data) and had been constructed with refined methodology and analytical methods.

For all comparative analyses in this work, the phylogeny proposed by Nyakatura & Bininda-Emonds (2012) was used, although slightly modified as follows (Fig. III.1):

- All species for which no data was available were pruned from the tree.
- Species names follow Wilson & Mittermeier (2009). However, some synonyms were kept from Wozencraft (2005) as in the original phylogeny, namely *Aonyx cinerea*, *Lycalopex*, *Proteles cristata*, and *Puma yagouaroundi*.
- *Genetta felina* was added after Gaubert & Begg (2007), since it did not appear in the original phylogeny.
- Finally, some divergence times were changed:
 - **Canidae**: Following Slater et al. (2009), the clade (*Speothos* + (*Chrysocyon* + *Dusicyon*)) was considered sister to the rest of South-American canids, since it is supported by nuclear polymorphisms. Given that divergence time estimates were older in Slater et al. (2009), the minimum values of the 95% confidence intervals of their estimates were used, so the clade would fit inside the South-American canids clade in the supertree.
 - **Felidae**: The topology and divergence times obtained by Johnson et al. (2006) were used.
 - **Hyaenidae**: Since both Koepfli et al. (2006) and Eizirik et al. (2010) recovered similar divergence times, approximately 5 Mya-older than the supertree, the divergence times proposed by Koepfli et al. (2006) were used.
 - **Mustelidae**: The more conservative result of monophyletic Galictinae, Helictidinae, and Lutrinae proposed by Koepfli et al. (2008) was used. Also, the more resolved phylogeny for *Mustela* of that study was used.
 - **Procyonidae**: Since resolution of this clade in the supertree is very poor, the topology and divergence times proposed by Koepfli et al. (2007) were used instead.

- *Viverridae*: Following Patou et al. (2008), *Paradoxurinae* was considered monophyletic. To place *Arctogalidia* back into *Paradoxurinae*, the minimum value of the 95% confidence interval for the age of that node, as well as the maximum value of the 95% confidence interval for the age of the split between *Hemigalinae* and *Paradoxurinae*, had to be used.

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Appendix 2 – Regression results

As indicated in Table III.3, the following tables present the regression results for each variable. Both the results using traditional regression methods and phylogenetically independent contrasts (PIC) are shown for the whole sample and each of the subsamples (fissipeds, by Family, by locomotor type, and by habitat). In each case, it is indicated (in the “sim.” columns) whether the theoretical values proposed by the geometric similarity hypothesis (G), the elastic similarity hypothesis (E), or both (B), are included in the 95% confidence interval for the slope b (95% CI _{b}). Furthermore, when neither theoretical value is included in the 95% CI _{b} , it is indicated whether there is positive allometry (+; b is higher than both theoretical values), negative allometry (-; b is lower than both theoretical values), or both (nei.; b is higher than one theoretical values and lower than the other). Finally, the results of the comparison between the allometric coefficients obtained with each methodology are presented in the last column ($b_{\text{trad}} \neq b_{\text{PIC}}$): a cross (×) indicates no significant differences, while a tick (✓) denotes that the slopes are significantly different from each other ($p < 0.05$).

Variable names and abbreviations are given in Table III.3, while the following abbreviations are common to all following tables: 95% CI _{a} , 95% confidence interval for the coefficient a ; 95% CI _{b} , 95% confidence interval for the allometric coefficient b ; n, sample size; n.s., unable to test differences due to non-significant regression; R, correlation coefficient; sim., similarity. Results in *grey italics* denote non-significant regressions.

III.A1 – L_s		traditional regression					PLC regression						
whole sample	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}	
fissipeds	137	3.098	2.662 – 3.682	0.356	0.336 – 0.374	0.957	+	136	0.338	0.318 – 0.358	0.940	G	×
Family	130	2.667	2.280 – 3.166	0.376	0.356 – 0.394	0.957	+	129	0.346	0.325 – 0.367	0.940	G	✓
Canidae	17	1.622	1.043 – 3.210	0.445	0.368 – 0.493	0.973	+	16	0.435	0.369 – 0.501	0.961	+	×
Mustelidae	32	2.970	2.214 – 3.985	0.341	0.304 – 0.378	0.956	G	31	0.330	0.283 – 0.377	0.923	G	×
Procyonidae	7	2.121	0.266 – 16.901	0.396	0.139 – 0.653	0.825	B	6	0.376	0.105 – 0.647	0.815	B	×
Ursidae	7	6.492	2.710 – 15.551	0.284	0.210 – 0.359	0.974	B	6	0.287	0.203 – 0.371	0.972	B	×
Felidae	26	5.271	4.163 – 6.674	0.313	0.288 – 0.338	0.982	G	25	0.317	0.283 – 0.351	0.968	G	×
Herpestidae	12	4.577	3.107 – 6.741	0.308	0.254 – 0.362	0.968	G	11	0.300	0.251 – 0.349	0.974	G	×
Eupleridae	5	4.173	0.881 – 19.767	0.329	0.115 – 0.543	0.935	B						
Viverridae	14	5.077	2.677 – 9.630	0.299	0.220 – 0.378	0.907	B	13	0.313	0.223 – 0.403	0.893	B	×
Locomotor type													
arboreal	7	2.219	0.414 – 11.900	0.382	0.174 – 0.590	0.881	B	6	0.216	0.201 – 0.231	0.998	-	×
semiarboreal	10	5.179	3.296 – 8.138	0.301	0.242 – 0.359	0.971	B	9	0.288	0.185 – 0.391	0.903	B	×
scansorial	45	4.017	3.297 – 4.894	0.335	0.314 – 0.356	0.978	G	44	0.334	0.309 – 0.359	0.970	G	×
terrestrial	49	2.056	1.540 – 2.961	0.411	0.367 – 0.447	0.963	+	48	0.339	0.301 – 0.377	0.925	G	✓
semifossorial	7	3.086	1.197 – 7.958	0.345	0.226 – 0.464	0.954	B	6	0.355	0.220 – 0.490	0.952	B	×
semiaquatic	11	3.334	1.226 – 9.068	0.329	0.212 – 0.446	0.881	B	10	0.349	0.231 – 0.467	0.897	B	×
aquatic	8	3.484	0.494 – 24.560	0.324	0.161 – 0.488	0.863	B	7	0.358	0.154 – 0.562	0.841	B	×
Preferred habitat													
forest	38	3.279	2.468 – 4.358	0.349	0.314 – 0.383	0.956	G	37	0.341	0.300 – 0.382	0.935	G	×
mosaic	40	2.643	2.030 – 3.439	0.380	0.350 – 0.411	0.970	+	39	0.349	0.318 – 0.380	0.964	G	✓
open	17	2.082	1.397 – 3.956	0.411	0.331 – 0.455	0.966	G	16	0.360	0.300 – 0.420	0.954	G	×
freshwater	13	3.735	1.389 – 6.804	0.322	0.205 – 0.438	0.838	B	12	0.348	0.224 – 0.472	0.848	B	×
marine	10	2.649	1.031 – 6.804	0.348	0.267 – 0.428	0.959	G	9	0.378	0.257 – 0.499	0.924	G	×
variable	19	2.585	1.641 – 4.073	0.385	0.335 – 0.436	0.967	+	18	0.320	0.271 – 0.369	0.955	G	✓

III.A2 – S	traditional regression						PIC regression						
	n	a	95% CI _a	<i>b</i> _{trad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{trad} ≠ <i>b</i> _{PIC}	
whole sample	137	0.897	0.728 – 1.112	0.378	0.351 – 0.403	0.967	+	136	0.348	0.326 – 0.370	0.930	G	✓
fissipeds	130	1.045	0.915 – 1.216	0.358	0.342 – 0.373	0.971	+	129	0.335	0.314 – 0.356	0.933	G	✓
Family													
Canidae	17	0.498	0.305 – 1.212	0.432	0.335 – 0.486	0.956	+	16	0.438	0.360 – 0.516	0.947	+	×
Mustelidae	32	1.089	0.838 – 1.416	0.354	0.321 – 0.388	0.967	G	31	0.337	0.291 – 0.383	0.932	G	×
Procyonidae	7	1.615	0.315 – 8.270	0.311	0.109 – 0.513	0.825	B	6	<i>0.292</i>	<i>0.086 – 0.498</i>	<i>0.822</i>	B	n.s.
Ursidae	7	5.843	3.181 – 10.732	0.212	0.161 – 0.264	0.977	E	6	0.215	0.158 – 0.272	0.977	E	×
Felidae	26	1.608	1.239 – 2.086	0.320	0.292 – 0.347	0.979	G	25	0.322	0.282 – 0.362	0.956	G	×
Herpestidae	12	1.430	1.110 – 1.842	0.308	0.272 – 0.343	0.987	G	11	0.298	0.260 – 0.336	0.984	G	×
Eupleridae	5	1.291	0.725 – 2.299	0.336	0.257 – 0.416	0.992	G						
Viverridae	14	1.720	0.963 – 3.072	0.298	0.226 – 0.370	0.924	B	13	<i>0.298</i>	<i>0.134 – 0.462</i>	<i>0.497</i>	B	n.s.
Locomotor type													
arboreal	7	0.733	0.350 – 1.538	0.407	0.315 – 0.498	0.981	G	6	0.343	0.342 – 0.344	1.000	+	×
semiarboreal	10	1.614	0.972 – 2.680	0.318	0.252 – 0.384	0.967	G	9	0.302	0.188 – 0.416	0.892	B	×
scansorial	45	1.266	1.066 – 1.503	0.343	0.325 – 0.362	0.984	G	44	0.330	0.299 – 0.361	0.953	G	×
terrestrial	49	1.154	0.995 – 1.369	0.338	0.318 – 0.357	0.983	G	48	0.336	0.304 – 0.368	0.945	G	×
semifossorial	7	0.537	0.097 – 2.959	0.420	0.205 – 0.635	0.895	B	6	0.389	0.166 – 0.612	0.888	B	×
semiaquatic	11	1.038	0.545 – 1.977	0.362	0.287 – 0.438	0.961	G	10	0.401	0.295 – 0.507	0.939	G	×
aquatic	8	<i>0.203</i>	<i>0.001 – 28.536</i>	<i>0.517</i>	<i>0.103 – 0.931</i>	<i>0.597</i>	B	7	<i>0.388</i>	<i>0.130 – 0.646</i>	<i>0.773</i>	B	n.s.
Preferred habitat													
forest	38	1.098	0.850 – 1.419	0.355	0.324 – 0.386	0.966	G	37	0.360	0.317 – 0.403	0.936	G	×
mosaic	40	1.044	0.862 – 1.265	0.360	0.338 – 0.383	0.982	+	39	0.325	0.297 – 0.353	0.964	G	✓
open	17	0.834	0.546 – 1.609	0.374	0.301 – 0.418	0.957	G	16	0.347	0.275 – 0.419	0.926	G	×
freshwater	13	1.049	0.589 – 1.867	0.361	0.293 – 0.429	0.959	G	12	0.415	0.306 – 0.524	0.920	G	×
marine	10	0.519	0.047 – 5.745	0.435	0.230 – 0.640	0.815	B	9	0.376	0.219 – 0.533	0.867	B	×
variable	19	1.180	0.809 – 1.722	0.343	0.301 – 0.385	0.971	G	18	0.328	0.283 – 0.373	0.965	G	×

III.A3 – I		traditional regression						PIC regression					
whole sample	n	a	95% CI_a	<i>b</i>_{rad}	95% CI_b	R	sim.	n	<i>b</i>_{PIC}	95% CI_b	R	sim.	<i>b</i>_{rad} ≠ <i>b</i>_{PIC}
fissipeds	137	0.716	0.538 – 0.939	0.423	0.392 – 0.453	0.927	+	136	0.386	0.356 – 0.416	0.892	+	✓
Family	130	0.614	0.460 – 0.806	0.443	0.412 – 0.474	0.924	+	129	0.384	0.358 – 0.410	0.922	+	✓
Canidae	17	0.978	0.509 – 2.697	0.399	0.286 – 0.472	0.933	G	16	0.418	0.324 – 0.512	0.914	G	×
Mustelidae	32	0.450	0.228 – 0.705	0.440	0.383 – 0.497	0.937	+	31	0.416	0.350 – 0.482	0.904	+	×
Procyonidae	7	4.282	1.564 – 11.724	0.233	0.108 – 0.357	0.885	B	<i>6</i>	<i>0.238</i>	<i>0.066 – 0.410</i>	<i>0.812</i>	<i>B</i>	n.s.
Ursidae	7	9.192	2.518 – 33.546	0.204	0.094 – 0.314	0.883	E	<i>6</i>	<i>0.202</i>	<i>0.086 – 0.318</i>	<i>0.866</i>	<i>E</i>	n.s.
Felidae	26	1.884	1.410 – 2.517	0.330	0.299 – 0.360	0.975	G	25	0.347	0.302 – 0.392	0.951	G	×
Herpestidae	12	1.830	1.083 – 3.094	0.316	0.243 – 0.390	0.944	B	11	0.317	0.248 – 0.386	0.953	B	×
Eupleridae	5	0.624	0.068 – 5.761	0.451	0.145 – 0.758	0.929	B						
Viverridae	14	2.579	1.429 – 4.653	0.289	0.216 – 0.362	0.916	B	13	0.323	0.234 – 0.412	0.901	B	×
Locomotor type													
arboreal	7	1.561	0.735 – 3.316	0.357	0.264 – 0.450	0.974	G	6	0.357	0.255 – 0.459	0.973	G	×
semi-arboreal	10	1.883	0.769 – 4.606	0.320	0.204 – 0.437	0.895	B	9	0.299	0.219 – 0.379	0.947	B	×
scansorial	45	1.113	0.850 – 1.458	0.385	0.356 – 0.414	0.969	+	44	0.385	0.340 – 0.430	0.925	+	×
terrestrial	49	0.450	0.294 – 0.763	0.477	0.418 – 0.526	0.932	+	48	0.362	0.317 – 0.407	0.907	G	✓
semifossorial	7	0.497	0.089 – 2.781	0.446	0.229 – 0.662	0.906	B	6	0.475	0.249 – 0.701	0.924	B	×
semiaquatic	11	0.425	0.085 – 2.115	0.449	0.261 – 0.637	0.832	G	10	0.459	0.293 – 0.625	0.883	G	×
aquatic	<i>8</i>	<i>0.151</i>	<i>0.001 – 16.286</i>	<i>0.527</i>	<i>0.135 – 0.919</i>	<i>0.667</i>	<i>B</i>	<i>7</i>	<i>0.556</i>	<i>0.024 – 1.088</i>	<i>0.412</i>	<i>B</i>	n.s.
Preferred habitat													
forest	38	0.770	0.491 – 1.207	0.425	0.371 – 0.480	0.925	+	37	0.410	0.346 – 0.474	0.886	+	×
mosaic	40	0.770	0.514 – 1.154	0.421	0.374 – 0.468	0.941	+	39	0.362	0.318 – 0.406	0.928	G	✓
open	17	0.495	0.216 – 1.541	0.465	0.324 – 0.555	0.923	G	16	0.378	0.298 – 0.458	0.923	G	×
freshwater	13	0.386	0.064 – 2.331	0.475	0.264 – 0.686	0.742	G	12	0.470	0.283 – 0.657	0.806	G	×
marine	10	0.256	0.030 – 2.216	0.484	0.299 – 0.668	0.884	G	<i>9</i>	<i>0.508</i>	<i>0.194 – 0.822</i>	<i>0.674</i>	<i>B</i>	n.s.
variable	19	0.369	0.199 – 0.686	0.496	0.427 – 0.564	0.963	+	18	0.395	0.330 – 0.460	0.947	G	✓

III.A4 – A	traditional regression						PIC regression						
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	137	1.774	1.500 – 2.112	0.392	0.373 – 0.410	0.970	+	136	0.355	0.333 – 0.377	0.931	G	✓
fissipeds	130	1.785	1.518 – 2.087	0.391	0.374 – 0.409	0.965	+	129	0.353	0.332 – 0.374	0.940	G	✓
Family													
Canidae	17	1.391	0.776 – 3.607	0.419	0.316 – 0.483	0.954	G	16	0.428	0.348 – 0.508	0.941	+	×
Mustelidae	32	1.564	1.134 – 2.157	0.387	0.346 – 0.428	0.959	+	31	0.366	0.313 – 0.414	0.921	G	×
Procyonidae	7	4.772	1.770 – 12.868	0.285	0.162 – 0.408	0.927	B	6	<i>0.286</i>	<i>0.111 – 0.461</i>	<i>0.870</i>	B	n.s.
Ursidae	7	18.339	8.036 – 41.855	0.191	0.121 – 0.261	0.948	E	6	0.191	0.116 – 0.266	0.949	E	×
Felidae	26	3.476	2.743 – 4.405	0.327	0.302 – 0.352	0.983	G	25	0.335	0.298 – 0.372	0.965	G	×
Herpestidae	12	3.643	2.675 – 4.961	0.301	0.258 – 0.344	0.979	G	11	0.300	0.255 – 0.345	0.978	G	×
Eupleridae	5	2.216	0.745 – 6.586	0.369	0.218 – 0.519	0.975	B						
Viverridae	14	4.444	2.757 – 7.164	0.288	0.229 – 0.347	0.945	B	13	0.297	0.237 – 0.357	0.948	B	×
Locomotor type													
arboreal	7	2.544	1.433 – 4.517	0.360	0.288 – 0.431	0.985	G	6	0.358	0.278 – 0.438	0.984	G	×
semiarboreal	10	4.124	2.636 – 6.452	0.300	0.241 – 0.358	0.971	B	9	0.277	0.210 – 0.344	0.958	B	×
scansorial	45	2.386	1.964 – 2.899	0.365	0.344 – 0.386	0.982	+	44	0.360	0.325 – 0.395	0.951	G	×
terrestrial	49	1.612	1.281 – 2.121	0.399	0.369 – 0.425	0.969	+	48	0.345	0.309 – 0.381	0.935	G	✓
semifossorial	7	1.304	0.392 – 4.336	0.409	0.258 – 0.560	0.947	G	6	0.420	0.262 – 0.578	0.953	G	×
semiaquatic	11	1.449	0.598 – 3.512	0.399	0.295 – 0.502	0.939	G	10	0.425	0.317 – 0.533	0.943	G	×
aquatic	8	0.997	0.038 – 26.417	0.439	0.165 – 0.714	0.780	B	7	<i>0.373</i>	<i>0.090 – 0.656</i>	<i>0.693</i>	B	n.s.
Preferred habitat													
forest	38	1.975	1.458 – 2.674	0.384	0.347 – 0.421	0.959	+	37	0.382	0.330 – 0.434	0.917	G	×
mosaic	40	1.903	1.491 – 2.430	0.387	0.358 – 0.415	0.975	+	39	0.342	0.312 – 0.372	0.964	G	✓
open	17	1.604	1.078 – 2.942	0.397	0.329 – 0.440	0.960	G	16	0.350	0.286 – 0.414	0.944	G	×
freshwater	13	1.492	0.555 – 4.010	0.402	0.286 – 0.518	0.900	G	12	0.442	0.313 – 0.571	0.901	G	×
marine	10	1.142	0.235 – 5.543	0.426	0.291 – 0.560	0.921	G	9	0.370	0.206 – 0.534	0.848	B	×
variable	19	1.451	0.960 – 2.192	0.413	0.367 – 0.459	0.976	+	18	0.364	0.313 – 0.415	0.962	G	×

III.A5 – H_s		traditional regression					PLC regression						
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}
fissipeds	137	0.171	0.100 – 0.292	0.454	0.393 – 0.515	0.822	+	136	0.463	0.416 – 0.510	0.804	+	×
Family	130	0.114	0.068 – 0.198	0.510	0.449 – 0.568	0.897	+	129	0.474	0.429 – 0.519	0.839	+	×
Canidae	17	0.166	0.100 – 0.440	0.480	0.374 – 0.534	0.947	+	16	0.441	0.353 – 0.529	0.933	+	×
Mustelidae	32	0.073	0.032 – 0.165	0.548	0.444 – 0.653	0.860	+	31	0.497	0.384 – 0.610	0.791	+	×
Procyonidae	7	0.111	0.008 – 1.459	0.531	0.212 – 0.850	0.852	B	<i>6</i>	<i>0.523</i>	<i>0.152 – 0.894</i>	<i>0.821</i>	<i>B</i>	n.s.
Ursidae	7	2.019	0.341 – 11.971	0.237	0.086 – 0.389	0.831	B	<i>6</i>	<i>0.235</i>	<i>0.071 – 0.399</i>	<i>0.829</i>	<i>B</i>	n.s.
Felidae	26	0.320	0.192 – 0.532	0.407	0.353 – 0.461	0.949	+	25	0.437	0.361 – 0.513	0.913	+	×
Herpestidae	12	0.827	0.434 – 1.573	0.278	0.188 – 0.368	0.887	B	11	0.250	0.158 – 0.342	0.858	B	×
Eupleridae	5	0.310	0.036 – 2.665	0.397	0.101 – 0.693	0.914	B						
Viverridae	14	0.223	0.102 – 0.484	0.431	0.335 – 0.528	0.935	+	13	0.450	0.329 – 0.571	0.906	G	×
Locomotor type													
arboreal	7	0.219	0.044 – 1.098	0.429	0.229 – 0.628	0.914	B	6	0.425	0.215 – 0.635	0.917	B	×
semiarboreal	10	0.220	0.084 – 0.576	0.442	0.317 – 0.567	0.938	G	9	0.441	0.232 – 0.650	0.825	B	×
scansorial	45	0.270	0.201 – 0.364	0.420	0.388 – 0.452	0.968	+	44	0.435	0.384 – 0.486	0.924	+	×
terrestrial	49	0.096	0.044 – 0.224	0.535	0.434 – 0.625	0.916	+	48	0.455	0.388 – 0.522	0.866	+	×
semifossorial	<i>7</i>	<i>0.005</i>	<i>0.000 – 2.586</i>	<i>0.866</i>	<i>0.089 – 1.644</i>	<i>0.626</i>	<i>B</i>	<i>6</i>	<i>0.564</i>	<i>0.068 – 1.060</i>	<i>0.706</i>	<i>B</i>	n.s.
semiaquatic	11	0.024	0.002 – 0.369	0.667	0.349 – 0.985	0.775	+	<i>10</i>	<i>0.847</i>	<i>0.338 – 1.356</i>	<i>0.623</i>	+	n.s.
aquatic	<i>8</i>	<i>0.038</i>	<i>0.000 – 11.844</i>	<i>0.483</i>	<i>0.000 – 0.965</i>	<i>0.004</i>	<i>B</i>	<i>7</i>	<i>0.580</i>	<i>-0.007 – 1.167</i>	<i>0.263</i>	<i>B</i>	n.s.
Preferred habitat													
forest	38	0.199	0.136 – 0.292	0.449	0.403 – 0.495	0.952	+	37	0.482	0.416 – 0.548	0.914	+	×
mosaic	40	0.104	0.058 – 0.185	0.526	0.458 – 0.593	0.921	+	39	0.526	0.443 – 0.609	0.878	+	×
open	17	0.086	0.021 – 1.006	0.546	0.259 – 0.699	0.836	G	16	0.257	0.234 – 0.280	0.987	E	✓
freshwater	13	0.026	0.002 – 0.291	0.665	0.382 – 0.948	0.767	+	12	0.886	0.431 – 1.341	0.644	+	×
marine	<i>10</i>	<i>0.131</i>	<i>0.004 – 4.356</i>	<i>0.393</i>	<i>0.094 – 0.692</i>	<i>0.359</i>	<i>B</i>	<i>9</i>	<i>0.469</i>	<i>0.110 – 0.828</i>	<i>0.406</i>	<i>B</i>	n.s.
variable	19	0.088	0.031 – 0.250	0.537	0.422 – 0.652	0.908	+	18	0.503	0.382 – 0.624	0.885	+	×

III.A6 – L _h	traditional regression						PIC regression						
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	137	5.994	4.878 – 7.355	0.318	0.293 – 0.344	0.909	G	136	0.311	0.289 – 0.333	0.911	nei.	×
fissipeds	130	4.580	3.959 – 5.399	0.354	0.334 – 0.370	0.946	+	129	0.311	0.290 – 0.332	0.924	nei.	✓
Family													
Canidae	17	3.350	1.705 – 11.350	0.401	0.263 – 0.478	0.920	G	16	0.415	0.314 – 0.516	0.898	G	×
Mustelidae	32	6.018	4.208 – 8.608	0.298	0.252 – 0.344	0.912	G	31	0.292	0.244 – 0.340	0.897	B	×
Procyonidae	7	13.706	5.597 – 33.563	0.224	0.113 – 0.335	0.902	B	6	<i>0.219</i>	<i>0.081 – 0.357</i>	<i>0.861</i>	<i>B</i>	n.s.
Ursidae	7	13.772	6.344 – 29.899	0.252	0.186 – 0.318	0.974	E	6	0.256	0.186 – 0.326	0.975	E	×
Felidae	26	9.680	7.805 – 12.006	0.285	0.263 – 0.308	0.982	nei.	25	0.295	0.264 – 0.326	0.969	nei.	×
Herpestidae	12	6.732	3.892 – 11.644	0.299	0.222 – 0.375	0.931	B	11	0.285	0.213 – 0.357	0.935	B	×
Eupleridae	5	5.553	3.834 – 8.042	0.338	0.287 – 0.389	0.997	G						
Viverridae	14	11.070	6.159 – 19.896	0.248	0.175 – 0.321	0.885	E	13	0.282	0.204 – 0.360	0.901	B	×
Locomotor type													
arboreal	7	5.956	2.087 – 16.997	0.334	0.204 – 0.463	0.941	B	6	0.334	0.193 – 0.475	0.940	B	×
semiarboreal	10	10.101	6.958 – 14.664	0.270	0.222 – 0.319	0.975	E	9	0.241	0.147 – 0.335	0.884	B	×
scansorial	45	6.878	5.800 – 8.156	0.316	0.298 – 0.335	0.982	G	44	0.314	0.289 – 0.339	0.966	G	×
terrestrial	49	3.645	2.899 – 5.137	0.381	0.338 – 0.408	0.959	+	48	0.323	0.282 – 0.364	0.900	G	✓
semifossorial	7	4.750	1.793 – 12.584	0.324	0.201 – 0.446	0.944	B	6	0.336	0.197 – 0.475	0.942	B	×
semiaquatic	11	8.410	3.903 – 18.128	0.256	0.166 – 0.346	0.885	B	10	0.269	0.183 – 0.355	0.911	B	×
aquatic	8	10.127	1.925 – 53.281	0.222	0.083 – 0.361	0.779	B	7	<i>0.237</i>	<i>0.090 – 0.384</i>	<i>0.808</i>	<i>B</i>	n.s.
Preferred habitat													
forest	38	6.167	4.623 – 8.227	0.322	0.287 – 0.356	0.947	G	37	0.302	0.260 – 0.344	0.913	G	×
mosaic	40	4.451	3.453 – 5.739	0.360	0.330 – 0.389	0.968	G	39	0.326	0.298 – 0.354	0.964	G	✓
open	17	3.162	1.899 – 7.408	0.403	0.296 – 0.460	0.949	G	16	0.350	0.277 – 0.423	0.926	G	×
freshwater	13	8.206	3.333 – 20.202	0.267	0.161 – 0.373	0.862	B	12	0.269	0.168 – 0.370	0.827	B	×
marine	10	4.007	0.765 – 21.003	0.307	0.166 – 0.449	0.826	B	9	0.311	0.193 – 0.429	0.891	B	×
variable	19	4.282	2.747 – 6.676	0.364	0.315 – 0.413	0.965	G	18	0.301	0.254 – 0.348	0.954	G	✓

III.A7 – d _{sh}		traditional regression					PIC regression						
whole sample	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}	
fissipeds	137	0.396	0.352 – 0.454	0.376	0.362 – 0.389	0.975	E	136	0.383	0.359 – 0.407	0.933	E	×
Family	130	0.371	0.329 – 0.432	0.385	0.368 – 0.399	0.971	E	129	0.387	0.361 – 0.413	0.927	E	×
Canidae	17	0.138	0.071 – 0.467	0.488	0.355 – 0.560	0.959	E	16	0.454	0.372 – 0.536	0.945	E	×
Mustelidae	32	0.326	0.226 – 0.469	0.399	0.352 – 0.445	0.950	E	31	0.386	0.319 – 0.453	0.883	B	×
Procyonidae	7	0.496	0.117 – 2.092	0.370	0.191 – 0.548	0.908	B	6	0.366	0.147 – 0.585	0.876	B	n.s.
Ursidae	7	0.962	0.607 – 1.522	0.293	0.254 – 0.332	0.993	-	6	0.295	0.252 – 0.338	0.993	G	×
Felidae	26	0.353	0.271 – 0.459	0.393	0.365 – 0.421	0.986	E	25	0.382	0.341 – 0.423	0.968	E	×
Herpestidae	12	0.676	0.424 – 1.078	0.302	0.237 – 0.368	0.952	G	11	0.322	0.262 – 0.382	0.966	B	×
Eupleridae	5	0.151	0.043 – 0.529	0.515	0.342 – 0.688	0.983	E						
Viverridae	14	0.474	0.209 – 1.077	0.349	0.248 – 0.451	0.887	B	13	0.338	0.263 – 0.413	0.937	B	×
Locomotor type													
arboreal	7	0.443	0.269 – 0.730	0.375	0.313 – 0.437	0.990	B	6	0.371	0.305 – 0.437	0.990	B	×
semiarboreal	10	0.320	0.189 – 0.542	0.416	0.347 – 0.485	0.979	E	9	0.418	0.333 – 0.503	0.970	B	×
scansorial	45	0.374	0.302 – 0.465	0.384	0.360 – 0.407	0.980	E	44	0.382	0.347 – 0.417	0.956	E	×
terrestrial	49	0.372	0.300 – 0.500	0.381	0.347 – 0.406	0.968	E	48	0.354	0.312 – 0.396	0.917	B	×
semifossorial	7	0.502	0.211 – 1.197	0.337	0.227 – 0.446	0.959	B	6	0.350	0.211 – 0.489	0.948	B	×
semiaquatic	11	0.294	0.094 – 0.922	0.418	0.284 – 0.552	0.906	B	10	0.527	0.279 – 0.775	0.791	B	×
aquatic	8	0.249	0.025 – 2.525	0.407	0.213 – 0.601	0.879	B	7	0.443	0.261 – 0.625	0.920	B	n.s.
Preferred habitat													
forest	38	0.353	0.259 – 0.482	0.391	0.354 – 0.429	0.959	E	37	0.392	0.345 – 0.439	0.934	E	×
mosaic	40	0.408	0.330 – 0.505	0.373	0.349 – 0.398	0.980	E	39	0.374	0.344 – 0.404	0.970	E	×
open	17	0.332	0.248 – 0.550	0.391	0.338 – 0.425	0.972	E	16	0.365	0.300 – 0.430	0.947	B	×
freshwater	13	0.284	0.108 – 0.747	0.422	0.308 – 0.536	0.914	B	12	0.507	0.323 – 0.691	0.842	B	×
marine	10	0.653	0.219 – 1.941	0.328	0.235 – 0.421	0.937	B	9	0.377	0.275 – 0.479	0.946	B	×
variable	19	0.374	0.261 – 0.538	0.384	0.344 – 0.424	0.979	E	18	0.351	0.302 – 0.400	0.962	B	×

III.A8 – d th	traditional regression						PIC regression						
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}	
whole sample	137	0.319	0.281 – 0.365	0.369	0.354 – 0.384	0.973	E	136	0.347	0.324 – 0.370	0.923	G	×
fissipeds	130	0.322	0.285 – 0.372	0.368	0.353 – 0.383	0.968	E	129	0.341	0.319 – 0.363	0.931	G	✓
Family													
Canidae	17	0.185	0.084 – 0.505	0.430	0.320 – 0.517	0.941	B	16	0.426	0.328 – 0.524	0.910	B	×
Mustelidae	32	0.466	0.348 – 0.623	0.307	0.270 – 0.344	0.946	G	31	0.319	0.270 – 0.368	0.910	G	×
Procyonidae	7	0.810	0.370 – 1.772	0.267	0.170 – 0.364	0.949	G	6	0.261	0.167 – 0.355	0.957	G	×
Ursidae	7	2.289	0.776 – 6.751	0.208	0.116 – 0.300	0.923	-	6	0.209	0.109 – 0.309	0.922	-	×
Felidae	26	0.381	0.288 – 0.505	0.354	0.324 – 0.384	0.980	B	25	0.339	0.301 – 0.377	0.964	B	×
Herpestidae	12	0.811	0.494 – 1.330	0.242	0.173 – 0.312	0.913	-	11	0.254	0.189 – 0.319	0.934	-	×
Eupleridae	5	0.204	0.084 – 0.496	0.439	0.316 – 0.561	0.988	B						
Viverridae	14	0.430	0.225 – 0.825	0.331	0.251 – 0.412	0.922	B	13	0.488	0.308 – 0.668	0.814	B	×
Locomotor type													
arboreal	7	0.533	0.280 – 1.015	0.318	0.238 – 0.398	0.976	B	6	0.315	0.228 – 0.402	0.975	B	×
semiarboreal	10	0.363	0.184 – 0.716	0.362	0.274 – 0.451	0.954	B	9	0.374	0.233 – 0.515	0.892	B	×
scansorial	45	0.303	0.253 – 0.363	0.379	0.359 – 0.398	0.986	E	44	0.349	0.320 – 0.378	0.963	B	✓
terrestrial	49	0.335	0.281 – 0.426	0.361	0.334 – 0.382	0.967	E	48	0.342	0.301 – 0.383	0.915	B	×
semifossorial	7	0.432	0.196 – 0.954	0.322	0.222 – 0.421	0.963	B	6	0.335	0.188 – 0.482	0.935	B	×
semiaquatic	11	0.671	0.312 – 1.444	0.263	0.173 – 0.353	0.892	G	10	0.307	0.194 – 0.420	0.878	B	×
aquatic	8	0.084	0.005 – 1.511	0.479	0.237 – 0.720	0.863	B	7	0.450	0.152 – 0.748	0.775	B	n.s.
Preferred habitat													
forest	38	0.306	0.229 – 0.407	0.378	0.343 – 0.412	0.962	E	37	0.365	0.323 – 0.407	0.941	B	×
mosaic	40	0.315	0.252 – 0.394	0.374	0.348 – 0.400	0.977	E	39	0.346	0.310 – 0.382	0.949	B	×
open	17	0.308	0.242 – 0.446	0.370	0.327 – 0.404	0.978	B	16	0.340	0.279 – 0.401	0.946	B	×
freshwater	13	0.558	0.246 – 1.265	0.288	0.192 – 0.384	0.864	B	12	0.345	0.226 – 0.464	0.858	B	×
marine	10	0.173	0.046 – 0.653	0.418	0.304 – 0.531	0.943	B	9	0.389	0.222 – 0.556	0.858	B	×
variable	19	0.335	0.237 – 0.473	0.365	0.327 – 0.403	0.979	B	18	0.348	0.290 – 0.406	0.945	B	×

III.A9 – T		traditional regression						PIC regression						
	<i>n</i>	<i>a</i>	95% CI _{<i>a</i>}	<i>b</i> _{trad}	95% CI _{<i>b</i>}	R	sim.	<i>n</i>	<i>b</i> _{PIC}	95% CI _{<i>b</i>}	R	sim.	<i>b</i> _{trad} ≠ <i>b</i> _{PIC}	
whole sample	137	0.558	0.162 – 1.071	6.14 · 10 ⁻⁵	2.68 · 10 ⁻⁵ – 7.63 · 10 ⁻⁵	0.619	+	136	4.12 · 10 ⁻⁵	3.43 · 10 ⁻⁵ – 4.81 · 10 ⁻⁵	0.190	+	×	
fissipeds	130	0.447	0.137 – 0.927	6.56 · 10 ⁻⁵	4.68 · 10 ⁻⁵ – 9.11 · 10 ⁻⁵	0.251	+	129	4.22 · 10 ⁻⁵	3.49 · 10 ⁻⁶ – 4.95 · 10 ⁻⁵	0.157	+	n.s.	
Family														
Canidae	17	1.560	0.840 – 2.499	1.88 · 10 ⁻⁴	6.55 · 10 ⁻⁵ – 2.55 · 10 ⁻⁴	0.763	+	16	1.34 · 10 ⁻⁴	7.12 · 10 ⁻⁵ – 1.97 · 10 ⁻⁴	0.530	+	×	
Mustelidae	32	0.545	0.127 – 1.824	-1.17 · 10 ⁻⁴	-4.22 · 10 ⁻⁴ – -7.62 · 10 ⁻⁵	0.288	-	31	-1.19 · 10 ⁻⁴	-1.59 · 10 ⁻⁴ – -7.87 · 10 ⁻⁵	0.419	-	n.s.	
Procyonidae	7	-1.081	-2.525 – -0.362	3.00 · 10 ⁻⁴	2.72 · 10 ⁻⁶ – 0.001	0.174	+	6	3.34 · 10 ⁻⁴	-7.96 · 10 ⁻⁵ – 7.48 · 10 ⁻⁴	0.075	B	n.s.	
Ursidae	7	-2.861	-6.636 – -0.913	2.09 · 10 ⁻⁵	-3.87 · 10 ⁻⁵ – 5.91 · 10 ⁻⁵	0.462	B	6	2.25 · 10 ⁻⁵	-3.93 · 10 ⁻⁶ – 4.89 · 10 ⁻⁵	0.327	B	n.s.	
Felidae	26	1.374	0.832 – 1.916	5.71 · 10 ⁻⁵	1.38 · 10 ⁻⁵ – 7.08 · 10 ⁻⁵	0.892	+	25	5.47 · 10 ⁻⁵	4.24 · 10 ⁻⁵ – 6.70 · 10 ⁻⁵	0.847	+	×	
Herpestidae	12	0.248	-0.187 – 0.683	4.50 · 10 ⁻⁴	3.00 · 10 ⁻⁴ – 0.001	0.710	+	11	4.42 · 10 ⁻⁴	1.75 · 10 ⁻⁴ – 7.09 · 10 ⁻⁴	0.530	+	n.s.	
Eupleridae	5	1.408	-0.147 – 6.976	-5.63 · 10 ⁻⁴	-0.005 – -3.75 · 10 ⁻⁴	0.271	-							
Viverridae	14	-0.339	-1.351 – 0.674	3.28 · 10 ⁻⁴	1.13 · 10 ⁻⁴ – 8.69 · 10 ⁻⁴	0.560	+	13	2.93 · 10 ⁻⁴	1.50 · 10 ⁻⁴ – 4.36 · 10 ⁻⁴	0.637	+	×	
Locomotor type														
arboreal	7	-0.584	-5.474 – 1.021	1.71 · 10 ⁻⁴	-6.07 · 10 ⁻⁴ – 0.002	0.063	B	6	6.30 · 10 ⁻⁵	4.10 · 10 ⁻⁵ – 8.50 · 10 ⁻⁵	0.960	+	n.s.	
semiarboreal	10	-0.769	-2.612 – -0.087	2.55 · 10 ⁻⁴	4.97 · 10 ⁻⁵ – 9.93 · 10 ⁻⁴	0.508	+	9	2.53 · 10 ⁻⁴	1.02 · 10 ⁻⁴ – 4.04 · 10 ⁻⁴	0.702	+	n.s.	
scansorial	45	0.233	-0.487 – 0.929	4.64 · 10 ⁻⁵	2.16 · 10 ⁻⁵ – 6.63 · 10 ⁻⁵	0.440	+	44	5.14 · 10 ⁻⁵	4.33 · 10 ⁻⁵ – 5.95 · 10 ⁻⁵	0.861	+	×	
terrestrial	49	1.596	-0.963 – 3.215	7.61 · 10 ⁻⁵	-2.15 · 10 ⁻⁴ – 1.99 · 10 ⁻⁴	0.131	B	48	1.31 · 10 ⁻⁴	1.10 · 10 ⁻⁴ – 1.52 · 10 ⁻⁴	0.838	+	n.s.	
semifossorial	7	-0.264	-0.728 – 0.151	1.96 · 10 ⁻⁴	1.34 · 10 ⁻⁴ – 2.90 · 10 ⁻⁴	0.898	+	6	1.89 · 10 ⁻⁴	7.46 · 10 ⁻⁵ – 3.03 · 10 ⁻⁴	0.873	+	n.s.	
semiaquatic	11	0.705	-0.246 – 2.327	-9.49 · 10 ⁻⁵	-2.74 · 10 ⁻⁴ – 7.69 · 10 ⁻⁵	0.115	B	10	-8.41 · 10 ⁻⁵	-1.47 · 10 ⁻⁴ – -2.11 · 10 ⁻⁵	0.229	-	n.s.	
aquatic	8	1.444	-21.620 – 14.430	5.67 · 10 ⁻⁵	-2.95 · 10 ⁻⁵ – 1.92 · 10 ⁻⁴	0.642	B	7	4.75 · 10 ⁻⁵	1.82 · 10 ⁻⁵ – 7.68 · 10 ⁻⁵	0.809	+	n.s.	
Preferred habitat														
forest	38	0.072	-1.793 – 0.873	8.63 · 10 ⁻⁵	-1.77 · 10 ⁻⁴ – 3.51 · 10 ⁻⁴	0.360	B	37	9.00 · 10 ⁻⁵	6.44 · 10 ⁻⁵ – 1.16 · 10 ⁻⁴	0.545	+	×	
mosaic	40	0.221	-0.909 – 1.351	8.44 · 10 ⁻⁵	-6.70 · 10 ⁻⁶ – 2.51 · 10 ⁻⁴	0.262	B	39	8.51 · 10 ⁻⁵	6.30 · 10 ⁻⁵ – 1.07 · 10 ⁻⁴	0.617	+	n.s.	
open	17	1.326	0.581 – 2.796	7.52 · 10 ⁻⁵	4.65 · 10 ⁻⁴ – 8.83 · 10 ⁻⁵	0.829	B	16	5.63 · 10 ⁻⁵	5.51 · 10 ⁻⁵ – 5.75 · 10 ⁻⁵	0.999	+	×	
freshwater	13	0.775	-0.213 – 2.410	-1.03 · 10 ⁻⁴	-2.93 · 10 ⁻⁴ – 7.53 · 10 ⁻⁵	0.166	B	12	1.17 · 10 ⁻⁴	3.88 · 10 ⁻⁵ – 1.95 · 10 ⁻⁴	0.115	+	n.s.	
marine	10	-1.147	-11.358 – 9.063	5.90 · 10 ⁻⁵	2.75 · 10 ⁻⁶ – 2.03 · 10 ⁻⁴	0.516	+	9	4.69 · 10 ⁻⁵	2.04 · 10 ⁻⁵ – 7.34 · 10 ⁻⁵	0.739	+	n.s.	
variable	19	1.337	-0.936 – 3.611	7.69 · 10 ⁻⁵	-1.97 · 10 ⁻⁴ – 1.32 · 10 ⁻⁴	0.206	B	18	5.59 · 10 ⁻⁵	2.98 · 10 ⁻⁵ – 8.20 · 10 ⁻⁵	0.421	+	n.s.	

III.A10 – HR	traditional regression						PIC regression					
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}
whole sample	137	0.029	0.023 – 0.036	0.156	0.128 – 0.184	0.499	136	0.221	0.186 – 0.256	0.388	+	✓
fissipeds	130	0.034	0.028 – 0.044	0.132	0.101 – 0.157	0.289	129	0.222	0.186 – 0.258	0.381	+	✓
Family												
Canidae	17	0.015	4.19 · 10 ⁻⁴ – 0.046	0.198	0.071 – 0.589	0.500	16	0.216	0.097 – 0.335	0.073	E	n.s.
Mustelidae	32	0.028	0.018 – 0.047	0.186	0.125 – 0.240	0.575	31	0.181	0.120 – 0.242	0.431	E	×
Procyonidae	7	0.024	4.28 · 10 ⁻⁴ – 0.071	0.200	0.060 – 0.674	0.674	6	0.201	0.014 – 0.388	0.662	E	n.s.
Ursidae	7	0.046	0.004 – 0.106	0.076	0.005 – 0.292	0.575	6	0.073	-0.006 – 0.152	0.495	B	n.s.
Felidae	26	0.030	0.023 – 0.040	0.130	0.098 – 0.154	0.823	25	0.134	0.090 – 0.178	0.626	E	×
Herpestidae	12	0.030	0.002 – 0.079	0.174	0.030 – 0.563	0.055	11	0.168	0.055 – 0.281	0.335	E	n.s.
Eupleridae	5	0.025	0.013 – 0.189	0.190	-0.118 – 0.275	0.909	B					
Viverridae	14	0.031	0.020 – 0.067	0.141	0.043 – 0.193	0.651	13	0.140	0.067 – 0.219	0.456	E	n.s.
Locomotor type												
arboreal	7	0.034	5.96 · 10 ⁻⁴ – 0.150	0.140	-0.059 – 0.646	0.408	6	0.124	-3.60 · 10 ⁻⁴ – 0.248	0.584	B	n.s.
semi-arboreal	10	0.024	0.013 – 0.057	0.180	0.069 – 0.252	0.806	9	0.246	0.097 – 0.395	0.690	E	×
scansorial	45	0.038	0.032 – 0.048	0.105	0.080 – 0.125	0.615	44	0.128	0.094 – 0.162	0.484	E	×
terrestrial	49	0.042	0.006 – 0.055	0.109	0.079 – 0.362	0.028	48	0.134	0.096 – 0.172	0.265	E	n.s.
semifossorial	7	0.064	0.014 – 0.092	0.076	0.021 – 0.260	0.227	6	0.064	-0.013 – 0.141	0.273	B	n.s.
semiaquatic	11	0.015	0.006 – 0.115	0.260	0.022 – 0.367	0.583	10	0.291	0.111 – 0.471	0.592	E	n.s.
aquatic	8	0.007	3.94 · 10 ⁻⁵ – 0.603	0.296	-0.058 – 0.744	0.625	7	0.261	0.094 – 0.428	0.794	E	n.s.
Preferred habitat												
forest	38	0.037	0.027 – 0.053	0.125	0.078 – 0.160	0.568	37	0.534	0.405 – 0.663	0.699	+	✓
mosaic	40	0.044	0.007 – 0.055	0.100	0.074 – 0.326	0.164	39	0.167	0.113 – 0.221	0.195	E	n.s.
open	17	0.269	0.152 – 3.309	-0.127	-0.426 – -0.040	0.015	16	0.123	0.056 – 0.190	0.172	E	n.s.
freshwater	13	0.014	0.005 – 0.086	0.265	0.057 – 0.374	0.643	12	0.313	0.153 – 0.473	0.652	+	×
marine	10	0.016	1.12 · 10 ⁻⁵ – 1.949	0.220	-0.153 – 0.840	0.242	9	0.208	0.057 – 0.359	0.497	E	n.s.
variable	19	0.049	0.010 – 0.081	0.085	0.032 – 0.265	0.286	18	0.099	0.055 – 0.143	0.498	E	n.s.

III.A11 – L_r		traditional regression					PIC regression						
whole sample	n	a	95% CI _a	b_{rad}	R	sim.	n	b_{PIC}	95% CI _b	R	sim.	$b_{rad} \neq b_{PIC}$	
fissipeds	137	3.503	2.778 – 4.515	0.362	0.331 – 0.390	0.896	G	136	0.352	0.326 – 0.378	0.899	G	×
Family	130	2.692	2.158 – 3.436	0.397	0.368 – 0.423	0.910	+	129	0.344	0.318 – 0.370	0.900	G	✓
Canidae	17	2.019	0.816 – 10.965	0.454	0.269 – 0.557	0.879	G	16	0.476	0.332 – 0.620	0.839	G	×
Mustelidae	32	3.649	2.378 – 5.600	0.325	0.270 – 0.379	0.893	G	31	0.318	0.266 – 0.370	0.897	G	×
Procyonidae	7	5.160	1.453 – 18.328	0.325	0.168 – 0.482	0.907	B	6	0.300	0.181 – 0.419	0.946	B	×
Ursidae	7	10.348	5.301 – 20.199	0.260	0.203 – 0.317	0.982	E	6	0.261	0.197 – 0.325	0.980	E	×
Felidae	26	8.534	5.789 – 12.579	0.288	0.246 – 0.329	0.940	E	25	0.337	0.282 – 0.392	0.922	G	×
Herpestidae	12	3.392	1.410 – 8.158	0.368	0.245 – 0.492	0.880	B	11	0.354	0.234 – 0.474	0.881	B	×
Eupleridae	5	8.373	1.676 – 41.831	0.269	0.048 – 0.491	0.894	B						
Viverridae	14	8.179	4.764 – 14.044	0.262	0.195 – 0.329	0.914	B	13	0.291	0.156 – 0.426	0.682	B	×
Locomotor type													
arboreal	7	3.606	0.891 – 14.601	0.363	0.190 – 0.536	0.910	B	6	0.368	0.184 – 0.552	0.915	B	×
semiarboreal	10	9.473	6.558 – 13.683	0.250	0.202 – 0.298	0.972	E	9	0.226	0.133 – 0.319	0.872	E	×
scansorial	45	5.991	4.633 – 7.748	0.317	0.290 – 0.345	0.958	G	44	0.336	0.300 – 0.372	0.939	G	×
terrestrial	49	1.709	1.167 – 2.768	0.457	0.396 – 0.506	0.941	+	48	0.361	0.312 – 0.410	0.890	G	✓
semifossorial	7	3.434	0.908 – 12.985	0.342	0.175 – 0.510	0.905	B	6	0.362	0.184 – 0.540	0.918	B	×
semiaquatic	11	4.515	1.267 – 16.083	0.293	0.144 – 0.442	0.739	B	10	0.239	0.142 – 0.336	0.850	B	×
aquatic	8	2.372	0.424 – 13.268	0.347	0.203 – 0.491	0.909	B	7	0.338	0.192 – 0.484	0.911	B	×
Preferred habitat													
forest	38	4.997	3.581 – 6.973	0.324	0.284 – 0.364	0.930	G	37	0.317	0.270 – 0.364	0.900	G	×
mosaic	40	2.560	1.792 – 3.658	0.406	0.365 – 0.448	0.951	+	39	0.371	0.335 – 0.407	0.955	+	×
open	17	1.912	0.957 – 6.009	0.451	0.309 – 0.531	0.924	G	16	0.384	0.289 – 0.479	0.895	G	×
freshwater	13	3.111	0.609 – 15.904	0.352	0.160 – 0.544	0.571	B	12	0.279	0.142 – 0.416	0.680	B	×
marine	10	2.069	0.719 – 5.956	0.362	0.272 – 0.452	0.952	G	9	0.345	0.253 – 0.437	0.947	G	×
variable	19	2.204	1.124 – 4.321	0.427	0.352 – 0.501	0.940	+	18	0.312	0.247 – 0.377	0.915	B	✓

III.A12 – d_{sr}		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	h_{rad}	R	sim.	n	h_{PIC}	95% CI_b	R	sim.	h_{rad} ≠ h_{PIC}	
fissipeds	137	0.282	0.244 – 0.327	0.335	0.318 – 0.352	0.961	G	136	0.358	0.331 – 0.385	0.894	B	×
Family	130	0.270	0.233 – 0.316	0.341	0.323 – 0.357	0.956	G	129	0.357	0.330 – 0.384	0.902	B	×
Canidae	17	0.096	0.052 – 0.327	0.465	0.329 – 0.531	0.936	B	16	0.427	0.326 – 0.528	0.905	B	×
Mustelidae	32	0.291	0.202 – 0.421	0.326	0.279 – 0.373	0.922	G	31	0.342	0.277 – 0.407	0.863	B	×
Procyonidae	7	0.485	0.154 – 1.528	0.275	0.133 – 0.417	0.893	B	6	0.254	0.129 – 0.379	0.917	B	×
Ursidae	7	0.314	0.035 – 2.851	0.320	0.132 – 0.508	0.860	B	6	0.328	0.127 – 0.529	0.870	B	n.s.
Felidae	26	0.154	0.107 – 0.221	0.391	0.353 – 0.430	0.972	E	25	0.395	0.339 – 0.451	0.942	E	×
Herpestidae	12	0.339	0.150 – 0.770	0.321	0.206 – 0.436	0.862	B	11	0.367	0.248 – 0.486	0.891	B	×
Eupleridae	5	0.325	0.129 – 0.819	0.318	0.191 – 0.445	0.976	B						
Viverridae	14	0.331	0.197 – 0.558	0.314	0.250 – 0.379	0.945	B	13	0.349	0.217 – 0.481	0.803	B	×
Locomotor type													
arboreal	7	0.219	0.068 – 0.705	0.361	0.216 – 0.506	0.937	B	6	0.362	0.208 – 0.516	0.939	B	×
semi-arboreal	10	0.672	0.443 – 1.021	0.228	0.173 – 0.282	0.956	-	9	0.232	0.164 – 0.300	0.937	-	×
scansorial	45	0.247	0.196 – 0.312	0.346	0.321 – 0.371	0.971	G	44	0.367	0.327 – 0.407	0.935	B	×
terrestrial	49	0.248	0.195 – 0.343	0.358	0.320 – 0.387	0.959	B	48	0.342	0.299 – 0.385	0.903	B	×
semifossorial	7	0.255	0.098 – 0.662	0.345	0.225 – 0.465	0.953	B	6	0.362	0.220 – 0.504	0.949	B	×
semiaquatic	11	0.183	0.072 – 0.466	0.382	0.273 – 0.492	0.925	B	10	0.459	0.286 – 0.632	0.872	B	×
aquatic	8	0.020	0.001 – 0.483	0.545	0.277 – 0.813	0.871	B	7	0.544	0.136 – 0.952	0.700	B	n.s.
Preferred habitat													
forest	38	0.276	0.195 – 0.389	0.337	0.296 – 0.379	0.931	B	37	0.365	0.312 – 0.418	0.903	B	×
mosaic	40	0.293	0.235 – 0.365	0.333	0.308 – 0.359	0.973	G	39	0.354	0.319 – 0.389	0.954	B	×
open	17	0.257	0.173 – 0.432	0.351	0.290 – 0.397	0.967	B	16	0.375	0.298 – 0.452	0.929	B	×
freshwater	13	0.165	0.070 – 0.386	0.396	0.296 – 0.496	0.924	B	12	0.479	0.312 – 0.646	0.855	B	×
marine	10	0.114	0.023 – 0.567	0.401	0.263 – 0.538	0.908	B	9	0.401	0.147 – 0.655	0.654	B	n.s.
variable	19	0.240	0.154 – 0.372	0.355	0.306 – 0.403	0.963	B	18	0.345	0.278 – 0.412	0.927	B	×

III.A13 – d_{tr}		traditional regression						PIC regression					
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}
fissipeds	137	0.140	0.117 – 0.171	0.442	0.420 – 0.463	0.962	+	136	0.403	0.375 – 0.431	0.910	+	✓
Family	130	0.160	0.136 – 0.198	0.425	0.400 – 0.444	0.953	+	129	0.389	0.361 – 0.417	0.914	E	✓
Canidae	17	0.134	0.081 – 0.348	0.465	0.364 – 0.519	0.947	E	16	0.478	0.388 – 0.570	0.938	+	×
Mustelidae	32	0.239	0.169 – 0.338	0.352	0.308 – 0.397	0.942	B	31	0.382	0.308 – 0.456	0.857	B	×
Procyonidae	7	0.320	0.077 – 1.335	0.355	0.178 – 0.531	0.901	B	6	0.347	0.163 – 0.531	0.904	B	×
Ursidae	7	0.301	0.038 – 2.387	0.357	0.181 – 0.534	0.903	B	6	0.317	0.167 – 0.467	0.925	B	×
Felidae	26	0.240	0.188 – 0.306	0.389	0.363 – 0.415	0.988	E	25	0.379	0.345 – 0.413	0.977	E	×
Herpestidae	12	0.336	0.112 – 1.002	0.318	0.165 – 0.472	0.729	B	11	0.310	0.158 – 0.462	0.728	B	×
Eupleridae	5	0.161	0.072 – 0.362	0.438	0.326 – 0.549	0.990	B						
Viverridae	14	0.253	0.116 – 0.552	0.360	0.263 – 0.456	0.904	B	13	0.420	0.265 – 0.575	0.816	B	×
Locomotor type													
arboreal	7	0.245	0.066 – 0.909	0.383	0.220 – 0.545	0.929	B	6	0.386	0.216 – 0.556	0.935	B	×
semiarboreal	10	0.213	0.090 – 0.502	0.397	0.286 – 0.509	0.939	B	9	0.366	0.253 – 0.479	0.929	B	×
scansorial	45	0.203	0.162 – 0.256	0.401	0.376 – 0.425	0.980	+	44	0.387	0.353 – 0.421	0.958	E	×
terrestrial	49	0.127	0.093 – 0.195	0.458	0.406 – 0.494	0.948	+	48	0.375	0.320 – 0.430	0.865	B	✓
semifossorial	7	0.209	0.051 – 0.860	0.376	0.157 – 0.554	0.911	B	6	0.401	0.182 – 0.620	0.898	B	×
semiaquatic	11	0.385	0.185 – 0.800	0.294	0.208 – 0.380	0.922	B	10	0.320	0.228 – 0.412	0.928	B	×
aquatic	8	0.031	0.003 – 0.277	0.581	0.398 – 0.764	0.949	+	7	0.500	0.264 – 0.736	0.893	B	×
Preferred habitat													
forest	38	0.170	0.115 – 0.253	0.416	0.368 – 0.463	0.940	E	37	0.389	0.331 – 0.447	0.899	B	×
mosaic	40	0.176	0.130 – 0.239	0.416	0.380 – 0.451	0.966	+	39	0.362	0.327 – 0.397	0.955	B	✓
open	17	0.143	0.095 – 0.324	0.446	0.347 – 0.490	0.958	E	16	0.395	0.308 – 0.482	0.918	B	×
freshwater	13	0.345	0.143 – 0.829	0.314	0.211 – 0.418	0.869	B	12	0.336	0.234 – 0.438	0.893	B	×
marine	10	0.039	0.008 – 0.196	0.556	0.418 – 0.694	0.953	+	9	0.505	0.354 – 0.656	0.934	E	×
variable	19	0.141	0.085 – 0.232	0.449	0.393 – 0.504	0.970	+	18	0.391	0.331 – 0.451	0.954	B	×

III.A14 – P	traditional regression						PIC regression						
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	137	0.101	0.085 – 0.122	0.426	0.404 – 0.446	0.956	+	136	0.412	0.380 – 0.444	0.892	+	×
fissipeds	130	0.088	0.074 – 0.108	0.444	0.421 – 0.464	0.952	+	129	0.414	0.381 – 0.447	0.888	+	×
Family													
Canidae	17	0.046	0.016 – 0.095	0.514	0.428 – 0.624	0.960	+	16	0.488	0.396 – 0.580	0.940	+	×
Mustelidae	32	0.161	0.110 – 0.236	0.350	0.302 – 0.399	0.929	G	31	0.347	0.276 – 0.418	0.838	G	×
Procyonidae	7	0.186	0.028 – 1.241	0.352	0.117 – 0.587	0.814	B	6	<i>0.325</i>	<i>0.095 – 0.555</i>	<i>0.820</i>	<i>B</i>	n.s.
Ursidae	7	0.147	0.016 – 1.360	0.399	0.210 – 0.589	0.911	B	6	0.357	0.159 – 0.555	0.894	B	×
Felidae	26	0.182	0.131 – 0.253	0.380	0.345 – 0.415	0.976	+	25	0.369	0.325 – 0.413	0.959	G	×
Herpestidae	12	0.164	0.075 – 0.361	0.374	0.264 – 0.484	0.908	G	11	0.353	0.241 – 0.465	0.897	B	×
Eupleridae	5	0.027	0.001 – 1.001	0.611	0.113 – 1.108	0.896	B						
Viverridae	14	0.096	0.029 – 0.321	0.424	0.275 – 0.574	0.828	G	13	0.483	0.292 – 0.674	0.783	G	×
Locomotor type													
arboreal	7	0.026	0.001 – 0.455	0.588	0.233 – 0.943	0.851	B	6	<i>0.589</i>	<i>0.211 – 0.967</i>	<i>0.935</i>	<i>B</i>	n.s.
semiarboreal	10	0.063	0.022 – 0.180	0.496	0.360 – 0.633	0.941	+	9	0.475	0.274 – 0.676	0.929	G	×
scansorial	45	0.089	0.066 – 0.119	0.448	0.416 – 0.480	0.972	+	44	0.421	0.373 – 0.469	0.958	+	×
terrestrial	49	0.092	0.070 – 0.130	0.442	0.400 – 0.475	0.956	+	48	0.294	0.255 – 0.333	0.865	G	✓
semifossorial	7	0.280	0.110 – 0.709	0.292	0.175 – 0.409	0.937	B	6	0.313	0.178 – 0.448	0.898	B	×
semiaquatic	11	0.117	0.028 – 0.478	0.386	0.220 – 0.551	0.823	B	10	<i>0.350</i>	<i>0.100 – 0.560</i>	<i>0.928</i>	<i>B</i>	n.s.
aquatic	8	0.037	0.004 – 0.354	0.487	0.298 – 0.676	0.922	G	7	0.481	0.277 – 0.685	0.893	G	×
Preferred habitat													
forest	38	0.064	0.039 – 0.104	0.482	0.422 – 0.541	0.931	+	37	0.478	0.398 – 0.558	0.870	+	×
mosaic	40	0.112	0.083 – 0.149	0.421	0.388 – 0.455	0.970	+	39	0.383	0.336 – 0.430	0.927	+	×
open	17	0.080	0.059 – 0.138	0.459	0.396 – 0.495	0.978	+	16	0.429	0.368 – 0.490	0.966	+	×
freshwater	13	0.118	0.032 – 0.443	0.389	0.233 – 0.544	0.799	B	12	0.380	0.215 – 0.545	0.736	B	×
marine	10	0.075	0.020 – 0.285	0.433	0.319 – 0.546	0.947	G	9	0.394	0.241 – 0.547	0.886	B	×
variable	19	0.105	0.063 – 0.176	0.431	0.374 – 0.488	0.966	+	18	0.396	0.325 – 0.467	0.936	G	×

III.A15 – RR		traditional regression				PIC regression							
whole sample	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}	
fissipeds	137	0.250	0.209 – 4.676	-0.158	-0.496 – -0.135	0.021	-	136	0.200	0.169 – 0.231	0.409	+	n.s.
Family	130	0.258	0.196 – 0.322	-0.169	-0.196 – -0.134	0.214	-	129	0.198	0.167 – 0.229	0.422	+	✓
Canidae	17	0.005	1.27 · 10 ⁻⁵ – 0.025	0.260	0.080 – 0.915	0.141	E	16	-0.324	-0.499 – -0.149	0.223	-	n.s.
Mustelidae	32	0.028	0.003 – 0.039	0.139	0.097 – 0.432	0.080	E	31	0.161	0.101 – 0.221	0.062	E	n.s.
Procyonidae	7	0.121	0.033 – 0.375	-0.081	-0.224 – 0.070	0.585	B	6	-0.088	-0.180 – 0.004	0.542	B	n.s.
Ursidae	7	0.008	1.43 · 10 ⁻⁵ – 0.055	0.169	0.002 – 0.712	0.082	E	6	0.168	-0.038 – 0.374	0.142	B	n.s.
Felidae	26	0.011	0.008 – 0.017	0.155	0.112 – 0.189	0.709	E	25	0.165	0.103 – 0.227	0.458	E	×
Herpestidae	12	0.449	0.155 – 46.774	-0.259	-0.922 – -0.116	0.177	-	11	0.243	0.070 – 0.416	0.096	E	n.s.
Eupleridae	5	0.028	0.005 – 0.107	0.093	-0.113 – 0.348	0.735	B						
Viverridae	14	0.026	0.019 – 0.046	0.108	0.038 – 0.147	0.543	E	13	0.108	0.045 – 0.171	0.396	E	n.s.
Locomotor type													
arboreal	7	0.009	5.40 · 10 ⁻⁷ – 0.029	0.237	0.106 – 1.454	0.047	E	6	-0.190	-0.425 – 0.045	0.030	B	n.s.
semiarboreal	10	0.124	0.085 – 0.691	-0.095	-0.326 – -0.051	0.263	-	9	0.106	0.018 – 0.194	0.115	E	n.s.
scansorial	45	0.016	0.011 – 0.023	0.129	0.093 – 0.171	0.242	E	44	0.142	0.099 – 0.185	0.189	E	n.s.
terrestrial	49	0.247	0.163 – 0.328	-0.164	-0.201 – -0.110	0.528	-	48	-0.165	-0.214 – -0.116	0.073	-	n.s.
semifossorial	7	0.033	0.004 – 0.067	0.104	0.002 – 0.361	0.193	E	6	0.120	-0.029 – 0.269	0.064	B	n.s.
semiaquatic	11	0.010	0.003 – 0.079	0.252	0.027 – 0.387	0.547	E	10	0.248	0.131 – 0.365	0.789	+	n.s.
aquatic	8	0.004	3.55 · 10 ⁻⁶ – 0.205	0.260	-0.061 – 0.832	0.613	B	7	0.266	0.239 – 0.293	0.276	+	n.s.
Preferred habitat													
forest	38	0.017	0.001 – 0.026	0.155	0.103 – 0.530	0.082	E	37	0.249	0.190 – 0.308	0.715	+	n.s.
mosaic	40	0.226	0.151 – 0.303	-0.153	-0.192 – -0.101	0.412	-	39	-0.125	-0.165 – -0.085	0.216	-	n.s.
open	17	0.264	0.098 – 0.486	-0.183	-0.256 – -0.055	0.428	-	16	0.156	0.070 – 0.242	0.029	E	n.s.
freshwater	13	0.004	0.001 – 0.040	0.336	0.097 – 0.510	0.491	E	12	0.384	0.169 – 0.599	0.550	+	n.s.
marine	10	0.013	6.75 · 10 ⁻⁶ – 0.127	0.164	-0.028 – 0.788	0.113	B	9	-0.214	-0.383 – -0.045	0.324	-	n.s.
variable	19	0.207	0.128 – 4.090	-0.145	-0.460 – -0.081	0.404	-	18	0.134	0.067 – 0.201	0.251	E	n.s.

III.A16 – L _u	traditional regression						PIC regression						
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}	
whole sample	136	3.841	3.046 – 4.922	0.358	0.327 – 0.385	0.897	G	135	0.347	0.321 – 0.373	0.897	G	×
fissipeds	129	2.926	2.411 – 3.644	0.394	0.367 – 0.418	0.916	+	128	0.340	0.314 – 0.366	0.902	G	✓
Family													
Canidae	16	2.170	0.856 – 12.076	0.452	0.258 – 0.556	0.884	G	15	0.474	0.326 – 0.622	0.841	G	×
Mustelidae	32	4.037	2.665 – 6.115	0.322	0.269 – 0.375	0.898	G	31	0.315	0.263 – 0.367	0.896	G	×
Procyonidae	7	5.692	1.569 – 20.645	0.318	0.159 – 0.478	0.900	B	6	0.293	0.174 – 0.412	0.945	B	×
Ursidae	7	10.831	6.606 – 17.759	0.262	0.220 – 0.304	0.990	E	6	0.263	0.216 – 0.310	0.990	E	×
Felidae	26	9.200	6.415 – 13.195	0.286	0.248 – 0.324	0.948	E	25	0.317	0.267 – 0.367	0.928	G	×
Herpestidae	12	3.710	1.629 – 8.452	0.363	0.247 – 0.478	0.892	B	11	0.334	0.230 – 0.438	0.900	B	×
Eupleridae	5	8.643	2.236 – 33.406	0.270	0.083 – 0.456	0.927	B						
Viverridae	14	8.785	5.053 – 15.275	0.260	0.191 – 0.328	0.908	E	13	0.291	0.147 – 0.435	0.631	B	×
Locomotor type													
arboreal	7	3.573	0.863 – 14.800	0.371	0.195 – 0.547	0.911	B	6	0.377	0.190 – 0.564	0.917	B	×
semiarboreal	10	9.563	6.305 – 14.505	0.257	0.203 – 0.311	0.966	E	9	0.227	0.130 – 0.324	0.860	E	×
scansorial	45	6.234	4.849 – 8.013	0.319	0.292 – 0.346	0.961	G	44	0.332	0.299 – 0.365	0.945	G	×
terrestrial	48	1.893	1.332 – 3.071	0.451	0.392 – 0.497	0.944	+	47	0.358	0.309 – 0.407	0.888	G	✓
semifossorial	7	3.904	1.139 – 13.375	0.333	0.178 – 0.488	0.914	B	6	0.349	0.180 – 0.518	0.921	B	×
semiaquatic	11	5.026	1.558 – 16.210	0.290	0.153 – 0.427	0.779	B	10	0.240	0.145 – 0.335	0.856	B	×
aquatic	8	4.077	0.572 – 29.063	0.303	0.139 – 0.468	0.840	B	7	0.298	0.123 – 0.473	0.830	B	×
Preferred habitat													
forest	38	5.048	3.609 – 7.061	0.330	0.289 – 0.370	0.931	G	37	0.318	0.271 – 0.365	0.899	G	×
mosaic	39	2.803	1.982 – 3.965	0.401	0.361 – 0.442	0.954	+	38	0.366	0.330 – 0.402	0.956	G	×
open	17	2.031	0.993 – 6.097	0.451	0.310 – 0.534	0.927	G	16	0.384	0.291 – 0.477	0.899	G	×
freshwater	13	3.620	0.781 – 16.783	0.343	0.163 – 0.523	0.610	B	12	0.275	0.141 – 0.409	0.689	B	×
marine	10	2.697	0.730 – 9.973	0.343	0.231 – 0.454	0.917	B	9	0.332	0.213 – 0.451	0.903	B	×
variable	19	2.532	1.322 – 4.847	0.418	0.346 – 0.490	0.942	+	18	0.307	0.246 – 0.368	0.922	B	✓

III.A17 – d_{SU}		traditional regression					PLC regression						
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}
fissipeds	136	0.263	0.223 – 0.320	0.369	0.348 – 0.387	0.948	E	135	0.365	0.336 – 0.394	0.886	E	×
Family	129	0.257	0.216 – 0.312	0.372	0.350 – 0.392	0.936	E	128	0.364	0.334 – 0.394	0.885	E	×
Canidae	16	0.057	0.018 – 0.291	0.505	0.325 – 0.626	0.915	B	15	0.433	0.308 – 0.558	0.865	B	×
Mustelidae	32	0.320	0.231 – 0.442	0.345	0.304 – 0.386	0.947	B	31	0.353	0.289 – 0.417	0.873	B	×
Procyonidae	7	0.167	0.011 – 2.592	0.457	0.117 – 0.796	0.763	B	<i>6</i>	<i>0.456</i>	<i>0.075 – 0.837</i>	<i>0.741</i>	<i>B</i>	n.s.
Ursidae	<i>7</i>	<i>1.015</i>	<i>0.098 – 10.539</i>	<i>0.258</i>	<i>0.059 – 0.457</i>	<i>0.741</i>	<i>B</i>	<i>6</i>	<i>0.246</i>	<i>0.040 – 0.452</i>	<i>0.738</i>	<i>B</i>	n.s.
Felidae	26	0.309	0.210 – 0.455	0.358	0.317 – 0.399	0.963	B	25	0.349	0.294 – 0.404	0.928	B	×
Herpestidae	12	0.265	0.101 – 0.697	0.363	0.228 – 0.499	0.848	B	11	0.357	0.215 – 0.499	0.831	B	×
Eupleridae	5	0.184	0.056 – 0.603	0.423	0.259 – 0.586	0.978	B						
Viverridae	14	0.374	0.142 – 0.985	0.330	0.210 – 0.450	0.815	B	<i>13</i>	<i>0.365</i>	<i>0.168 – 0.562</i>	<i>0.527</i>	<i>B</i>	n.s.
Locomotor type													
arboreal	7	0.192	0.048 – 0.770	0.427	0.254 – 0.599	0.936	B	6	0.435	0.242 – 0.628	0.934	B	×
semiarboreal	10	0.555	0.320 – 0.964	0.295	0.223 – 0.367	0.954	C	9	0.275	0.173 – 0.377	0.896	B	×
scansorial	45	0.266	0.198 – 0.357	0.376	0.344 – 0.408	0.961	E	44	0.366	0.315 – 0.417	0.891	B	×
terrestrial	48	0.298	0.226 – 0.407	0.338	0.304 – 0.372	0.931	C	47	0.359	0.304 – 0.414	0.857	B	×
semifossorial	7	0.258	0.127 – 0.524	0.379	0.290 – 0.468	0.979	B	6	0.382	0.266 – 0.498	0.970	B	×
semiaquatic	11	0.319	0.166 – 0.614	0.344	0.267 – 0.420	0.955	B	10	0.345	0.236 – 0.454	0.912	B	×
aquatic	8	0.115	0.007 – 1.916	0.434	0.198 – 0.670	0.839	B	<i>7</i>	<i>0.462</i>	<i>0.143 – 0.781</i>	<i>0.753</i>	<i>B</i>	n.s.
Preferred habitat													
forest	38	0.203	0.130 – 0.319	0.408	0.353 – 0.462	0.918	+	37	0.401	0.335 – 0.467	0.874	E	×
mosaic	39	0.297	0.220 – 0.402	0.358	0.323 – 0.393	0.956	B	38	0.358	0.314 – 0.402	0.931	B	×
open	17	0.199	0.116 – 0.433	0.385	0.306 – 0.452	0.915	B	16	0.340	0.261 – 0.419	0.909	B	×
freshwater	13	0.299	0.128 – 0.700	0.355	0.255 – 0.455	0.906	B	12	0.388	0.226 – 0.550	0.784	B	×
marine	10	0.245	0.068 – 0.878	0.370	0.261 – 0.480	0.933	B	9	0.368	0.206 – 0.530	0.849	B	×
variable	19	0.297	0.186 – 0.475	0.351	0.299 – 0.403	0.957	B	18	0.358	0.298 – 0.418	0.945	B	×

III.A18 – d _{tu}	traditional regression						PIC regression					
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}
whole sample	136	0.199	0.169 – 0.238	0.370	0.351 – 0.389	E	135	0.374	0.346 – 0.402	0.897	E	×
fissipeds	129	0.182	0.152 – 0.215	0.382	0.363 – 0.403	E	128	0.482	0.427 – 0.537	0.760	+	✓
Family												
Canidae	16	0.150	0.055 – 0.518	0.410	0.274 – 0.518	B	15	0.411	0.290 – 0.532	0.861	B	×
Mustelidae	32	0.247	0.166 – 0.367	0.334	0.283 – 0.384	B	31	0.368	0.294 – 0.442	0.844	B	×
Procyonidae	7	0.435	0.122 – 1.557	0.270	0.112 – 0.427	B	6	0.281	0.090 – 0.472	0.837	B	n.s.
Ursidae	7	0.173	0.010 – 3.127	0.395	0.148 – 0.641	B	6	0.409	0.138 – 0.680	0.845	B	n.s.
Felidae	26	0.119	0.068 – 0.208	0.419	0.360 – 0.479	E	25	0.388	0.314 – 0.462	0.892	B	×
Herpestidae	12	0.233	0.096 – 0.569	0.370	0.245 – 0.495	B	11	0.367	0.246 – 0.488	0.887	B	×
Eupleridae	5	0.225	0.154 – 0.328	0.363	0.310 – 0.415	B						
Viverridae	14	0.323	0.166 – 0.629	0.320	0.237 – 0.402	B	13	0.282	0.152 – 0.412	0.689	B	×
Locomotor type												
arboreal	7	0.250	0.068 – 0.914	0.342	0.181 – 0.502	B	6	0.222	0.219 – 0.225	1.000	-	×
semiarboreal	10	0.353	0.194 – 0.644	0.310	0.232 – 0.388	B	9	0.287	0.182 – 0.392	0.900	B	×
scansorial	45	0.139	0.101 – 0.191	0.408	0.374 – 0.442	E	44	0.409	0.352 – 0.466	0.893	E	×
terrestrial	48	0.186	0.148 – 0.242	0.386	0.357 – 0.412	E	47	0.375	0.329 – 0.421	0.909	B	×
semifossorial	7	0.106	0.053 – 0.524	0.374	0.230 – 0.518	B	6	0.377	0.225 – 0.529	0.945	B	×
semiaquatic	11	0.325	0.105 – 1.007	0.307	0.174 – 0.439	B	10	0.480	0.213 – 0.747	0.691	B	×
aquatic	8	0.033	0.006 – 0.181	0.503	0.361 – 0.645	E	7	0.479	0.336 – 0.622	0.959	E	×
Preferred habitat												
forest	38	0.194	0.134 – 0.281	0.378	0.334 – 0.423	E	37	0.369	0.315 – 0.423	0.901	B	×
mosaic	39	0.181	0.131 – 0.251	0.384	0.346 – 0.421	E	38	0.379	0.327 – 0.431	0.913	B	×
open	17	0.158	0.118 – 0.241	0.399	0.354 – 0.432	E	16	0.374	0.303 – 0.445	0.940	B	×
freshwater	13	0.296	0.109 – 0.802	0.316	0.199 – 0.433	B	12	0.439	0.242 – 0.636	0.744	B	×
marine	10	0.101	0.029 – 0.359	0.415	0.307 – 0.523	B	9	0.381	0.219 – 0.543	0.860	B	×
variable	19	0.168	0.105 – 0.269	0.389	0.336 – 0.441	E	18	0.409	0.331 – 0.487	0.928	B	×

III.A19 – O		traditional regression					PIC regression						
whole sample	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
fissipeds	136	0.721	0.633 – 0.831	0.368	0.351 – 0.384	0.976	+	135	0.369	0.349 – 0.389	0.950	+	×
Family	129	0.674	0.588 – 0.779	0.377	0.359 – 0.393	0.974	+	128	0.370	0.350 – 0.390	0.949	+	×
Canidae	16	0.425	0.263 – 0.902	0.436	0.352 – 0.488	0.959	+	15	0.378	0.298 – 0.458	0.930	G	×
Mustelidae	32	0.641	0.486 – 0.846	0.372	0.337 – 0.407	0.967	+	31	0.369	0.323 – 0.415	0.942	G	×
Procyonidae	7	0.543	0.068 – 4.328	0.400	0.143 – 0.657	0.829	B	6	0.409	0.077 – 0.741	0.756	B	n.s.
Ursidae	7	1.978	0.319 – 12.275	0.269	0.113 – 0.424	0.864	B	6	0.276	0.097 – 0.455	0.853	B	n.s.
Felidae	26	0.776	0.615 – 0.977	0.370	0.345 – 0.394	0.987	+	25	0.362	0.327 – 0.397	0.974	G	×
Herpestidae	12	0.962	0.588 – 1.573	0.334	0.265 – 0.403	0.956	G	11	0.347	0.288 – 0.406	0.971	G	×
Eupleridae	5	0.612	0.229 – 1.632	0.402	0.267 – 0.537	0.983	G						
Viverridae	14	0.626	0.350 – 1.122	0.384	0.312 – 0.456	0.954	G	13	0.405	0.323 – 0.487	0.948	G	×
Locomotor type													
arboreal	7	0.402	0.093 – 1.735	0.440	0.259 – 0.621	0.934	B	6	0.377	0.376 – 0.378	1.000	+	×
semiarboreal	10	0.560	0.311 – 1.008	0.401	0.325 – 0.478	0.972	G	9	0.378	0.245 – 0.511	0.906	B	×
scansorial	45	0.789	0.633 – 0.983	0.360	0.337 – 0.384	0.976	+	44	0.358	0.323 – 0.393	0.948	G	×
terrestrial	48	0.605	0.494 – 0.789	0.391	0.358 – 0.417	0.975	+	47	0.359	0.327 – 0.391	0.953	G	×
semifossorial	7	0.596	0.316 – 1.124	0.400	0.320 – 0.480	0.985	G	6	0.423	0.289 – 0.557	0.967	G	×
semiaquatic	11	0.640	0.281 – 1.459	0.375	0.278 – 0.471	0.940	G	10	0.419	0.295 – 0.543	0.923	G	×
aquatic	8	0.186	0.012 – 2.791	0.469	0.242 – 0.696	0.875	B	7	0.458	0.284 – 0.632	0.932	G	×
Preferred habitat													
forest	38	0.599	0.457 – 0.784	0.391	0.358 – 0.423	0.969	+	37	0.403	0.361 – 0.445	0.952	+	×
mosaic	39	0.677	0.543 – 0.843	0.377	0.352 – 0.403	0.979	+	38	0.381	0.351 – 0.411	0.972	+	×
open	17	0.569	0.474 – 0.787	0.400	0.361 – 0.421	0.991	+	16	0.372	0.336 – 0.408	0.985	+	×
freshwater	13	0.690	0.296 – 1.610	0.367	0.268 – 0.467	0.913	G	12	0.442	0.289 – 0.595	0.857	G	×
marine	10	0.520	0.148 – 1.827	0.384	0.276 – 0.491	0.939	G	9	0.354	0.226 – 0.482	0.902	B	×
variable	19	0.818	0.569 – 1.175	0.360	0.320 – 0.400	0.976	G	18	0.329	0.291 – 0.367	0.975	G	×

III.A20 - θ	traditional regression				PIC regression									
	n	a	95% CI _a	b_{rad}	R	sim.	n	b_{PIC}	95% CI _b	R	sim.	$b_{\text{rad}} \neq b_{\text{PIC}}$		
whole sample	136	0.078	0.008 - 0.090	9.70 · 10 ⁻⁷	4.60 · 10 ⁻⁷	-3.56 · 10 ⁻⁷	0.048	-	135	2.44 · 10 ⁻⁶	2.02 · 10 ⁻⁶	-2.86 · 10 ⁻⁶	0.047	n.s.
fissipeds	129	0.132	0.115 - 0.148	-1.52 · 10 ⁻⁶	-2.06 · 10 ⁻⁶	-9.73 · 10 ⁻¹⁰	0.100	-	128	2.58 · 10 ⁻⁶	2.13 · 10 ⁻⁶	-3.03 · 10 ⁻⁶	0.018	n.s.
Family														
Canidae	16	0.019	-0.059 - 0.042	3.63 · 10 ⁻⁶	5.98 · 10 ⁻⁷	-1.22 · 10 ⁻⁵	0.447	-	15	3.63 · 10 ⁻⁶	1.99 · 10 ⁻⁶	-5.27 · 10 ⁻⁶	0.623	n.s.
Mustelidae	32	0.110	-0.041 - 0.141	1.17 · 10 ⁻⁵	-1.51 · 10 ⁻⁷	-3.71 · 10 ⁻⁵	0.064	-	31	-2.93 · 10 ⁻⁵	-4.02 · 10 ⁻⁵	-1.84 · 10 ⁻⁵	0.081	n.s.
Procyonidae	7	0.025	-0.047 - 0.096	1.95 · 10 ⁻⁵	7.02 · 10 ⁻⁶	-3.15 · 10 ⁻⁵	0.689	-	6	2.08 · 10 ⁻⁵	-2.00 · 10 ⁻⁸	-4.16 · 10 ⁻⁵	0.594	n.s.
Ursidae	7	0.033	-0.020 - 0.085	2.52 · 10 ⁻⁷	-2.84 · 10 ⁻⁷	-1.63 · 10 ⁻⁶	0.241	-	6	2.71 · 10 ⁻⁷	-6.21 · 10 ⁻⁸	-6.04 · 10 ⁻⁷	0.154	n.s.
Felidae	26	0.059	-0.022 - 0.082	1.12 · 10 ⁻⁶	-4.11 · 10 ⁻⁷	-4.92 · 10 ⁻⁶	0.073	-	25	-1.43 · 10 ⁻⁶	-2.03 · 10 ⁻⁶	-8.26 · 10 ⁻⁷	0.006	n.s.
Herpestidae	12	0.027	-0.020 - 0.071	4.82 · 10 ⁻⁵	6.09 · 10 ⁻⁶	6.51 · 10 ⁻⁵	0.588	-	11	5.04 · 10 ⁻⁵	1.92 · 10 ⁻⁵	-8.16 · 10 ⁻⁵	0.497	n.s.
Eupleridae	5	0.085	0.018 - 0.152	2.40 · 10 ⁻⁵	1.85 · 10 ⁻⁴	-1.28 · 10 ⁻⁴	0.866	-	-	-	-	-	-	-
Viverridae	14	0.113	0.090 - 0.179	-7.14 · 10 ⁻⁶	-2.80 · 10 ⁻⁵	-3.26 · 10 ⁻⁶	0.428	-	13	-5.48 · 10 ⁻⁵	-8.94 · 10 ⁻⁵	-2.02 · 10 ⁻⁵	0.134	n.s.
Locomotor type														
arboreal	7	0.095	0.004 - 0.260	-7.49 · 10 ⁻⁶	-6.38 · 10 ⁻⁵	-2.51 · 10 ⁻⁵	0.462	-	6	-7.17 · 10 ⁻⁶	-7.76 · 10 ⁻⁶	-6.58 · 10 ⁻⁶	0.998	n.s.
semiarboreal	10	0.202	0.108 - 0.378	-2.22 · 10 ⁻⁵	-9.98 · 10 ⁻⁵	-3.73 · 10 ⁻⁵	0.168	-	9	-1.74 · 10 ⁻⁵	-3.18 · 10 ⁻⁵	-3.00 · 10 ⁻⁶	0.131	n.s.
scansorial	45	0.135	0.112 - 0.196	-1.04 · 10 ⁻⁶	-2.87 · 10 ⁻⁶	-2.12 · 10 ⁻⁷	0.180	-	44	-1.33 · 10 ⁻⁶	-1.74 · 10 ⁻⁶	-9.20 · 10 ⁻⁷	0.038	n.s.
terrestrial	48	0.111	0.060 - 0.167	-1.45 · 10 ⁻⁶	-3.93 · 10 ⁻⁶	-6.65 · 10 ⁻⁶	0.052	-	47	1.50 · 10 ⁻⁵	-2.87 · 10 ⁻⁵	-5.87 · 10 ⁻⁵	0.193	n.s.
semifossorial	7	0.047	-0.013 - 0.088	1.75 · 10 ⁻⁵	1.11 · 10 ⁻⁵	-2.56 · 10 ⁻⁵	0.885	-	6	1.68 · 10 ⁻⁵	3.50 · 10 ⁻⁶	-3.01 · 10 ⁻⁵	0.772	n.s.
semiaquatic	11	0.106	-0.064 - 0.160	8.20 · 10 ⁻⁶	-4.47 · 10 ⁻⁶	-3.40 · 10 ⁻⁵	0.070	-	10	-1.63 · 10 ⁻⁵	-2.82 · 10 ⁻⁵	-4.45 · 10 ⁻⁶	0.315	n.s.
aquatic	8	0.035	-0.318 - 0.215	5.07 · 10 ⁻⁷	-7.40 · 10 ⁻⁷	-2.50 · 10 ⁻⁶	0.314	-	7	5.75 · 10 ⁻⁷	1.28 · 10 ⁻⁷	-1.02 · 10 ⁻⁶	0.673	n.s.
Preferred habitat														
forest	38	0.137	0.096 - 0.212	-3.34 · 10 ⁻⁶	-1.19 · 10 ⁻⁵	-9.11 · 10 ⁻⁶	0.122	-	37	2.56 · 10 ⁻⁶	1.70 · 10 ⁻⁵	-3.42 · 10 ⁻⁵	0.101	n.s.
mosaic	39	0.139	0.113 - 0.228	-1.86 · 10 ⁻⁶	-6.06 · 10 ⁻⁶	-1.72 · 10 ⁻⁷	0.091	-	38	-2.53 · 10 ⁻⁷	-3.37 · 10 ⁻⁶	-1.69 · 10 ⁻⁶	0.011	n.s.
open	17	0.108	0.028 - 0.196	-1.96 · 10 ⁻⁶	-1.68 · 10 ⁻⁵	-2.21 · 10 ⁻⁵	0.043	-	16	-2.18 · 10 ⁻⁸	-2.78 · 10 ⁻⁷	-1.58 · 10 ⁻⁷	0.869	n.s.
freshwater	13	0.094	-0.076 - 0.152	8.80 · 10 ⁻⁶	-3.49 · 10 ⁻⁶	-3.72 · 10 ⁻⁵	0.141	-	12	-5.36 · 10 ⁻⁵	-8.84 · 10 ⁻⁵	-1.88 · 10 ⁻⁵	0.271	n.s.
marine	10	0.045	-0.230 - 0.134	-4.50 · 10 ⁻⁷	-1.25 · 10 ⁻⁷	-1.97 · 10 ⁻⁶	0.136	-	9	7.86 · 10 ⁻⁷	4.05 · 10 ⁻⁷	-1.17 · 10 ⁻⁶	0.815	n.s.
variable	19	0.124	0.062 - 0.201	-1.11 · 10 ⁻⁶	-4.35 · 10 ⁻⁶	-3.44 · 10 ⁻⁶	0.141	-	18	-1.78 · 10 ⁻⁷	-2.69 · 10 ⁻⁶	-8.66 · 10 ⁻⁷	0.065	n.s.

III.A21 - α		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	$b_{rad} \neq b_{PIC}$	
fissipeds	136	0.020	0.012 - 0.035	0.314	0.253 - 0.366	0.589	G	135	0.388	0.329 - 0.447	0.451	G	✓
Family	129	0.017	0.010 - 0.033	0.334	0.257 - 0.395	0.535	G	128	0.398	0.336 - 0.460	0.450	+	✓
Canidae	16	0.033	0.009 - 0.284	0.301	0.060 - 0.450	0.523	B	15	0.323	0.150 - 0.496	0.376	B	n.s.
Mustelidae	32	0.023	0.009 - 0.059	0.333	0.211 - 0.455	0.180	B	31	0.417	0.265 - 0.569	0.214	G	n.s.
Procyonidae	7	0.002	0.000 - 0.041	0.597	0.190 - 1.003	0.806	B	6	0.547	0.131 - 0.963	0.791	B	n.s.
Ursidae	7	0.005	0.000 - 0.974	0.385	-0.058 - 0.828	0.003	B	6	0.393	-0.095 - 0.881	0.022	B	n.s.
Felidae	26	0.016	0.008 - 0.031	0.309	0.235 - 0.383	0.822	B	25	0.369	0.269 - 0.469	0.766	G	×
Herpestidae	12	0.008	0.001 - 0.061	0.476	0.186 - 0.766	0.500	B	11	0.444	0.169 - 0.719	0.499	B	n.s.
Eupleridae	5	0.019	0.001 - 0.470	0.346	-0.095 - 0.788	0.720	B						
Viverridae	14	0.003	0.000 - 0.025	0.490	0.241 - 0.739	0.588	B	13	0.484	0.188 - 0.780	0.266	B	n.s.
Locomotor type													
arboreal	7	0.003	0.000 - 0.222	0.475	-0.062 - 1.012	0.178	B	6	0.475	-0.108 - 1.058	0.148	B	n.s.
semi-arboreal	10	0.005	0.000 - 0.079	0.474	0.124 - 0.824	0.422	B	9	0.429	0.100 - 0.758	0.395	B	n.s.
scansorial	45	0.024	0.016 - 0.038	0.268	0.221 - 0.314	0.822	E	44	0.326	0.252 - 0.400	0.674	G	×
terrestrial	48	0.023	0.007 - 0.104	0.334	0.157 - 0.470	0.556	B	47	0.404	0.289 - 0.519	0.281	G	n.s.
semifossorial	7	0.010	0.000 - 0.332	0.405	-0.032 - 0.842	0.347	B	6	0.397	-0.088 - 0.882	0.185	B	n.s.
semiaquatic	11	0.013	0.002 - 0.100	0.363	0.128 - 0.599	0.513	B	10	0.468	0.141 - 0.795	0.414	B	n.s.
aquatic	8	0.002	0.000 - 0.506	0.497	0.011 - 0.984	0.203	B	7	0.437	-0.022 - 0.896	0.000	B	n.s.
Preferred habitat													
forest	38	0.011	0.004 - 0.026	0.378	0.270 - 0.486	0.529	G	37	0.429	0.310 - 0.548	0.568	G	×
mosaic	39	0.014	0.006 - 0.030	0.351	0.259 - 0.422	0.623	G	38	0.437	0.305 - 0.569	0.415	G	×
open	17	0.023	0.005 - 0.176	0.323	0.074 - 0.486	0.452	B	16	0.403	0.219 - 0.587	0.568	B	n.s.
freshwater	13	0.011	0.002 - 0.067	0.385	0.171 - 0.600	0.545	B	12	0.519	0.206 - 0.832	0.438	B	n.s.
marine	10	0.011	0.001 - 0.167	0.329	0.100 - 0.558	0.518	B	9	0.290	0.051 - 0.529	0.182	B	n.s.
variable	19	0.062	0.026 - 0.149	0.208	0.111 - 0.305	0.416	E	18	0.204	0.112 - 0.296	0.485	E	n.s.

III.A22 – UR	traditional regression						PIC regression					
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}
whole sample	136	0.014	$4.28 \cdot 10^{-4} - 0.019$	0.198	0.166 – 0.605	0.141 +	135	0.188	0.156 – 0.220	0.142 +	0.142 +	n.s.
fissipeds	129	0.408	$0.300 - 15.740$	-0.389	-0.634 – -0.166	0.067 -	128	0.188	0.155 – 0.221	0.083 +	0.083 +	n.s.
Family												
Canidae	16	0.003	$3.17 \cdot 10^{-6} - 0.019$	0.302	0.077 – 1.045	0.212 E	15	-0.380	-0.597 – -0.163	0.167 -	0.167 -	n.s.
Mustelidae	32	0.032	$0.004 - 0.052$	0.139	0.084 – 0.407	0.272 E	31	0.143	0.090 – 0.196	0.175 E	0.175 E	n.s.
Procyonidae	7	0.005	$1.06 \cdot 10^{-8} - 0.026$	0.358	0.159 – 1.907	0.199 +	6	0.340	-0.074 – 0.754	0.201 B	0.201 B	n.s.
Ursidae	7	0.742	$0.051 - 273.527$	-0.181	-0.688 – 0.062	0.397 G	6	-0.179	-0.377 – 0.019	0.457 B	0.457 B	n.s.
Felidae	26	0.015	$0.009 - 0.024$	0.162	0.108 – 0.216	0.458 E	25	0.198	0.115 – 0.281	0.154 E	0.154 E	n.s.
Herpestidae	12	0.403	$0.123 - 41.976$	-0.243	-0.889 – -0.073	0.067 -	11	-0.234	-0.401 – -0.067	0.043 -	0.043 -	n.s.
Eupleridae	5	0.012	$4.22 \cdot 10^{-5} - 0.055$	0.238	-0.008 – 1.038	0.693 B						
Viverridae	14	0.024	$0.002 - 0.043$	0.143	0.068 – 0.484	0.229 E	13	0.130	0.054 – 0.206	0.405 E	0.405 E	n.s.
Locomotor type												
arboreal	7	0.018	$1.75 \cdot 10^{-5} - 0.037$	0.194	0.110 – 1.069	0.319 E	6	0.179	0.157 – 0.201	0.995 +	0.995 +	n.s.
semiarboreal	10	0.034	$0.003 - 0.052$	0.109	0.044 – 0.418	0.312 E	9	0.106	0.033 – 0.179	0.578 E	0.578 E	n.s.
scansorial	45	0.018	$0.013 - 0.027$	0.149	0.105 – 0.186	0.361 E	44	0.280	0.194 – 0.366	0.082 +	0.082 +	n.s.
terrestrial	48	0.416	$0.232 - 0.623$	-0.233	-0.289 – -0.156	0.477 -	47	-0.189	-0.245 – -0.133	0.050 -	0.050 -	n.s.
semifossorial	7	0.028	$0.003 - 0.066$	0.156	0.053 – 0.433	0.431 E	6	0.132	-0.029 – 0.293	0.175 B	0.175 B	n.s.
semiaquatic	11	0.019	$0.006 - 0.098$	0.199	0.014 – 0.317	0.516 E	10	0.113	0.056 – 0.170	0.754 E	0.754 E	n.s.
aquatic	8	0.013	$2.70 \cdot 10^{-5} - 0.313$	0.197	-0.076 – 0.700	0.552 B	7	0.233	0.011 – 0.455	0.424 E	0.424 E	n.s.
Preferred habitat												
forest	38	0.017	$0.010 - 0.028$	0.187	0.121 – 0.242	0.368 E	37	0.506	0.354 – 0.658	0.464 +	0.464 +	✓
mosaic	39	0.271	$0.179 - 2.587$	-0.567	-0.420 – -0.103	0.266 -	38	-0.151	-0.201 – -0.101	0.170 -	0.170 -	n.s.
open	17	0.470	$0.131 - 47.863$	-0.258	-0.798 – -0.083	0.258 -	16	-0.191	-0.295 – -0.087	0.187 -	0.187 -	n.s.
freshwater	13	0.010	$1.53 \cdot 10^{-4} - 0.055$	0.258	0.079 – 0.776	0.442 E	12	0.291	0.108 – 0.474	0.350 E	0.350 E	n.s.
marine	10	0.020	$8.75 \cdot 10^{-6} - 0.150$	0.156	-0.009 – 0.792	0.197 B	9	-0.173	-0.318 – -0.028	0.032 -	0.032 -	n.s.
variable	19	0.349	$0.171 - 17.783$	-0.190	-0.768 – -0.104	0.306 -	18	0.135	0.071 – 0.199	0.400 E	0.400 E	n.s.

III.A23 – IFA		traditional regression					PLC regression						
whole sample	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}	
fissipeds	136	0.062	0.053 – 0.075	0.138	0.117 – 0.156	0.275	+	135	0.161	0.135 – 0.187	0.332	+	×
Family	129	0.064	0.006 – 0.079	0.134	0.109 – 0.418	0.041	+	128	0.161	0.134 – 0.188	0.278	+	n.s.
Canidae	16	0.020	5.22 · 10 ⁻⁵ – 0.040	0.239	0.149 – 0.893	0.079	+	15	-0.285	-0.449 – -0.121	0.072	-	n.s.
Mustelidae	32	0.070	0.049 – 0.109	0.155	0.103 – 0.198	0.456	+	31	0.149	0.099 – 0.199	0.441	+	×
Procyonidae	7	0.025	3.36 · 10 ⁻⁶ – 0.374	0.249	-0.064 – 1.310	0.216	B	6	0.249	-0.054 – 0.552	0.197	B	n.s.
Ursidae	7	1.246	0.007 – 119.95	-0.157	-0.540 – 0.292	0.180	B	6	0.434	0.008 – 0.860	0.614	+	n.s.
Felidae	26	0.055	0.043 – 0.073	0.130	0.099 – 0.154	0.726	+	25	0.127	0.080 – 0.174	0.463	+	×
Herpestidae	12	0.838	0.566 – 35.400	-0.194	-0.724 – -0.138	0.021	-	11	0.177	0.053 – 0.301	0.209	+	n.s.
Eupleridae	5	0.059	0.011 – 0.212	0.158	-0.038 – 0.400	0.919	B						
Viverridae	14	0.046	0.026 – 0.089	0.179	0.088 – 0.251	0.731	+	13	0.180	0.085 – 0.275	0.565	+	×
Locomotor type													
arboreal	7	0.037	3.77 · 10 ⁻⁵ – 0.264	0.206	-0.052 – 1.067	0.350	B	6	-0.056	-0.066 – -0.046	0.990	-	n.s.
semiarboreal	10	0.049	0.030 – 0.091	0.168	0.080 – 0.231	0.849	+	9	0.184	0.092 – 0.276	0.802	+	×
scansorial	45	0.078	0.066 – 0.097	0.094	0.072 – 0.113	0.479	+	44	0.183	0.128 – 0.238	0.241	+	n.s.
terrestrial	48	0.535	0.379 – 0.686	-0.123	-0.155 – -0.079	0.355	-	47	0.155	0.109 – 0.201	0.156	+	n.s.
semifossorial	7	0.074	0.015 – 0.170	0.158	0.052 – 0.358	0.562	+	6	0.161	-0.016 – 0.338	0.471	B	n.s.
semiaquatic	11	0.053	0.024 – 0.213	0.189	0.034 – 0.275	0.673	+	10	0.249	0.114 – 0.384	0.707	+	×
aquatic	8	0.027	1.72 · 10 ⁻⁴ – 0.062	0.210	0.134 – 0.622	0.737	+	7	0.207	0.073 – 0.341	0.785	+	×
Preferred habitat													
forest	38	0.058	0.041 – 0.095	0.148	0.085 – 0.193	0.493	+	37	0.184	0.133 – 0.235	0.573	+	×
mosaic	39	0.453	0.356 – 2.768	-0.098	-0.310 – -0.067	0.137	-	38	-0.172	-0.227 – -0.117	0.264	-	n.s.
open	17	0.644	0.315 – 10.233	-0.153	-0.483 – -0.063	0.139	-	16	0.157	0.071 – 0.243	0.136	+	n.s.
freshwater	13	0.024	4.32 · 10 ⁻⁴ – 0.155	0.271	0.070 – 0.772	0.471	+	12	0.323	0.141 – 0.505	0.549	+	n.s.
marine	10	0.055	6.35 · 10 ⁻⁵ – 0.360	0.149	-0.004 – 0.704	0.308	B	9	0.160	0.026 – 0.294	0.009	+	n.s.
variable	19	0.521	0.282 – 0.829	-0.111	-0.159 – -0.043	0.387	-	18	0.117	0.060 – 0.174	0.316	+	n.s.

III.A24 – L _m	traditional regression						PIC regression						
	n	a	95% CI _a	h _{rad}	R	sim.	n	h _{PIC}	95% CI _b	R	sim.	h _{rad} ≠ h _{PIC}	
whole sample	136	1.498	1.174 – 1.972	0.351	0.315 – 0.380	0.873	G	135	0.347	0.319 – 0.375	0.885	G	×
fissipeds	129	1.171	0.907 – 1.567	0.383	0.347 – 0.415	0.884	+	128	0.348	0.320 – 0.376	0.887	G	×
Family													
Canidae	16	0.915	0.440 – 4.034	0.449	0.285 – 0.532	0.926	G	15	0.458	0.344 – 0.572	0.902	+	×
Mustelidae	32	2.017	1.281 – 3.176	0.294	0.236 – 0.352	0.849	B	31	0.299	0.240 – 0.358	0.847	B	×
Procyonidae	7	2.983	0.809 – 10.995	0.251	0.089 – 0.412	0.828	B	6	0.225	0.095 – 0.355	0.883	B	×
Ursidae	7	0.998	0.156 – 6.389	0.351	0.193 – 0.509	0.920	B	6	0.345	0.178 – 0.512	0.921	B	×
Felidae	26	2.709	1.964 – 3.738	0.310	0.275 – 0.344	0.965	G	25	0.336	0.292 – 0.380	0.951	G	×
Herpestidae	12	1.369	0.721 – 2.599	0.373	0.283 – 0.463	0.940	G	11	0.354	0.263 – 0.445	0.934	G	×
Eupleridae	5	4.309	1.684 – 11.025	0.217	0.088 – 0.346	0.946	B						
Viverridae	14	1.429	0.695 – 2.939	0.343	0.254 – 0.433	0.911	G	13	0.336	0.212 – 0.460	0.815	B	×
Locomotor type													
arboreal	7	1.114	0.093 – 13.348	0.369	0.062 – 0.677	0.689	B	6	0.379	0.049 – 0.709	0.714	B	n.s.
semi-arboreal	10	2.040	0.656 – 6.344	0.315	0.167 – 0.462	0.818	B	9	0.276	0.146 – 0.406	0.826	B	×
scansorial	45	2.240	1.535 – 3.268	0.314	0.273 – 0.354	0.905	G	44	0.318	0.282 – 0.354	0.929	G	×
terrestrial	48	0.788	0.507 – 1.360	0.497	0.377 – 0.505	0.934	+	47	0.355	0.310 – 0.400	0.904	G	✓
semifossorial	7	1.646	0.455 – 5.947	0.301	0.140 – 0.463	0.884	B	6	0.307	0.143 – 0.471	0.903	B	×
semiaquatic	11	2.832	1.128 – 7.113	0.257	0.149 – 0.365	0.831	B	10	0.281	0.166 – 0.396	0.847	B	×
aquatic	8	0.153	0.029 – 0.813	0.491	0.352 – 0.631	0.959	+	7	0.471	0.286 – 0.656	0.927	G	×
Preferred habitat													
forest	38	1.947	1.252 – 3.028	0.317	0.263 – 0.370	0.866	G	37	0.315	0.262 – 0.368	0.870	G	×
mosaic	40	1.182	0.770 – 1.815	0.385	0.336 – 0.435	0.920	+	39	0.356	0.316 – 0.396	0.941	G	×
open	17	0.748	0.371 – 2.210	0.458	0.315 – 0.542	0.926	G	16	0.433	0.339 – 0.527	0.920	+	×
freshwater	13	3.179	1.310 – 7.711	0.249	0.145 – 0.353	0.776	B	12	0.281	0.176 – 0.386	0.833	B	×
marine	10	0.732	0.202 – 2.649	0.365	0.255 – 0.475	0.929	G	9	0.349	0.177 – 0.521	0.809	B	×
variable	18	0.901	0.397 – 2.046	0.421	0.330 – 0.511	0.914	G	17	0.308	0.244 – 0.372	0.920	B	✓

III.A25 – d _{sm}		traditional regression				PIC regression							
whole sample	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}	
fissipeds	136	0.192	0.167 – 0.225	0.337	0.320 – 0.352	0.963	G	135	0.337	0.313 – 0.361	0.907	G	x
Family	129	0.178	0.153 – 0.214	0.346	0.326 – 0.363	0.957	G	128	0.335	0.310 – 0.360	0.909	G	x
Canidae	16	0.051	0.021 – 0.126	0.492	0.385 – 0.588	0.939	+	15	0.433	0.335 – 0.531	0.920	E	x
Mustelidae	32	0.212	0.152 – 0.294	0.320	0.278 – 0.362	0.937	G	31	0.311	0.259 – 0.363	0.894	G	x
Procyonidae	7	0.183	0.025 – 1.354	0.336	0.088 – 0.583	0.767	B	6	0.316	0.057 – 0.575	0.751	B	n.s.
Ursidae	7	0.884	0.307 – 2.549	0.197	0.107 – 0.287	0.918	-	6	0.176	0.086 – 0.266	0.912	-	x
Felidae	26	0.209	0.171 – 0.257	0.336	0.314 – 0.358	0.988	G	25	0.323	0.291 – 0.355	0.971	G	x
Herpestidae	12	0.328	0.174 – 0.618	0.281	0.192 – 0.370	0.893	G	11	0.281	0.193 – 0.369	0.898	G	x
Eupleridae	5	0.084	0.016 – 0.430	0.429	0.203 – 0.654	0.958	B						
Viverridae	14	0.197	0.092 – 0.420	0.326	0.232 – 0.420	0.889	B	13	0.362	0.234 – 0.490	0.830	B	x
Locomotor type													
arboreal	7	0.114	0.020 – 0.648	0.387	0.173 – 0.602	0.876	B	6	0.383	0.155 – 0.611	0.878	B	x
semiarboreal	10	0.174	0.075 – 0.405	0.352	0.242 – 0.462	0.924	B	9	0.350	0.178 – 0.522	0.810	B	x
scansorial	45	0.174	0.139 – 0.217	0.349	0.326 – 0.373	0.975	G	44	0.335	0.299 – 0.371	0.937	G	x
terrestrial	48	0.182	0.142 – 0.265	0.346	0.303 – 0.376	0.948	B	47	0.324	0.283 – 0.365	0.902	G	x
semifossorial	7	0.214	0.064 – 0.719	0.321	0.168 – 0.473	0.911	B	6	0.325	0.160 – 0.490	0.912	B	x
semiaquatic	11	0.160	0.068 – 0.378	0.359	0.259 – 0.460	0.929	B	10	0.364	0.227 – 0.501	0.871	B	x
aquatic	8	0.026	0.014 – 0.048	0.488	0.438 – 0.539	0.995	+	7	0.489	0.437 – 0.541	0.995	+	x
Preferred habitat													
forest	38	0.152	0.111 – 0.208	0.363	0.325 – 0.401	0.951	B	37	0.328	0.287 – 0.369	0.931	G	x
mosaic	40	0.174	0.133 – 0.227	0.351	0.320 – 0.381	0.964	B	39	0.352	0.311 – 0.393	0.934	B	x
open	17	0.189	0.127 – 0.405	0.345	0.260 – 0.390	0.938	B	16	0.357	0.266 – 0.448	0.888	B	x
freshwater	13	0.163	0.076 – 0.350	0.356	0.266 – 0.446	0.925	B	12	0.396	0.287 – 0.505	0.912	B	x
marine	10	0.139	0.050 – 0.386	0.351	0.263 – 0.438	0.952	B	9	0.340	0.203 – 0.477	0.876	B	x
variable	18	0.189	0.139 – 0.259	0.342	0.308 – 0.377	0.982	B	17	0.322	0.282 – 0.362	0.973	G	x

III.A26 – d _{tm}	traditional regression						PIC regression							
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}		
whole sample	136	0.200	0.176 – 0.232	0.339	0.321 – 0.354	0.964	G	135	0.364	0.341 – 0.387	0.932	E	✓	
fissipeds	129	0.180	0.155 – 0.209	0.353	0.334 – 0.370	0.962	nei.	128	0.362	0.338 – 0.386	0.930	E	×	
Family														
Canidae	16	0.091	0.051 – 0.346	0.436	0.295 – 0.496	0.919	B	15	0.406	0.314 – 0.498	0.919	B	×	
Mustelidae	32	0.191	0.144 – 0.254	0.341	0.305 – 0.377	0.959	B	31	0.375	0.326 – 0.424	0.937	B	×	
Procyonidae	7	<i>0.471</i>	<i>0.115 – 1.927</i>	<i>0.223</i>	<i>0.048 – 0.397</i>	<i>0.733</i>	<i>B</i>	6	<i>0.221</i>	<i>0.022 – 0.420</i>	<i>0.687</i>	<i>B</i>	n.s.	
Ursidae	7	0.593	0.205 – 1.714	0.236	0.146 – 0.327	0.943	-	6	0.237	0.140 – 0.334	0.944	G	×	
Felidae	26	0.179	0.127 – 0.253	0.358	0.322 – 0.395	0.970	B	25	0.364	0.318 – 0.410	0.953	B	×	
Herpestidae	12	0.347	0.191 – 0.629	0.280	0.197 – 0.364	0.906	G	11	0.263	0.176 – 0.350	0.885	G	×	
Eupleridae	5	0.129	0.030 – 0.559	0.391	0.189 – 0.594	0.959	B							
Viverridae	14	0.217	0.120 – 0.395	0.318	0.244 – 0.391	0.929	B	13	0.352	0.177 – 0.527	0.624	B	×	
Locomotor type														
arboreal	7	0.159	0.045 – 0.555	0.355	0.200 – 0.509	0.925	B	6	0.360	0.199 – 0.521	0.876	B	×	
semi-arboreal	10	0.156	0.075 – 0.323	0.371	0.276 – 0.466	0.949	B	9	0.409	0.249 – 0.569	0.924	B	×	
scansorial	45	0.181	0.142 – 0.232	0.351	0.324 – 0.377	0.969	B	44	0.369	0.328 – 0.410	0.975	B	×	
terrestrial	48	0.179	0.139 – 0.238	0.359	0.324 – 0.391	0.963	B	47	0.355	0.317 – 0.393	0.948	B	×	
semifossorial	7	0.153	0.048 – 0.489	0.372	0.226 – 0.518	0.940	B	6	0.375	0.210 – 0.540	0.911	B	×	
semiaquatic	11	0.206	0.076 – 0.557	0.327	0.210 – 0.444	0.881	B	10	0.366	0.212 – 0.520	0.929	B	×	
aquatic	8	0.098	0.023 – 0.421	0.382	0.260 – 0.505	0.947	B	7	0.382	0.259 – 0.505	0.995	B	×	
Preferred habitat														
forest	38	0.155	0.117 – 0.204	0.368	0.334 – 0.402	0.962	E	37	0.369	0.325 – 0.413	0.937	B	×	
mosaic	40	0.201	0.155 – 0.260	0.342	0.312 – 0.372	0.964	G	39	0.369	0.329 – 0.409	0.944	B	×	
open	17	0.155	0.106 – 0.231	0.378	0.330 – 0.416	0.973	B	16	0.373	0.310 – 0.436	0.952	B	×	
freshwater	13	0.232	0.091 – 0.592	0.314	0.204 – 0.424	0.849	B	12	0.370	0.252 – 0.488	0.879	B	×	
marine	10	0.178	0.088 – 0.357	0.333	0.273 – 0.392	0.976	B	9	0.346	0.279 – 0.413	0.973	B	×	
variable	18	0.190	0.131 – 0.275	0.353	0.312 – 0.394	0.976	B	17	0.314	0.270 – 0.358	0.964	G	×	

III.A27 – MR		traditional regression				PLC regression					
n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}
whole sample											
136	0.031	0.002 – 0.039	0.150	0.127 – 0.459	0.122 +	135	0.168	0.139 – 0.197	0.043 +		n.s.
129	0.427	0.352 – 7.313	-0.159	-0.494 – -0.133	0.050 -	128	0.172	0.142 – 0.202	0.004 +		n.s.
Family											
Canidae											
16	0.012	8.81 · 10 ⁻⁵ – 0.028	0.219	0.109 – 0.757	0.226 E	15	-0.231	-0.364 – -0.098	0.039 -		n.s.
Mustelidae											
32	0.038	0.022 – 0.065	0.157	0.095 – 0.224	0.315 E	31	0.167	0.105 – 0.229	0.139 E		n.s.
Procyonidae											
7	0.022	1.21 · 10 ⁻⁴ – 0.057	0.214	0.093 – 0.833	0.284 E	6	0.238	-0.049 – 0.525	0.228 B		n.s.
Ursidae											
7	1.315	0.225 – 4.209	-0.188	-0.290 – -0.035	0.773 -	6	-0.187	-0.337 – -0.037	0.765 -		×
Felidae											
26	0.036	0.005 – 0.055	0.109	0.064 – 0.331	0.302 E	25	-0.137	-0.195 – -0.079	0.048 -		n.s.
Herpestidae											
12	0.496	0.288 – 11.350	-0.195	-0.634 – -0.112	0.503 -	11	-0.188	-0.310 – -0.066	0.422 -		n.s.
Eupleridae											
5	0.016	1.42 · 10 ⁻⁴ – 0.471	0.243	-0.279 – 0.902	0.851 B						
Viverridae											
14	0.384	-0.715 – 0.975	-0.145	-0.544 – -0.060	0.143 -	13	-0.176	-0.284 – -0.068	0.260 -		n.s.
Locomotor type											
arboreal											
7	0.019	4.10 · 10 ⁻⁴ – 0.460	0.227	-0.179 – 0.689	0.379 B	6	-0.203	-0.453 – 0.047	0.114 B		n.s.
semiarboreal											
10	0.017	1.99 · 10 ⁻⁴ – 0.087	0.245	0.022 – 0.855	0.278 E	9	0.269	0.063 – 0.475	0.404 E		n.s.
scansorial											
45	0.033	0.026 – 0.042	0.130	0.102 – 0.156	0.428 E	44	0.142	0.099 – 0.185	0.130 E		n.s.
terrestrial											
48	0.393	0.272 – 0.527	-0.165	-0.205 – -0.116	0.539 -	47	-0.175	-0.226 – -0.124	0.164 G		n.s.
semifossorial											
7	0.069	0.010 – 0.130	0.101	0.021 – 0.351	0.263 E	6	0.118	-0.026 – 0.262	0.163 B		n.s.
semiaquatic											
11	0.038	0.028 – 0.073	0.148	0.070 – 0.187	0.811 E	10	0.154	0.055 – 0.253	0.546 E		n.s.
aquatic											
8	0.041	1.73 · 10 ⁻⁴ – 0.226	0.118	-0.029 – 0.571	0.122 B	7	0.148	4.25 · 10 ⁻⁴ – 0.296	0.320 E		n.s.
Preferred habitat											
forest											
38	0.027	0.018 – 0.041	0.178	0.120 – 0.221	0.406 E	37	-0.343	-0.459 – -0.227	0.065 -		n.s.
mosaic											
40	0.314	0.240 – 3.063	-0.124	-0.388 – -0.090	0.134 -	39	-0.125	-0.166 – -0.084	0.066 -		n.s.
open											
17	0.552	0.211 – 0.998	-0.209	-0.297 – -0.074	0.486 -	16	-0.186	-0.278 – -0.094	0.445 -		n.s.
freshwater											
13	0.028	0.016 – 0.069	0.181	0.075 – 0.239	0.762 E	12	0.201	0.096 – 0.306	0.627 E		×
marine											
10	0.503	0.023 – 8.704	-0.098	-0.345 – 0.148	0.064 B	9	0.120	0.022 – 0.218	0.180 +		n.s.
variable											
19	0.379	0.198 – 6.265	-0.145	-0.448 – -0.070	0.335 -	17	0.126	0.061 – 0.191	0.237 +		n.s.

III.A28 – % _{prox}	traditional regression						PIC regression					
	n	a	95% CI _a	b _{rad}	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}
whole sample	137	16.881	15.596 – 18.365	0.058	0.048 – 0.067	0.416	136	0.066	0.055 – 0.077	0.240	+	×
fissipeds	130	17.894	16.368 – 19.789	0.050	0.039 – 0.060	0.172	129	0.061	0.051 – 0.071	0.272	+	n.s.
Family												
Canidae	17	11.899	1.718 – 17.783	0.090	0.043 – 0.304	0.398	16	-0.112	-0.174 – -0.050	0.024	-	n.s.
Mustelidae	32	17.535	15.276 – 20.941	0.062	0.041 – 0.078	0.529	31	0.049	0.032 – 0.066	0.409	+	×
Procyonidae	7	7.280	0.619 – 29.174	0.154	-0.009 – 0.474	0.416	6	0.151	-0.023 – 0.324	0.384	B	n.s.
Ursidae	7	19.134	9.449 – 23.714	0.030	0.012 – 0.089	0.556	6	0.032	-0.002 – 0.066	0.511	B	n.s.
Felidae	26	18.184	16.218 – 20.654	0.043	0.030 – 0.054	0.525	25	0.042	0.025 – 0.059	0.245	+	n.s.
Herpestidae	12	43.421	39.811 – 124.738	-0.060	-0.208 – -0.045	0.004	11	0.056	0.016 – 0.096	0.183	+	n.s.
Eupleridae	5	19.996	10.046 – 33.963	0.041	-0.043 – 0.130	0.267	B					
Viverridae	14	10.940	1.239 – 16.482	0.114	0.061 – 0.382	0.258	13	0.114	0.042 – 0.186	0.066	+	n.s.
Locomotor type												
arboreal	7	8.619	0.504 – 37.239	0.126	-0.071 – 0.478	0.095	6	-0.115	-0.253 – 0.023	0.261	B	n.s.
semiarboreal	10	17.235	9.829 – 25.527	0.056	-0.001 – 0.125	0.496	9	0.060	0.030 – 0.090	0.799	+	n.s.
scansorial	45	19.829	18.408 – 21.429	0.033	0.025 – 0.041	0.426	44	0.042	0.029 – 0.055	0.251	+	n.s.
terrestrial	49	38.380	35.156 – 81.283	-0.040	-0.132 – -0.029	0.002	48	0.051	0.036 – 0.066	0.130	+	n.s.
semifossorial	7	20.893	9.643 – 26.546	0.043	0.016 – 0.141	0.346	6	0.038	-0.008 – 0.084	0.249	B	n.s.
semiaquatic	11	18.143	15.704 – 25.942	0.058	0.017 – 0.074	0.822	10	0.058	0.028 – 0.088	0.725	+	×
aquatic	8	20.970	4.901 – 36.224	0.046	0.001 – 0.164	0.486	7	0.049	-8.77·10 ⁻⁴ – 0.099	0.240	B	n.s.
Preferred habitat												
forest	38	14.928	12.246 – 18.967	0.071	0.041 – 0.094	0.320	37	0.081	0.056 – 0.106	0.391	+	n.s.
mosaic	40	20.366	10.280 – 22.182	0.036	0.025 – 0.116	0.045	39	0.038	0.026 – 0.050	0.236	+	n.s.
open	17	39.537	31.261 – 99.083	-0.047	-0.157 – -0.016	0.029	16	0.047	0.021 – 0.073	0.140	+	n.s.
freshwater	13	13.989	10.023 – 24.831	0.085	0.023 – 0.121	0.505	12	0.099	0.046 – 0.152	0.591	+	n.s.
marine	10	13.896	0.281 – 19.143	0.078	0.054 – 0.402	0.284	9	0.073	0.017 – 0.129	0.402	+	n.s.
variable	19	35.375	31.769 – 67.298	-0.028	-0.097 – -0.014	0.042	18	0.058	0.045 – 0.071	0.899	+	n.s.

III.A29 – % _{mid}		traditional regression						PIC regression					
whole sample	n	a	95% CI _a	<i>b</i> _{rad}	95% CI _b	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}
fissipeds	137	57.597	54.325 – 61.094	-0.046	-0.053 – -0.039	0.595	-	136	-0.044	-0.050 – -0.038	0.508	-	×
Family	130	53.530	50.699 – 55.976	-0.037	-0.042 – -0.030	0.418	-	129	-0.039	-0.045 – -0.033	0.454	-	×
Canidae	17	52.881	44.361 – 59.704	-0.039	-0.053 – -0.019	0.720	-	16	-0.039	-0.057 – -0.021	0.531	-	×
Mustelidae	32	51.916	48.529 – 55.081	-0.031	-0.039 – -0.022	0.701	-	31	-0.028	-0.036 – -0.020	0.681	-	×
Procyonidae	7	82.092	44.055 – 142.561	-0.088	-0.154 – -0.016	0.705	-	6	-0.084	-0.156 – -0.012	0.721	-	n.s.
Ursidae	7	63.416	34.514 – 175.388	-0.040	-0.127 – -0.013	0.290	B	6	-0.046	-0.102 – -0.010	0.070	B	n.s.
Felidae	26	46.957	42.756 – 72.277	-0.022	-0.068 – -0.012	0.193	-	25	-0.030	-0.042 – -0.018	0.328	-	n.s.
Herpestidae	12	53.174	42.756 – 86.298	-0.043	-0.108 – -0.011	0.473	-	11	-0.040	-0.064 – -0.016	0.554	-	n.s.
Eupleridae	5	23.025	4.328 – 37.757	0.070	-0.011 – -0.309	0.581	B						
Viverridae	14	71.945	50.003 – 272.898	-0.074	-0.239 – -0.030	0.299	-	13	-0.057	-0.090 – -0.024	0.424	-	n.s.
Locomotor type													
arboreal	7	65.253	27.290 – 158.489	-0.052	-0.158 – -0.061	0.184	B	6	0.024	0.019 – 0.029	0.984	+	n.s.
semiarboreal	10	50.548	41.305 – 87.297	-0.028	-0.099 – -0.002	0.017	B	9	-0.026	-0.047 – -0.005	0.241	-	n.s.
scansorial	45	47.676	45.082 – 73.790	-0.022	-0.071 – -0.016	0.102	-	44	-0.031	-0.040 – -0.022	0.328	-	n.s.
terrestrial	49	54.125	50.699 – 57.544	-0.042	-0.050 – -0.033	0.720	-	48	-0.032	-0.040 – -0.024	0.508	-	✓
semifossorial	7	46.644	42.658 – 71.450	-0.025	-0.078 – -0.012	0.324	-	6	-0.026	-0.055 – -0.003	0.444	B	n.s.
semiaquatic	11	56.312	48.529 – 131.522	-0.039	-0.136 – -0.018	0.397	-	10	0.030	0.011 – 0.049	0.604	+	n.s.
aquatic	8	92.066	68.391 – 163.682	-0.091	-0.139 – -0.068	0.929	-	7	-0.089	-0.137 – -0.041	0.857	-	×
Preferred habitat													
forest	38	59.279	52.000 – 138.038	-0.048	-0.151 – -0.031	0.130	-	37	-0.052	-0.069 – -0.035	0.212	-	n.s.
mosaic	40	50.711	47.206 – 54.200	-0.031	-0.040 – -0.022	0.587	-	39	-0.031	-0.039 – -0.023	0.639	-	×
open	17	46.838	42.170 – 51.286	-0.025	-0.035 – -0.010	0.636	-	16	-0.010	-0.012 – -0.008	0.943	-	×
freshwater	13	58.894	51.286 – 149.624	-0.046	-0.155 – -0.028	0.267	-	12	-0.039	-0.063 – -0.015	0.365	-	n.s.
marine	10	96.383	37.239 – 3706.807	-0.093	-0.395 – -0.017	0.612	-	9	-0.083	-0.139 – -0.027	0.587	-	n.s.
variable	19	52.324	45.709 – 57.148	-0.036	-0.047 – -0.020	0.618	-	18	-0.028	-0.042 – -0.014	0.126	-	n.s.

III.A30 – % _{dist}	traditional regression					PIC regression							
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	137	22.631	21.429 – 24.099	0.044	0.037 – 0.051	0.187	+	136	0.050	0.041 – 0.059	0.098	+	n.s.
fissipeds	130	21.807	20.464 – 23.496	0.050	0.040 – 0.057	0.222	+	129	-0.063	-0.074 – -0.052	0.001	-	n.s.
Family													
Canidae	17	19.738	4.642 – 29.923	0.067	0.023 – 0.231	0.032	+	16	0.082	0.037 – 0.127	0.070	+	n.s.
Mustelidae	32	42.374	37.844 – 84.333	-0.042	-0.133 – -0.030	0.077	-	31	0.067	0.042 – 0.092	0.041	+	n.s.
Procyonidae	7	20.663	8.674 – 75.858	0.063	-0.088 – 0.172	0.475	B	6	0.062	-0.005 – 0.129	0.490	B	n.s.
Ursidae	7	47.610	34.995 – 168.267	-0.032	-0.140 – -0.003	0.005	-	6	-0.031	-0.069 – 0.007	0.071	B	n.s.
Felidae	26	51.109	44.771 – 115.611	-0.042	-0.131 – -0.029	0.331	-	25	0.046	0.027 – 0.065	0.035	+	n.s.
Herpestidae	12	18.030	4.642 – 22.961	0.082	0.044 – 0.273	0.312	+	11	0.076	0.024 – 0.128	0.287	+	n.s.
Eupleridae	5	57.438	24.831 – 189.234	-0.069	-0.237 – 0.062	0.797	B						
Viverridae	14	45.930	36.644 – 109.901	-0.042	-0.148 – -0.011	0.053	-	13	0.104	0.039 – 0.169	0.191	+	n.s.
Locomotor type													
arboreal	7	20.142	3.648 – 79.433	0.062	-0.111 – 0.278	0.099	B	6	0.049	-0.010 – 0.108	0.264	B	n.s.
semiarboreal	10	40.105	36.644 – 42.855	-0.026	-0.034 – -0.014	0.792	-	9	0.072	0.012 – 0.132	0.026	+	n.s.
scansorial	45	45.867	42.658 – 80.538	-0.032	-0.095 – -0.024	0.267	-	44	0.048	0.033 – 0.063	0.069	+	n.s.
terrestrial	49	21.434	19.861 – 23.933	0.055	0.041 – 0.066	0.634	+	48	0.053	0.038 – 0.068	0.276	+	n.s.
semifossorial	7	44.066	37.325 – 95.060	-0.040	-0.146 – -0.016	0.094	-	6	0.029	-0.002 – 0.060	0.514	B	n.s.
semiaquatic	11	51.098	27.925 – 80.353	-0.064	-0.113 – 0.002	0.400	B	10	-0.072	-0.088 – -0.056	0.957	-	n.s.
aquatic	8	12.791	2.191 – 25.351	0.078	0.035 – 0.226	0.749	+	7	0.079	0.001 – 0.157	0.368	+	n.s.
Preferred habitat													
forest	38	45.175	40.272 – 86.298	-0.038	-0.117 – -0.023	0.262	-	37	-0.081	-0.107 – -0.055	0.350	-	n.s.
mosaic	40	23.714	22.131 – 25.882	0.040	0.028 – 0.049	0.497	+	39	0.042	0.030 – 0.054	0.536	+	×
open	17	22.589	10.162 – 28.445	0.052	0.021 – 0.146	0.370	+	16	0.051	0.023 – 0.079	0.140	+	n.s.
freshwater	13	75.353	34.754 – 516.416	-0.105	-0.341 – -0.024	0.247	-	12	-0.105	-0.171 – -0.039	0.367	-	n.s.
marine	10	18.336	13.583 – 36.475	0.048	-0.006 – 0.075	0.722	B	9	0.055	0.010 – 0.100	0.222	+	n.s.
variable	19	22.080	9.886 – 26.002	0.049	0.029 – 0.134	0.564	+	18	-0.039	-0.059 – -0.019	0.135	-	n.s.

Supplementary Material

	whole sample	phylogeny						locomotor type						preferred habitat								
		Canidae	Mustelidae	Procyonidae	Ursidae	Felidae	Herpestidae	Viverridae	arboreal	semiarboreal	scansorial	terrestrial	semifossorial	semiaquatic	aquatic	forest	mosaic	open	freshwater	marine	variable	
L_s	$\rho_{0.5}$	Nee	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	exp.	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.6}$	$\rho_{0.8}$	In	Nee	$\rho_{0.9}$	In
S	$\rho_{0.5}$	Nee	Nee	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	$\rho_{1.7}$	exp.	$\rho_{0.8}$	Nee	In	untr.	Nee	untr.	$\rho_{0.6}$	$\rho_{0.8}$	In	Nee	$\rho_{0.9}$	In
I	Nee	Nee	$\rho_{0.5}$	$\rho_{0.5}$	In	$\rho_{0.5}$	$\rho_{0.5}$	In	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.6}$	$\rho_{0.8}$	In	Nee	$\rho_{0.9}$	In
A	Nee	Nee	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.6}$	$\rho_{0.8}$	In	Nee	$\rho_{0.9}$	In
H_s	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	Gra.	Nee	In	$\rho_{0.6}$	$\rho_{0.8}$	exp.	Nee	$\rho_{0.9}$	In
L_h	Nee	$\rho_{0.5}$	In	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	Nee	$\rho_{0.6}$	In	In	Nee	$\rho_{0.9}$	In
d_{sh}	Nee	$\rho_{0.5}$	Nee	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	untr.	Nee	$\rho_{0.1}$	In	Nee	In	$\rho_{0.3}$	exp.	In	Nee	$\rho_{0.8}$	In	Nee	In	In
d_{th}	Nee	$\rho_{0.5}$	In	$\rho_{0.5}$	Nee	$\rho_{0.1}$	$\rho_{0.5}$	untr.	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.6}$	$\rho_{0.8}$	In	Nee	$\rho_{0.9}$	In
T	exp.	exp.	Gra.	$\rho_{0.5}$	$\rho_{0.5}$	Nee	untr.	$\rho_{2.0}$	$\rho_{1.7}$	exp.	Nee	exp.	exp.	untr.	Gra.	untr.	In	untr.	exp.	Gra.	untr.	Gra.
HR	exp.	exp.	Nee	$\rho_{0.5}$	untr.	$\rho_{0.5}$	$\rho_{0.5}$	untr.	Nee	$\rho_{0.1}$	Gra.	Nee	$\rho_{0.5}$	Gra.	Nee	$\rho_{0.8}$	exp.	exp.	In	Nee	$\rho_{0.9}$	In
L_r	Nee	$\rho_{0.5}$	In	$\rho_{0.5}$	Nee	$\rho_{0.1}$	untr.	$\rho_{0.5}$	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Gra.	$\rho_{0.8}$	Nee	In	In	Gra.	untr.	In
d_{sr}	Nee	Nee	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	untr.	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.5}$	Nee	In	Nee	$\rho_{0.9}$	In
d_{tr}	Nee	$\rho_{0.5}$	$\rho_{0.5}$	In	Nee	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	Nee	untr.	In	Nee	$\rho_{0.9}$	In
P	Nee	Nee	Nee	$\rho_{0.5}$	untr.	Nee	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	exp.	untr.	Gra.	In	$\rho_{0.5}$	$\rho_{0.8}$	In	Nee	untr.	In
RR	exp.	exp.	Nee	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	In	Nee	In	untr.	exp.	Nee	exp.	Nee	In	Nee	Nee	In
L_u	Nee	$\rho_{0.5}$	In	$\rho_{0.5}$	Nee	$\rho_{0.1}$	$\rho_{0.5}$	In	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Gra.	$\rho_{0.8}$	Nee	In	In	Gra.	$\rho_{0.9}$	In
d_{su}	$\rho_{0.5}$	$\rho_{0.5}$	In	$\rho_{0.5}$	Nee	Nee	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	untr.	Nee	$\rho_{0.8}$	Nee	Nee	In	Nee	Nee	In
d_{tu}	Nee	exp.	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	$\rho_{1.7}$	exp.	$\rho_{0.8}$	Nee	In	untr.	exp.	$\rho_{0.8}$	Nee	$\rho_{0.8}$	In	exp.	$\rho_{0.9}$	$\rho_{0.5}$
O	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	exp.	$\rho_{0.8}$	Nee	In	untr.	Nee	In	$\rho_{0.6}$	Nee	In	Nee	$\rho_{0.9}$	In
θ	exp.	exp.	Nee	exp.	$\rho_{0.5}$	Nee	untr.	In	exp.	exp.	Nee	$\rho_{0.5}$	exp.	$\rho_{0.5}$	exp.	In	exp.	$\rho_{0.5}$	exp.	exp.	exp.	Gra.
α	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	In	In	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	In	Nee	In	$\rho_{0.3}$	Nee	Nee	$\rho_{0.6}$	In	In	Nee	Nee	$\rho_{0.5}$
UR	$\rho_{0.5}$	$\rho_{0.5}$	Nee	In	Nee	$\rho_{0.1}$	$\rho_{0.5}$	untr.	Nee	exp.	Nee	exp.	In	Gra.	exp.	$\rho_{0.8}$	exp.	Nee	In	Nee	Nee	In
IFA	$\rho_{0.5}$	$\rho_{0.5}$	In	$\rho_{0.5}$	Nee	exp.	$\rho_{0.5}$	In	Nee	exp.	$\rho_{0.8}$	exp.	In	$\rho_{0.3}$	Nee	$\rho_{0.8}$	$\rho_{0.5}$	exp.	In	Nee	Nee	In
L_m	Nee	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.1}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{1.7}$	$\rho_{0.1}$	In	Nee	In	Nee	exp.	$\rho_{0.8}$	Nee	$\rho_{0.8}$	In	Nee	untr.	In
d_{sm}	Nee	Nee	In	$\rho_{0.5}$	untr.	Nee	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	In	Nee	In	$\rho_{0.3}$	Gra.	Nee	$\rho_{0.6}$	Nee	In	Nee	Nee	In
d_{tm}	Nee	$\rho_{0.5}$	Nee	In	In	$\rho_{0.1}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	In	$\rho_{0.3}$	Gra.	Nee	$\rho_{0.6}$	Nee	In	Nee	Nee	In
MR	$\rho_{0.5}$	$\rho_{0.5}$	In	$\rho_{0.5}$	In	$\rho_{0.1}$	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.5}$	Gra.	$\rho_{0.5}$	In	$\rho_{0.3}$	Nee	In	exp.	Nee	In	Nee	$\rho_{0.9}$	In
%_{prox}	Nee	$\rho_{0.5}$	Nee	In	untr.	$\rho_{0.1}$	$\rho_{0.5}$	In	Nee	$\rho_{0.1}$	$\rho_{0.8}$	$\rho_{0.5}$	In	Gra.	exp.	Nee	$\rho_{0.6}$	Nee	$\rho_{0.5}$	Nee	$\rho_{0.9}$	exp.
%_{mid}	Nee	Nee	In	Nee	untr.	$\rho_{0.5}$	untr.	untr.	$\rho_{1.7}$	exp.	Nee	Nee	In	$\rho_{0.3}$	exp.	Nee	$\rho_{0.6}$	In	exp.	Gra.	Nee	Gra.
%_{dist}	$\rho_{0.5}$	exp.	In	exp.	Nee	$\rho_{0.1}$	$\rho_{0.5}$	untr.	exp.	$\rho_{0.1}$	exp.	Nee	In	Gra.	exp.	$\rho_{0.8}$	exp.	Nee	In	Nee	$\rho_{0.9}$	In

Table III.S1. Branch length transformations used for phylogenetically independent contrasts. Variable names are listed in Table III.3. Abbreviations: exp., exponential transformation; Gra., transformation of Grafen; In, natural logarithm transformation; Nee, transformation of Nee; ρ_x , Grafen's rho transform, where x indicates the value of rho; untr., untransformed branch lengths.

Tables III.S2 to III.S30.

Results of the complex allometry test.

In each case, it is indicated

(in the “ $D \neq 1$ ” column)

whether the exponent of

complex allometry (D) is

significantly different from

1. Results in *grey italics*

denote non-significant

regressions. Variable names

are listed in Table

III.3. Abbreviations: 95%

CI_C , 95% confidence interval

for the coefficient (C);

95% CI_D , 95% confidence

interval for the exponent

of complex allometry

(D); 95% CI_{lnA} , 95% confidence

interval for $ln A$; n ,

sample size; n.c., the

model did not converge

in a realistic solution;

n.s., although the model

did converge in a realistic

solution, it was not

significant according to

the associated correlation

coefficient (R).

III.S2 – L _s	n	ln A	95% CI _{lnA}	C	95% CI _C	D	95% CI _D	R	D ≠ 1
whole sample	137	5.527	5.377 – 5.677	0.181	0.108 – 0.253	1.284	1.102 – 1.465	0.960	✓ ($D > 1$)
fissipeds	130	5.568	5.390 – 5.746	0.270	0.167 – 0.373	1.129	0.957 – 1.300	0.958	×
Family									
Canidae	17	5.133	4.964 – 5.301	0.449	0.272 – 0.625	0.971	0.675 – 1.266	0.973	×
Mustelidae	32	4.604	4.392 – 4.817	0.383	0.188 – 0.578	0.911	0.641 – 1.182	0.957	×
Procyonidae	7	4.245	3.576 – 4.915	0.409	-0.440 – 1.258	0.754	1.207 – 2.715	0.833	×
Ursidae	7	5.438	5.365 – 5.511	0.200	0.114 – 0.287	1.472	0.930 – 2.014	0.991	×
Felidae	26	5.458	5.330 – 5.586	0.360	0.236 – 0.484	0.908	0.713 – 1.103	0.982	×
Herpestidae	12	4.153	4.013 – 4.293	0.433	0.266 – 0.600	0.647	0.341 – 0.953	0.981	✓ ($D < 1$)
Eupleridae	5	4.236	3.718 – 4.753	0.166	-0.361 – 0.693	1.728	-1.648 – 5.104	0.962	×
Viverridae	14	4.400	4.215 – 4.585	0.237	0.040 – 0.434	1.120	0.223 – 1.818	0.908	×
Locomotor type									
arboreal	7	4.287	3.913 – 4.661	0.187	-0.154 – 0.529	1.748	-0.231 – 3.728	0.917	×
semiarboreal	10	4.518	4.326 – 4.710	0.368	0.150 – 0.586	0.820	0.393 – 1.246	0.974	×
scansorial	45	5.426	5.296 – 5.557	0.238	0.140 – 0.336	1.168	0.952 – 1.385	0.979	×
terrestrial	49	5.705	5.388 – 6.021	0.286	0.122 – 0.451	1.139	0.892 – 1.387	0.964	×
semifossorial	7	4.297	3.963 – 4.630	0.320	-0.274 – 0.913	1.026	-0.637 – 2.689	0.953	×
semiaquatic	11	4.312	4.025 – 4.598	0.093	-0.117 – 0.302	1.863	0.151 – 3.575	0.904	×
aquatic	8	5.402	5.006 – 5.799	0.174	-0.226 – 0.573	1.410	-0.438 – 3.258	0.881	×
Preferred habitat									
forest	38	5.187	4.963 – 5.411	0.390	0.200 – 0.580	0.918	0.671 – 1.166	0.957	×
mosaic	40	5.410	5.225 – 5.596	0.284	0.154 – 0.414	1.133	0.903 – 1.363	0.971	×
open	17	5.465	5.102 – 5.828	0.295	0.062 – 0.528	1.149	0.760 – 1.538	0.967	×
freshwater	13	–	–	–	–	–	–	–	n.c.
marine	10	5.437	5.177 – 5.697	0.200	-0.042 – 0.442	1.311	0.589 – 2.033	0.967	×
variable	19	5.463	5.151 – 5.775	0.212	0.044 – 0.380	1.266	0.896 – 1.636	0.973	×
III.S3 – S									
whole sample	137	4.941	4.737 – 5.146	0.443	0.301 – 0.585	0.918	0.784 – 1.052	0.967	×
fissipeds	130	4.581	4.421 – 4.742	0.360	0.253 – 0.466	0.985	0.857 – 1.113	0.971	×
Family									
Canidae	17	3.827	3.616 – 4.037	0.445	0.223 – 0.667	0.942	0.570 – 1.314	0.957	×
Mustelidae	32	3.826	3.630 – 4.021	0.485	0.297 – 0.672	0.814	0.615 – 1.012	0.971	×
Procyonidae	7	3.243	2.680 – 3.806	0.346	-0.344 – 1.037	0.683	-1.074 – 2.440	0.838	×
Ursidae	7	4.449	4.359 – 4.540	0.183	0.074 – 0.292	1.173	0.453 – 1.893	0.979	×
Felidae	26	4.272	4.140 – 4.405	0.282	0.163 – 0.401	1.062	0.814 – 1.310	0.979	×
Herpestidae	12	2.913	2.831 – 2.995	0.324	0.223 – 0.425	0.932	0.634 – 1.231	0.987	×
Eupleridae	5	3.210	2.951 – 3.468	0.351	-0.014 – 0.716	0.940	-0.169 – 2.049	0.992	×
Viverridae	14	3.444	3.225 – 3.663	0.422	0.163 – 0.680	0.643	0.199 – 1.088	0.935	×
Locomotor type									
arboreal	7	3.528	3.331 – 3.725	0.372	0.149 – 0.595	1.085	0.426 – 1.744	0.981	×
semiarboreal	10	3.552	3.347 – 3.757	0.435	0.199 – 0.672	0.737	0.358 – 1.115	0.975	×
scansorial	45	4.400	4.282 – 4.518	0.265	0.174 – 0.357	1.126	0.947 – 1.305	0.985	×
terrestrial	49	4.550	4.363 – 4.737	0.421	0.298 – 0.544	0.901	0.782 – 1.020	0.984	×
semifossorial	7	3.548	1.737 – 5.360	0.921	-1.285 – 3.127	0.372	-0.756 – 1.500	0.933	×
semiaquatic	11	3.771	3.501 – 4.040	0.425	0.147 – 0.704	0.861	0.439 – 1.284	0.963	×
aquatic	8	–	–	–	–	–	–	–	n.c.
Preferred habitat									
forest	38	4.260	4.053 – 4.467	0.482	0.296 – 0.668	0.826	0.635 – 1.016	0.969	×
mosaic	40	4.368	4.216 – 4.521	0.369	0.248 – 0.490	0.980	0.819 – 1.140	0.982	×
open	17	4.270	3.871 – 4.670	0.411	0.099 – 0.722	0.933	0.570 – 1.296	0.958	×
freshwater	13	3.767	3.519 – 4.015	0.417	0.166 – 0.668	0.873	0.486 – 1.260	0.961	×
marine	10	–	–	–	–	–	–	–	n.c.
variable	19	4.394	4.078 – 4.709	0.342	0.123 – 0.561	0.988	0.701 – 1.275	0.971	×

III.S4 – I	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	4.807	4.580 – 5.034	0.194	0.088 – 0.300	1.315	1.067 – 1.563	0.931	✓ (<i>D</i> >1)
fissipeds	130	4.816	4.549 – 5.083	0.280	0.131 – 0.428	1.171	0.931 – 1.412	0.925	×
Family									
Canidae	17	4.178	3.924 – 4.432	0.453	0.181 – 0.725	0.847	0.415 – 1.278	0.936	×
Mustelidae	32	3.680	3.363 – 3.997	0.448	0.162 – 0.734	0.954	0.611 – 1.297	0.938	×
Procyonidae	7	3.478	3.214 – 3.742	0.197	-0.187 – 0.580	1.057	-1.220 – 3.334	0.885	×
Ursidae	7	4.806	4.578 – 5.035	0.200	-0.073 – 0.473	0.859	-0.649 – 2.367	0.885	×
Felidae	26	4.585	4.431 – 4.739	0.334	0.190 – 0.479	0.977	0.728 – 1.226	0.975	×
Herpestidae	12	3.305	3.094 – 3.515	0.444	0.193 – 0.695	0.631	0.191 – 1.071	0.961	×
Eupleridae	5	3.395	2.527 – 4.263	0.273	-0.697 – 1.243	1.506	-2.279 – 5.292	0.944	×
Viverridae	14	3.791	3.543 – 4.040	0.456	0.163 – 0.749	0.557	0.125 – 0.989	0.932	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	3.845	3.642 – 4.048	0.393	0.142 – 0.643	0.850	0.154 – 1.547	0.976	×
semiarboreal	10	3.698	3.290 – 4.107	0.434	-0.040 – 0.908	0.689	-0.056 – 1.433	0.905	×
scansorial	45	4.695	4.526 – 4.863	0.238	0.118 – 0.358	1.237	0.969 – 1.504	0.971	×
terrestrial	49	4.942	4.441 – 5.442	0.326	0.065 – 0.588	1.134	0.789 – 1.478	0.933	×
semifossorial	7	3.291	2.880 – 3.701	0.121	-0.232 – 0.474	2.165	-0.506 – 4.835	0.934	×
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	4.595	4.234 – 4.956	0.483	0.173 – 0.793	0.894	0.570 – 1.217	0.926	×
mosaic	40	4.684	4.374 – 4.994	0.371	0.135 – 0.607	1.033	0.718 – 1.348	0.941	×
open	17	4.478	3.901 – 5.055	0.237	-0.081 – 0.555	1.302	0.629 – 1.975	0.929	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	4.739	4.201 – 5.276	0.182	-0.275 – 0.640	1.530	0.003 – 3.057	0.907	×
variable	19	4.758	4.350 – 5.165	0.242	0.034 – 0.449	1.323	0.919 – 1.726	0.971	×

III.S5 – A	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	5.619	5.447 – 5.791	0.320	0.217 – 0.424	1.075	0.934 – 1.215	0.971	×
fissipeds	130	5.435	5.257 – 5.614	0.331	0.220 – 0.441	1.059	0.911 – 1.206	0.965	×
Family									
Canidae	17	4.735	4.519 – 4.950	0.454	0.226 – 0.683	0.900	0.530 – 1.269	0.955	×
Mustelidae	32	4.461	4.226 – 4.696	0.455	0.237 – 0.673	0.889	0.637 – 1.142	0.960	×
Procyonidae	7	4.059	3.784 – 4.334	0.271	-0.113 – 0.654	0.969	-0.606 – 2.543	0.927	×
Ursidae	7	5.347	5.202 – 5.492	0.200	0.027 – 0.373	0.869	-0.092 – 1.830	0.949	×
Felidae	26	5.151	5.028 – 5.275	0.313	0.199 – 0.427	1.015	0.804 – 1.227	0.983	×
Herpestidae	12	3.814	3.711 – 3.917	0.353	0.226 – 0.480	0.816	0.490 – 1.142	0.982	×
Eupleridae	5	3.982	3.606 – 4.359	0.253	-0.185 – 0.691	1.410	-0.434 – 3.253	0.984	×
Viverridae	14	4.284	4.116 – 4.451	0.390	0.193 – 0.587	0.695	0.317 – 1.073	0.954	×
Locomotor type									
arboreal	7	4.344	4.187 – 4.501	0.361	0.177 – 0.545	0.976	0.414 – 1.538	0.985	×
semiarboreal	10	4.341	4.177 – 4.505	0.452	0.262 – 0.643	0.670	0.386 – 0.955	0.984	✓ (<i>D</i> <1)
scansorial	45	5.266	5.141 – 5.391	0.252	0.159 – 0.345	1.185	0.991 – 1.379	0.984	×
terrestrial	49	5.483	5.186 – 5.781	0.375	0.199 – 0.550	1.014	0.817 – 1.210	0.970	×
semifossorial	7	4.052	3.548 – 4.556	0.458	-0.440 – 1.356	0.850	-0.811 – 2.511	0.948	×
semiaquatic	11	4.290	3.971 – 4.609	0.250	-0.043 – 0.544	1.293	0.461 – 2.124	0.943	×
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	5.162	4.916 – 5.409	0.505	0.285 – 0.724	0.837	0.622 – 1.053	0.961	×
mosaic	40	5.249	5.059 – 5.440	0.370	0.222 – 0.518	1.009	0.812 – 1.206	0.975	×
open	17	5.108	4.711 – 5.506	0.344	0.065 – 0.624	1.051	0.655 – 1.446	0.960	×
freshwater	13	4.183	3.907 – 4.458	0.102	-0.089 – 0.293	1.955	0.527 – 3.383	0.920	×
marine	10	5.493	5.174 – 5.813	0.139	-0.118 – 0.395	1.650	0.517 – 2.784	0.953	×
variable	19	5.296	4.989 – 5.602	0.281	0.100 – 0.461	1.169	0.872 – 1.466	0.979	×

III.S6 – H_S	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	3.235	3.010 – 3.460	0.041	3.76 · 10 ⁻⁴ – 0.082	2.049	1.570 – 2.528	0.860	✓ (D>1)
fissipeds	130	3.719	3.412 – 4.025	0.213	0.072 – 0.354	1.352	1.043 – 1.661	0.902	✓ (D>1)
Family									
Canidae	17	3.258	2.991 – 3.524	0.536	0.252 – 0.821	0.871	0.486 – 1.257	0.950	×
Mustelidae	32	2.579	2.141 – 3.018	0.248	-0.057 – 0.553	1.375	0.660 – 2.091	0.868	×
Procyonidae	7	2.424	1.717 – 3.131	0.459	-0.535 – 1.453	0.984	-1.447 – 3.415	0.852	×
Ursidae	7	3.644	3.412 – 3.876	0.132	-0.139 – 0.403	1.599	-1.010 – 4.207	0.857	×
Felidae	26	3.507	3.308 – 3.705	0.182	0.043 – 0.320	1.471	0.996 – 1.946	0.960	×
Herpestidae	12	2.253	1.857 – 2.649	0.480	0.035 – 0.925	0.448	-0.101 – 0.997	0.923	✓ (D=0)
Eupleridae	5	2.169	1.861 – 2.478	0.106	-0.119 – 0.332	2.454	0.194 – 4.713	0.991	×
Viverridae	14	2.471	2.272 – 2.669	0.279	0.084 – 0.475	1.339	0.742 – 1.936	0.943	×
Locomotor type									
arboreal	7	2.457	2.043 – 2.870	0.307	-0.129 – 0.743	1.308	-0.243 – 2.859	0.921	×
semiarboreal	10	2.679	2.257 – 3.100	0.514	0.035 – 0.992	0.833	0.159 – 1.508	0.939	×
scansorial	45	3.626	3.469 – 3.783	0.202	0.102 – 0.301	1.375	1.108 – 1.643	0.975	✓ (D>1)
terrestrial	49	3.758	3.217 – 4.299	0.201	-0.012 – 0.413	1.395	0.920 – 1.869	0.924	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	3.425	3.142 – 3.708	0.397	0.176 – 0.618	1.039	0.748 – 1.330	0.952	×
mosaic	40	3.548	3.224 – 3.871	0.189	0.031 – 0.346	1.495	1.057 – 1.933	0.933	✓ (D>1)
open	17	3.625	2.567 – 4.683	0.370	-0.337 – 1.077	1.106	0.168 – 2.043	0.837	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	3.753	2.998 – 4.508	0.267	-0.132 – 0.666	1.284	0.584 – 1.983	0.914	×
III.S7 – L_h	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	5.513	5.363 – 5.663	0.081	0.031 – 0.132	1.583	1.290 – 1.876	0.922	✓ (D>1)
fissipeds	130	5.868	5.673 – 6.063	0.277	0.159 – 0.395	1.084	0.895 – 1.274	0.947	×
Family									
Canidae	17	5.402	5.133 – 5.672	0.417	0.131 – 0.702	0.905	0.400 – 1.409	0.921	×
Mustelidae	32	4.722	4.501 – 4.944	0.208	0.029 – 0.387	1.152	0.667 – 1.637	0.914	×
Procyonidae	7	4.610	4.321 – 4.898	0.257	-0.106 – 0.620	0.734	-0.577 – 2.044	0.910	×
Ursidae	7	5.804	5.692 – 5.917	0.211	0.076 – 0.346	1.215	0.434 – 1.995	0.977	×
Felidae	26	5.688	5.574 – 5.802	0.281	0.175 – 0.386	0.999	0.782 – 1.217	0.982	×
Herpestidae	12	4.467	4.215 – 4.719	0.435	0.139 – 0.732	0.587	0.083 – 1.091	0.946	×
Eupleridae	5	4.665	4.555 – 4.774	0.289	0.149 – 0.428	1.179	0.662 – 1.696	0.998	×
Viverridae	14	4.098	4.399 – 5.798	0.686	-0.064 – 1.436	0.256	-0.116 – 0.626	0.932	✓ (D=0)
Locomotor type									
arboreal	7	4.957	4.662 – 5.251	0.380	0.005 – 0.755	0.768	-0.294 – 1.830	0.946	×
semiarboreal	10	4.940	4.803 – 5.076	0.391	0.233 – 0.548	0.704	0.426 – 0.981	0.985	✓ (D<1)
scansorial	45	5.720	5.615 – 5.826	0.206	0.130 – 0.282	1.216	1.020 – 1.413	0.984	✓ (D>1)
terrestrial	49	5.977	5.657 – 6.296	0.307	0.130 – 0.485	1.073	0.828 – 1.319	0.960	×
semifossorial	7	4.536	4.181 – 4.891	0.311	-0.325 – 0.947	0.986	-0.832 – 2.803	0.944	×
semiaquatic	11	4.555	4.330 – 4.780	0.078	-0.092 – 0.247	1.807	0.164 – 3.450	0.906	×
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	5.565	5.328 – 5.802	0.424	0.212 – 0.636	0.830	0.583 – 1.077	0.949	×
mosaic	40	5.710	5.525 – 5.894	0.286	0.153 – 0.418	1.101	0.868 – 1.333	0.969	×
open	17	5.727	5.308 – 6.146	0.253	-0.001 – 0.506	1.209	0.711 – 1.708	0.953	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	5.346	4.774 – 5.918	0.225	-0.347 – 0.797	1.072	-0.391 – 2.535	0.826	×
variable	19	5.717	5.409 – 6.025	0.200	0.034 – 0.365	1.267	0.879 – 1.655	0.970	×

III.S8 – d_{sh}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	3.985	3.824 – 4.146	0.348	0.246 – 0.449	1.023	0.898 – 1.149	0.975	×
fissipeds	130	3.842	3.675 – 4.008	0.358	0.251 – 0.465	1.019	0.888 – 1.150	0.971	×
Family									
Canidae	17	3.056	2.850 – 3.261	0.415	0.207 – 0.623	1.100	0.710 – 1.489	0.960	×
Mustelidae	32	3.047	2.773 – 3.321	0.511	0.251 – 0.772	0.838	0.574 – 1.101	0.952	×
Procyonidae	7	2.529	2.137 – 2.921	0.338	-0.216 – 0.891	0.993	-0.856 – 2.842	0.908	×
Ursidae	7	3.691	3.617 – 3.766	0.286	0.197 – 0.376	1.025	0.658 – 1.391	0.993	×
Felidae	26	3.660	3.522 – 3.799	0.384	0.256 – 0.512	1.004	0.811 – 1.198	0.985	×
Herpestidae	12	2.121	1.960 – 2.282	0.329	0.131 – 0.527	0.862	0.302 – 1.422	0.953	×
Eupleridae	5	2.545	2.462 – 2.629	0.304	0.214 – 0.394	1.596	1.282 – 1.910	0.999	✓ (<i>D</i> > 1)
Viverridae	14	2.632	2.313 – 2.952	0.476	0.099 – 0.853	0.642	0.068 – 1.216	0.898	×
Locomotor type									
arboreal	7	2.715	2.609 – 2.822	0.313	0.197 – 0.428	1.217	0.812 – 1.621	0.993	×
semiarboreal	10	2.843	2.628 – 3.058	0.511	0.267 – 0.755	0.825	0.480 – 1.170	0.983	×
scansorial	45	3.625	3.487 – 3.764	0.261	0.158 – 0.363	1.192	0.986 – 1.399	0.982	×
terrestrial	49	3.910	3.613 – 4.206	0.447	0.255 – 0.639	0.919	0.743 – 1.095	0.969	×
semifossorial	7	2.382	2.136 – 2.628	0.215	-0.149 – 0.580	1.387	-0.184 – 2.958	0.964	×
semiaquatic	11	2.858	2.456 – 3.259	0.242	-0.123 – 0.607	1.329	0.254 – 2.404	0.915	×
aquatic	8	4.227	3.651 – 4.803	0.716	0.071 – 1.361	0.504	-0.054 – 1.062	0.936	×
Preferred habitat									
forest	38	3.390	3.154 – 3.626	0.377	0.188 – 0.567	0.997	0.736 – 1.257	0.959	×
mosaic	40	3.655	3.477 – 3.832	0.452	0.302 – 0.602	0.896	0.736 – 1.055	0.980	×
open	17	3.633	3.299 – 3.968	0.494	0.219 – 0.788	0.873	0.609 – 1.136	0.974	×
freshwater	13	2.865	2.512 – 3.218	0.254	-0.064 – 0.572	1.304	0.416 – 2.192	0.922	×
marine	10	4.186	3.801 – 4.571	0.667	0.251 – 1.082	0.583	0.279 – 0.886	0.967	✓ (<i>D</i> < 1)
variable	19	3.691	3.400 – 3.982	0.326	0.137 – 0.514	1.066	0.803 – 1.329	0.980	×
III.S9 – d_{th}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	3.808	3.626 – 3.990	0.439	0.312 – 0.565	0.915	0.795 – 1.035	0.973	×
fissipeds	130	3.649	3.462 – 3.836	0.463	0.328 – 0.598	0.887	0.764 – 1.009	0.969	×
Family									
Canidae	17	2.849	2.539 – 3.105	0.491	0.217 – 0.765	0.850	0.448 – 1.253	0.944	×
Mustelidae	32	2.379	2.170 – 2.588	0.328	0.138 – 0.518	0.933	0.624 – 1.242	0.947	×
Procyonidae	7	2.143	1.923 – 2.362	0.267	-0.036 – 0.569	0.941	-0.299 – 2.182	0.949	×
Ursidae	7	3.418	3.292 – 3.545	0.127	-0.021 – 0.274	1.613	0.135 – 3.090	0.947	×
Felidae	26	3.246	3.103 – 3.389	0.315	0.186 – 0.444	1.059	0.819 – 1.298	0.980	×
Herpestidae	12	1.762	1.614 – 1.909	0.210	0.029 – 0.391	1.054	0.193 – 1.916	0.914	×
Eupleridae	5	2.246	1.853 – 2.638	0.407	-0.116 – 0.929	1.074	-0.301 – 2.450	0.988	×
Viverridae	14	2.398	2.152 – 2.645	0.490	0.198 – 0.781	0.613	0.192 – 1.035	0.939	×
Locomotor type									
arboreal	7	2.403	2.228 – 2.577	0.353	0.183 – 0.569	0.841	0.175 – 1.507	0.978	×
semiarboreal	10	2.479	2.198 – 2.761	0.494	0.169 – 0.819	0.731	0.274 – 1.189	0.964	×
scansorial	45	3.435	3.303 – 3.566	0.323	0.217 – 0.428	1.076	0.908 – 1.244	0.986	×
terrestrial	49	3.572	3.289 – 3.855	0.436	0.251 – 0.621	0.908	0.734 – 1.081	0.968	×
semifossorial	7	2.102	1.872 – 2.332	0.225	-0.134 – 0.584	1.304	-0.172 – 2.779	0.967	×
semiaquatic	11	2.207	1.906 – 2.508	0.202	-0.091 – 0.495	1.107	0.111 – 2.103	0.893	×
aquatic	8	3.593	3.090 – 4.096	0.179	-0.297 – 0.656	1.730	-0.485 – 3.946	0.901	×
Preferred habitat									
forest	38	3.208	2.977 – 3.440	0.477	0.274 – 0.681	0.859	0.647 – 1.072	0.964	×
mosaic	40	3.443	3.254 – 3.632	0.491	0.327 – 0.656	0.856	0.697 – 1.014	0.979	×
open	17	3.263	2.979 – 3.546	0.418	0.196 – 0.639	0.930	0.676 – 1.183	0.979	×
freshwater	13	2.191	1.896 – 2.485	0.143	-0.114 – 0.399	1.408	0.111 – 2.705	0.873	×
marine	10	3.628	3.224 – 4.032	0.268	-0.118 – 0.654	1.233	0.382 – 2.083	0.948	×
variable	19	3.431	3.141 – 3.721	0.378	0.175 – 0.582	0.974	0.733 – 1.214	0.979	×

III.S10 – HR	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	4.224	-25.155 – 33.603	6.108	-23.324 – 35.540	0.038	-0.144 – 0.219	0.607	✓ (<i>D</i> =0)
fissipeds	130	-2.049	-2.351 – -1.746	0.070	-0.173 – 0.312	0.749	-0.633 – 2.130	0.292	×
Family									
Canidae	17	-2.320	-2.495 – -2.145	0.032	-0.089 – 0.152	2.042	-1.137 – 5.222	0.548	×
Mustelidae	32	-1.509	-2.425 – -0.592	0.486	-0.484 – 1.457	0.330	-0.303 – 0.963	0.620	✓ (<i>D</i> =0)
Procyonidae	7	-2.055	-2.378 – -1.733	0.108	-0.408 – 0.624	1.296	-4.827 – 7.419	0.681	n.s.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	-2.026	-2.182 – -1.871	0.105	-0.039 – 0.248	1.011	0.219 – 1.803	0.823	×
Herpestidae	12	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-2.118	-2.260 – -1.977	0.033	-0.048 – 0.114	2.911	0.284 – 5.537	0.991	×
Viverridae	14	-2.209	-2.365 – -2.053	0.078	-0.087 – 0.242	1.155	-0.628 – 2.939	0.653	×
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-2.079	-2.357 – -1.801	0.142	-0.163 – 0.447	1.017	-0.621 – 2.656	0.806	×
scansorial	45	-2.099	-2.268 – -1.930	0.053	-0.080 – 0.186	1.101	-0.192 – 2.394	0.616	×
terrestrial	49	-	-	-	-	-	-	-	n.c.
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-1.743	-2.269 – -1.217	0.120	-0.382 – 0.622	1.171	-1.742 – 4.083	0.586	n.s.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	-2.154	-2.285 – -2.023	0.005	-0.021 – 0.031	2.533	-0.467 – 5.534	0.600	×
mosaic	40	-	-	-	-	-	-	-	n.c.
open	17	-	-	-	-	-	-	-	n.c.
freshwater	13	-1.738	-2.235 – -1.240	0.196	-0.305 – 0.696	0.906	-0.753 – 2.565	0.643	×
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-2.082	-2.523 – -1.641	0.108	-0.348 – 0.565	0.429	-1.114 – 1.971	0.345	n.s.
III.S11 – L_r	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	5.470	5.287 – 5.653	0.088	0.027 – 0.149	1.600	1.277 – 1.924	0.909	✓ (<i>D</i> >1)
fissipeds	130	5.654	5.414 – 5.894	0.202	0.081 – 0.322	1.266	0.990 – 1.543	0.913	×
Family									
Canidae	17	5.444	5.060 – 5.829	0.482	0.070 – 0.893	0.854	0.238 – 1.471	0.882	×
Mustelidae	32	4.431	4.185 – 4.678	0.184	-0.002 – 0.370	1.261	0.684 – 1.839	0.897	×
Procyonidae	7	4.667	4.153 – 5.182	0.533	-0.039 – 1.104	0.460	-0.227 – 1.147	0.950	×
Ursidae	7	5.613	5.534 – 5.693	0.209	0.114 – 0.304	1.285	0.723 – 1.846	0.988	×
Felidae	26	5.531	5.333 – 5.730	0.245	0.066 – 0.423	1.060	0.632 – 1.489	0.941	×
Herpestidae	12	4.288	3.934 – 4.643	0.428	-0.002 – 0.858	0.727	-0.130 – 1.584	0.885	×
Eupleridae	5	4.417	3.765 – 5.070	0.155	-0.571 – 0.881	1.517	-3.462 – 6.496	0.909	×
Viverridae	14	4.724	4.484 – 4.964	0.463	0.183 – 0.743	0.488	0.114 – 0.862	0.944	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	4.692	4.306 – 5.078	0.346	-0.113 – 0.805	0.943	-0.516 – 2.402	0.910	×
semiarboreal	10	4.678	4.535 – 4.821	0.362	0.197 – 0.527	0.649	0.386 – 1.012	0.981	×
scansorial	45	5.538	5.386 – 5.691	0.173	0.070 – 0.276	1.300	0.981 – 1.619	0.962	×
terrestrial	49	5.909	5.496 – 6.322	0.238	0.049 – 0.428	1.258	0.909 – 1.606	0.946	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	5.395	5.001 – 5.788	0.287	-0.128 – 0.703	1.078	-0.026 – 2.181	0.910	×
Preferred habitat									
forest	38	5.316	5.048 – 5.584	0.374	0.143 – 0.605	0.887	0.576 – 1.198	0.931	×
mosaic	40	5.560	5.340 – 5.780	0.216	0.085 – 0.347	1.301	0.990 – 1.613	0.957	×
open	17	5.626	5.105 – 6.147	0.193	-0.068 – 0.454	1.394	0.711 – 2.078	0.935	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	5.499	5.118 – 5.879	0.350	-0.038 – 0.737	0.992	0.365 – 1.619	0.952	×
variable	19	5.611	5.215 – 6.007	0.144	-0.025 – 0.314	1.490	0.929 – 2.052	0.956	×

III.S12 – d_{sr}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	3.112	2.928 – 3.296	0.326	0.207 – 0.445	0.994	0.838 – 1.149	0.961	×
fissipeds	130	3.017	2.824 – 3.209	0.363	0.232 – 0.494	0.952	0.797 – 1.108	0.956	×
Family									
Canidae	17	2.466	2.210 – 2.721	0.415	0.152 – 0.678	1.039	0.554 – 1.525	0.936	×
Mustelidae	32	2.013	1.772 – 2.255	0.266	0.061 – 0.471	1.069	0.644 – 1.495	0.923	×
Procyonidae	7	1.774	1.352 – 2.196	0.374	-0.121 – 0.869	0.582	-0.450 – 1.614	0.918	×
Ursidae	7	2.780	2.541 – 3.018	0.120	-0.138 – 0.379	2.206	-0.579 – 4.992	0.902	×
Felidae	26	2.831	2.635 – 3.026	0.416	0.229 – 0.602	0.947	0.691 – 1.203	0.973	×
Herpestidae	12	1.528	1.268 – 1.789	0.284	-0.037 – 0.604	0.976	-0.127 – 2.079	0.861	×
Eupleridae	5	1.624	1.330 – 1.918	0.210	-0.125 – 0.546	1.454	-0.247 – 3.155	0.987	×
Viverridae	14	2.024	1.845 – 2.203	0.526	0.316 – 0.737	0.546	0.280 – 0.812	0.972	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	2.059	1.428 – 2.689	0.635	-0.149 – 1.418	0.367	-0.433 – 1.167	0.974	×
semiarboreal	10	1.700	1.541 – 1.860	0.169	0.002 – 0.335	1.210	0.429 – 1.990	0.960	×
scansorial	45	2.864	2.679 – 3.050	0.343	0.186 – 0.500	0.989	0.759 – 1.219	0.971	×
terrestrial	49	3.084	2.776 – 3.393	0.336	0.153 – 0.519	1.009	0.781 – 1.237	0.959	×
semifossorial	7	1.769	1.509 – 2.029	0.198	-0.162 – 0.558	1.485	-0.203 – 3.174	0.960	×
semiaquatic	11	2.114	1.746 – 2.482	0.309	-0.049 – 0.668	1.096	0.301 – 1.890	0.926	×
aquatic	8	3.011	2.414 – 3.608	0.236	-0.345 – 0.816	1.607	-0.422 – 3.635	0.898	×
Preferred habitat									
forest	38	2.658	2.366 – 2.950	0.479	0.211 – 0.747	0.784	0.512 – 1.056	0.934	×
mosaic	40	2.857	2.670 – 3.044	0.434	0.271 – 0.598	0.857	0.679 – 1.034	0.974	×
open	17	2.794	2.466 – 3.122	0.353	0.108 – 0.598	0.981	0.645 – 1.316	0.967	×
freshwater	13	2.113	1.781 – 2.446	0.288	-0.024 – 0.600	1.173	0.921 – 1.924	0.927	×
marine	10	3.095	2.506 – 3.684	0.393	-0.211 – 0.998	0.954	0.092 – 1.816	0.908	×
variable	19	2.832	2.486 – 3.179	0.271	0.055 – 0.487	1.108	0.743 – 1.473	0.965	×
III.S13 – d_{tr}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	137	4.031	3.757 – 4.304	0.590	0.391 – 0.789	0.862	0.725 – 1.000	0.963	×
fissipeds	130	3.467	3.234 – 3.700	0.384	0.235 – 0.534	1.023	0.853 – 1.193	0.953	×
Family									
Canidae	17	2.897	2.634 – 3.160	0.538	0.256 – 0.820	0.844	0.468 – 1.220	0.950	×
Mustelidae	32	2.365	2.088 – 2.642	0.580	0.304 – 0.856	0.707	0.474 – 0.940	0.950	✓ (<i>D</i> <1)
Procyonidae	7	1.956	1.574 – 2.338	0.315	-0.232 – 0.861	1.022	-0.970 – 3.014	0.901	×
Ursidae	7	3.330	2.976 – 3.685	0.341	-0.083 – 0.766	0.927	-0.487 – 2.341	0.904	×
Felidae	26	3.210	3.086 – 3.334	0.352	0.240 – 0.464	1.053	0.867 – 1.240	0.988	×
Herpestidae	12	1.592	0.867 – 2.318	0.432	-0.391 – 1.254	0.472	-0.710 – 1.653	0.751	×
Eupleridae	5	1.998	1.663 – 2.334	0.386	-0.049 – 0.826	1.127	-0.080 – 2.334	0.991	×
Viverridae	14	2.303	1.897 – 2.709	0.735	0.271 – 1.199	0.401	0.066 – 0.736	0.951	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	2.194	1.832 – 2.557	0.366	-0.061 – 0.793	0.967	-0.317 – 2.250	0.929	×
semiarboreal	10	2.363	2.019 – 2.707	0.658	0.255 – 1.062	0.590	0.196 – 0.983	0.964	✓ (<i>D</i> <1)
scansorial	45	3.240	3.088 – 3.392	0.290	0.174 – 0.405	1.159	0.951 – 1.368	0.981	×
terrestrial	49	3.580	3.141 – 4.019	0.390	0.139 – 0.641	1.045	0.773 – 1.317	0.948	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	2.130	1.806 – 2.453	0.422	0.077 – 0.767	0.704	0.206 – 1.203	0.933	×
aquatic	8	4.097	3.622 – 4.572	0.444	-0.051 – 0.939	1.180	0.314 – 2.046	0.952	×
Preferred habitat									
forest	38	2.923	2.622 – 3.224	0.404	0.160 – 0.648	0.983	0.671 – 1.296	0.941	×
mosaic	40	3.217	2.976 – 3.459	0.408	0.218 – 0.598	0.992	0.763 – 1.221	0.966	×
open	17	3.247	2.792 – 3.702	0.373	0.059 – 0.688	1.068	0.656 – 1.479	0.959	×
freshwater	13	2.052	1.691 – 2.412	0.251	-0.097 – 0.600	1.059	0.121 – 1.997	0.869	×
marine	10	3.926	3.433 – 4.418	0.355	-0.114 – 0.824	1.241	0.461 – 2.021	0.957	×
variable	19	3.354	2.989 – 3.720	0.286	0.076 – 0.495	1.198	0.857 – 1.539	0.974	×

III.S14 – P	n	<i>ln A</i>	95% <i>CI_{ln A}</i>	<i>C</i>	95% <i>CI_C</i>	<i>D</i>	95% <i>CI_D</i>	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	3.190	2.960 – 3.421	0.357	0.216 – 0.497	1.057	0.887 – 1.228	0.957	×
fissipeds	130	3.269	2.996 – 3.542	0.521	0.328 – 0.714	0.909	0.752 – 1.066	0.952	×
Family									
Canidae	17	2.086	1.949 – 2.223	0.283	0.162 – 0.405	1.477	1.127 – 1.827	0.977	✓ (<i>D</i> >1)
Mustelidae	32	1.672	1.421 – 1.923	0.291	0.077 – 0.505	1.062	0.652 – 1.468	0.929	×
Procyonidae	7	1.470	0.757 – 2.183	0.422	-0.426 – 1.270	0.612	-0.018 – 2.242	0.835	×
Ursidae	7	3.253	2.791 – 3.726	0.533	-0.005 – 1.071	0.561	-0.329 – 1.452	0.937	×
Felidae	26	2.823	2.652 – 2.994	0.355	0.198 – 0.511	1.026	0.769 – 1.283	0.976	×
Herpestidae	12	1.500	1.020 – 1.980	0.665	0.127 – 1.204	0.441	-0.032 – 0.914	0.941	✓ (<i>D</i> =0)
Eupleridae	5	1.480	1.136 – 1.823	0.114	-0.093 – 0.321	2.844	0.910 – 4.778	0.995	×
Viverridae	14	1.608	1.218 – 1.997	0.396	-0.046 – 0.839	0.894	-0.010 – 1.799	0.829	×
Locomotor type									
arboreal	7	1.750	1.008 – 2.491	0.382	-0.390 – 1.153	1.346	-0.859 – 3.552	0.861	×
semiarboreal	10	1.780	1.378 – 2.182	0.342	-0.072 – 0.755	1.256	0.291 – 2.221	0.944	×
scansorial	45	2.889	2.714 – 3.063	0.254	0.135 – 0.373	1.286	1.034 – 1.537	0.976	✓ (<i>D</i> >1)
terrestrial	49	3.349	2.947 – 3.751	0.566	0.295 – 0.836	0.879	0.685 – 1.072	0.957	×
semifossorial	7	1.356	1.179 – 1.532	0.082	-0.069 – 0.233	2.174	0.490 – 3.859	0.972	×
semiaquatic	11	–	–	–	–	–	–	–	n.c.
aquatic	8	2.925	2.557 – 3.292	0.217	-0.139 – 0.572	1.632	0.278 – 2.986	0.952	×
Preferred habitat									
forest	38	2.596	2.239 – 2.952	0.391	0.119 – 0.663	1.073	0.707 – 1.440	0.931	×
mosaic	40	2.881	2.644 – 3.119	0.461	0.266 – 0.655	0.941	0.736 – 1.145	0.970	×
open	17	2.933	2.585 – 3.282	0.481	0.217 – 0.744	0.966	0.702 – 1.230	0.979	×
freshwater	13	–	–	–	–	–	–	–	n.c.
marine	10	3.107	2.632 – 3.582	0.408	-0.075 – 0.891	1.002	0.332 – 1.673	0.947	×
variable	19	3.092	2.655 – 3.528	0.459	0.149 – 0.770	0.956	0.654 – 1.257	0.966	×

III.S15 – RR	n	<i>ln A</i>	95% <i>CI_{ln A}</i>	<i>C</i>	95% <i>CI_C</i>	<i>D</i>	95% <i>CI_D</i>	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	-2.792	-2.856 – -2.728	-1.25 · 10 ⁻⁷	-1.85 · 10 ⁻⁶ – 1.61 · 10 ⁻⁶	7.165	0.438 – 13.891	0.251	×
fissipeds	130	-2.838	-2.912 – -2.763	-1.48 · 10 ⁻⁵	-1.37 · 10 ⁻⁴ – 1.07 · 10 ⁻⁴	5.090	0.940 – 9.240	0.319	×
Family									
Canidae	17	-2.917	-3.140 – -2.693	0.005	-0.089 – 0.100	2.954	-11.798 – 17.706	0.207	n.s.
Mustelidae	32	-2.477	-2.851 – -2.103	0.022	-0.353 – 0.397	0.686	-7.398 – 8.769	0.089	n.s.
Procyonidae	7	–	–	–	–	–	–	–	n.c.
Ursidae	7	–	–	–	–	–	–	–	n.c.
Felidae	26	-2.704	-2.975 – -2.432	0.166	-0.113 – 0.445	0.769	-0.127 – 1.666	0.714	×
Herpestidae	12	–	–	–	–	–	–	–	n.c.
Eupleridae	5	-2.786	-3.188 – -2.385	0.074	-0.506 – 0.655	0.908	-7.186 – 9.002	0.736	n.s.
Viverridae	14	-2.678	-2.858 – -2.499	0.088	-0.124 – 0.300	0.665	-1.106 – 2.437	0.556	×
Locomotor type									
arboreal	7	–	–	–	–	–	–	–	n.c.
semiarboreal	10	–	–	–	–	–	–	–	n.c.
scansorial	45	-2.742	-3.261 – -2.223	0.112	-0.424 – 0.648	0.467	-1.287 – 2.221	0.266	n.s.
terrestrial	49	-2.940	-3.156 – -2.724	-0.004	-0.026 – 0.017	2.452	-0.081 – 4.985	0.578	×
semifossorial	7	–	–	–	–	–	–	–	n.c.
semiaquatic	11	-2.133	-2.784 – -1.483	0.229	-0.469 – 0.928	0.674	-1.156 – 2.503	0.566	n.s.
aquatic	8	–	–	–	–	–	–	–	n.c.
Preferred habitat									
forest	38	–	–	–	–	–	–	–	n.c.
mosaic	40	-2.920	-3.063 – -2.777	-0.001	-0.009 – 0.006	3.237	0.050 – 6.423	0.539	×
open	17	-2.974	-3.262 – -2.686	-4.47 · 10 ⁻⁴	-0.006 – 0.005	3.866	-3.067 – 10.800	0.560	×
freshwater	13	-2.097	-3.064 – -1.129	0.372	-0.676 – 1.422	0.523	-0.984 – 2.030	0.533	n.s.
marine	10	–	–	–	–	–	–	–	n.c.
variable	19	-2.947	-3.127 – -2.767	-3.08 · 10 ⁻⁴	-0.004 – 0.003	3.762	-1.735 – 9.259	0.575	×

III.S16 – L_u	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	5.510	5.331 – 5.688	0.085	0.027 – 0.143	1.613	1.291 – 1.936	0.911	✓ (<i>D</i> >1)
fissipeds	129	5.736	5.499 – 5.972	0.216	0.092 – 0.339	1.235	0.972 – 1.497	0.919	×
Family									
Canidae	16	5.491	5.102 – 5.881	0.473	0.054 – 0.891	0.869	0.228 – 1.511	0.886	×
Mustelidae	32	4.525	4.278 – 4.772	0.199	0.007 – 0.390	1.215	0.666 – 1.764	0.901	×
Procyonidae	7	4.721	4.162 – 5.281	0.540	-0.074 – 1.155	0.435	-0.256 – 1.125	0.947	×
Ursidae	7	5.703	5.630 – 5.776	0.239	0.151 – 0.327	1.115	0.673 – 1.557	0.991	×
Felidae	26	5.593	5.409 – 5.778	0.245	0.080 – 0.411	1.060	0.663 – 1.456	0.949	×
Herpestidae	12	4.305	4.007 – 4.603	0.384	0.019 – 0.750	0.824	-0.042 – 1.689	0.894	×
Eupleridae	5	4.469	3.923 – 5.015	0.172	-0.455 – 0.799	1.439	-2.444 – 5.322	0.938	×
Viverridae	14	4.816	4.534 – 5.099	0.516	0.191 – 0.840	0.417	0.072 – 0.762	0.949	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	4.762	4.370 – 5.155	0.358	-0.111 – 0.827	0.929	-0.509 – 2.368	0.912	×
semiarboreal	10	4.779	4.623 – 4.934	0.407	0.226 – 0.589	0.633	0.339 – 0.926	0.981	✓ (<i>D</i> <1)
scansorial	45	5.599	5.452 – 5.746	0.172	0.073 – 0.271	1.308	1.000 – 1.616	0.964	×
terrestrial	48	5.986	5.573 – 6.400	0.258	0.060 – 0.456	1.219	0.883 – 1.554	0.947	×
semifossorial	7	–	–	–	–	–	–	–	n.c.
semiaquatic	11	–	–	–	–	–	–	–	n.c.
aquatic	8	5.306	4.878 – 5.734	0.188	-0.253 – 0.629	1.257	-0.590 – 3.105	0.847	×
Preferred habitat									
forest	38	5.406	5.135 – 5.678	0.393	0.156 – 0.630	0.872	0.570 – 1.173	0.932	×
mosaic	39	5.616	5.397 – 5.836	0.228	0.092 – 0.364	1.269	0.962 – 1.576	0.959	×
open	17	5.696	5.181 – 6.212	0.202	-0.063 – 0.466	1.372	0.711 – 2.033	0.938	×
freshwater	13	–	–	–	–	–	–	–	n.c.
marine	10	5.448	5.001 – 5.895	0.272	-0.173 – 0.717	1.086	0.142 – 2.029	0.918	×
variable	19	5.668	5.279 – 6.058	0.148	-0.022 – 0.319	1.467	0.918 – 2.016	0.957	×

III.S17 – d_{su}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.585	3.328 – 3.843	0.442	0.260 – 0.624	0.901	0.731 – 1.071	0.948	×
fissipeds	129	3.466	3.189 – 3.743	0.492	0.286 – 0.697	0.852	0.679 – 1.025	0.938	×
Family									
Canidae	16	2.289	1.984 – 2.594	0.378	0.071 – 0.685	1.167	0.529 – 1.804	0.918	×
Mustelidae	32	2.429	2.191 – 2.667	0.407	0.185 – 0.629	0.880	0.593 – 1.167	0.949	×
Procyonidae	7	2.100	1.546 – 2.655	0.247	-0.720 – 1.214	1.498	-3.882 – 6.877	0.784	×
Ursidae	7	3.249	2.832 – 3.667	0.214	-0.284 – 0.712	0.852	-1.712 – 3.416	0.744	n.s.
Felidae	26	3.165	2.952 – 3.379	0.424	0.214 – 0.633	0.880	0.604 – 1.157	0.964	×
Herpestidae	12	1.752	1.261 – 2.243	0.497	-0.077 – 1.071	0.568	-0.267 – 1.403	0.867	×
Eupleridae	5	2.057	1.554 – 2.560	0.561	-0.239 – 1.362	0.661	-0.767 – 2.090	0.985	×
Viverridae	14	–	–	–	–	–	–	–	n.c.
Locomotor type									
arboreal	7	2.568	1.808 – 3.328	0.742	-0.206 – 1.690	0.372	-0.469 – 1.212	0.971	×
semiarboreal	10	2.243	2.008 – 2.479	0.384	0.114 – 0.655	0.763	0.267 – 1.258	0.961	×
scansorial	45	3.229	3.016 – 3.443	0.304	0.135 – 0.474	1.089	0.802 – 1.377	0.961	×
terrestrial	48	3.342	2.960 – 3.723	0.591	0.301 – 0.881	0.743	0.552 – 0.935	0.939	✓ (<i>D</i> <1)
semifossorial	7	2.220	1.857 – 2.583	0.539	-0.052 – 1.130	0.679	-0.156 – 1.514	0.982	×
semiaquatic	11	2.333	2.067 – 2.599	0.323	0.058 – 0.589	1.010	0.458 – 1.563	0.955	×
aquatic	8	3.351	2.823 – 3.879	0.185	-0.329 – 0.699	1.596	-0.693 – 3.885	0.873	×
Preferred habitat									
forest	38	3.104	2.732 – 3.475	0.511	0.181 – 0.840	0.840	0.520 – 1.160	0.921	×
mosaic	39	3.213	2.943 – 3.484	0.519	0.273 – 0.766	0.798	0.578 – 1.018	0.959	×
open	17	3.107	2.522 – 3.693	0.618	0.081 – 1.154	0.732	0.333 – 1.131	0.926	×
freshwater	13	2.301	1.964 – 2.638	0.261	-0.058 – 0.580	1.148	0.306 – 1.989	0.907	×
marine	10	3.372	2.971 – 3.772	0.247	-0.140 – 0.633	1.204	0.284 – 2.124	0.937	×
variable	19	3.301	2.910 – 3.693	0.525	0.210 – 0.839	0.801	0.542 – 1.059	0.962	×

III.S18 – d_{tu}	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.316	3.089 – 3.543	0.426	0.269 – 0.584	0.992	0.768 – 1.076	0.958	×
fissipeds	129	3.370	3.108 – 3.632	0.585	0.382 – 0.788	0.798	0.657 – 0.939	0.953	✓ (<i>D</i> <1)
Family									
Canidae	16	2.392	2.067 – 2.717	0.443	0.093 – 0.793	0.861	0.291 – 1.432	0.906	×
Mustelidae	32	1.887	1.639 – 2.134	0.238	0.037 – 0.439	1.141	0.667 – 1.615	0.915	×
Procyonidae	7	1.677	1.041 – 2.314	0.436	-0.262 – 1.134	0.432	-0.535 – 1.400	0.903	×
Ursidae	7	3.083	2.751 – 3.415	0.133	-0.221 – 0.486	2.313	-1.158 – 5.784	0.870	×
Felidae	26	2.974	2.654 – 3.293	0.545	0.223 – 0.867	0.815	0.491 – 1.139	0.945	×
Herpestidae	12	1.618	1.269 – 1.968	0.422	-0.002 – 0.846	0.741	-0.126 – 1.607	0.884	×
Eupleridae	5	1.687	1.516 – 1.858	0.358	0.124 – 0.592	1.010	0.310 – 1.710	0.997	×
Viverridae	14	1.941	1.714 – 2.169	0.398	0.132 – 0.664	0.738	0.225 – 1.250	0.924	×
Locomotor type									
arboreal	7	1.772	1.455 – 2.090	0.222	-0.100 – 0.543	1.432	-0.149 – 3.012	0.926	×
semiarboreal	10	1.968	1.724 – 2.212	0.455	0.171 – 0.739	0.676	0.254 – 1.098	0.965	×
scansorial	45	3.157	2.877 – 3.437	0.512	0.258 – 0.766	0.866	0.627 – 1.106	0.962	×
terrestrial	48	3.313	2.994 – 3.631	0.472	0.262 – 0.682	0.901	0.719 – 1.083	0.965	×
semifossorial	7	1.689	1.154 – 2.225	0.462	-0.458 – 1.383	0.763	-0.848 – 2.375	0.946	×
semiaquatic	11	1.814	1.421 – 2.207	0.140	-0.204 – 0.484	1.436	-0.345 – 3.217	0.833	×
aquatic	8	3.036	2.853 – 3.219	0.235	0.058 – 0.413	1.622	0.999 – 2.244	0.989	×
Preferred habitat									
forest	38	2.875	2.556 – 3.194	0.619	0.315 – 0.923	0.720	0.488 – 0.951	0.945	✓ (<i>D</i> <1)
mosaic	39	3.094	2.798 – 3.390	0.615	0.338 – 0.892	0.752	0.547 – 0.958	0.961	✓ (<i>D</i> <1)
open	17	2.923	2.585 – 3.261	0.431	0.171 – 0.691	0.949	0.660 – 1.239	0.974	×
freshwater	13	1.830	1.458 – 2.203	0.172	-0.164 – 0.507	1.309	-0.079 – 2.697	0.837	×
marine	10	3.222	2.753 – 3.690	0.451	-0.033 – 0.935	0.921	0.324 – 1.518	0.949	×
variable	19	2.998	2.601 – 3.395	0.385	0.110 – 0.660	0.988	0.668 – 1.308	0.964	×
III.S19 – O	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	4.300	4.176 – 4.424	0.224	0.159 – 0.290	1.209	1.079 – 1.339	0.978	✓ (<i>D</i> >1)
fissipeds	129	4.199	4.064 – 4.334	0.256	0.180 – 0.331	1.163	1.029 – 1.297	0.975	✓ (<i>D</i> >1)
Family									
Canidae	16	3.667	3.465 – 3.868	0.394	0.185 – 0.603	1.048	0.642 – 1.454	0.959	×
Mustelidae	32	3.305	3.122 – 3.488	0.324	0.168 – 0.480	1.059	0.793 – 1.324	0.967	×
Procyonidae	7	2.837	2.325 – 3.348	0.294	-0.482 – 1.071	1.155	-2.079 – 4.389	0.831	×
Ursidae	7	4.395	2.809 – 5.982	0.608	-1.027 – 2.242	0.225	-0.664 – 1.113	0.927	×
Felidae	26	4.192	4.069 – 4.315	0.385	0.268 – 0.501	0.969	0.795 – 1.143	0.987	×
Herpestidae	12	2.711	2.556 – 2.866	0.325	0.134 – 0.515	0.984	0.409 – 1.558	0.956	×
Eupleridae	5	3.001	2.629 – 3.373	0.311	-0.145 – 0.767	1.279	-0.287 – 2.846	0.987	×
Viverridae	14	3.117	2.951 – 3.283	0.314	0.138 – 0.489	1.141	0.670 – 1.612	0.956	×
Locomotor type									
arboreal	7	3.207	2.815 – 3.600	0.379	-0.063 – 0.822	1.099	-0.184 – 2.381	0.934	×
semiarboreal	10	3.109	2.942 – 3.438	0.395	0.121 – 0.669	0.990	0.465 – 1.515	0.972	×
scansorial	45	4.058	3.927 – 4.188	0.217	0.125 – 0.308	1.257	1.032 – 1.482	0.980	✓ (<i>D</i> >1)
terrestrial	48	4.304	4.050 – 4.557	0.297	0.161 – 0.434	1.107	0.911 – 1.304	0.976	×
semifossorial	7	3.184	2.952 – 3.416	0.403	-0.013 – 0.820	0.979	0.063 – 1.894	0.985	×
semiaquatic	11	3.257	2.953 – 3.562	0.256	-0.029 – 0.541	1.232	0.449 – 2.014	0.944	×
aquatic	8	4.232	3.830 – 4.634	0.135	-0.223 – 0.493	1.982	-0.279 – 4.244	0.927	×
Preferred habitat									
forest	38	3.873	3.677 – 4.070	0.334	0.183 – 0.484	1.067	0.830 – 1.305	0.969	×
mosaic	39	4.044	3.886 – 4.202	0.300	0.186 – 0.414	1.105	0.915 – 1.296	0.980	×
open	17	4.165	3.972 – 4.359	0.373	0.235 – 0.511	1.030	0.850 – 1.211	0.991	×
freshwater	13	3.238	2.912 – 3.563	0.244	-0.057 – 0.545	1.228	0.365 – 2.092	0.916	×
marine	10	4.326	3.913 – 4.740	0.287	-0.120 – 0.693	1.137	0.313 – 1.961	0.941	×
variable	19	3.950	3.759 – 4.140	0.155	0.064 – 0.246	1.389	1.112 – 1.667	0.987	✓ (<i>D</i> >1)

III.S20 – θ	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	R	<i>D</i> ≠ 1
whole sample	136	-2.520	-3.115 – -1.925	-0.009	-0.279 – 0.260	1.344	-11.773 – 14.461	0.045	n.s.
fissipeds	129	-2.716	-3.947 – -1.484	-0.105	-1.167 – 0.957	0.642	-3.144 – 4.428	0.100	n.s.
Family									
Canidae	16	-	-	-	-	-	-	-	n.c.
Mustelidae	32	-	-	-	-	-	-	-	n.c.
Procyonidae	7	-2.082	-2.977 – -1.187	0.374	-1.110 – 1.858	1.365	-3.892 – 6.622	0.753	n.s.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	-	-	-	-	-	-	-	n.c.
Herpestidae	12	-1.920	-2.686 – -1.154	0.277	-0.599 – 1.153	1.546	-1.792 – 4.884	0.608	×
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-	-	-	-	-	-	-	n.c.
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	-	-	-	-	-	-	-	n.c.
terrestrial	48	-3.009	-4.259 – -1.759	-0.036	-0.496 – 0.423	1.455	-4.256 – 7.166	0.207	n.s.
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	-	-	-	-	-	-	-	n.c.
mosaic	39	-	-	-	-	-	-	-	n.c.
open	17	-	-	-	-	-	-	-	n.c.
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-	-	-	-	-	-	-	n.c.
III.S21 – α	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	R	<i>D</i> ≠ 1
whole sample	136	-0.365	-0.877 – 0.146	0.192	-0.144 – 0.528	0.982	0.239 – 1.724	0.586	×
fissipeds	129	-0.412	-1.009 – 0.184	0.243	-0.194 – 0.681	0.867	0.116 – 1.617	0.535	×
Family									
Canidae	16	-0.518	-0.856 – -0.180	0.092	-0.213 – 0.397	1.480	-1.207 – 4.166	0.539	×
Mustelidae	32	-	-	-	-	-	-	-	n.c.
Procyonidae	7	-1.193	-2.295 – -0.092	0.630	-0.741 – 2.000	0.712	-1.264 – 2.687	0.817	×
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	-0.719	-1.016 – -0.423	0.120	-0.087 – 0.326	1.471	0.391 – 2.551	0.832	×
Herpestidae	12	-1.087	-2.235 – 0.062	0.406	-0.929 – 1.740	0.548	-1.764 – 2.859	0.526	n.s.
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-1.463	-1.941 – -0.985	0.127	-0.258 – 0.512	1.792	-0.812 – 4.396	0.624	×
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	-0.636	-0.910 – -0.362	0.137	-0.056 – 0.330	1.251	0.502 – 1.999	0.826	×
terrestrial	48	-0.271	-1.096 – 0.554	0.143	-0.300 – 0.586	1.110	-0.213 – 2.434	0.556	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	-0.425	-1.521 – 0.670	0.578	-0.566 – 1.721	0.503	-0.302 – 1.309	0.550	×
mosaic	39	-0.538	-1.176 – 0.099	0.235	-0.282 – 0.753	0.963	-0.111 – 2.037	0.623	×
open	17	-0.566	-1.624 – 0.492	0.157	-0.646 – 0.960	0.964	-1.496 – 3.423	0.454	n.s.
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-	-	-	-	-	-	-	n.c.

III.S22 – UR	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1	
whole sample	136	-	-	-	-	-	-	-	n.c.	
fissipeds	129	-2.659	-2.749 – -2.570	-5.03 · 10 ⁻⁶	-8.56 · 10 ⁻⁵	-7.55 · 10 ⁻⁵	5.440	-2.626 – 13.506	0.179	×
Family										
Canidae	16	-3.109	-3.384 – -2.833	0.012	-0.123 – 0.146	2.720	-6.867 – 12.306	0.297	n.s.	
Mustelidae	32	-1.900	-4.729 – 0.929	0.409	-2.494 – 3.312	0.161	-1.039 – 1.362	0.349	n.s.	
Procyonidae	7	-	-	-	-	-	-	-	n.c.	
Ursidae	7	-	-	-	-	-	-	-	n.c.	
Felidae	26	-2.400	-2.966 – -1.835	0.209	-0.414 – 0.832	0.469	-0.797 – 1.736	0.475	×	
Herpestidae	12	-	-	-	-	-	-	-	n.c.	
Eupleridae	5	-	-	-	-	-	-	-	n.c.	
Viverridae	14	-	-	-	-	-	-	-	n.c.	
Locomotor type										
arboreal	7	-	-	-	-	-	-	-	n.c.	
semiarboreal	10	-2.497	-2.756 – -2.239	0.027	-0.244 – 0.299	1.193	-6.714 – 9.100	0.315	n.s.	
scansorial	45	-2.336	-2.914 – -1.758	0.182	-0.415 – 0.779	0.463	-0.733 – 1.658	0.374	×	
terrestrial	48	-3.039	-3.337 – -2.740	-0.004	-0.028 – 0.020	2.605	-0.232 – 5.441	0.551	×	
semifossorial	7	-	-	-	-	-	-	-	n.c.	
semiaquatic	11	-1.965	-2.772 – -1.157	0.287	-0.606 – 1.181	0.412	-1.062 – 1.886	0.576	n.s.	
aquatic	8	-	-	-	-	-	-	-	n.c.	
Preferred habitat										
forest	38	-2.299	-2.740 – -1.857	0.117	-0.300 – 0.534	0.733	-0.953 – 2.418	0.370	×	
mosaic	39	-2.716	-2.893 – -2.539	-0.002	-0.020 – 0.016	2.753	-1.832 – 7.338	0.370	×	
open	17	-3.017	-3.430 – -2.603	-2.43 · 10 ⁻⁴	-0.005 – 0.004	4.267	-5.908 – 14.442	0.452	n.s.	
freshwater	13	-1.873	-3.536 – -0.210	0.463	-1.326 – 2.253	0.288	-1.073 – 1.649	0.533	n.s.	
marine	10	-	-	-	-	-	-	-	n.c.	
variable	19	-2.859	-3.140 – -2.577	-0.001	-0.013 – 0.011	3.237	-2.788 – 9.261	0.489	×	
III.S23 – IFA	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1	
whole sample	136	-0.422	-4.259 – 3.416	0.992	-2.882 – 4.866	0.114	-0.315 – 0.543	0.341	✓ (<i>D</i> =0)	
fissipeds	129	-1.358	-10.852 – 8.137	0.235	-9.312 – 9.782	0.068	-2.713 – 2.850	0.055	n.s.	
Family										
Canidae	16	-1.753	-1.917 – -1.589	0.001	-0.018 – 0.019	4.920	-23.901 – 33.741	0.237	n.s.	
Mustelidae	32	-1.243	-1.575 – -0.910	0.104	-0.216 – 0.425	0.795	-0.762 – 2.352	0.459	×	
Procyonidae	7	-	-	-	-	-	-	-	n.c.	
Ursidae	7	-	-	-	-	-	-	-	n.c.	
Felidae	26	-1.398	-1.620 – -1.176	0.142	-0.086 – 0.370	0.765	-0.088 – 1.618	0.730	×	
Herpestidae	12	-	-	-	-	-	-	-	n.c.	
Eupleridae	5	-1.458	-1.856 – -1.059	0.162	-0.421 – 0.745	0.881	-2.828 – 4.589	0.920	×	
Viverridae	14	-1.531	-1.628 – -1.435	0.023	-0.025 – 0.071	2.685	0.930 – 4.440	0.867	×	
Locomotor type										
arboreal	7	-	-	-	-	-	-	-	n.c.	
semiarboreal	10	-1.557	-1.705 – -1.409	0.036	-0.060 – 0.132	2.199	-0.092 – 4.491	0.891	×	
scansorial	45	-1.552	-1.718 – -1.386	0.036	-0.093 – 0.166	1.116	-0.750 – 2.982	0.480	×	
terrestrial	48	-1.763	-2.028 – -1.498	-0.010	-0.084 – 0.064	1.683	-1.743 – 5.109	0.374	×	
semifossorial	7	-	-	-	-	-	-	-	n.c.	
semiaquatic	11	-1.047	-1.482 – -0.613	0.217	-0.251 – 0.685	0.655	-0.628 – 1.938	0.693	×	
aquatic	8	-1.027	-1.156 – -0.899	0.009	-0.045 – 0.062	3.696	-1.901 – 9.294	0.911	×	
Preferred habitat										
forest	38	-1.517	-1.649 – -1.386	0.001	-0.008 – 0.010	3.462	-1.210 – 8.133	0.534	×	
mosaic	39	-1.659	-1.770 – -1.547	-3.27 · 10 ⁻⁴	-0.008 – 0.007	3.068	-6.315 – 12.450	0.207	n.s.	
open	17	-	-	-	-	-	-	-	n.c.	
freshwater	13	-0.974	-2.162 – 0.215	0.411	-0.887 – 1.708	0.366	-0.990 – 1.721	0.539	n.s.	
marine	10	-1.112	-1.524 – -0.700	0.027	-0.353 – 0.406	1.340	-7.170 – 9.849	0.313	n.s.	
variable	19	-1.740	-2.002 – -1.478	-0.007	-0.076 – 0.062	1.914	-3.090 – 6.918	0.411	n.s.	

III.S24 – L_m	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	4.449	4.254 – 4.644	0.080	0.017 – 0.143	1.620	1.248 – 1.993	0.887	✓ (<i>D</i> >1)
fissipeds	129	4.566	4.323 – 4.810	0.157	0.045 – 0.268	1.356	1.023 – 1.690	0.890	✓ (<i>D</i> >1)
Family									
Canidae	16	4.589	4.290 – 4.888	0.454	0.135 – 0.772	0.930	0.409 – 1.451	0.926	×
Mustelidae	32	3.477	3.236 – 3.718	0.127	-0.038 – 0.292	1.395	0.636 – 2.153	0.857	×
Procyonidae	7	3.529	2.596 – 4.462	0.513	-0.461 – 1.487	0.311	-0.513 – 1.134	0.912	×
Ursidae	7	4.505	4.156 – 4.855	0.409	-0.003 – 0.821	0.707	-0.315 – 1.730	0.931	×
Felidae	26	4.635	4.478 – 4.792	0.239	0.103 – 0.375	1.135	0.796 – 1.473	0.966	×
Herpestidae	12	3.492	3.220 – 3.764	0.512	0.188 – 0.836	0.642	0.142 – 1.141	0.951	×
Eupleridae	5	3.315	3.038 – 3.591	0.106	-0.169 – 0.382	1.774	-0.979 – 4.527	0.976	×
Viverridae	14	3.593	3.365 – 3.821	0.340	0.082 – 0.597	0.927	0.309 – 1.545	0.911	×
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	3.699	3.142 – 4.256	0.430	-0.221 – 1.081	0.620	-0.373 – 1.613	0.830	×
scansorial	45	4.384	4.199 – 4.569	0.098	0.002 – 0.195	1.579	1.035 – 2.123	0.918	✓ (<i>D</i> >1)
terrestrial	48	4.942	4.531 – 5.353	0.200	0.024 – 0.375	1.325	0.935 – 1.715	0.942	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	3.716	3.269 – 4.164	0.369	-0.115 – 0.852	0.639	-0.134 – 1.412	0.844	×
aquatic	8	4.643	4.250 – 5.036	0.523	0.100 – 0.945	0.916	0.319 – 1.514	0.960	×
Preferred habitat									
forest	38	4.089	3.778 – 4.401	0.213	-0.013 – 0.440	1.136	0.569 – 1.703	0.868	×
mosaic	40	4.474	4.219 – 4.728	0.170	0.031 – 0.309	1.384	0.958 – 1.810	0.930	×
open	17	4.759	4.244 – 5.274	0.192	-0.063 – 0.448	1.406	0.735 – 2.076	0.939	×
freshwater	13	3.674	3.259 – 4.089	0.282	-0.150 – 0.714	0.747	-0.193 – 1.686	0.780	×
marine	10	4.745	4.274 – 5.215	0.647	0.141 – 1.153	0.649	0.254 – 1.044	0.954	×
variable	18	4.638	4.133 – 5.143	0.143	-0.079 – 0.366	1.475	0.733 – 2.218	0.932	×
III.S25 – d_{sm}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	2.692	2.524 – 2.860	0.283	0.180 – 0.385	1.060	0.903 – 1.217	0.963	×
fissipeds	129	2.575	2.397 – 2.753	0.296	0.185 – 0.407	1.050	0.884 – 1.216	0.957	×
Family									
Canidae	16	1.987	1.781 – 2.194	0.291	0.099 – 0.483	1.396	0.861 – 1.931	0.951	×
Mustelidae	32	1.717	1.482 – 1.952	0.339	0.125 – 0.553	0.933	0.595 – 1.270	0.937	×
Procyonidae	7	1.248	0.595 – 1.901	0.325	-0.498 – 1.149	0.742	-1.622 – 3.105	0.776	×
Ursidae	7	2.385	2.200 – 2.571	0.197	-0.024 – 0.419	0.887	-0.372 – 2.146	0.918	×
Felidae	26	2.454	2.348 – 2.560	0.320	0.223 – 0.418	1.021	0.844 – 1.198	0.988	×
Herpestidae	12	1.223	0.979 – 1.446	0.322	0.026 – 0.618	0.754	-0.046 – 1.554	0.901	×
Eupleridae	5	1.196	0.616 – 1.776	0.248	-0.379 – 0.875	1.586	-1.106 – 4.278	0.973	×
Viverridae	14	1.453	1.204 – 1.703	0.345	0.058 – 0.631	0.848	0.183 – 1.514	0.892	×
Locomotor type									
arboreal	7	1.348	0.997 – 1.699	0.162	-0.138 – 0.463	1.939	-0.073 – 3.952	0.928	×
semiarboreal	10	1.700	1.326 – 2.075	0.573	0.133 – 1.013	0.589	0.096 – 1.081	0.946	×
scansorial	45	2.370	2.254 – 2.487	0.174	0.099 – 0.250	1.358	1.125 – 1.591	0.980	✓ (<i>D</i> >1)
terrestrial	48	2.587	2.251 – 2.923	0.303	0.108 – 0.498	1.034	0.763 – 1.305	0.948	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	1.797	1.445 – 2.149	0.343	-0.011 – 0.696	0.982	0.293 – 1.670	0.929	×
aquatic	8	2.806	2.672 – 2.940	0.454	0.313 – 0.596	1.054	0.817 – 1.291	0.995	×
Preferred habitat									
forest	38	2.157	1.931 – 2.383	0.291	0.121 – 0.461	1.092	0.783 – 1.400	0.951	×
mosaic	40	2.436	2.224 – 2.647	0.352	0.184 – 0.520	0.980	0.746 – 1.214	0.964	×
open	17	2.444	1.998 – 2.889	0.400	0.042 – 0.759	0.896	0.470 – 1.322	0.939	×
freshwater	13	1.814	1.483 – 2.145	0.382	0.048 – 0.715	0.898	0.332 – 1.463	0.926	×
marine	10	2.849	2.488 – 3.210	0.577	0.191 – 0.962	0.697	0.352 – 1.043	0.968	×
variable	18	2.462	2.222 – 2.703	0.261	0.111 – 0.411	1.118	0.854 – 1.382	0.983	×

III.S26 – d_{tm}										
	n	$\ln A$	95% $CI_{\ln A}$	C	95% CI_C	D	95% CI_D	R	$D \neq 1$	
whole sample	136	2.709	2.553 – 2.865	0.251	0.161 – 0.342	1.115	0.957 – 1.273	0.965	×	
fissipeds	129	2.670	2.499 – 2.841	0.304	0.197 – 0.412	1.048	0.892 – 1.203	0.962	×	
Family										
Canidae	16	2.142	1.839 – 2.444	0.438	0.115 – 0.760	0.929	0.383 – 1.475	0.920	×	
Mustelidae	32	1.825	1.626 – 2.024	0.347	0.169 – 0.526	0.966	0.689 – 1.243	0.959	×	
Procyonidae	7	1.204	0.719 – 1.689	0.217	-0.382 – 0.817	0.699	-1.773 – 3.171	0.744	n.s.	
Ursidae	7	2.469	2.297 – 2.641	0.215	0.009 – 0.422	1.047	-0.083 – 2.178	0.944	×	
Felidae	26	2.580	2.393 – 2.766	0.372	0.195 – 0.548	0.961	0.689 – 1.233	0.970	×	
Herpestidae	12	1.315	1.046 – 1.584	0.375	0.055 – 0.695	0.632	-0.033 – 1.297	0.917	×	
Eupleridae	5	1.342	0.713 – 1.972	0.324	-0.481 – 1.130	1.171	-1.486 – 3.828	0.962	×	
Viverridae	14	1.505	1.309 – 1.702	0.363	0.136 – 0.590	0.821	0.325 – 1.317	0.933	×	
Locomotor type										
arboreal	7	1.465	1.139 – 1.791	0.278	-0.077 – 0.633	1.206	-0.193 – 2.606	0.929	×	
semiarboreal	10	1.709	1.398 – 2.019	0.495	0.138 – 0.852	0.743	0.239 – 1.247	0.958	×	
scansorial	45	2.491	2.334 – 2.649	0.234	0.118 – 0.349	1.197	0.936 – 1.459	0.971	×	
terrestrial	48	2.695	2.407 – 2.983	0.283	0.124 – 0.441	1.087	0.848 – 1.326	0.963	×	
semifossorial	7	1.782	0.735 – 2.829	0.757	-0.585 – 2.098	0.424	-0.521 – 1.369	0.958	×	
semiaquatic	11	1.937	1.427 – 2.447	0.592	0.032 – 1.153	0.538	0.018 – 1.059	0.907	×	
aquatic	8	2.837	2.513 – 3.160	0.523	0.167 – 0.878	0.717	0.241 – 1.192	0.962	×	
Preferred habitat										
forest	38	2.318	2.103 – 2.532	0.371	0.196 – 0.545	0.976	0.733 – 1.219	0.962	×	
mosaic	40	2.531	2.316 – 2.746	0.396	0.216 – 0.576	0.910	0.691 – 1.129	0.965	×	
open	17	2.527	2.219 – 2.835	0.323	0.108 – 0.537	1.062	0.738 – 1.387	0.974	×	
freshwater	13	1.960	1.410 – 2.511	0.622	0.021 – 1.222	0.478	-0.014 – 0.970	0.881	✓ ($D=0$)	
marine	10	2.820	2.586 – 3.053	0.505	0.257 – 0.753	0.752	0.492 – 1.011	0.984	×	
variable	18	2.490	2.242 – 2.738	0.202	0.065 – 0.338	1.252	0.935 – 1.569	0.981	×	
III.S27 – MR										
	n	$\ln A$	95% $CI_{\ln A}$	C	95% CI_C	D	95% CI_D	R	$D \neq 1$	
whole sample	136	-	-	-	-	-	-	-	n.c.	
fissipeds	129	-2.218	-2.285 – -2.152	-1.25 · 10 ⁻⁶	-2.47 · 10 ⁻⁵	-2.22 · 10 ⁻⁵	5.970	-3.414 – 15.354	0.164	n.s.
Family										
Canidae	16	-	-	-	-	-	-	-	n.c.	
Mustelidae	32	-1.700	-2.840 – -0.560	0.283	-0.919 – 1.484	0.287	-0.923 – 1.498	0.370	×	
Procyonidae	7	-	-	-	-	-	-	-	n.c.	
Ursidae	7	-	-	-	-	-	-	-	n.c.	
Felidae	26	-2.197	-2.495 – -1.899	0.064	-0.255 – 0.383	0.645	-1.841 – 3.131	0.310	n.s.	
Herpestidae	12	-	-	-	-	-	-	-	n.c.	
Eupleridae	5	-2.104	-2.858 – -1.350	0.169	-0.779 – 1.118	1.225	-4.711 – 7.160	0.853	n.s.	
Viverridae	14	-	-	-	-	-	-	-	n.c.	
Locomotor type										
arboreal	7	-	-	-	-	-	-	-	n.c.	
semiarboreal	10	-2.003	-2.841 – -1.164	0.137	-0.852 – 1.126	0.523	-3.848 – 4.894	0.295	n.s.	
scansorial	45	-1.965	-2.372 – -1.559	0.138	-0.272 – 0.547	0.582	-0.639 – 1.804	0.436	×	
terrestrial	48	-2.507	-2.740 – -2.274	-0.006	-0.036 – 0.023	2.279	-0.054 – 4.613	0.595	×	
semifossorial	7	-	-	-	-	-	-	-	n.c.	
semiaquatic	11	-1.860	-2.037 – -1.682	0.050	-0.092 – 0.192	1.668	-0.452 – 3.788	0.833	×	
aquatic	8	-	-	-	-	-	-	-	n.c.	
Preferred habitat										
forest	38	-1.889	-2.295 – -1.483	0.118	-0.261 – 0.497	0.751	-0.788 – 2.290	0.406	×	
mosaic	40	-2.263	-2.388 – -2.137	-3.28 · 10 ⁻⁴	-0.005 – 0.004	3.526	-3.602 – 10.654	0.293	n.s.	
open	17	-2.511	-2.847 – -2.175	-0.002	-0.016 – 0.013	3.320	-1.643 – 8.283	0.633	×	
freshwater	13	-1.830	-2.103 – -1.558	0.128	-0.136 – 0.392	1.048	-0.345 – 2.442	0.761	×	
marine	10	-	-	-	-	-	-	-	n.c.	
variable	18	-2.357	-2.627 – -2.087	-0.002	-0.032 – 0.027	2.596	-3.302 – 8.494	0.447	n.s.	

III.S28 – %_{prox}	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	3.702	3.217 – 4.187	0.271	-0.218 – 0.760	0.229	-0.129 – 0.587	0.469	✓ (<i>D</i> ≠0)
fissipeds	130	3.355	3.241 – 3.469	0.014	-0.075 – 0.104	0.785	-1.706 – 3.275	0.173	×
Family									
Canidae	17	3.307	3.232 – 3.381	0.006	-0.032 – 0.044	2.613	-2.580 – 7.805	0.459	n.s.
Mustelidae	32	3.724	2.566 – 4.882	0.345	-0.840 – 1.531	0.152	-0.397 – 0.701	0.630	✓ (<i>D</i> ≠0)
Procyonidae	7	-	-	-	-	-	-	-	n.c.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	3.412	3.224 – 3.601	0.082	-0.125 – 0.290	0.374	-0.553 – 1.301	0.563	×
Herpestidae	12	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-	-	-	-	-	-	-	n.c.
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	3.366	3.252 – 3.480	0.041	-0.075 – 0.158	0.521	-0.576 – 1.618	0.438	×
terrestrial	49	-	-	-	-	-	-	-	n.c.
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	3.339	3.224 – 3.454	0.009	-0.052 – 0.070	1.516	-2.307 – 5.339	0.326	×
mosaic	40	-	-	-	-	-	-	-	n.c.
open	17	-	-	-	-	-	-	-	n.c.
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-	-	-	-	-	-	-	n.c.

III.S29 – %_{mid}	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	137	3.212	2.813 – 3.611	-0.330	-0.734 – 0.073	0.205	-0.017 – 0.427	0.632	✓ (<i>D</i> ≠0)
fissipeds	130	3.631	3.604 – 3.658	-0.001	-0.004 – 0.002	2.449	0.669 – 4.229	0.462	×
Family									
Canidae	17	3.571	3.521 – 3.620	-0.034	-0.088 – 0.019	0.836	-0.281 – 1.953	0.714	×
Mustelidae	32	3.616	3.530 – 3.703	-0.068	-0.159 – 0.024	0.450	-0.076 – 0.976	0.727	✓ (<i>D</i> ≠0)
Procyonidae	7	-	-	-	-	-	-	-	n.c.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	3.633	3.576 – 3.690	-0.007	-0.068 – 0.053	0.695	-3.588 – 4.979	0.195	n.s.
Herpestidae	12	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-	-	-	-	-	-	-	n.c.
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	-	-	-	-	-	-	-	n.c.
terrestrial	49	3.564	3.509 – 3.618	-0.004	-0.015 – 0.007	1.953	0.664 – 3.241	0.767	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	3.675	3.598 – 3.752	-0.002	-0.036 – 0.032	1.718	-8.741 – 12.178	0.141	n.s.
mosaic	40	3.621	3.590 – 3.652	-0.002	-0.007 – 0.004	2.343	0.551 – 4.135	0.664	×
open	17	3.625	3.600 – 3.651	-7.11 · 10 ⁻⁶	-7.89 · 10 ⁻⁵ – 6.47 · 10 ⁻⁵	5.175	-0.263 – 10.613	0.752	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	3.438	3.274 – 3.603	-0.014	-0.132 – 0.104	1.858	-3.306 – 7.023	0.623	n.s.
variable	19	3.597	3.541 – 3.653	-0.002	-0.010 – 0.007	2.362	-0.358 – 5.082	0.696	×

III.S28 – %_{dist}	n	<i>In A</i>	95% CI_{<i>In A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	R	<i>D</i> ≠ 1
whole sample	137	3.516	3.497 – 3.535	$3.27 \cdot 10^{-7}$	$-2.79 \cdot 10^{-6} - 3.44 \cdot 10^{-6}$	6.190	1.549 – 10.832	0.318	✓ (<i>D</i> >1)
fissipeds	130	3.519	3.498 – 3.540	$2.68 \cdot 10^{-6}$	$-1.93 \cdot 10^{-5} - 2.46 \cdot 10^{-5}$	5.354	1.226 – 9.482	0.329	✓ (<i>D</i> >1)
Family									
Canidae	17	3.599	3.301 – 3.897	0.012	-0.308 – 0.332	0.372	-11.387 – 12.132	0.071	n.s.
Mustelidae	32	3.425	3.400 – 3.450	$4.38 \cdot 10^{-8}$	$-1.98 \cdot 10^{-6} - 2.07 \cdot 10^{-6}$	8.423	-19.191 – 36.036	0.235	n.s.
Procyonidae	7	-	-	-	-	-	-	-	n.c.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	3.452	3.115 – 3.789	-0.070	-0.433 – 0.293	0.278	-1.231 – 1.787	0.363	n.s.
Herpestidae	12	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-	-	-	-	-	-	-	n.c.
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	3.481	3.356 – 3.607	-0.029	-0.157 – 0.100	0.485	-1.202 – 2.171	0.285	n.s.
terrestrial	49	3.598	3.533 – 3.664	0.002	-0.005 – 0.009	2.400	0.574 – 4.226	0.696	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	3.687	3.034 – 4.339	0.208	-0.479 – 0.896	0.249	-0.821 – 1.318	0.832	×
Preferred habitat									
forest	38	3.442	3.285 – 3.599	-0.036	-0.204 – 0.132	0.412	-1.287 – 2.112	0.272	n.s.
mosaic	40	3.548	3.511 – 3.585	0.001	-0.002 – 0.003	2.957	0.558 – 5.356	0.621	×
open	17	-	-	-	-	-	-	-	n.c.
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	3.575	3.511 – 3.639	0.001	-0.004 – 0.005	2.880	-0.234 – 5.994	0.701	×

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Scaling pattern of the carnivoran hind limb: Locomotor types and differential scaling



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Abstract

The scaling pattern of the hind limb in Carnivora was determined using a sample of 13 variables measured on the femur, tibia, and calcaneus, of 429 specimens belonging to 141 species. Standardised major axis (SMA) regressions on body mass were calculated for all variables, using both traditional regression methods and phylogenetically independent contrasts (PIC). Significant differences were found between the allometric slopes obtained both with traditional and PIC regression methods, emphasizing the need to take into account phylogenetic relatedness in scaling studies. Overall, the scaling of the carnivoran hind limb conformed to geometric similarity, although some deviations from its predictions (including differential scaling) were detected, especially in relation with swimming adaptations. The scaling pattern of several phyletic lines and locomotor habits within Carnivora was also determined. Significant deviations from the scaling pattern of the order were found in some phyletic lines, but not in the locomotor habit subsamples, which suggests that the scaling of the carnivoran hind limb is more heavily influenced by phylogenetic relatedness than by locomotor specializations, and also that the scaling pattern of the carnivoran hind limb is more conservative than that of the forelimb. Finally, together with our previous work on the carnivoran forelimb, the results of the present study suggest that, in large non-aquatic carnivorans, size-related increases in bone stresses are compensated primarily by limb posture changes instead of by modifying limb bone scaling. However, increasing bone robusticity might also occur in the forelimb in response to the heavier stresses acting on the forelimbs due to asymmetrical body weight distribution.

Keywords: biomechanics; Carnivora; differential scaling; habitat; hind limb; locomotor type; phylogenetically independent contrasts; scaling

Introduction

The morphofunctional properties of the bones and muscles of animals change at different rates as their size increases, which is known as scaling (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003). In order to understand the consequences of scaling, several hypotheses have been proposed which provide theoretical values to these rates of change based on different biomechanical constraints. For instance, the geometric similarity hypothesis derives from the notion that if all linear dimensions of an object are multiplied by a constant, its volume increases by the cube of this constant, which translates into linear dimensions being proportional to body mass^{0.33} (e.g. Alexander, 2002). On the other hand, the elastic similarity hypothesis proposes that, in order that different-sized animals are able to withstand similarly the effect of gravity, their lengths should be proportional to body mass^{0.25} and their diameters to body mass^{0.375} (McMahon, 1973). However, empirical evidence has shown that neither of these hypotheses adequately describes the scaling pattern of mammalian bones (Bou et al., 1987; Bertram & Biewener, 1990; Christiansen, 1999*a,b*; Carrano, 2001; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012; Chapter III). This is probably related to factors such as phylogenetic constraints to bone morphology (Flynn et al., 1988; Bertram & Biewener, 1990; Day & Jayne, 2007), adaptations to particular locomotor patterns (Bou et al., 1987), or the different biomechanical requirements of locomotion in large and small mammals (Fischer & Blickhan, 2006), which can cause deviations from the theoretical values proposed by the different similarity hypotheses (or even non-linear relationships between those morphofunctional properties and body mass, which is known as differential scaling or complex allometry; Economos, 1983; Bertram & Biewener, 1990; Silva, 1998; Christiansen, 1999*a,b*; Carrano, 2001).

In order to clarify the effect of these factors on the scaling of the appendicular skeleton, the present work complements a previous work on the scaling of the carnivoran forelimb (Chapter III) by presenting here the results obtained for the carnivoran hind limb, as well as an interlimb comparison. The aims of the present study are thus: 1) to determine the scaling pattern of the carnivoran hind limb, and to assess whether differential scaling can be found in this pattern; 2) to analyze whether the main phyletic lines (families) within Carnivora deviated from it, and if so, then how; and 3) to test whether particular locomotor habits within Carnivora cause deviations from the general scaling pattern for the order.

The order Carnivora was chosen because it is a monophyletic group spanning a size range of four orders of magnitude, and presenting one of the widest locomotor diversities among mammals (Van Valkenburgh, 1987; Bertram & Biewener, 1990; Wilson & Mittermeier, 2009; Nyakatura & Bininda-Emonds, 2012).

Material and Methods

The sample for the hind limb consisted of 429 specimens from 141 species of Carnivora (Table IV.1). For each specimen, measurements were taken on the femur, tibia, and calcaneus. The specimens and variables have already been described in Chapter II, as were the locomotor type and preferred habitat categories used to build the subsamples (Table IV.2). As in the previous studies, locomotor type was used to represent locomotor specialization, and preferred habitat as an indicator of the ability to perform different modes of locomotion (running, swimming, climbing, digging) and thus maximize resource exploitation by being able to navigate all substrates available in their preferred habitat. As described elsewhere (Chapter III), taxonomy follows Wilson & Mittermeier (2009), except for a few species for which the synonyms in Wozencraft (2005) were preferred.

The 13 studied variables included 11 linear measurements and 2 bone robusticities (**FR**, **TR**), and are summarized in Table IV.3. The linear measurements could be subdivided into bone lengths (represented as L_x , where x indicates each particular bone, e.g. L_f for femur length), bone diameters (d_{sx} , d_{tx}), and other measurements (**N**, **r**). Bone robusticities were calculated dividing sagittal diameter by bone length ($XR = d_{sx} / L_x$). Since the scapula has been shown to be the main propulsive element of the forelimb (Fischer et al., 2002; Lilje & Fischer, 2001), it is thus considered here the most proximal segment of the forelimb and, correspondingly, the functional homologue of the femur.

Following Chapter III, all variables were regressed to body mass (M_b) using the standardised major axis method (SMA), and assuming the power equation for all variables:

$$Y = a \cdot X^b \quad . \quad (\text{Eq. 1})$$

All regressions were calculated using PAST (Hammer et al. 2001), and 95% confidence intervals were obtained for both the coefficient (a) and the allometric exponent (b_{trad}). Furthermore, all the SMA regression slopes using phylogenetically independent contrasts (PIC) were also calculated, since the hierarchical sequence of interspecific data introduces a phylogenetic signal that could cause correlation of the error terms due to the lack of independence among species (Felsenstein, 1985; Grafen, 1989; Harvey & Pagel, 1991;

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Canidae									
<i>Alopex lagopus</i>	3	terr	op	1	<i>Lycalopex gymnocercus</i>	4	terr	op	1
<i>Canis adustus</i>	4	terr	mo	1	<i>Lycaon pictus</i>	3	terr	mo	1
<i>Canis aureus</i>	6	terr	va	1	<i>Nyctereutes procyonoides</i>	3	terr	fo	1
<i>Canis latrans</i>	3	terr	va	1	<i>Otocyon megalotis</i>	1	terr	op	1
<i>Canis lupus</i>	4	terr	va	2, 3	<i>Speothos venaticus</i>	6	terr	fo	1
<i>Canis mesomelas</i>	6	terr	op	1	<i>Urocyon cinereoargenteus</i>	1	terr	mo	1
<i>Cerdocyon thous</i>	2	terr	mo	1	<i>Vulpes chama</i>	1	terr	op	1
<i>Chrysocyon brachyurus</i>	6	terr	op	4	<i>Vulpes vulpes</i>	12	terr	va	5
<i>Cuon alpinus</i>	3	terr	fo	1	<i>Vulpes zerda</i>	2	terr	op	1
<i>Lycalopex culpaeus</i>	3	terr	va	1					
Mustelidae									
<i>Aonyx cinereus</i>	2	saq	fw	1	<i>Martes foina</i>	23	scan	mo	8
<i>Arctonyx collaris</i>	1	sfos	fo	1	<i>Martes martes</i>	8	sarb	fo	8
<i>Eira barbara</i>	2	sarb	fo	1	<i>Martes zibellina</i>	1	scan	fo	1
<i>Enhydra lutris</i>	1	aq	ma	1	<i>Meles meles</i>	5	sfos	mo	9
<i>Galictis cuja</i>	2	terr	va	1	<i>Mellivora capensis</i>	2	sfos	va	1
<i>Galictis vittata</i>	2	terr	mo	1	<i>Melogale moschata</i>	1	terr	mo	1
<i>Gulo gulo</i>	2	scan	mo	1	<i>Melogale orientalis</i>	1	terr	mo	1
<i>Ictonyx lybicus</i>	2	terr	op	1	<i>Mustela erminea</i>	8	terr	mo	8
<i>Ictonyx striatus</i>	1	terr	va	1	<i>Mustela eversmannii</i>	1	terr	op	1
<i>Lontra felina</i>	3	saq	ma	1	<i>Mustela lutreola</i>	1	saq	fw	1
<i>Lontra longicaudis</i>	2	saq	fw	1	<i>Mustela nivalis</i>	5	terr	va	8
<i>Lontra provocax</i>	1	saq	fw	6	<i>Mustela nudipes</i>	2	terr	fo	1
<i>Lutra lutra</i>	4	saq	fw	7	<i>Mustela putorius</i>	6	terr	mo	1
<i>Lutrogale perspicillata</i>	1	saq	fw	1	<i>Mustela vison</i>	2	saq	fw	1
<i>Lyncodon patagonicus</i>	2	terr	op	1	<i>Pteronura brasiliensis</i>	2	saq	fw	1
<i>Martes americana</i>	1	sarb	fo	1	<i>Vormela peregusna</i>	3	sfos	va	1
Mephitidae									
<i>Conepatus chinga</i>	2	sfos	op	1	<i>Spilogale gracilis</i>	2	terr	mo	1
<i>Conepatus humboldti</i>	1	sfos	va	1					
Otariidae									
<i>Arctocephalus australis</i>	1	aq	ma	10	<i>Otaria flavescens</i>	2	aq	ma	11
<i>Arctocephalus gazella</i>	1	aq	ma	10	<i>Zalophus californianus</i>	2	aq	ma	11
Phocidae									
<i>Hydrurga leptonyx</i>	1	aq	ma	11	<i>Phoca vitulina</i>	2	aq	ma	12
<i>Mirounga leonina</i>	1	aq	ma	12					
Ailuridae									
<i>Ailurus fulgens</i>	7	scan	fo	13					
Procyonidae									
<i>Bassaricyon gabbii</i>	1	arb	fo	1	<i>Potos flavus</i>	4	arb	fo	1
<i>Bassariscus astutus</i>	1	scan	mo	1	<i>Procyon cancrivorus</i>	3	scan	fw	1
<i>Nasua narica</i>	4	scan	fo	14	<i>Procyon lotor</i>	5	scan	fw	1
<i>Nasua nasua</i>	6	scan	mo	15					
Prionodontidae									
<i>Prionodon linsang</i>	1	arb	fo	1					

Table IV.1. Measured species. See legend on next page.

Table IV.1. Measured species. (cont.) See legend on next page.

species	n	loctyp	habitat	M _b	species	n	loctyp	habitat	M _b
Ursidae									
<i>Ailuropoda melanoleuca</i>	2	scan	fo	1	<i>Ursus americanus</i>	1	scan	mo	1
<i>Helarctos malayanus</i>	1	scan	fo	1	<i>Ursus arctos</i>	6	scan	va	1
<i>Melursus ursinus</i>	1	scan	mo	1	<i>Ursus maritimus</i>	4	terr	ma	1
<i>Tremarctos ornatus</i>	2	scan	mo	1					
Viverridae									
<i>Arctictis binturong</i>	4	arb	fo	1	<i>Genetta tigrina</i>	1	sarb	mo	1
<i>Arctogalidia trivirgata</i>	2	arb	fo	1	<i>Hemigalus derbyanus</i>	4	sarb	fo	1
<i>Civettictis civetta</i>	4	terr	mo	20	<i>Paradoxurus hermaphroditus</i>	2	arb	fo	1
<i>Cynogale benettii</i>	1	saq	fw	1	<i>Poiana richardsoni</i>	1	sarb	fo	1
<i>Genetta felina</i>	5	scan	mo	1	<i>Viverra tangalunga</i>	4	terr	fo	1
<i>Genetta genetta</i>	7	scan	mo	1	<i>Viverra zibetha</i>	2	terr	fo	1
<i>Genetta maculata</i>	3	sarb	mo	1	<i>Viverricula indica</i>	4	scan	mo	1
Herpestidae									
<i>Atilax paludinosus</i>	2	saq	fw	1	<i>Herpestes brachyurus</i>	1	terr	fo	1
<i>Crossarchus obscurus</i>	2	terr	fo	8	<i>Herpestes edwardsii</i>	2	terr	mo	1
<i>Cynictis penicillata</i>	4	terr	op	1	<i>Herpestes ichneumon</i>	4	terr	op	1
<i>Galerella pulverulenta</i>	4	terr	fo	1	<i>Ichneumia albicauda</i>	2	terr	mo	1
<i>Galerella sanguinea</i>	1	terr	mo	1	<i>Suricata suricatta</i>	4	sfos	op	1
<i>Helogale parvula</i>	2	terr	mo	1					
Eupleridae									
<i>Cryptoprocta ferox</i>	2	sarb	fo	1	<i>Mungotictis decemlineata</i>	1	scan	fo	1
<i>Fossa fossa</i>	2	terr	fo	1	<i>Salanoia concolor</i>	2	scan	fo	1
<i>Galidia elegans</i>	4	scan	fo	1					
Hyaenidae									
<i>Crocuta crocuta</i>	2	terr	mo	8	<i>Parahyaena brunnea</i>	1	terr	va	1
<i>Hyaena hyaena</i>	3	terr	va	1	<i>Proteles cristatus</i>	2	terr	op	8
Felidae									
<i>Acinonyx jubatus</i>	3	scan	mo	1	<i>Neofelis nebulosa</i>	1	sarb	fo	17
<i>Caracal caracal</i>	5	scan	mo	1	<i>Otocolobus manul</i>	2	scan	op	1
<i>Felis chaus</i>	1	scan	va	1	<i>Panthera leo</i>	7	scan	op	1
<i>Felis nigripes</i>	2	scan	mo	16	<i>Panthera onca</i>	2	scan	fo	1
<i>Felis silvestris</i>	15	scan	mo	1	<i>Panthera pardus</i>	8	scan	va	12
<i>Leopardus colocolo</i>	2	scan	va	1	<i>Panthera tigris</i>	9	scan	mo	18
<i>Leopardus geoffroyi</i>	2	scan	mo	1	<i>Panthera uncia</i>	4	scan	op	19
<i>Leopardus pardalis</i>	2	scan	fo	1	<i>Pardofelis marmorata</i>	1	arb	fo	1
<i>Leopardus tigrinus</i>	1	scan	fo	1	<i>Prionailurus bengalensis</i>	1	scan	mo	1
<i>Leopardus wiedii</i>	1	arb	fo	1	<i>Prionailurus planiceps</i>	1	scan	fw	1
<i>Leptailurus serval</i>	6	scan	mo	12	<i>Prionailurus viverrinus</i>	1	scan	fw	1
<i>Lynx canadensis</i>	1	scan	mo	1	<i>Profelis aurata</i>	1	scan	fo	1
<i>Lynx lynx</i>	3	scan	mo	1	<i>Puma concolor</i>	5	scan	va	1
<i>Lynx pardinus</i>	4	scan	mo	12	<i>Puma yaguaroundi</i>	3	scan	mo	1
<i>Lynx rufus</i>	1	scan	va	1					
Nandiniidae									
<i>Nandinia binotata</i>	5	sarb	fo	1					

Table III.1. Measured species. (cont.) For each species, the table shows the number of measured specimens, the assigned category for both locomotor type and preferred habitat, and the references from which the mean body mass value for that species was taken (M_b). Abbreviations: aq, aquatic; arb, arboreal; fo, forest; fw, freshwater; loctyp, locomotor type; ma, marine; mo, mosaic; n, measured specimens; op, open; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial; va, variable. See Table II.3 for a description of locomotor type and preferred habitat categories. References: 1. Wilson & Mittermeier, 2009; 2. Blanco et al., 2002; 3. Mech, 2006; 4. Dietz, 1984; 5. Cavallini, 1995; 6. Reyes-Küppers, 2007; 7. Yom-Tov et al., 2006; 8. Grzimek, 1988; 9. Virgós et al., 2011; 10. Perrin et al., 2002; 11. MacDonald, 2001; 12. Silva & Downing, 1995; 13. Roberts & Gittleman, 1984; 14. Gompper, 1995; 15. Gompper & Decker, 1998; 16. Sliwa, 2004; 17. Sunquist & Sunquist, 2002; 18. Mazák, 1981; 19. IUCN Cat Specialist Group, 2011; 20. Ray, 1995.

Christiansen, 2002*a, b*). PIC regression slopes were calculated using the PDAP: PDTREE module of Mesquite (Maddison & Maddison, 2010; Midford et al., 2010). The structure of the phylogenetic tree used in the present study is discussed elsewhere (Chapter III). The PIC slopes (b_{PIC}) were compared to b_{rad} values with an F-test ($p < 0.05$) to assess whether

Locomotor type	Description
arboreal	species that spend most of their life in trees (over 75%), rarely descending to the ground
semiarboreal	species that spend a large amount of their time in the trees (between 50% and 75%), both foraging and resting, but also on ground surface
scansorial	species that, although mostly terrestrial (over half their time is spent on the ground), can climb well and will readily do so to chase arboreal prey or escape, and might nest in trees for protection against terrestrial predators
terrestrial	species that rarely or never climb or swim, and that might dig to modify a burrow but not regularly for food
semifossorial	species that dig regularly for both food and shelter, but that still show considerable ability to move around on the surface
semiaquatic	species that forage regularly underwater and usually plunge into the water to escape, but must spend time ashore to groom,...
aquatic	species that carry out most of their life cycle in water, although some part of this cycle can be confined to land (parturition, mating, rearing the young)
Preferred habitat	Description
open	areas with low to nonexistent tree cover (e.g. grasslands, steppes, tundra,...). Carnivorans inhabiting open habitats could probably be good diggers, maybe also capable swimmers, but should lack climbing skills.
mosaic	this category was created for species that either live in forested areas with scarce tree cover (e.g. savannah), or require the presence of both forested and open areas within their home range, thus, they are expected to be good climbers, while also could be capable diggers or swimmers.
forest	areas with a high density of trees (e.g. rain forest, taiga, deciduous forest,...). Carnivorans inhabiting forested areas should probably be adept climbers, even though not completely arboreal, to be able to chase prey that flee to the canopy. They can also be capable swimmers and diggers.
freshwater	this category was created for species that dwell in or near freshwater systems (e.g. rivers, lakes, swamps,...). Carnivorans inhabiting freshwater habitats are expected to be capable swimmers, while also can present some ability to climb or dig.
marine	saltwater systems and their coastal regions. Marine carnivorans are expected to be very good swimmers, rarely dig, and possess an almost nonexistent ability to climb.
variable	this category includes all species that appear indistinctly in two or more of the other categories and thus probably contains species with highly variable locomotor skills.

Table IV.2. Description of locomotor type and preferred habitat categories. Locomotor type categories were adapted from previous works on the relationship between locomotor behavior and forelimb morphology (Eisenberg, 1981; Van Valkenburgh, 1985, 1987).

Table IV.3. Variable names and abbreviations.

For each variable, it is also indicated in which table of the Appendix its regression results are shown.

Abbr.	Name	Appendix
M_b	Body mass	
L_f	Femur functional length	IV.A1
N	Neck–head length	IV.A2
d_{sf}	Femur sagittal diameter	IV.A3
d_{tf}	Femur transverse diameter	IV.A4
FR	Femur robusticity	IV.A5
L_t	Tibia functional length	IV.A6
d_{st}	Tibia sagittal diameter	IV.A7
d_{tt}	Tibia transverse diameter	IV.A8
TR	Tibia robusticity	IV.A9
L_c	Calcaneus length	IV.A10
r	Ankle extensors moment arm	IV.A11
d_{sc}	Calcaneus sagittal diameter	IV.A12
d_{tc}	Calcaneus transverse diameter	IV.A13

the phylogenetic signal had any effect on the results.

As in the previous work (Chapter III), for each variable and methodology (traditional and PIC), separate regressions were calculated for the whole sample, the fissiped subsample, and also for several subsamples by family, locomotor type, and preferred habitat. Regressions were not calculated for any subsample with a sample size lower than 5, which was the case for Hyaenidae, Mephitidae, Phocidae, Otariidae, the monotypic families (Ailuridae, Nandiniidae,

Prionodontidae), and Eupleridae when using PIC regression, plus a few other groups in the case of calcaneal variables (Ursidae, Herpestidae, Eupleridae, and aquatic, marine and semifossorial carnivorans, plus semiarboreal carnivorans when using PIC regression). Then, all allometric exponents were compared to the theoretical values proposed by the geometric similarity hypothesis (all variables $\propto M_b^{0.33}$, except for **FR**, **TR** $\propto M_b^0$) and the elastic similarity hypothesis ($L_x, N, r \propto M_b^{0.25}$; $d_{sx}, d_{tx} \propto M_b^{0.375}$; **FR**, **TR** $\propto M_b^{0.125}$). Allometric exponents were considered to deviate significantly from the predictions of any similarity hypothesis when their 95%CI did not include the corresponding theoretical value. Furthermore, for each variable, allometric exponents were compared between the whole sample and the fissiped subsample, and between the different family, locomotor type, and preferred habitat subsamples.

Finally, also for each variable and each subsample, the presence of differential scaling was assessed using the model proposed by Jolicoeur (1989), which was fitted with SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), and 95% confidence intervals were calculated for all parameters.

Results

Tables IV.A1 through IV.A13 in the Appendix show the regression results for each variable. As observed in previous studies comparing traditional and PIC regressions (Christiansen, 2002*a,b*; Gálvez-López & Casinos, 2012, Chapter III), the correlation

coefficients (R) from the PIC analyses were lower than those from traditional regressions in most cases, which sometimes resulted in regressions no longer being significant (e.g. Table IV.A13). Some authors have attributed this phenomenon to a higher risk of type I errors (i.e., indicating a significant correlation between two variables when there was none) when the effect of phylogeny is neglected in correlation analyses (Grafen, 1989; Christiansen, 2002a). In several cases, however, R actually increased after taking into account the effect of phylogeny, which in some cases resulted in regressions becoming significant (e.g. Table IV.A1).

Figures IV.1 through IV.3 illustrate the allometric exponents' comparison between Families (Fig. IV.1), locomotor types (Fig. IV.2), and preferred habitats (Fig. IV.3). Branch lengths ought to be transformed in most cases before performing the PIC regressions (Table IV.S1).

Whole sample vs. Fissiped subsample

As in the forelimb (Chapter III), removal of Pinnipedia from the sample caused a generalized increase of the allometric exponents (especially when using traditional regression methods), although this increase was only significant for L_f , N , d_{sf} , and d_{st} , and then only for b_{trad} (Tables IV.A1–IV.A3, IV.A7). Overall, PIC slopes tended to be lower than those obtained using traditional regression methods, being significantly lower for L_f and L_t in the fissiped subsample (Tables IV.A1, IV.A6). Significant differences between the allometric exponents obtained using traditional and PIC regressions were also found for the carnivoran forelimb (Chapter III), but not in other previous studies comparing both methodologies (Christiansen, 2002b; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012).

Regarding conformity with the similarity hypotheses, Table IV.4 presents the percentage of linear measurements that conform to each similarity hypothesis in both the whole sample and the fissiped subsample, and also using either traditional regression methods or PIC. Contrary to the results obtained for the forelimb (Chapter III), the scaling pattern of the hind limb in Carnivora conformed clearly the geometric similarity hypothesis. However, the removal of Pinnipedia from the sample produced conflicting results between both methodologies (Table IV.4): while traditional regression results indicated low conformity to either similarity hypotheses, PIC slopes conformed to the geometric similarity hypothesis, like in the whole sample. Finally, both bone robusticities scaled elastically, whatever the sample or methodology (Tables IV.A5, IV.A9).

Table IV.4. Conformity to the similarity hypotheses summary.

For each subsample, the number of linear measurements conforming to geometric (G) or elastic similarity (E) is given, as is the percentage of the significant regressions for that subsample that they represent. Values in grey indicate that the number of variables conforming to a particular similarity hypothesis is either less than half the number of variables, or over 20% lower than the number of variables conforming to the other similarity hypothesis.

		traditional	PIC		traditional	PIC
whole sample	G	8/11 (72.7%)	10/11 (90.9%)	scansorial	G	7/11 (63.6%)
	E	0/11 (0%)	2/11 (18.2%)		E	1/11 (9.1%)
fissipeds	G	4/11 (36.4%)	9/11 (81.8%)	terrestrial	G	7/11 (63.6%)
	E	3/11 (27.3%)	2/11 (18.2%)		E	3/11 (27.3%)
Canidae	G	8/11 (72.7%)	7/11 (63.6%)	semifossorial	G	7/7 (100%)
	E	7/11 (63.6%)	6/11 (54.5%)		E	6/7 (85.7%)
Mustelidae	G	11/11 (100%)	10/11 (90.9%)	semiaquatic	G	11/11 (100%)
	E	6/11 (54.5%)	8/11 (72.7%)		E	10/11 (90.9%)
Procyonidae	G	7/7 (100%)	6/6 (100%)	aquatic	G	4/4 (100%)
	E	7/7 (100%)	6/6 (100%)		E	3/4 (75.0%)
Ursidae	G	8/8 (100%)	3/3 (100%)	forest	G	9/11 (81.8%)
	E	8/8 (100%)	3/3 (100%)		E	4/11 (36.4%)
Felidae	G	8/11 (72.7%)	10/11 (90.9%)	mosaic	G	6/11 (54.5%)
	E	5/11 (45.5%)	5/11 (45.5%)		E	5/11 (45.5%)
Herpestidae	G	6/7 (87.5%)	5/7 (71.4%)	open	G	11/11 (70.3%)
	E	3/7 (42.9%)	3/7 (42.9%)		E	6/11 (37.8%)
Eupleridae	G	5/7 (71.4%)	–	freshwater	G	11/11 (100%)
	E	4/7 (57.1%)	–		E	11/11 (100%)
Viverridae	G	8/11 (72.7%)	10/11 (90.9%)	marine	G	6/6 (100%)
	E	5/11 (45.5%)	9/11 (81.8%)		E	5/6 (83.3%)
arboreal	G	11/11 (100%)	6/10 (60.0%)	variable	G	11/11 (100%)
	E	10/11 (90.9%)	5/10 (50.0%)		E	6/11 (54.5%)
semiarboreal	G	9/11 (81.8%)	5/7 (71.4%)			
	E	10/11 (90.9%)	7/7 (100%)			

Family subsamples

No significant differences were found between the allometric exponents obtained with each method (Tables IV.A1–IV.A13), which agrees with previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012) and with a previous work on forelimb scaling in the same carnivoran families (Chapter III).

Like in the whole sample, the scaling pattern of the carnivoran hind limb conformed to geometric similarity in most families (Mustelidae, Felidae, Herpestidae, and Viverridae), although for Mustelidae and Viverridae the elastic similarity hypothesis was also a likely explanation after taking into account the effect of phylogenetic relatedness (Table IV.4; PIC results). In Ursidae and Procyonidae, however, small sample sizes resulted in low correlation coefficients (R) and 95%CI_b wide enough to include the theoretic value for both hypotheses in most of the variables, and thus no similarity hypothesis could be ruled out

(Table IV.4). Finally, in the case of Canidae, conformity to both similarity hypotheses was low, especially considering PIC results.

Regarding bone robusticities, when significant, **TR** always scaled elastically (Table IV.A9). In the case of **FR**, the slopes calculated using traditional regression methods presented intermediate values between the theoretical values proposed by both similarity hypotheses. PIC slopes for **FR**, however, conformed to the elastic similarity hypothesis (Table IV.A5).

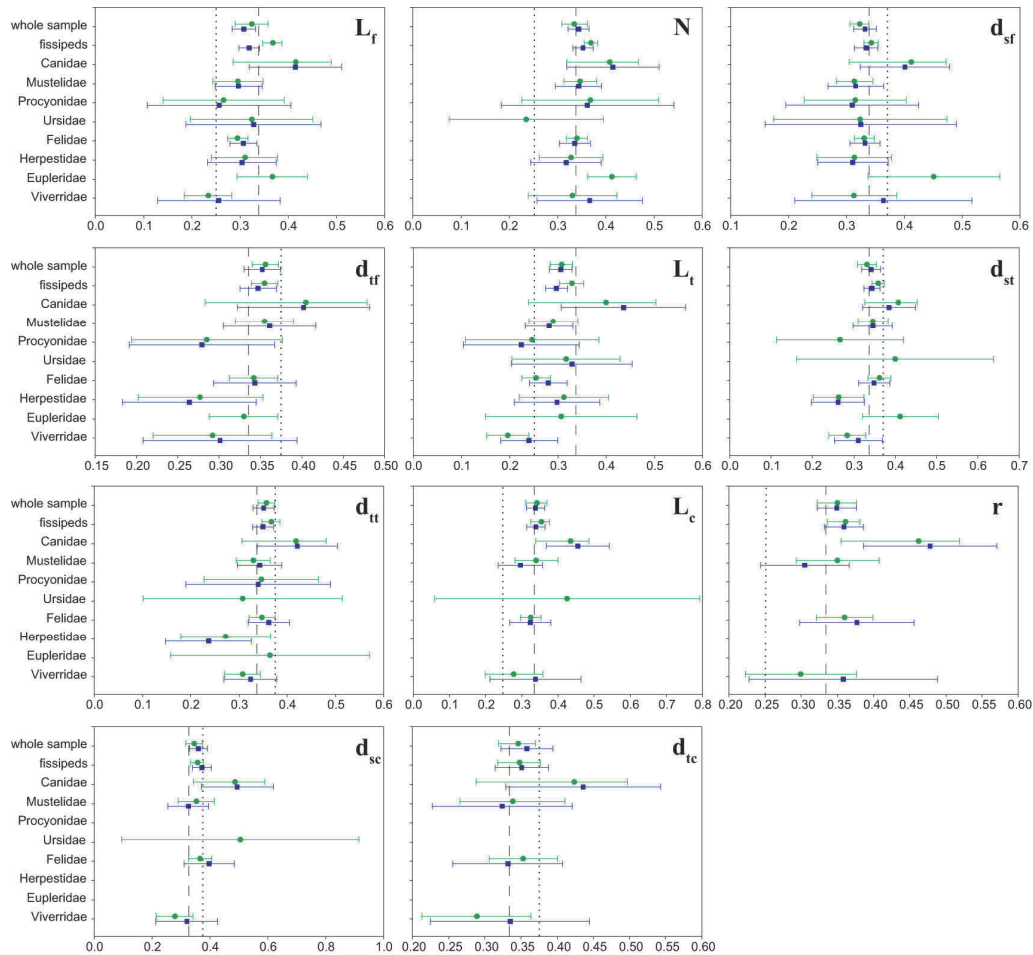


Figure IV.1. Allometric exponents by family. For each subsample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissiped subsample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dotted line corresponds to that proposed by the elastic similarity hypothesis. Variable names are listed in Table IV.3.

Figure IV.1 shows comparisons of the allometric exponents between different families for each variable, which are summarized in Table IV.5. No significant differences between families were found for **TR**. Overall, Canidae and Eupleridae scaled faster than all other families, while Herpestidae and Viverridae present lower allometric slopes than most families.

Locomotor type subsamples

Contrary to previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012) but in agreement with a previous work on forelimb scaling in Carnivora (Chapter III), significant differences between the allometric exponents obtained with each methodology were observed: for both L_f and L_t traditional slopes were significantly higher than PIC slopes in terrestrial carnivorans (Tables IV.A1, IV.A6).

The scaling pattern of scansorial and terrestrial carnivorans conformed better to the geometric similarity hypothesis (Table IV.4). In the rest of locomotor type subsamples, the

	< Can	< Mus	< Urs	< Fel	< Her	< Eup	< Viv
Mus < both: r PIC: L_f , d_{sf} , L_t , L_c , d_{sc} , d_{tc}	-	-	-	-	-	trad.: N , d_{sf}	-
Pro < both: L_f PIC: d_{tf} , L_t	-	-	-	-	-	trad.: d_{sf}	-
Urs < trad.: N	-	-	-	-	-	trad.: N	-
Fel < both: L_c PIC: L_f , L_t , r	-	-	-	-	-	trad.: N , d_{sf}	trad.: FR
Her < both: d_{tf} , d_{st} , d_{tt} PIC: L_f , N , d_{sf} , L_t	both: d_{tf} , d_{st}	-	both: d_{st}	-	-	trad.: N , d_{sf} , d_{st}	-
Viv < trad.: L_c , r PIC: d_{tf} , d_{tt}	trad.: L_f , L_t , d_{st} , d_{sc}	trad.: L_t	trad.: L_f , L_t , d_{st} , d_{tt} , d_{sc}	trad.: L_f , L_t	trad.: L_f , L_t	trad.: L_f , d_{sf} , d_{st}	-

Table IV.5. Differences in the allometric exponents between families. In each cell, row indicates the family with an allometric exponent (b) significantly lower than the column family for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; Can, Canidae; Eup, Eupleridae; Fel, Felidae; Her, Herpestidae; Mus, Mustelidae; PIC, regression using phylogenetically independent contrasts; Pro, Procyonidae; trad., traditional regression methods; Urs, Ursidae; Viv, Viverridae. Variable names are listed in Table IV.3.

95% CI_b were wide enough to include the theoretic value for both hypotheses in most of the variables and thus no similarity hypothesis could be ruled out. When considering PIC results, however, it is worth noting that semiarboreal carnivorans scaled elastically, and that conformity to both similarity hypotheses was low in arboreal carnivorans (due to the particular scaling of calcaneal variables) (Table IV.4).

Regarding bone robusticities, when significant, they scaled elastically, except for **FR** in

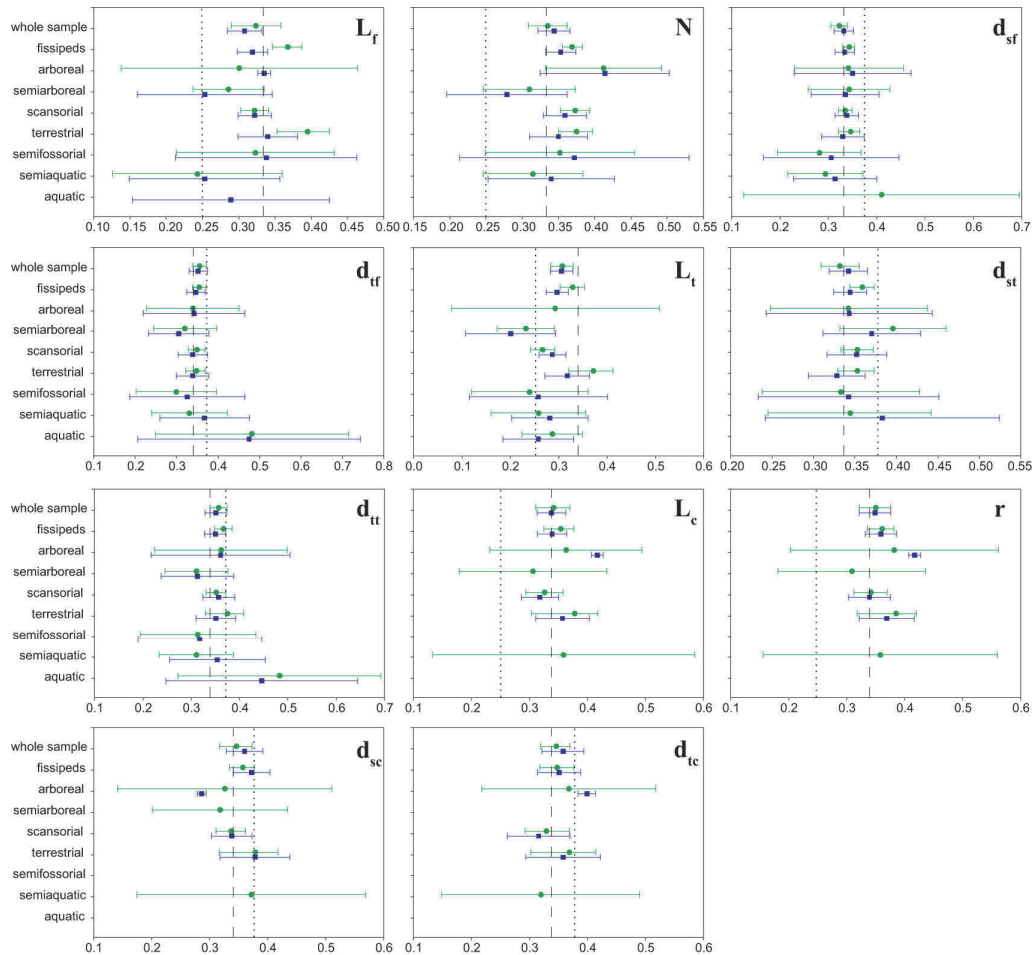


Figure IV.2. Allometric exponents by locomotor type. For each sub-sample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissipeds sub-sample are included as a reference. The allometric exponents obtained for the whole sample and the fissipeds sub-sample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dot-ted line corresponds to that proposed by the elastic similarity hypothesis. See Table IV.2 for a description of locomotor type categories. Variable names are listed in Table IV.3.

terrestrial carnivorans, which decreased with increasing body mass values (Tables IV.A5, IV.A9).

Figure IV.2 shows comparisons of the allometric exponents between different locomotor types for each variable, which are summarized in Table IV.6. Most significant differences between locomotor types were found either among traditional or PIC slopes, but not both.

Preferred habitat subsamples

As observed for the locomotor type subsamples, significant differences between the allometric exponents obtained using traditional and PIC regression methods were observed for some preferred habitat categories, which opposes previous studies comparing both methodologies (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012) but agrees with previous results on the scaling of the carnivoran forelimb (Chapter III). Carnivorans inhabiting mosaic or variable habitats presented significantly lower PIC slopes for several variables (Tables IV.A1–IV.A10), while in forest-dwelling species higher PIC slopes were obtained for all calcaneal variables (Tables IV.A10–IV.A13).

Overall, the scaling pattern of habitat subsamples conformed better to the geometric similarity hypotheses (Table IV.4). However, for freshwater and marine carnivorans the 95% CI_b included the theoretical values of both hypotheses, so no similarity hypotheses could be ruled out. In the mosaic habitat subsample, when considering the results from the traditional regressions, conformity with either similarity hypotheses was low, but PIC slopes clearly conformed to the geometric similarity hypothesis. On the other hand, the opposite was true for forest-dwelling carnivorans (i.e., geometric scaling according to traditional regression results, but low conformity to either similarity hypotheses in PIC slopes).

Table IV.6. Differences in the allometric exponents between locomotor types. In each cell, row indicates the locomotor type with an allometric exponent (*b*) significantly lower than the locomotor type of that column for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; PIC, regression using phylogenetically independent contrasts; trad., traditional regression methods. Other abbreviations as in Table IV.1. Variable names are listed in Table IV.3.

	< arb	< scan	< terr	< saq
arb <	–	PIC: d_{sc}	PIC: d_{sc}	–
sarb <	both: N	–	both: L_t trad: L_f, N	–
scan <	PIC: L_c, r, d_{tc}	–	trad: L_f, L_t	–
terr <	PIC: L_c, r	–	–	trad: FR
sfos <	–	–	trad: L_t	–
saq <	trad: N	–	trad: L_f, L_t	–
aq <	–	–	trad: L_f, L_t	–

Similarly to the family subsamples, **TR** always scaled elastically when the regressions were significant, while the scaling of **FR** varied among subsamples (Tables IV.A5, IV.A9).

Figure IV.3 shows comparisons of the allometric exponents between different preferred habitats for each variable, which are summarized in Table IV.7. As in the locomotor type subsamples, most significant differences between preferred habitats were found either among traditional or PIC slopes, but not both.

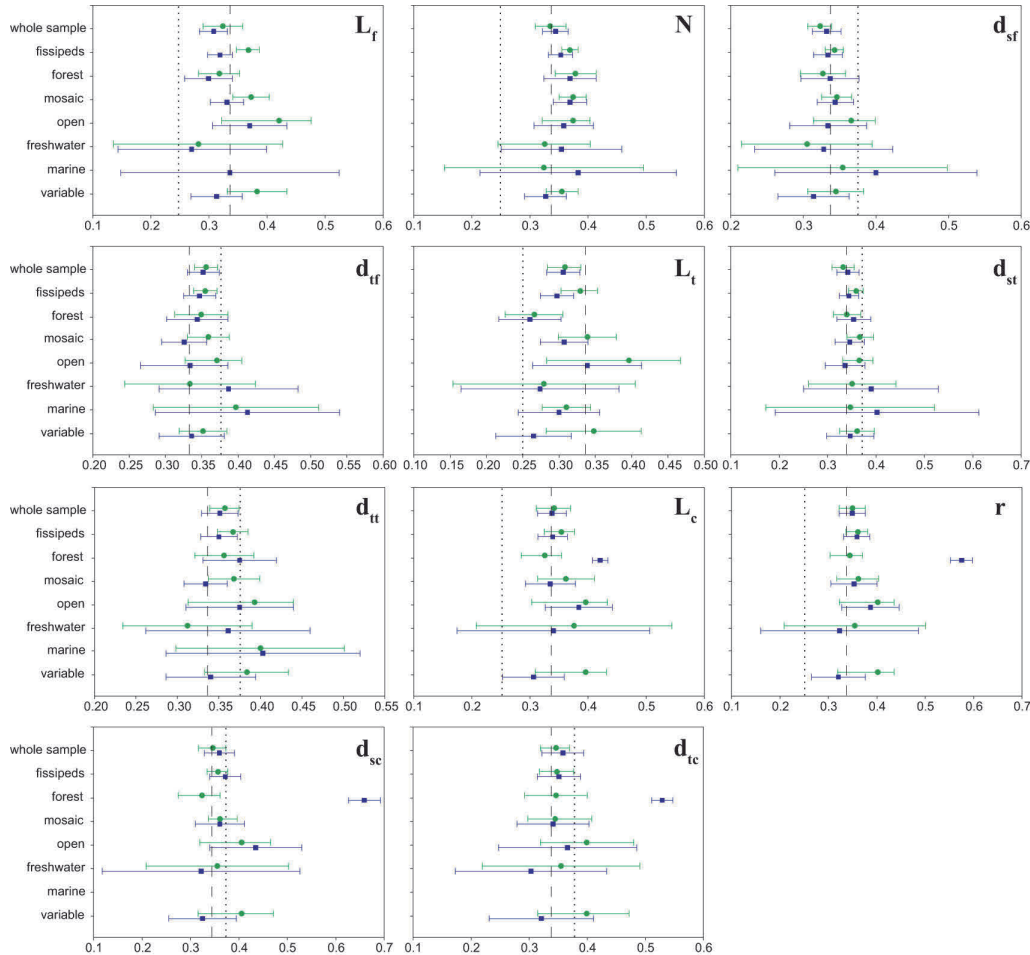


Figure IV.3. Allometric exponents by preferred habitat. For each sub-sample, the allometric exponents obtained using traditional regression methods (green) and phylogenetically independent contrasts (blue), as well as their 95% confidence intervals, are shown. Only the results of significant regressions are presented. The allometric exponents obtained for the whole sample and the fissipeds subsample are included as a reference. The dashed line represents the theoretical value proposed by the geometric similarity hypothesis, while the dotted line corresponds to that proposed by the elastic similarity hypothesis. See Table IV.2 for a description of preferred habitat categories. Variable names are listed in Table IV.3.

Complex allometry

Results for the test for complex allometry are shown in Tables IV.S2 through IV.S14.

In the whole sample, evidence for complex allometry was found in half of the variables. In the case of L_f , N , L_t , d_{st} , L_c , and r , D was significantly higher than 1, indicating that these variables scale faster in small species; while in d_{ff} D was significantly lower than 1, suggesting that these variables scale faster in large species.

As observed for the carnivoran forelimb (Chapter III), after removing Pinnipedia from the sample (i.e. in the fissiped subsample), evidence for complex allometry was not recovered in most cases. Only for L_t and L_c was D still significantly different from 1 ($D > 1$ in both cases). Furthermore, significant evidence for complex allometry was also found for **TR**, which presented $D < 1$. However, the 95% CI_D for **TR** included 0, which, as formulated by Gálvez-López & Casinos (Chapter III), indicates independence from body mass.

Overall, significant evidence for complex allometry was scarce in the family subsamples. Differential scaling was found in Mustelidae (d_{sf}), Herpestidae (L_f , N , L_t , d_{ff}), and Viverridae (L_f , N , d_{sf} , d_{ff} , L_t , d_{st} , d_{tc}), with $D < 1$ in all cases. However, as observed for the whole sample when $D < 1$, in some cases the 95% CI_D also included 0, indicating independence from body mass: N in Viverridae, and L_t and d_{ff} in Herpestidae.

In the locomotor type subsamples, significant evidence for complex allometry was even less frequent than in the family subsamples. In all locomotor types but scansorial, when complex allometry was detected, it suggested that large carnivorans scaled faster than small species (i.e. $D < 1$). This was the case for N and d_{ff} in arboreal carnivorans, for L_f in semiarboreal species, and for **TR** in semifossorial carnivorans. In the case of scansorial

	< forest	< mosaic	< open	< freshwater	< marine	< variable
forest <	–	both: L_t trad: L_f	both: L_f , L_t	–	trad: L_t	trad: L_f , L_t
mosaic < PIC: TR , L_c , r , d_{sc} , d_{tc}	–	–	–	trad: FR	–	–
open < PIC: r , d_{sc} , d_{tc}	–	–	trad: d_{ff}	–	–	–
freshwater < PIC: FR , r , d_{tc}	–	–	trad: d_{ff}	–	–	–
variable < PIC: r , d_{sc} , d_{tc}	–	PIC: N	PIC: L_c , r , d_{sc}	–	–	–

Table IV.7. Differences in the allometric exponents between preferred habitats. In each cell, row indicates the preferred habitat with an allometric exponent (b) significantly lower than the preferred habitat of that column for each methodology (both, trad., PIC). Abbreviations: both, allometric exponents are significantly different using both methodologies; PIC, regression using phylogenetically independent contrasts; trad., traditional regression methods. Variable names are listed in Table IV.3.

carnivorans, on the other hand, large species scaled lower (L_f , d_{sf} , L_t , L_c). As previously observed, in some cases when $D < 1$ the 95% CI_D also included 0. This was the case for d_{tf} in arboreal carnivorans, and **TR** in semifossorial species.

Finally, evidence for complex allometry was only found in a few cases in the preferred habitat subsamples. Large carnivorans scaled significantly faster than small species ($D < 1$) in forest (**N**, d_{tf} , d_{tc}) and mosaic (**TR**) habitats; while the opposite was true for L_c , r , and d_{tc} , in species inhabiting mosaic habitats. Again, the 95% CI_D for **TR** also included 0.

Discussion

Considerations on the scaling pattern of the carnivoran hind limb

Previous studies on hind limb scaling have found scarce conformity to either the geometric or the elastic similarity hypotheses (Bou et al., 1987; Bertram & Biewener, 1990; Cubo & Casinos, 1998; Heinrich & Biknevicius, 1998; Christiansen, 1999*a,b*; Carrano, 2001; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012). In the present study, however, high conformity to geometric scaling was the norm in most subsamples, especially when considering the results of phylogenetically independent contrasts (PIC; Table IV.4). Regardless of conformity, significant evidence for complex allometry was found in most of the studied variables, which agrees with previous studies (Economos, 1983; Bertram & Biewener, 1990; Silva, 1998; Christiansen, 1999*a,b*; Carrano, 2001). Finally, in agreement with previous results on the carnivoran forelimb (Chapter III), but contrary to previous studies comparing traditional and PIC regression methods (Christiansen, 2002*b*; Christiansen & Adolfssen, 2005; Gálvez-López & Casinos, 2012), significant differences between the slopes of both methodologies were found, especially in the fissiped subsample. Thus, in order to avoid any possible artefacts caused by the phylogenetic relatedness of the species in our sample, only the PIC results will be further discussed.

It has been proposed that differential scaling is a consequence of the need of large mammals (over 200kg) to develop progressively more robust limb bones in order to endure the higher bone stresses caused by increasing body mass (Biewener, 1990; Christiansen, 1999*a,b*; Carrano, 2001). At body mass values under that threshold, postural modifications alone (limb straightening) should reduce the magnitude of those stresses, and thus no changes in bone scaling would be required (Biewener, 2003; Carrano, 2001). Since only a handful of non-aquatic carnivoran species attain such large body sizes, limb straightening should be their primary strategy to reduce bone stresses, not changing limb

bone scaling (i.e. differential scaling). In the present study, however, significant evidence for differential scaling was found in several variables, indicating that hind limb scaling does change with size in Carnivora. As observed previously for the carnivoran forelimb (Chapter III), differential scaling was not recovered for most variables after removing Pinnipedia from the sample (i.e. in the fissiped subsample), probably indicating that scaling changes were related to the locomotor specialization of that group (swimming). Furthermore, no significant evidence for differential scaling was found in any of the “large” carnivoran families (Canidae, Felidae, Ursidae; Tables IV.S2–IV.S14). Thus, together with our previous work on the carnivoran forelimb (Chapter III), the results of the present study suggest that, in large non-aquatic carnivorans, size-related increases in bone stresses are compensated by limb posture changes instead of by modifying limb bone scaling.

As observed in previous studies, femur generally presented higher correlation coefficients than tibia, which has been interpreted as proximal proximal limb segments being more conservative in lengthening with increasing body mass than distal ones (McMahon, 1975; Lilje et al., 2003; Schmidt & Fischer, 2009; Chapter III). Interestingly, all subsamples including species adapted to swimming (whole sample; semiaquatic and aquatic carnivorans; freshwater and marine species) deviated from this tendency, presenting more variability in the length of the femur than in the tibia. This is probably related to the limb bone shortening described previously in carnivorans adapted to swimming, which was particularly evident for the femur (Chapter II).

Previous studies had reported scaling differences between femur and tibia (Casinos et al., 1986; Wayne, 1986; Bertram & Biewener, 1990; Raich & Casinos, 1991; Heinrich & Biknevicius, 1998; Christiansen, 1999*a*; Llorens et al., 2001; Lilje et al., 2003; Casinos et al., 2012). In those studies, the length of the tibia tended to scale slower than the length of the femur. In the present study, although the tibia presented the lowest allometric exponent in most subsamples, significant differences were only found for semiarboreal carnivorans. Furthermore, both femur and tibia length scaled slower than calcaneus length in most subsamples. The scaling of bone diameters also tends to be faster in the femur than in the tibia (Llorens et al., 2001; Lilje et al., 2003; but see Cubo & Casinos, 1998). The results of the present study, however, suggest that both sagittal and transverse diameters of femur and tibia scale no differently from each other in Carnivora. In fact, only for Herpestidae were some differences between bone diameters significant (d_{sf} scaled faster than d_{tt} ; Tables IV.A12, IV.A13). Thus, together with our previous study on forelimb scaling (Chapter III), the results of the present study suggest that the scaling pattern of the carnivoran hind limb

is more conservative than that of the forelimb.

Phylogeny, locomotor habit and the scaling of the carnivoran hind limb

Overall, the scaling patterns found for the hind limb in the different carnivoran families were similar to the pattern found for the whole order. Only Canidae and Herpestidae deviated significantly from it (Fig. IV.1). In the case of Canidae, bone lengths (L_f , L_t , L_c) and the moment arm of the ankle extensors (r) scaled faster than in the rest of Carnivora; while in Herpestidae several bone diameters presented lower slopes than those of the whole order and the fissiped subsample (d_{tf} , d_{st} , d_{tt}). Furthermore, when comparing the allometric exponents obtained for each variable between families, Canidae and Eupleridae tended to scale faster than other families, while Herpestidae and Viverridae presented lower allometric slopes than most families. In canids this could be explained by size selection, which seems to be one of the main forces driving canid evolution (Wayne, 1986; Chapter III). The slow scaling of bone lengths in Viverridae could be related to arboreality, since presenting short limbs has been described in this family as a strategy to increase stability in arboreal supports (Cartmill, 1985). In the case of Herpestidae, the low allometric slopes found for bone diameters could reflect a reduction in fossorial habits with increasing size, since fossorial species tend to have more robust limb bones than less specialized species (Lehmann, 1963; Casinos et al., 1993; Elissamburu & Vizcaíno, 2004; Chapter II). Finally, it should be noted that the wide confidence intervals (95%CI_b) obtained for some families could be obscuring further significant deviations from the ordinal scaling pattern (e.g. Procyonidae, Eupleridae).

The lack of significant differences between traditional and PIC slopes in the family subsamples agrees with a previous study stating that most morphological variability of the appendicular skeleton in Carnivora occurs at the family level (Chapter II), and also with the results found in the carnivoran forelimb (Chapter III). Also in agreement with previous results on the carnivoran forelimb, significant differences between both methodologies were found for several locomotor type and preferred habitat subsamples (Chapter III).

Previous studies on the scaling of the appendicular skeleton in Carnivora have been restricted to fissiped carnivorans, and thus comparisons with the literature will only be discussed for that subsample. Overall, our results using traditional regression methods tended to agree with those of Bertram & Biewener (1990) regarding conformity to the similarity hypotheses. However, since they regressed bone lengths onto bone diameters, no direct comparison could be made. Similarly, the PIC slopes obtained for both femur and

tibia length matched those obtained by Christiansen (1999*a*). Conformity to the geometric similarity hypothesis was high in Felidae, in agreement with previous studies on the scaling of their appendicular skeleton (Day & Jayne, 2007; Gálvez-López & Casinos, 2012, Chapter III). Finally, Heinrich & Biknevičius (1998) obtained lower allometric slopes than those proposed by any similarity hypothesis for the hind limbs of scansorial mustelids (i.e., Martinae), which were not recovered in the present study for either Mustelidae or scansorial carnivorans (no specific regressions were carried out for any subfamily).

Contrary to the forelimbs, which are involved in both locomotion and prey capture/handling in Carnivora (Iwaniuk et al., 1999), the hind limbs are merely locomotor. Furthermore, even within their locomotor function, the forelimbs generally perform a wider variety of tasks than the hindlimbs (e.g. semifossorial carnivorans dig exclusively with their forelimbs; Wilson & Mittermeier, 2009). Thus, selective pressures acting on the hind limb are probably similar for all carnivoran species, regardless of locomotor habit, which would explain that neither locomotor type nor preferred habitat subsamples deviated significantly from the scaling pattern of the whole sample (Figs. IV.2, IV.3). Another possible explanation could be that bone scaling was more heavily influenced by phylogenetic relatedness than by other factors (Lilje et al., 2003). This argument is supported by the lower amount of significant differences in the allometric slopes among locomotor type or preferred habitat subsamples than among carnivoran families, especially when considering PIC results (Tables IV.5–IV.7), which was also observed in the carnivoran forelimb (Chapter III). Finally, it is worth noting that calcaneal variables did deviate from the scaling pattern of the whole sample in arboreal and forest-dwelling carnivorans. However, judging by the unexpectedly high correlation coefficients and narrow 95%CI_b's for such low sample sizes (Tables IV.A10–II.A13), these results are probably spurious and were thus not taken into account.

Similarly to previous results on the carnivoran forelimb (Chapter III), significant evidences for complex allometry were found in several variables measured on the carnivoran hind limb. Again, the causes of this differential scaling are hard to ascertain, since it was detected in subsamples with wide and narrow body mass ranges (e.g. the whole sample and Herpestidae), in those including a wide variety of locomotor types (e.g. Viverridae), and in some locomotor type subsamples (e.g. semiarboreal and scansorial carnivorans). Thus, neither body mass range (Economos, 1983; Bertram & Biewener, 1990), varying locomotor requirements (Biewener, 1990, 2003; Christiansen, 1999*a,b*; Carrano, 2001), nor the inclusion of different locomotor types in the same sample (Gálvez-López &

Casinos, 2012), provide a sound explanation for differential scaling in Carnivora.

Interlimb scaling in Carnivora

Previous interlimb comparisons of the scaling of bone lengths have revealed that the distal forelimb segments (i.e. radius/ulna, metacarpals) scale faster than both the femur and the tibia (Wayne, 1986; Raich & Casinos, 1991; Heinrich & Biknevičius, 1998; Christiansen, 1999a; Llorens et al., 2001; Lilje et al., 2003). However, conflicting results exist on the relationships between the proximal limb segments (i.e. scapula and humerus in the forelimb and femur and tibia in the hind limb). In their study on the scaling of the appendicular skeleton in some scansorial mustelids, Heinrich & Biknevičius (1998) obtained higher allometric slopes for humerus than for femur. Similar results were obtained by Llorens et al. (2001) in *Platyrrhina*. As Heinrich & Biknevičius (1998) pointed out, this would indicate a greater straightening of the hind limbs with increasing body mass, since pivot height, and thus functional length, is the same for both the forelimbs and the hind limbs in mammals (Fischer & Blickhan, 2006). On the other hand, whereas in Carnivora the length of femur, humerus and ulna scaled no differently from each other, and all of them faster than tibia length (Raich & Casinos, 1991), in Canidae the length of the femur scaled faster than that of both the humerus and the tibia, but no differently from from scapular length (Wayne, 1986). Furthermore, Christiansen (1999a) found no significant differences in the scaling of the length of humerus, femur and tibia in mammals. However, in the same study he described a lower slope for the tibia than for humerus and femur in Carnivora, which was also later observed by Lilje et al. (2003) in Ruminantia. In the present study, both tibia and femur length scale slower (often significantly) than the length of all forelimb bones except for humerus, which suggests that indeed limb straightening is greater in the hind limbs than in the forelimbs. In the case of Ursidae, femur and tibia length scale faster than the length of any forelimb bone but the third metacarpal, which might be interpreted as the forelimbs straighten further than the hind limbs. However, bears have plantigrade feet, and thus the higher slopes for femur and tibia length probably compensate the loss of the distal (metatarsal) segment. The rest of subsamples generally follow the scaling pattern found for Carnivora, although with slight deviations which probably do not affect the limb straightening relationship (e.g. both ulna and radius length scale slower than femur length in semiarboreal mammals).

In the case of bone diameters, previous interlimb comparisons agree on hind limb diameters scaling slower than forelimb diameters (Cubo & Casinos, 1998; Heinrich &

Biknevicius, 1998; Llorens et al., 2001; Lilje et al., 2003), which was also recovered for most subsamples in the present study. These results agree with those of Carrano (2001), who stated that hind limb bones are relatively more slender than forelimb bones. The only exceptions to this trend were 1) the sagittal diameter of the third metacarpal, which scaled significantly slower than femur sagittal diameter in Ursidae and than tibia transverse diameter in forest-dwelling carnivorans; and 2) radius sagittal diameter, which scaled significantly slower than all hind limb diameters in semiarboreal carnivorans.

Thus, in Carnivora, hind limbs are straightened more with increasing size than forelimbs, while bone robusticity increases faster in the forelimbs than the hind limbs, which would suggest that each pair of limbs presents a different strategy to cope with the higher bone stresses caused by increasing body mass (Biewener, 1990; Christiansen, 1999*a,b*; Carrano, 2001). In turn, this might be related to the asymmetrical distribution of body weight in most mammals, which imposes heavier loads on the forelimb than on the hind limbs (Schmitt & Lemelin, 2002).

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Appendix – Regression results

As indicated in Table IV.3, the following tables present the regression results for each variable. Both the results using traditional regression methods and phylogenetically independent contrasts (PIC) are shown for the whole sample and each of the subsamples (fissipeds, by Family, by locomotor type, and by habitat). In each case, it is indicated (in the “sim.” columns) whether the theoretical values proposed by the geometric similarity hypothesis (G), the elastic similarity hypothesis (E), or both (B), are included in the 95% confidence interval for the slope b (95% CI _{b}). Furthermore, when neither theoretical value is included in the 95% CI _{b} , it is indicated whether there is positive allometry (+; b is higher than both theoretical values), negative allometry (-; b is lower than both theoretical values), or both (nei.; b is higher than one theoretical values and lower than the other). Finally, the results of the comparison between the allometric coefficients obtained with each methodology are presented in the last column ($b_{\text{trad}} \neq b_{\text{PIC}}$): a cross (×) indicates no significant differences, while a tick (✓) denotes that the slopes are significantly different from each other ($p < 0.05$).

Variable names and abbreviations are given in Table IV.3, while the following abbreviations are common to all following tables: 95% CI _{a} , 95% confidence interval for the coefficient a ; 95% CI _{b} , 95% confidence interval for the allometric coefficient b ; n , sample size; n.s., unable to test differences due to non-significant regression; R , correlation coefficient; sim., similarity. Results in *grey italics* denote non-significant regressions.

IV.A1 – L_f		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}
fissipeds	136	5.977	4.641 – 7.734	0.324	0.290 – 0.358	0.818	G	135	0.308	0.284 – 0.332	0.887	G	×
Family	129	4.385	3.704 – 5.217	0.368	0.347 – 0.387	0.934	+	128	0.319	0.298 – 0.340	0.928	G	✓
Canidae	17	3.151	1.641 – 10.351	0.416	0.286 – 0.489	0.935	G	16	0.415	0.319 – 0.511	0.908	G	×
Mustelidae	32	6.192	4.118 – 9.310	0.296	0.244 – 0.348	0.882	B	31	0.297	0.248 – 0.346	0.894	B	×
Procyonidae	7	10.662	3.852 – 29.513	0.266	0.140 – 0.392	0.911	B	6	0.257	0.108 – 0.406	0.885	B	×
Ursidae	7	6.463	1.458 – 28.650	0.324	0.197 – 0.451	0.940	B	6	0.328	0.188 – 0.468	0.939	B	×
Felidae	26	9.953	8.163 – 12.134	0.295	0.274 – 0.316	0.986	nei.	25	0.307	0.279 – 0.335	0.977	G	×
Herpestidae	11	6.725	4.106 – 11.016	0.310	0.241 – 0.378	0.956	B	10	0.304	0.233 – 0.375	0.953	B	×
Eupleridae	5	5.076	2.990 – 8.616	0.367	0.294 – 0.440	0.994	G						
Viverridae	14	13.607	9.100 – 20.347	0.234	0.184 – 0.283	0.941	E	13	0.256	0.129 – 0.383	0.622	B	×
Locomotor type													
arboreal	7	8.163	2.193 – 30.900	0.301	0.138 – 0.464	0.883	B	6	0.335	0.326 – 0.344	1.000	G	×
semiarboreal	10	9.910	6.787 – 14.138	0.286	0.237 – 0.335	0.977	B	9	0.253	0.160 – 0.346	0.899	B	×
scansorial	45	7.244	6.084 – 8.894	0.322	0.303 – 0.341	0.982	G	44	0.322	0.299 – 0.345	0.972	G	×
terrestrial	48	3.469	2.694 – 4.897	0.395	0.353 – 0.425	0.964	+	47	0.340	0.299 – 0.381	0.915	G	✓
semifossorial	7	5.100	2.139 – 12.958	0.323	0.214 – 0.432	0.956	B	6	0.338	0.213 – 0.463	0.954	B	×
semiaquatic	11	9.210	3.391 – 25.068	0.243	0.126 – 0.360	0.769	B	10	0.253	0.149 – 0.357	0.844	B	×
aquatic	8	13.106	1.968 – 87.560	0.168	0.010 – 0.327	0.330	E	7	0.289	0.153 – 0.425	0.894	B	n.s.
Preferred habitat													
forest	38	6.937	5.176 – 9.297	0.318	0.282 – 0.353	0.944	G	37	0.299	0.258 – 0.340	0.916	G	×
mosaic	39	4.418	3.353 – 5.820	0.373	0.341 – 0.404	0.967	+	38	0.331	0.302 – 0.360	0.965	G	✓
open	17	2.854	1.757 – 6.125	0.421	0.322 – 0.476	0.962	G	16	0.370	0.306 – 0.434	0.950	G	×
freshwater	13	7.357	2.125 – 25.468	0.282	0.136 – 0.427	0.624	B	12	0.270	0.143 – 0.399	0.714	B	×
marine	10	1.811	0.109 – 30.078	0.350	0.110 – 0.590	0.541	B	9	0.336	0.148 – 0.524	0.744	B	n.s.
variable	19	3.906	2.471 – 6.174	0.383	0.332 – 0.434	0.966	G	18	0.313	0.269 – 0.357	0.963	G	✓

IV.A2 – N	traditional regression						PIC regression						
	n	a	95% CI _a	<i>h</i> _{rad}	R	sim.	n	<i>h</i> _{PIC}	95% CI _b	R	sim.	<i>h</i> _{rad} ≠ <i>h</i> _{PIC}	
whole sample	136	0.699	0.571 – 0.860	0.335	0.309 – 0.362	0.945	G	135	0.344	0.322 – 0.366	0.929	G	×
fissipeds	129	0.541	0.483 – 0.610	0.369	0.355 – 0.383	0.977	+	128	0.353	0.332 – 0.374	0.943	G	×
Family													
Canidae	17	0.383	0.228 – 0.852	0.408	0.319 – 0.468	0.937	G	16	0.415	0.319 – 0.511	0.908	G	×
Mustelidae	32	0.604	0.460 – 0.791	0.347	0.313 – 0.381	0.964	G	31	0.344	0.296 – 0.392	0.928	G	×
Procyonidae	7	0.592	0.188 – 1.864	0.368	0.226 – 0.510	0.942	B	6	0.362	0.183 – 0.541	0.917	B	×
Ursidae	7	2.879	0.441 – 18.788	0.235	0.075 – 0.395	0.807	B	6	0.236	0.065 – 0.407	0.811	B	n.s.
Felidae	26	0.694	0.563 – 0.854	0.340	0.318 – 0.362	0.988	G	25	0.336	0.304 – 0.368	0.975	G	×
Herpestidae	11	0.770	0.480 – 1.233	0.328	0.262 – 0.394	0.964	G	10	0.318	0.245 – 0.391	0.955	B	×
Eupleridae	5	0.410	0.285 – 0.589	0.413	0.363 – 0.463	0.998	+						
Viverridae	14	0.719	0.341 – 1.514	0.331	0.239 – 0.423	0.897	B	13	0.367	0.258 – 0.476	0.885	G	×
Locomotor type													
arboreal	7	0.390	0.205 – 0.744	0.412	0.332 – 0.492	0.986	G	6	0.414	0.325 – 0.503	0.985	G	×
semiarboreal	10	0.915	0.561 – 1.492	0.310	0.246 – 0.373	0.968	B	9	0.279	0.196 – 0.362	0.934	B	×
scansorial	45	0.533	0.443 – 0.641	0.373	0.353 – 0.393	0.984	+	44	0.359	0.329 – 0.389	0.961	G	×
terrestrial	48	0.509	0.425 – 0.638	0.375	0.350 – 0.397	0.974	+	47	0.350	0.310 – 0.390	0.923	G	×
semifossorial	7	0.639	0.282 – 1.450	0.352	0.249 – 0.455	0.967	B	6	0.372	0.214 – 0.530	0.940	B	×
semiaquatic	11	0.774	0.429 – 1.397	0.315	0.246 – 0.384	0.957	B	10	0.340	0.253 – 0.427	0.943	G	×
aquatic	8	0.646	0.041 – 10.165	0.297	0.066 – 0.528	0.627	B	7	0.296	0.064 – 0.528	0.666	B	n.s.
Preferred habitat													
forest	38	0.501	0.374 – 0.671	0.378	0.343 – 0.414	0.961	+	37	0.369	0.324 – 0.414	0.932	G	×
mosaic	39	0.526	0.428 – 0.647	0.374	0.350 – 0.397	0.982	+	38	0.369	0.340 – 0.398	0.973	+	×
open	17	0.522	0.404 – 0.811	0.374	0.321 – 0.403	0.981	G	16	0.358	0.307 – 0.409	0.966	G	×
freshwater	13	0.742	0.376 – 1.461	0.325	0.245 – 0.404	0.929	B	12	0.354	0.250 – 0.458	0.900	B	×
marine	10	0.518	0.070 – 3.830	0.324	0.153 – 0.495	0.763	B	9	0.383	0.214 – 0.552	0.850	B	×
variable	19	0.635	0.495 – 0.810	0.355	0.328 – 0.383	0.989	G	18	0.327	0.291 – 0.363	0.977	G	×

IV.A3 – d_{sf}		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}
fissipeds	136	0.505	0.441 – 0.583	0.323	0.306 – 0.339	0.961	G	135	0.332	0.312 – 0.352	0.935	G	×
Family	129	0.433	0.388 – 0.486	0.343	0.330 – 0.355	0.972	G	128	0.334	0.314 – 0.354	0.940	G	×
Canidae	17	0.228	0.133 – 0.593	0.412	0.305 – 0.472	0.951	B	16	0.401	0.324 – 0.478	0.938	B	×
Mustelidae	32	0.485	0.379 – 0.622	0.314	0.283 – 0.346	0.963	G	31	0.316	0.268 – 0.364	0.912	G	×
Procyonidae	7	0.601	0.295 – 1.223	0.315	0.227 – 0.403	0.970	B	6	0.310	0.195 – 0.425	0.954	B	×
Ursidae	7	0.524	0.090 – 3.062	0.324	0.174 – 0.474	0.915	B	6	0.325	0.160 – 0.490	0.912	B	×
Felidae	26	0.514	0.438 – 0.603	0.331	0.314 – 0.348	0.993	G	25	0.332	0.306 – 0.358	0.983	G	×
Herpestidae	11	0.576	0.364 – 0.912	0.314	0.249 – 0.378	0.963	B	10	0.311	0.250 – 0.372	0.967	G	×
Eupleridae	5	0.229	0.100 – 0.525	0.451	0.337 – 0.565	0.990	E						
Viverridae	14	0.562	0.311 – 1.019	0.313	0.240 – 0.387	0.928	B	13	0.364	0.211 – 0.517	0.749	B	×
Locomotor type													
arboreal	7	0.470	0.190 – 1.163	0.342	0.230 – 0.455	0.958	B	6	0.350	0.229 – 0.471	0.960	B	×
semiarboreal	10	0.484	0.253 – 0.927	0.343	0.258 – 0.427	0.953	B	9	0.335	0.265 – 0.405	0.969	B	×
scansorial	45	0.484	0.424 – 0.552	0.335	0.321 – 0.349	0.990	G	44	0.338	0.314 – 0.362	0.973	G	×
terrestrial	48	0.409	0.346 – 0.511	0.346	0.321 – 0.365	0.969	G	47	0.330	0.286 – 0.374	0.896	G	×
semifossorial	7	0.653	0.328 – 1.301	0.282	0.195 – 0.368	0.963	G	6	0.306	0.166 – 0.446	0.930	B	×
semiaquatic	11	0.581	0.298 – 1.134	0.294	0.216 – 0.372	0.936	G	10	0.314	0.228 – 0.400	0.934	B	×
aquatic	8	0.133	0.004 – 4.009	0.410	0.125 – 0.695	0.718	B	7	0.392	0.137 – 0.647	0.784	B	n.s.
Preferred habitat													
forest	38	0.508	0.393 – 0.656	0.327	0.296 – 0.358	0.960	G	37	0.337	0.297 – 0.377	0.936	B	×
mosaic	39	0.431	0.361 – 0.516	0.346	0.325 – 0.367	0.984	G	38	0.344	0.319 – 0.369	0.976	G	×
open	17	0.347	0.259 – 0.550	0.366	0.314 – 0.399	0.974	B	16	0.334	0.281 – 0.387	0.959	B	×
freshwater	13	0.559	0.260 – 1.203	0.305	0.215 – 0.395	0.895	B	12	0.328	0.233 – 0.423	0.902	B	×
marine	10	0.274	0.051 – 1.479	0.354	0.210 – 0.498	0.867	B	9	0.400	0.261 – 0.539	0.910	B	×
variable	19	0.421	0.298 – 0.596	0.345	0.306 – 0.383	0.976	B	18	0.314	0.265 – 0.363	0.953	G	×

IV.A4 – d _{tf}	traditional regression						PIC regression						
	n	a	95% CI _a	h _{rad}	R	sim.	n	h _{PIC}	95% CI _b	R	sim.	h _{rad} ≠ h _{PIC}	
whole sample	136	0.417	0.361 – 0.480	0.356	0.340 – 0.372	0.972	nei.	135	0.352	0.330 – 0.374	0.932	G	×
fissipeds	129	0.421	0.362 – 0.488	0.355	0.339 – 0.371	0.967	nei.	128	0.347	0.325 – 0.369	0.932	G	×
Family													
Canidae	17	0.247	0.126 – 0.724	0.405	0.283 – 0.479	0.952	B	16	0.402	0.322 – 0.482	0.934	B	×
Mustelidae	32	0.377	0.287 – 0.496	0.355	0.320 – 0.390	0.965	B	31	0.361	0.305 – 0.417	0.910	G	×
Procyonidae	7	0.831	0.399 – 1.729	0.285	0.194 – 0.376	0.961	B	6	0.279	0.191 – 0.367	0.967	B	×
Ursidae	7	<i>1.691</i>	<i>0.193 – 14.835</i>	<i>0.240</i>	<i>0.055 – 0.425</i>	<i>0.743</i>	<i>B</i>	<i>6</i>	<i>0.241</i>	<i>0.043 – 0.439</i>	<i>0.748</i>	<i>B</i>	n.s.
Felidae	26	0.494	0.375 – 0.652	0.342	0.312 – 0.371	0.979	G	25	0.343	0.293 – 0.393	0.939	G	×
Herpestidae	11	0.812	0.472 – 1.398	0.277	0.202 – 0.353	0.932	G	10	0.264	0.183 – 0.345	0.918	G	×
Eupleridae	5	0.605	0.449 – 0.815	0.330	0.288 – 0.371	0.998	G						
Viverridae	14	0.733	0.409 – 1.314	0.292	0.220 – 0.364	0.919	G	13	0.301	0.208 – 0.394	0.874	B	×
Locomotor type													
arboreal	7	0.522	0.212 – 1.285	0.339	0.228 – 0.451	0.958	B	6	0.342	0.219 – 0.465	0.957	B	×
semi-arboreal	10	0.603	0.336 – 1.085	0.320	0.244 – 0.397	0.956	B	9	0.305	0.232 – 0.378	0.958	B	×
scansorial	45	0.470	0.390 – 0.566	0.349	0.328 – 0.369	0.982	G	44	0.339	0.304 – 0.374	0.944	G	×
terrestrial	48	0.418	0.341 – 0.526	0.348	0.323 – 0.369	0.965	G	47	0.339	0.300 – 0.378	0.921	B	×
semifossorial	7	0.612	0.284 – 1.320	0.299	0.202 – 0.396	0.960	B	6	0.326	0.187 – 0.465	0.939	B	×
semiaquatic	11	0.486	0.224 – 1.057	0.331	0.240 – 0.422	0.931	B	10	0.367	0.259 – 0.475	0.923	B	×
aquatic	8	0.092	0.006 – 1.479	0.482	0.249 – 0.715	0.875	B	7	0.475	0.206 – 0.744	0.842	B	×
Preferred habitat													
forest	38	0.456	0.336 – 0.619	0.349	0.313 – 0.386	0.950	B	37	0.344	0.302 – 0.386	0.934	B	×
mosaic	39	0.411	0.319 – 0.529	0.359	0.330 – 0.388	0.970	B	38	0.326	0.295 – 0.357	0.959	G	✓
open	17	0.347	0.259 – 0.517	0.371	0.327 – 0.405	0.973	B	16	0.334	0.266 – 0.386	0.946	B	×
freshwater	13	0.488	0.227 – 1.048	0.334	0.244 – 0.424	0.914	B	12	0.387	0.291 – 0.483	0.930	B	×
marine	10	0.248	0.065 – 0.943	0.397	0.283 – 0.511	0.936	B	9	0.413	0.286 – 0.540	0.930	B	×
variable	19	0.418	0.310 – 0.563	0.352	0.319 – 0.385	0.983	B	18	0.336	0.291 – 0.381	0.966	B	×

IV.A5 – FR		traditional regression					PIC regression						
	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}	
whole sample	136	0.024	0.018 – 0.033	0.142	0.108 – 0.177	0.318	E	135	0.131	0.110 – 0.152	0.289	E	×
fissipeds	129	0.182	0.153 – 1.056	-0.097	-0.305 – -0.076	0.104	-	128	-0.135	-0.159 – -0.111	0.001	-	n.s.
Family													
Canidae	17	0.027	0.002 – 0.048	0.106	0.039 – 0.394	0.030	E	16	-0.129	-0.199 – -0.059	0.175	-	n.s.
Mustelidae	32	0.033	0.005 – 0.049	0.129	0.084 – 0.368	0.321	E	31	-0.151	-0.206 – -0.096	0.249	-	n.s.
Procyonidae	7	0.041	0.004 – 0.053	0.088	0.054 – 0.377	0.721	E	6	0.087	0.023 – 0.151	0.800	E	n.s.
Ursidae	7	0.175	0.080 – 2.071	-0.066	-0.275 – 0.006	0.149	B	6	-0.061	-0.140 – 0.006	0.237	B	n.s.
Felidae	26	0.040	0.033 – 0.050	0.064	0.040 – 0.081	0.587	nei.	25	0.076	0.046 – 0.106	0.346	nei.	n.s.
Herpestidae	11	0.032	0.003 – 0.079	0.140	0.010 – 0.483	0.045	E	10	0.139	0.032 – 0.246	0.086	E	n.s.
Eupleridae	5	0.040	0.007 – 0.130	0.101	-0.080 – 0.361	0.833	B						
Viverridae	14	0.037	0.031 – 0.046	0.094	0.066 – 0.117	0.767	nei.	13	0.110	0.060 – 0.160	0.701	E	×
Locomotor type													
arboreal	7	0.033	0.001 – 0.096	0.112	-0.029 – 0.541	0.571	B	6	0.089	0.085 – 0.093	0.999	E	n.s.
semiarboreal	10	0.029	0.005 – 0.061	0.124	0.021 – 0.346	0.385	E	9	0.142	0.038 – 0.246	0.490	E	n.s.
scansorial	45	0.044	0.038 – 0.052	0.058	0.041 – 0.073	0.274	nei.	44	0.078	0.055 – 0.101	0.203	nei.	n.s.
terrestrial	48	0.165	0.130 – 0.197	-0.090	-0.112 – -0.060	0.508	-	47	-0.103	-0.133 – -0.073	0.192	-	n.s.
semifossorial	7	0.147	0.116 – 0.298	-0.059	-0.146 – -0.025	0.641	-	6	-0.066	-0.124 – -0.008	0.702	-	n.s.
semiaquatic	11	0.036	0.025 – 0.078	0.119	0.031 – 0.157	0.750	E	10	0.130	0.051 – 0.209	0.616	E	×
aquatic	8	0.003	1.95 · 10 ⁻⁴ – 0.401	0.334	-0.044 – 0.582	0.718	B	7	0.306	0.070 – 0.542	0.676	E	n.s.
Preferred habitat													
forest	38	0.040	0.010 – 0.053	0.082	0.050 – 0.258	0.176	E	37	0.286	0.216 – 0.356	0.693	+	n.s.
mosaic	39	0.157	0.117 – 0.530	-0.082	-0.222 – -0.046	0.240	-	38	0.079	0.053 – 0.105	0.142	nei.	n.s.
open	17	0.164	0.109 – 0.204	-0.091	-0.122 – -0.035	0.528	-	16	-0.084	-0.128 – -0.040	0.361	-	n.s.
freshwater	13	0.028	0.018 – 0.059	0.142	0.060 – 0.189	0.697	E	12	0.150	0.078 – 0.222	0.694	E	×
marine	10	0.007	9.06 · 10 ⁻⁷ – 1.577	0.273	-0.164 – 1.027	0.429	B	9	0.279	0.076 – 0.482	0.498	E	n.s.
variable	19	0.151	0.112 – 0.616	-0.076	-0.227 – -0.040	0.434	-	18	-0.109	-0.165 – -0.053	0.022	-	n.s.

IV.A6 – L _t	traditional regression						PIC regression						
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	136	7.202	5.931 – 8.798	0.308	0.284 – 0.330	0.915	nei.	135	0.306	0.283 – 0.329	0.897	nei.	×
fissipeds	129	6.122	4.999 – 7.628	0.329	0.303 – 0.353	0.911	G	128	0.297	0.274 – 0.320	0.901	nei.	✓
Family													
Canidae	17	3.834	1.530 – 17.140	0.400	0.239 – 0.503	0.873	B	16	0.436	0.307 – 0.565	0.847	G	×
Mustelidae	32	6.849	4.608 – 10.179	0.290	0.240 – 0.341	0.885	B	31	0.282	0.233 – 0.331	0.885	E	×
Procyonidae	7	12.561	4.110 – 38.393	0.246	0.108 – 0.385	0.872	B	6	0.224	0.104 – 0.344	0.902	B	×
Ursidae	7	5.304	1.425 – 19.739	0.317	0.205 – 0.429	0.952	B	6	0.329	0.204 – 0.454	0.952	B	×
Felidae	26	14.249	10.755 – 18.878	0.255	0.225 – 0.285	0.961	E	25	0.280	0.241 – 0.319	0.945	E	×
Herpestidae	11	6.902	3.537 – 13.470	0.312	0.219 – 0.406	0.918	B	10	0.298	0.209 – 0.387	0.922	B	×
Eupleridae	5	8.448	2.701 – 26.422	0.307	0.150 – 0.464	0.960	B						
Viverridae	14	18.548	13.015 – 26.433	0.196	0.153 – 0.240	0.935	-	13	0.240	0.181 – 0.299	0.922	E	×
Locomotor type													
arboreal	7	8.552	1.515 – 48.267	0.293	0.079 – 0.508	0.772	B	6	0.297	0.068 – 0.526	0.783	B	n.s.
semiarboreal	10	15.163	9.625 – 23.888	0.232	0.173 – 0.291	0.950	E	9	0.201	0.108 – 0.294	0.832	E	×
scansorial	45	11.576	9.164 – 14.622	0.267	0.242 – 0.292	0.951	E	44	0.287	0.259 – 0.315	0.949	nei.	×
terrestrial	48	4.287	3.100 – 6.433	0.372	0.321 – 0.412	0.934	G	47	0.318	0.272 – 0.364	0.871	G	✓
semifossorial	7	9.724	3.727 – 25.372	0.240	0.120 – 0.361	0.899	B	6	0.258	0.115 – 0.401	0.896	B	×
semiaquatic	11	8.964	3.880 – 20.710	0.258	0.160 – 0.356	0.864	B	10	0.282	0.203 – 0.361	0.931	B	×
aquatic	8	6.817	3.210 – 14.474	0.287	0.224 – 0.350	0.976	B	7	0.258	0.185 – 0.331	0.963	E	×
Preferred habitat													
forest	38	10.476	7.548 – 14.541	0.266	0.226 – 0.305	0.899	E	37	0.260	0.217 – 0.303	0.874	E	×
mosaic	39	5.810	4.108 – 8.219	0.339	0.299 – 0.379	0.935	G	38	0.307	0.274 – 0.340	0.947	G	×
open	17	3.760	2.054 – 8.964	0.396	0.283 – 0.467	0.940	G	16	0.339	0.264 – 0.414	0.916	G	×
freshwater	13	8.194	2.819 – 23.817	0.279	0.154 – 0.405	0.736	B	12	0.274	0.165 – 0.383	0.807	B	×
marine	10	5.198	3.509 – 7.699	0.310	0.277 – 0.344	0.991	G	9	0.300	0.244 – 0.356	0.975	B	×
variable	19	5.278	2.911 – 9.570	0.348	0.282 – 0.413	0.929	G	18	0.265	0.213 – 0.317	0.923	B	✓

IV.A7 – d_{st}		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	b_{rad}	95% CI_b	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}
fissipeds	136	0.491	0.409 – 0.593	0.332	0.309 – 0.355	0.952	G	135	0.342	0.319 – 0.365	0.921	G	×
Family	129	0.400	0.353 – 0.460	0.359	0.344 – 0.373	0.973	nei.	128	0.344	0.324 – 0.364	0.944	G	×
Canidae	17	0.246	0.159 – 0.511	0.408	0.327 – 0.454	0.968	B	16	0.385	0.321 – 0.449	0.954	B	×
Mustelidae	32	0.403	0.302 – 0.537	0.346	0.310 – 0.383	0.959	B	31	0.346	0.299 – 0.393	0.931	B	×
Procyonidae	7	0.888	0.256 – 3.077	0.267	0.113 – 0.420	0.865	B	<i>6</i>	<i>0.255</i>	<i>0.082 – 0.428</i>	<i>0.839</i>	<i>B</i>	n.s.
Ursidae	7	0.239	0.015 – 3.912	0.400	0.162 – 0.638	0.856	B	<i>6</i>	<i>0.409</i>	<i>0.145 – 0.673</i>	<i>0.854</i>	<i>B</i>	n.s.
Felidae	26	0.417	0.320 – 0.543	0.362	0.334 – 0.390	0.983	E	25	0.349	0.311 – 0.387	0.966	B	×
Herpestidae	11	0.885	0.572 – 1.370	0.263	0.202 – 0.324	0.951	-	10	0.262	0.198 – 0.326	0.948	-	×
Eupleridae	5	0.309	0.159 – 0.601	0.412	0.321 – 0.504	0.993	B						
Viverridae	14	0.731	0.510 – 1.048	0.284	0.240 – 0.329	0.968	-	13	0.311	0.253 – 0.369	0.956	G	×
Locomotor type													
arboreal	7	0.475	0.222 – 1.019	0.342	0.248 – 0.437	0.971	B	6	0.343	0.243 – 0.443	0.972	B	×
semiarboreal	10	0.329	0.201 – 0.538	0.396	0.332 – 0.460	0.980	B	9	0.370	0.311 – 0.429	0.982	E	×
scansorial	45	0.444	0.370 – 0.532	0.353	0.333 – 0.372	0.983	G	44	0.352	0.316 – 0.388	0.942	B	×
terrestrial	48	0.407	0.339 – 0.514	0.353	0.329 – 0.373	0.970	G	47	0.328	0.294 – 0.362	0.938	G	×
semifossorial	7	0.471	0.222 – 1.001	0.333	0.238 – 0.428	0.969	B	6	0.342	0.233 – 0.451	0.967	B	×
semiaquatic	11	0.410	0.176 – 0.954	0.344	0.245 – 0.442	0.924	B	10	0.383	0.242 – 0.524	0.877	B	×
aquatic	<i>8</i>	<i>0.261</i>	<i>0.007 – 10.243</i>	<i>0.351</i>	<i>0.044 – 0.659</i>	<i>0.483</i>	<i>B</i>	<i>7</i>	<i>0.377</i>	<i>0.027 – 0.727</i>	<i>0.466</i>	<i>B</i>	n.s.
Preferred habitat													
forest	38	0.468	0.371 – 0.592	0.340	0.312 – 0.369	0.969	G	37	0.354	0.319 – 0.389	0.957	B	×
mosaic	39	0.390	0.307 – 0.495	0.367	0.340 – 0.395	0.974	E	38	0.346	0.316 – 0.376	0.965	B	×
open	17	0.373	0.291 – 0.516	0.366	0.332 – 0.394	0.981	B	16	0.336	0.295 – 0.377	0.975	B	×
freshwater	13	0.397	0.185 – 0.852	0.351	0.261 – 0.441	0.823	B	12	0.390	0.251 – 0.529	0.848	B	×
marine	10	0.293	0.038 – 2.253	0.347	0.173 – 0.521	0.789	B	9	0.402	0.192 – 0.612	0.780	B	×
variable	19	0.388	0.279 – 0.538	0.361	0.325 – 0.397	0.981	B	18	0.347	0.298 – 0.396	0.962	B	×

IV.A8 – d _{tt}	traditional regression					PIC regression							
	n	a	95% CI _a	<i>b</i> _{rad}	R	sim.	n	<i>b</i> _{PIC}	95% CI _b	R	sim.	<i>b</i> _{rad} ≠ <i>b</i> _{PIC}	
whole sample	136	0.334	0.286 – 0.392	0.357	0.339 – 0.374	0.964	nei.	135	0.351	0.329 – 0.373	0.934	G	×
fissipeds	129	0.309	0.262 – 0.366	0.367	0.348 – 0.385	0.961	E	128	0.350	0.328 – 0.372	0.934	G	×
Family													
Canidae	17	0.212	0.119 – 0.591	0.418	0.306 – 0.481	0.947	B	16	0.421	0.338 – 0.504	0.934	E	×
Mustelidae	32	0.357	0.270 – 0.472	0.330	0.294 – 0.365	0.957	G	31	0.343	0.297 – 0.389	0.933	B	×
Procyonidae	7	0.361	0.139 – 0.942	0.347	0.228 – 0.465	0.955	B	6	0.340	0.190 – 0.490	0.935	B	×
Ursidae	7	0.552	0.049 – 6.234	0.308	0.101 – 0.514	0.812	B	6	<i>0.309</i>	<i>0.093 – 0.525</i>	<i>0.826</i>	<i>B</i>	n.s.
Felidae	26	0.408	0.316 – 0.526	0.348	0.321 – 0.375	0.983	B	25	0.362	0.319 – 0.405	0.960	B	×
Herpestidae	11	0.690	0.353 – 1.350	0.272	0.179 – 0.366	0.890	G	10	0.237	0.148 – 0.326	0.873	-	×
Eupleridae	5	0.357	0.080 – 1.597	0.364	0.158 – 0.571	0.951	B						
Viverridae	14	0.493	0.367 – 0.661	0.308	0.271 – 0.344	0.982	G	13	0.324	0.269 – 0.379	0.964	B	×
Locomotor type													
arboreal	7	0.318	0.105 – 0.961	0.362	0.225 – 0.499	0.944	B	6	0.361	0.217 – 0.505	0.947	B	×
semi-arboreal	10	0.506	0.307 – 0.834	0.311	0.246 – 0.376	0.967	B	9	0.313	0.238 – 0.388	0.958	B	×
scansorial	45	0.374	0.310 – 0.453	0.352	0.331 – 0.372	0.982	G	44	0.357	0.324 – 0.390	0.954	B	×
terrestrial	48	0.291	0.218 – 0.431	0.375	0.330 – 0.409	0.954	B	47	0.351	0.310 – 0.392	0.921	B	×
semifossorial	7	0.380	0.148 – 0.981	0.314	0.195 – 0.434	0.944	B	6	0.318	0.190 – 0.446	0.947	B	×
semiaquatic	11	0.433	0.226 – 0.831	0.311	0.234 – 0.387	0.945	B	10	0.354	0.255 – 0.453	0.931	B	×
aquatic	8	0.063	0.005 – 0.765	0.483	0.273 – 0.692	0.900	B	7	0.446	0.248 – 0.644	0.905	B	×
Preferred habitat													
forest	38	0.338	0.252 – 0.454	0.356	0.321 – 0.392	0.955	B	37	0.375	0.331 – 0.419	0.937	B	×
mosaic	39	0.319	0.243 – 0.418	0.368	0.337 – 0.399	0.967	E	38	0.334	0.308 – 0.360	0.972	G	✓
open	17	0.255	0.169 – 0.496	0.393	0.313 – 0.440	0.967	B	16	0.375	0.310 – 0.440	0.950	B	×
freshwater	13	0.444	0.229 – 0.862	0.312	0.234 – 0.390	0.927	B	12	0.361	0.262 – 0.460	0.913	B	×
marine	10	0.169	0.052 – 0.552	0.400	0.298 – 0.501	0.951	B	9	0.403	0.286 – 0.520	0.938	B	×
variable	19	0.267	0.169 – 0.421	0.384	0.333 – 0.434	0.966	B	18	0.340	0.286 – 0.394	0.952	B	×

IV.A9 – TR		traditional regression					PIC regression						
whole sample	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}	
fissipeds	136	0.031	0.027 – 0.036	0.114	0.097 – 0.128	0.297	E	135	0.141	0.119 – 0.163	0.393	E	✓
Family	129	0.029	0.025 – 0.035	0.124	0.105 – 0.140	0.398	E	128	0.134	0.113 – 0.155	0.466	E	×
Canidae	17	0.014	2.36 · 10 ⁻⁴ – 0.028	0.176	0.093 – 0.629	0.259	E	16	-0.242	-0.372 – -0.112	0.251	-	n.s.
Mustelidae	32	0.035	0.025 – 0.053	0.124	0.075 – 0.161	0.603	E	31	0.117	0.083 – 0.151	0.621	E	×
Procyonidae	7	0.033	0.002 – 0.052	0.116	0.059 – 0.452	0.138	E	6	0.124	-0.028 – 0.276	0.121	B	n.s.
Ursidae	7	0.023	2.14 · 10 ⁻⁴ – 0.165	0.139	-0.031 – 0.538	0.272	B	6	0.156	-0.024 – 0.336	0.359	B	n.s.
Felidae	26	0.021	0.016 – 0.028	0.145	0.110 – 0.170	0.767	E	25	0.142	0.090 – 0.194	0.510	E	×
Herpestidae	11	0.257	0.140 – 3.761	-0.147	-0.526 – -0.067	0.254	-	10	-0.143	-0.250 – -0.036	0.229	-	n.s.
Eupleridae	5	0.022	5.02 · 10 ⁻⁴ – 0.046	0.173	0.091 – 0.718	0.664	E						
Viverridae	14	0.031	0.026 – 0.046	0.116	0.068 – 0.142	0.787	E	13	0.115	0.065 – 0.165	0.735	E	×
Locomotor type													
arboreal	7	0.021	1.05 · 10 ⁻⁴ – 0.072	0.170	0.014 – 0.838	0.628	E	6	0.192	0.052 – 0.332	0.809	E	n.s.
semiarboreal	10	0.018	0.011 – 0.033	0.186	0.108 – 0.248	0.900	E	9	0.201	0.108 – 0.294	0.833	E	×
scansorial	45	0.027	0.022 – 0.034	0.125	0.101 – 0.147	0.744	E	44	0.134	0.097 – 0.171	0.442	E	×
terrestrial	48	0.206	0.165 – 0.646	-0.114	-0.357 – -0.086	0.046	-	47	0.132	0.093 – 0.171	0.126	E	n.s.
semifossorial	7	0.041	0.030 – 0.059	0.115	0.072 – 0.153	0.927	E	6	0.109	0.055 – 0.163	0.917	E	×
semiaquatic	11	0.027	0.015 – 0.062	0.146	0.051 – 0.212	0.654	E	10	0.190	0.065 – 0.315	0.508	E	n.s.
aquatic	8	3.323	0.080 – 4.71 · 10 ⁶	-0.311	-1.298 – -0.018	0.357	-	7	-0.312	-0.630 – 0.006	0.240	G	n.s.
Preferred habitat													
forest	38	0.027	0.021 – 0.036	0.137	0.099 – 0.165	0.677	E	37	0.156	0.117 – 0.195	0.670	E	×
mosaic	39	0.032	0.005 – 0.042	0.116	0.088 – 0.341	0.359	E	38	0.109	0.075 – 0.143	0.337	E	×
open	17	0.222	0.137 – 2.363	-0.129	-0.408 – -0.061	0.101	-	16	0.110	0.050 – 0.170	0.119	E	n.s.
freshwater	13	0.015	0.006 – 0.051	0.207	0.075 – 0.303	0.581	E	12	0.233	0.095 – 0.371	0.472	E	n.s.
marine	10	0.855	0.054 – 5701.643	-0.197	-0.934 – 0.028	0.174	B	9	0.217	0.036 – 0.398	0.063	E	n.s.
variable	19	0.034	0.006 – 0.063	0.102	0.041 – 0.304	0.303	E	18	0.120	0.080 – 0.160	0.753	E	n.s.

IV.A10 – L_c		traditional regression						PIC regression					
whole sample	n	a	95% CI_L	b_{trad}	95% CI_b	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{trad} ≠ b_{PIC}
fissipeds	84	1.280	1.049 – 1.638	0.354	0.325 – 0.377	0.961	G	83	0.339	0.314 – 0.364	0.943	G	×
Family													
Canidae	19	0.643	0.407 – 1.531	0.435	0.339 – 0.486	0.943	+	18	0.455	0.368 – 0.542	0.929	+	×
Mustelidae	15	1.256	0.794 – 1.987	0.340	0.281 – 0.400	0.957	G	14	0.296	0.235 – 0.357	0.941	B	×
Procyonidae													
Ursidae	5	0.412	0.005 – 33.229	0.425	0.059 – 0.792	0.883	B						
Felidae	21	1.876	1.427 – 2.467	0.325	0.297 – 0.353	0.984	G	20	0.324	0.267 – 0.381	0.932	G	×
Herpestidae													
Eupleridae													
Viverridae	9	2.375	1.239 – 4.552	0.278	0.198 – 0.358	0.947	B	8	0.338	0.212 – 0.464	0.905	B	×
Locomotor type													
arboreal	6	1.171	0.399 – 3.437	0.363	0.232 – 0.494	0.966	B	5	0.417	0.407 – 0.427	1.000	+	×
semiarboreal	5	2.067	0.774 – 5.521	0.306	0.179 – 0.433	0.974	B						
scansorial	35	1.697	1.272 – 2.238	0.326	0.294 – 0.358	0.963	G	33	0.318	0.286 – 0.350	0.960	G	×
terrestrial	30	1.023	0.715 – 1.912	0.378	0.304 – 0.418	0.961	G	30	0.357	0.311 – 0.403	0.941	G	×
semifossorial													
semiaquatic	6	1.103	0.175 – 6.945	0.359	0.133 – 0.585	0.891	B	5	<i>0.362</i>	<i>0.110 – 0.614</i>	<i>0.899</i>	<i>B</i>	n.s.
aquatic													
Preferred habitat													
forest	23	1.645	1.315 – 2.317	0.325	0.285 – 0.354	0.965	G	22	0.421	0.408 – 0.434	0.998	+	✓
mosaic	27	1.190	0.767 – 1.753	0.362	0.313 – 0.411	0.958	G	26	0.335	0.292 – 0.378	0.950	G	×
open	13	0.926	0.654 – 2.063	0.396	0.303 – 0.433	0.980	G	12	0.384	0.326 – 0.442	0.975	G	×
freshwater	7	0.989	0.242 – 4.031	0.376	0.208 – 0.544	0.921	B	6	0.340	0.174 – 0.506	0.920	B	×
marine													
variable	13	0.926	0.653 – 1.965	0.396	0.309 – 0.432	0.980	G	11	0.306	0.253 – 0.359	0.970	G	✓

IV.A11 – r		traditional regression				PLC regression						
n	a	95% CI_r	b_{rad}	95% CI_b	R	sim.	n	b_{PLC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PLC}
whole sample												
85	0.997	0.806 – 1.264	0.350	0.322 – 0.376	0.964	G	84	0.349	0.322 – 0.376	0.938	G	×
fissipeds												
84	0.914	0.770 – 1.135	0.361	0.336 – 0.381	0.969	+	83	0.359	0.332 – 0.386	0.939	G	×
Family												
Canidae												
19	0.384	0.227 – 1.015	0.462	0.355 – 0.519	0.945	+	18	0.478	0.386 – 0.570	0.927	+	×
Mustelidae												
15	0.904	0.579 – 1.409	0.350	0.293 – 0.408	0.962	G	14	0.305	0.244 – 0.366	0.946	B	×
Procyonidae												
Ursidae												
5	<i>0.253</i>	<i>0.001 – 45.479</i>	<i>0.449</i>	<i>0.016 – 0.882</i>	<i>0.851</i>	<i>B</i>						
Felidae												
21	0.981	0.668 – 1.440	0.360	0.321 – 0.399	0.974	G	20	0.377	0.298 – 0.456	0.899	G	×
Herpestidae												
Eupleridae												
Viverridae												
9	1.497	0.805 – 2.786	0.299	0.223 – 0.376	0.959	B	8	0.358	0.228 – 0.488	0.919	B	×
Locomotor type												
arboreal												
6	0.751	0.172 – 3.283	0.382	0.203 – 0.562	0.941	B	5	0.417	0.407 – 0.427	1.000	+	×
semiarboreal												
5	1.508	0.563 – 4.038	0.309	0.181 – 0.436	0.974	B						
scansorial												
35	1.102	0.856 – 1.425	0.342	0.312 – 0.370	0.972	G	33	0.339	0.303 – 0.375	0.955	G	×
terrestrial												
30	0.741	0.544 – 1.316	0.385	0.318 – 0.420	0.965	G	30	0.369	0.322 – 0.416	0.942	G	×
semifossorial												
semiaquatic												
6	0.873	0.169 – 4.522	0.358	0.156 – 0.560	0.913	B	5	<i>0.355</i>	<i>0.127 – 0.583</i>	<i>0.914</i>	<i>B</i>	n.s.
aquatic												
Preferred habitat												
forest												
23	1.067	0.854 – 1.511	0.344	0.304 – 0.371	0.965	G	22	0.575	0.552 – 0.598	0.996	+	✓
mosaic												
27	0.894	0.616 – 1.267	0.362	0.318 – 0.404	0.969	G	26	0.353	0.306 – 0.400	0.947	G	×
open												
13	0.658	0.480 – 1.332	0.402	0.323 – 0.436	0.981	G	12	0.387	0.328 – 0.446	0.973	G	×
freshwater												
7	0.898	0.264 – 3.048	0.355	0.209 – 0.501	0.934	B	6	0.323	0.160 – 0.486	0.914	B	×
marine												
variable												
13	0.658	0.480 – 1.375	0.402	0.319 – 0.436	0.981	G	11	0.321	0.266 – 0.376	0.971	G	×

IV.A12 – d_{sc}		traditional regression					PIC regression						
	n	a	95% CI_a	b_{rad}	R	sim.	n	b_{PIC}	95% CI_b	R	sim.	b_{rad} ≠ b_{PIC}	
whole sample	85	0.495	0.391 – 0.636	0.346	0.317 – 0.373	0.961	84	0.360	0.329 – 0.391	0.919	B	×	
fissipeds	84	0.452	0.377 – 0.556	0.357	0.334 – 0.377	0.967	83	0.372	0.340 – 0.404	0.922	E	×	
Family													
Canidae	19	0.137	0.055 – 0.511	0.486	0.342 – 0.589	0.905	18	0.494	0.370 – 0.618	0.874	E	×	
Mustelidae	15	0.452	0.278 – 0.734	0.353	0.290 – 0.416	0.955	14	0.325	0.255 – 0.395	0.934	B	×	
Procyonidae													
Ursidae	5	0.070	0.001 – 9.631	0.505	0.094 – 0.915	0.896	B						
Felidae	21	0.431	0.292 – 0.636	0.366	0.326 – 0.406	0.974	B	20	0.397	0.310 – 0.484	0.890	B	×
Herpestidae													
Eupleridae													
Viverridae	9	0.878	0.523 – 1.474	0.278	0.214 – 0.341	0.967	G	8	0.320	0.213 – 0.427	0.933	B	×
Locomotor type													
arboreal	6	0.544	0.119 – 2.494	0.336	0.141 – 0.511	0.912	B	5	0.286	0.278 – 0.294	1.000	-	×
semiarboreal	5	0.700	0.285 – 1.718	0.318	0.201 – 0.434	0.980	B						
scansorial	35	0.557	0.444 – 0.715	0.337	0.311 – 0.362	0.981	G	33	0.338	0.303 – 0.373	0.956	G	×
terrestrial	30	0.364	0.256 – 0.640	0.379	0.316 – 0.418	0.954	B	30	0.378	0.318 – 0.438	0.909	B	×
semifossorial													
semiaquatic	6	0.402	0.080 – 2.005	0.372	0.174 – 0.569	0.924	B	5	<i>0.348</i>	<i>0.073 – 0.623</i>	<i>0.868</i>	<i>B</i>	n.s.
aquatic													
Preferred habitat													
forest	23	0.604	0.443 – 0.945	0.324	0.275 – 0.361	0.934	G	22	0.659	0.626 – 0.692	0.994	+	✓
mosaic	27	0.432	0.317 – 0.537	0.361	0.337 – 0.397	0.977	E	26	0.361	0.310 – 0.412	0.940	B	×
open	13	0.304	0.185 – 0.644	0.406	0.319 – 0.466	0.976	B	12	0.435	0.340 – 0.530	0.946	E	×
freshwater	7	0.449	0.131 – 1.536	0.356	0.209 – 0.503	0.933	B	6	0.322	0.118 – 0.526	0.860	B	×
marine													
variable	13	0.304	0.176 – 0.646	0.406	0.316 – 0.471	0.976	B	11	0.325	0.255 – 0.395	0.953	B	×

IV.A12 – d_{IC}		traditional regression					PIC regression						
whole sample	n	a	95% CI _a	b _{rad}	95% CI _b	R	sim.	n	b _{PIC}	95% CI _b	R	sim.	b _{rad} ≠ b _{PIC}
fissipeds	85	0.241	0.194 – 0.306	0.346	0.319 – 0.370	0.952	G	84	0.358	0.322 – 0.394	0.890	B	×
Family	84	0.236	0.185 – 0.309	0.348	0.318 – 0.377	0.948	B	83	0.351	0.314 – 0.388	0.876	B	×
Canidae	19	0.122	0.063 – 0.401	0.424	0.288 – 0.497	0.908	B	18	0.436	0.329 – 0.543	0.879	B	×
Mustelidae	15	0.239	0.136 – 0.419	0.339	0.266 – 0.411	0.934	B	14	0.324	0.227 – 0.421	0.870	B	×
Procyonidae													
Ursidae	5	0.001	0.000 – 476.235	0.763	-0.305 – 1.831	0.648	B						
Felidae	21	0.243	0.154 – 0.385	0.353	0.306 – 0.400	0.961	B	20	0.332	0.256 – 0.408	0.879	B	×
Herpestidae													
Eupleridae													
Viverridae	9	0.393	0.212 – 0.728	0.289	0.213 – 0.364	0.956	G	8	0.335	0.225 – 0.445	0.935	B	×
Locomotor type													
arboreal	6	0.192	0.056 – 0.656	0.368	0.218 – 0.518	0.956	B	5	0.399	0.384 – 0.414	1.000	+	×
semiarboreal	5	0.319	0.036 – 2.806	0.314	0.033 – 0.596	0.873	B						
scansorial	35	0.286	0.198 – 0.404	0.329	0.292 – 0.369	0.933	G	33	0.316	0.262 – 0.370	0.879	G	×
terrestrial	30	0.194	0.128 – 0.349	0.369	0.302 – 0.415	0.953	B	30	0.358	0.294 – 0.422	0.883	B	×
semifossorial													
semiaquatic	6	0.287	0.072 – 1.148	0.320	0.149 – 0.490	0.923	B	5	0.316	0.118 – 0.514	0.919	B	n.s.
aquatic													
Preferred habitat													
forest	23	0.245	0.154 – 0.409	0.346	0.292 – 0.400	0.956	B	22	0.529	0.511 – 0.547	0.997	+	✓
mosaic	27	0.240	0.139 – 0.351	0.345	0.298 – 0.408	0.932	B	26	0.341	0.279 – 0.403	0.899	B	×
open	13	0.152	0.076 – 0.318	0.399	0.319 – 0.480	0.951	B	12	0.366	0.247 – 0.485	0.876	B	×
freshwater	7	0.225	0.072 – 0.703	0.355	0.219 – 0.491	0.943	B	6	0.303	0.173 – 0.433	0.938	B	×
marine													
variable	13	0.152	0.081 – 0.337	0.399	0.315 – 0.472	0.951	B	11	0.321	0.231 – 0.411	0.921	B	×

Supplementary Material

Table IV.S1. Branch length transformations used for phylogenetically independent contrasts. Variable names are listed in Table IV.3. Abbreviations: exp., exponential transformation; Gra., transformation of Grafen; ln, natural logarithm transformation; Nee, transformation of Nee; ρ_x , Grafen's rho transform, where x indicates the value of rho; untr., untransformed branch lengths.

	whole sample		phylogeny							locomotor type						preferred habitat						
	fi	ss	Canidae	Mustelidae	Procyonidae	Ursidae	Felidae	Herpestidae	Viverridae	arboreal	semiarboreal	scansorial	terrestrial	semifossorial	semiaquatic	aquatic	forest	mosaic	open	freshwater	marine	variable
L_f	$\rho_{0.5}$	$\rho_{0.5}$	ln	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{1.7}$	exp.	$\rho_{0.8}$	Nee	ln	$\rho_{0.3}$	Nee	exp.	$\rho_{0.6}$	$\rho_{0.8}$	ln	Nee	$\rho_{0.9}$	ln
N	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.5}$	$\rho_{0.5}$	ln	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	ln	Nee	Nee	Nee	Nee	Nee	ln	Nee	$\rho_{0.9}$	ln
d_{sf}	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	ln	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	ln	untr.	Nee	Nee	$\rho_{0.5}$	Nee	ln	Nee	Nee	ln
d_{tf}	$\rho_{0.5}$	$\rho_{0.5}$	ln	ln	Nee	$\rho_{0.5}$	$\rho_{0.5}$	ln	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	ln	untr.	Nee	ln	Nee	$\rho_{0.8}$	ln	Nee	Nee	ln
FR	$\rho_{0.5}$	exp.	ln	exp.	ln	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	Nee	exp.	Nee	Nee	$\rho_{0.5}$	$\rho_{0.3}$	Nee	$\rho_{0.8}$	exp.	Nee	ln	Nee	Nee	exp.
L_t	Nee	$\rho_{0.5}$	ln	$\rho_{0.5}$	untr.	$\rho_{0.1}$	$\rho_{0.5}$	untr.	Nee	$\rho_{0.1}$	$\rho_{0.8}$	Nee	ln	$\rho_{0.3}$	exp.	$\rho_{0.8}$	Nee	$\rho_{0.8}$	ln	Nee	$\rho_{0.9}$	ln
d_{st}	Nee	Nee	Nee	$\rho_{0.5}$	untr.	$\rho_{0.5}$	$\rho_{0.5}$	ln	$\rho_{1.7}$	$\rho_{0.1}$	$\rho_{0.8}$	Nee	ln	$\rho_{0.3}$	Nee	Nee	$\rho_{0.6}$	$\rho_{0.8}$	ln	Nee	Nee	ln
d_{tt}	Nee	Nee	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{0.5}$	$\rho_{0.5}$	untr.	$\rho_{1.7}$	$\rho_{0.1}$	ln	Nee	Nee	$\rho_{0.3}$	Nee	ln	$\rho_{0.5}$	ln	ln	Nee	$\rho_{0.9}$	ln
TR	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.5}$	ln	$\rho_{0.5}$	$\rho_{0.5}$	$\rho_{0.5}$	Nee	$\rho_{0.1}$	ln	Nee	Nee	$\rho_{0.3}$	Nee	Nee	Nee	Nee	$\rho_{0.5}$	Nee	Nee	ln
L_c	Nee	$\rho_{0.5}$	Nee	ln			untr.	$\rho_{1.7}$	exp.		Nee	Nee		Nee		exp.	$\rho_{0.8}$	ln	Nee			ln
r	$\rho_{0.5}$	$\rho_{0.5}$	Nee	ln			untr.	exp.	exp.		Nee	Nee		Nee		exp.	$\rho_{0.8}$	ln	Nee			ln
d_{sc}	$\rho_{0.5}$	$\rho_{0.5}$	ln	ln			untr.	$\rho_{1.7}$	exp.		Nee	ln		Nee		exp.	$\rho_{0.8}$	ln	Nee			ln
d_{tc}	Nee	$\rho_{0.5}$	$\rho_{0.5}$	ln			untr.	$\rho_{1.7}$	exp.		Nee	ln		Nee		exp.	$\rho_{0.8}$	ln	Gra.			$\rho_{0.5}$

Tables IV.S2 to IV.S14. Results of the complex allometry test. In each case, it is indicated (in the “ $D \neq 1$ ” column) whether the exponent of complex allometry (D) is significantly different from 1. Results in *grey italics* denote non-significant regressions. Variable names are listed in Table IV.3. Abbreviations: 95% CI_C, 95% confidence interval for the coefficient (C); 95% CI_D, 95% confidence interval for the exponent of complex allometry (D); 95% CI_{ln A}, 95% confidence interval for $\ln A$; n, sample size; n.c., the model did not converge in a realistic solution; n.s., although the model did converge in a realistic solution, it was not significant according to the associated correlation coefficient (R).

IV.S2 – L_f	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	5.365	5.198 – 5.532	0.032	-1.72 · 10 ⁻⁴ – 0.065	1.999	1.514 – 2.484	0.853	✓ (<i>D</i> >1)
fissipeds	129	5.968	5.745 – 6.191	0.279	0.145 – 0.413	1.093	0.879 – 1.307	0.934	×
Family									
Canidae	17	5.469	5.229 – 5.709	0.396	0.145 – 0.646	0.986	0.508 – 1.464	0.934	×
Mustelidae	32	4.631	4.420 – 4.842	0.128	-0.014 – 0.270	1.417	0.767 – 2.067	0.932	×
Procyonidae	7	4.738	4.411 – 5.064	0.308	-0.103 – 0.719	0.737	-0.504 – 1.977	0.919	×
Ursidae	7	5.922	5.741 – 6.104	0.217	0.002 – 0.431	1.497	0.251 – 2.744	0.957	×
Felidae	26	5.785	5.691 – 5.880	0.232	0.151 – 0.314	1.136	0.927 – 1.346	0.987	×
Herpestidae	11	4.590	4.376 – 4.804	0.484	0.235 – 0.734	0.555	0.191 – 0.919	0.973	✓ (<i>D</i> <1)
Eupleridae	5	4.831	4.633 – 5.028	0.317	0.063 – 0.570	1.165	0.309 – 2.021	0.996	×
Viverridae	14	4.922	4.769 – 5.076	0.376	0.195 – 0.557	0.565	0.239 – 0.891	0.960	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	4.922	4.556 – 5.288	0.293	-0.153 – 0.738	0.883	-0.785 – 2.550	0.884	×
semiarboreal	10	5.072	4.939 – 5.206	0.410	0.255 – 0.565	0.710	0.450 – 0.970	0.987	✓ (<i>D</i> <1)
scansorial	45	5.829	5.725 – 5.933	0.199	0.125 – 0.273	1.245	1.048 – 1.442	0.984	✓ (<i>D</i> >1)
terrestrial	48	6.069	5.764 – 6.375	0.292	0.130 – 0.455	1.114	0.875 – 1.352	0.965	×
semifossorial	7	4.573	4.324 – 4.823	0.211	-0.164 – 0.587	1.361	-0.289 – 3.011	0.960	×
semiaquatic	11	-	-	-	-	-	-	-	n.c.
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	5.563	5.332 – 5.793	0.346	0.152 – 0.540	0.925	0.640 – 1.211	0.944	×
mosaic	39	5.839	5.646 – 6.032	0.284	0.148 – 0.420	1.122	0.880 – 1.363	0.967	×
open	17	5.827	5.460 – 6.195	0.250	0.035 – 0.465	1.244	0.816 – 1.672	0.967	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	5.845	5.529 – 6.160	0.209	0.040 – 0.378	1.270	0.891 – 1.649	0.972	×
IV.S3 – N	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.735	3.583 – 3.888	0.153	0.083 – 0.222	1.328	1.119 – 1.538	0.950	✓ (<i>D</i> >1)
fissipeds	129	4.146	3.991 – 4.301	0.429	0.321 – 0.537	0.925	0.817 – 1.032	0.977	×
Family									
Canidae	17	3.258	3.036 – 3.480	0.362	0.133 – 0.590	1.046	0.562 – 1.530	0.938	×
Mustelidae	32	3.035	2.847 – 3.223	0.347	0.179 – 0.514	0.980	0.719 – 1.242	0.964	×
Procyonidae	7	2.706	2.389 – 3.022	0.356	-0.085 – 0.798	0.967	-0.410 – 2.343	0.942	×
Ursidae	7	3.992	3.702 – 4.281	0.166	-0.181 – 0.514	1.185	-1.352 – 3.722	0.809	×
Felidae	26	3.764	3.652 – 3.875	0.398	0.290 – 0.507	0.901	0.747 – 1.054	0.989	×
Herpestidae	11	2.607	2.445 – 2.770	0.543	0.355 – 0.731	0.525	0.291 – 0.759	0.988	✓ (<i>D</i> <1)
Eupleridae	5	2.730	2.569 – 2.891	0.410	0.190 – 0.631	1.004	0.429 – 1.578	0.998	×
Viverridae	14	3.105	2.574 – 3.637	0.737	0.143 – 1.332	0.348	-0.029 – 0.725	0.936	✓ (<i>D</i> =0)
Locomotor type									
arboreal	7	3.033	2.933 – 3.132	0.539	0.407 – 0.672	0.664	0.410 – 0.919	0.996	✓ (<i>D</i> <1)
semiarboreal	10	2.833	2.625 – 3.041	0.324	0.092 – 0.556	0.938	0.404 – 1.472	0.968	×
scansorial	45	3.968	3.824 – 4.113	0.363	0.242 – 0.484	1.006	0.837 – 1.174	0.984	×
terrestrial	48	4.140	3.875 – 4.405	0.421	0.253 – 0.590	0.940	0.776 – 1.105	0.974	×
semifossorial	7	2.770	2.539 – 3.001	0.236	-0.114 – 0.585	1.352	-0.025 – 2.729	0.972	×
semiaquatic	11	2.837	2.641 – 3.032	0.188	0.011 – 0.365	1.347	0.675 – 2.020	0.965	×
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	3.848	3.606 – 4.090	0.621	0.392 – 0.850	0.730	0.555 – 0.905	0.968	✓ (<i>D</i> <1)
mosaic	39	3.912	3.744 – 4.079	0.450	0.308 – 0.592	0.899	0.747 – 1.050	0.982	×
open	17	3.768	3.502 – 4.034	0.354	0.161 – 0.547	1.018	0.754 – 1.282	0.981	×
freshwater	13	2.809	2.614 – 3.003	0.123	-0.030 – 0.276	1.671	0.746 – 2.596	0.951	×
marine	10	3.632	2.819 – 4.444	0.387	-0.476 – 1.249	0.752	-0.426 – 1.929	0.773	×
variable	19	3.866	3.669 – 4.062	0.296	0.171 – 0.422	1.079	0.885 – 1.272	0.989	×

IV.S4 – d_{sf}	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.398	3.250 – 3.546	0.220	0.137 – 0.302	1.152	0.986 – 1.318	0.962	×
fissipeds	129	3.520	3.368 – 3.672	0.353	0.251 – 0.455	0.975	0.850 – 1.100	0.972	×
Family									
Canidae	17	2.785	2.587 – 2.983	0.371	0.167 – 0.575	1.044	0.623 – 1.465	0.951	×
Mustelidae	32	2.623	2.436 – 2.809	0.461	0.279 – 0.643	0.775	0.576 – 0.974	0.968	✓ (D<1)
Procyonidae	7	2.263	2.068 – 2.459	0.311	0.037 – 0.585	0.979	-0.007 – 1.965	0.970	×
Ursidae	7	3.431	3.159 – 3.703	0.262	-0.064 – 0.588	1.172	-0.335 – 2.680	0.917	×
Felidae	26	3.260	3.184 – 3.336	0.274	0.207 – 0.340	1.110	0.967 – 1.254	0.993	×
Herpestidae	11	2.050	1.897 – 2.204	0.336	0.145 – 0.527	0.891	0.359 – 1.423	0.963	×
Eupleridae	5	2.470	2.109 – 2.831	0.415	-0.064 – 0.894	1.085	-0.150 – 2.320	0.991	×
Viverridae	14	2.513	2.274 – 2.752	0.495	0.213 – 0.777	0.567	0.179 – 0.954	0.895	✓ (D<1)
Locomotor type									
arboreal	7	2.521	2.272 – 2.770	0.419	0.094 – 0.743	0.709	-0.111 – 1.530	0.966	×
semiarboreal	10	2.477	2.205 – 2.748	0.321	0.023 – 0.618	1.015	0.308 – 1.722	0.953	×
scansorial	45	3.335	3.249 – 3.422	0.252	0.186 – 0.318	1.144	1.007 – 1.281	0.991	✓ (D>1)
terrestrial	48	3.531	3.264 – 3.797	0.382	0.214 – 0.551	0.945	0.763 – 1.126	0.969	×
semifossorial	7	2.160	1.932 – 2.389	0.243	-0.154 – 0.639	1.103	-0.381 – 2.586	0.964	×
semiaquatic	11	2.372	2.119 – 2.624	0.212	-0.027 – 0.452	1.188	0.400 – 1.976	0.939	×
aquatic	8	3.707	2.063 – 5.351	0.830	-0.975 – 2.635	0.336	-0.687 – 1.359	0.820	×
Preferred habitat									
forest	38	3.072	2.871 – 3.273	0.360	0.191 – 0.529	0.928	0.689 – 1.167	0.960	×
mosaic	39	3.333	3.191 – 3.475	0.372	0.256 – 0.487	0.956	0.805 – 1.108	0.984	×
open	17	3.282	2.981 – 3.583	0.369	0.144 – 0.593	0.983	0.690 – 1.277	0.975	×
freshwater	13	2.310	2.078 – 2.542	0.100	-0.076 – 0.276	1.754	0.427 – 3.081	0.914	×
marine	10	3.610	2.893 – 4.327	0.650	-0.125 – 1.424	0.596	0.011 – 1.181	0.895	×
variable	19	3.334	3.053 – 3.616	0.299	0.115 – 0.483	1.055	0.776 – 1.335	0.976	×
IV.S5 – d_{if}	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.942	3.756 – 4.127	0.459	0.326 – 0.592	0.880	0.761 – 0.999	0.973	✓ (D<1)
fissipeds	129	3.665	3.491 – 3.838	0.387	0.268 – 0.506	0.947	0.815 – 1.079	0.967	×
Family									
Canidae	17	2.794	2.602 – 2.986	0.361	0.164 – 0.558	1.055	0.635 – 1.474	0.952	×
Mustelidae	32	2.787	2.581 – 2.993	0.500	0.301 – 0.699	0.797	0.595 – 1.000	0.969	×
Procyonidae	7	2.361	2.141 – 2.581	0.334	0.052 – 0.616	0.779	-0.038 – 1.595	0.966	×
Ursidae	7	3.483	3.199 – 3.767	0.112	-0.216 – 0.441	1.698	-2.038 – 5.433	0.773	×
Felidae	26	3.350	3.210 – 3.491	0.299	0.173 – 0.425	1.066	0.819 – 1.313	0.979	×
Herpestidae	11	2.129	1.915 – 2.343	0.352	0.092 – 0.611	0.703	0.090 – 1.316	0.941	×
Eupleridae	5	2.392	2.260 – 2.523	0.336	0.153 – 0.519	0.974	0.391 – 1.557	0.998	×
Viverridae	14	2.637	2.360 – 2.913	0.551	0.230 – 0.872	0.449	0.111 – 0.788	0.952	✓ (D<1)
Locomotor type									
arboreal	7	2.691	2.438 – 2.945	0.565	0.236 – 0.894	0.418	-0.018 – 0.854	0.991	✓ (D=0)
semiarboreal	10	2.564	2.317 – 2.811	0.407	0.124 – 0.690	0.782	0.289 – 1.275	0.962	×
scansorial	45	3.549	3.401 – 3.696	0.345	0.221 – 0.470	0.995	0.814 – 1.177	0.982	×
terrestrial	48	3.552	3.269 – 3.835	0.371	0.195 – 0.548	0.957	0.761 – 1.154	0.965	×
semifossorial	7	2.247	2.005 – 2.488	0.234	-0.168 – 0.637	1.191	-0.386 – 2.768	0.961	×
semiaquatic	11	2.603	2.289 – 2.916	0.296	-0.015 – 0.607	1.029	0.319 – 1.739	0.932	×
aquatic	8	4.109	3.417 – 4.801	0.675	-0.092 – 1.442	0.644	-0.128 – 1.415	0.901	×
Preferred habitat									
forest	38	3.381	3.124 – 3.638	0.557	0.315 – 0.799	0.739	0.532 – 0.945	0.957	✓ (D<1)
mosaic	39	3.516	3.305 – 3.727	0.472	0.287 – 0.658	0.851	0.665 – 1.037	0.972	×
open	17	3.343	3.028 – 3.659	0.376	0.140 – 0.612	0.980	0.677 – 1.283	0.973	×
freshwater	13	2.560	2.270 – 2.850	0.212	-0.053 – 0.476	1.266	0.383 – 2.148	0.918	×
marine	10	4.039	3.520 – 4.558	0.620	0.066 – 1.174	0.714	0.250 – 1.179	0.947	×
variable	19	3.434	3.191 – 3.676	0.313	0.153 – 0.473	1.047	0.815 – 1.278	0.983	×

IV.S6 – FR	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	136	-	-	-	-	-	-	-	n.c.
fissipeds	129	-2.542	-2.582 – -2.503	-7.87 · 10 ⁻⁷	-1.30 · 10 ⁻⁵ – 1.15 · 10 ⁻⁵	6.052	-1.755 – 13.858	0.197	×
Family									
Canidae	17	-	-	-	-	-	-	-	n.c.
Mustelidae	32	-	-	-	-	-	-	-	n.c.
Procyonidae	7	-	-	-	-	-	-	-	n.c.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	-2.529	-2.639 – -2.418	0.038	-0.065 – 0.140	1.000	-0.573 – 2.573	0.587	×
Herpestidae	11	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-2.343	-2.841 – -1.845	0.124	-0.650 – 0.897	0.604	-4.965 – 6.173	0.840	n.s.
Viverridae	14	-2.405	-2.543 – -2.266	0.122	-0.041 – 0.286	0.568	-0.341 – 1.476	0.777	×
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-	-	-	-	-	-	-	n.c.
scansorial	45	-2.502	-2.718 – -2.285	0.049	-0.173 – 0.271	0.504	-1.226 – 2.234	0.288	n.s.
terrestrial	48	-2.654	-2.787 – -2.521	-0.003	-0.021 – 0.015	2.236	-0.296 – 4.768	0.558	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	-2.133	-2.366 – -1.899	0.137	-0.112 – 0.385	0.718	-0.395 – 1.831	0.762	×
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	-2.487	-2.663 – -2.312	0.016	-0.129 – 0.161	0.956	-3.760 – 5.673	0.176	n.s.
mosaic	39	-2.596	-2.686 – -2.507	-0.001	-0.007 – 0.005	3.062	-2.627 – 8.752	0.324	×
open	17	-2.655	-2.790 – -2.520	-0.001	-0.005 – 0.004	3.471	-0.977 – 7.919	0.689	×
freshwater	13	-2.106	-2.439 – -1.773	0.218	-0.144 – 0.580	0.517	-0.362 – 1.397	0.732	×
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-2.624	-2.731 – -2.516	-0.001	-0.006 – 0.005	3.111	-1.447 – 7.670	0.582	×
IV.S7 – L_t	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	136	5.628	5.474 – 5.782	0.097	0.039 – 0.156	1.486	1.205 – 1.766	0.953	✓ (<i>D</i> >1)
fissipeds	129	5.643	5.456 – 5.830	0.146	0.058 – 0.234	1.332	1.051 – 1.613	0.915	✓ (<i>D</i> >1)
Family									
Canidae	17	5.504	5.163 – 5.845	0.407	0.043 – 0.770	0.881	0.229 – 1.533	0.875	×
Mustelidae	32	4.783	4.524 – 5.041	0.222	0.004 – 0.439	1.082	0.539 – 1.626	0.885	×
Procyonidae	7	4.818	4.307 – 5.328	0.394	-0.171 – 0.960	0.452	-0.451 – 1.355	0.917	×
Ursidae	7	5.637	5.497 – 5.777	0.206	0.042 – 0.371	1.558	0.551 – 2.566	0.973	×
Felidae	26	5.622	5.494 – 5.749	0.162	0.060 – 0.265	1.252	0.867 – 1.636	0.964	×
Herpestidae	11	4.687	4.283 – 5.092	0.547	0.091 – 1.003	0.454	-0.045 – 0.953	0.942	✓ (<i>D</i> =0)
Eupleridae	5	4.779	4.358 – 5.199	0.200	-0.280 – 0.679	1.457	-1.103 – 4.017	0.972	×
Viverridae	14	4.847	4.715 – 4.979	0.295	0.139 – 0.451	0.611	0.237 – 0.986	0.951	✓ (<i>D</i> <1)
Locomotor type									
arboreal	7	4.851	4.362 – 5.340	0.257	-0.346 – 0.860	0.846	-1.714 – 3.406	0.775	×
semiarboreal	10	4.971	4.778 – 5.164	0.343	0.119 – 0.567	0.670	0.229 – 1.111	0.962	×
scansorial	45	5.552	5.434 – 5.669	0.105	0.037 – 0.173	1.478	1.124 – 1.831	0.960	✓ (<i>D</i> >1)
terrestrial	48	5.794	5.440 – 6.147	0.179	0.023 – 0.335	1.290	0.905 – 1.674	0.939	×
semifossorial	7	-	-	-	-	-	-	-	n.c.
semiaquatic	11	4.657	4.377 – 4.936	0.101	-0.130 – 0.332	1.586	-0.103 – 3.275	0.872	×
aquatic	8	5.699	5.527 – 5.870	0.259	0.078 – 0.440	1.066	0.533 – 1.599	0.976	×
Preferred habitat									
forest	38	5.303	5.055 – 5.552	0.241	0.041 – 0.441	0.995	0.564 – 1.425	0.897	×
mosaic	39	5.580	5.373 – 5.787	0.165	0.046 – 0.283	1.341	0.969 – 1.714	0.942	×
open	17	5.722	5.316 – 6.127	0.182	-0.027 – 0.391	1.366	0.786 – 1.946	0.950	×
freshwater	13	-	-	-	-	-	-	-	n.c.
marine	10	5.712	5.586 – 5.838	0.258	0.133 – 0.384	1.104	0.824 – 1.383	0.992	×
variable	19	5.578	5.218 – 5.938	0.114	-0.039 – 0.267	1.498	0.858 – 2.137	0.944	×

IV.S8 – d_{st}	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.385	3.237 – 3.533	0.170	0.098 – 0.242	1.278	1.086 – 1.470	0.956	✓(D>1)
fissipeds	129	3.676	3.516 – 3.836	0.392	0.283 – 0.501	0.950	0.830 – 1.070	0.973	×
Family									
Canidae	17	2.876	2.704 – 3.048	0.428	0.246 – 0.609	0.936	0.621 – 1.251	0.968	×
Mustelidae	32	2.708	2.494 – 2.922	0.436	0.235 – 0.638	0.852	0.611 – 1.092	0.961	×
Procyonidae	7	2.248	1.842 – 2.653	0.296	-0.213 – 0.804	0.731	-0.859 – 2.321	0.875	×
Ursidae	7	3.505	3.196 – 3.814	0.179	-0.167 – 0.525	1.968	-0.525 – 4.462	0.901	×
Felidae	26	3.362	3.246 – 3.477	0.243	0.149 – 0.338	1.232	0.998 – 1.467	0.986	×
Herpestidae	11	2.139	1.955 – 2.322	0.390	0.173 – 0.606	0.592	0.179 – 1.005	0.967	×
Eupleridae	5	2.478	2.274 – 2.682	0.520	0.204 – 0.835	0.732	0.105 – 1.359	0.997	×
Viverridae	14	2.482	2.369 – 2.596	0.427	0.294 – 0.561	0.634	0.409 – 0.859	0.982	✓(D<1)
Locomotor type									
arboreal	7	2.508	2.298 – 2.717	0.362	0.108 – 0.615	0.897	0.128 – 1.665	0.972	×
semiarboreal	10	2.637	2.428 – 2.847	0.423	0.189 – 0.658	0.931	0.519 – 1.343	0.980	×
scansorial	45	3.485	3.355 – 3.615	0.292	0.188 – 0.395	1.090	0.908 – 1.273	0.984	×
terrestrial	48	3.665	3.398 – 3.931	0.426	0.252 – 0.600	0.909	0.742 – 1.076	0.971	×
semifossorial	7	2.308	2.055 – 2.561	0.294	-0.148 – 0.737	1.084	-0.278 – 2.446	0.969	×
semiaquatic	11	2.569	2.224 – 2.913	0.318	-0.026 – 0.662	0.999	0.273 – 1.726	0.925	×
aquatic	8	–	–	–	–	–	–	–	n.c.
Preferred habitat									
forest	38	3.117	2.938 – 3.296	0.342	0.196 – 0.487	0.981	0.762 – 1.201	0.969	×
mosaic	39	3.529	3.333 – 3.725	0.445	0.278 – 0.612	0.893	0.712 – 1.073	0.975	×
open	17	3.413	3.150 – 3.675	0.417	0.212 – 0.623	0.926	0.690 – 1.162	0.981	×
freshwater	13	2.542	2.246 – 2.838	0.248	-0.028 – 0.524	1.191	0.416 – 1.965	0.926	×
marine	10	–	–	–	–	–	–	–	n.c.
variable	19	3.427	3.168 – 3.685	0.292	0.128 – 0.457	1.089	0.832 – 1.345	0.981	×
IV.S9 – d_{tt}	n	ln A	95% CI_{lnA}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	136	3.484	3.312 – 3.656	0.287	0.184 – 0.390	1.078	0.922 – 1.235	0.964	×
fissipeds	129	3.388	3.208 – 3.568	0.316	0.204 – 0.429	1.048	0.891 – 1.206	0.961	×
Family									
Canidae	17	2.830	2.603 – 3.057	0.442	0.202 – 0.682	0.914	0.512 – 1.315	0.921	×
Mustelidae	32	2.393	2.188 – 2.599	0.395	0.203 – 0.587	0.878	0.623 – 1.133	0.959	×
Procyonidae	7	2.042	1.767 – 2.318	0.359	-0.014 – 0.733	0.904	-0.204 – 2.012	0.955	×
Ursidae	7	3.205	2.905 – 3.505	0.148	-0.196 – 0.492	1.785	-1.195 – 4.766	0.846	×
Felidae	26	3.233	3.107 – 3.360	0.296	0.184 – 0.408	1.087	0.864 – 1.311	0.983	×
Herpestidae	11	2.101	1.591 – 2.610	0.556	0.001 – 1.111	0.363	-0.120 – 0.847	0.938	✓(D=0)
Eupleridae	5	2.110	1.507 – 2.713	0.250	-0.459 – 0.958	1.383	-1.644 – 4.410	0.959	×
Viverridae	14	2.258	2.169 – 2.347	0.376	0.273 – 0.479	0.810	0.594 – 1.026	0.986	×
Locomotor type									
arboreal	7	2.248	1.953 – 2.544	0.313	-0.019 – 0.645	1.111	-0.055 – 2.277	0.946	×
semiarboreal	10	2.252	2.040 – 2.465	0.327	0.090 – 0.565	0.932	0.392 – 1.473	0.967	×
scansorial	45	3.243	3.122 – 3.365	0.240	0.150 – 0.329	1.191	0.995 – 1.388	0.983	×
terrestrial	48	3.336	3.008 – 3.664	0.277	0.101 – 0.452	1.111	0.840 – 1.382	0.955	×
semifossorial	7	1.968	1.512 – 2.424	0.401	-0.372 – 1.175	0.740	-0.797 – 2.276	0.948	×
semiaquatic	11	2.369	2.092 – 2.646	0.372	0.085 – 0.659	0.838	0.343 – 1.333	0.949	×
aquatic	8	3.618	3.018 – 4.217	0.516	-0.132 – 1.164	0.863	-0.054 – 1.779	0.903	×
Preferred habitat									
forest	38	3.083	2.842 – 3.323	0.478	0.262 – 0.694	0.825	0.602 – 1.047	0.958	×
mosaic	39	3.244	3.034 – 3.455	0.365	0.198 – 0.533	0.986	0.761 – 1.211	0.967	×
open	17	3.179	2.836 – 3.522	0.297	0.071 – 0.522	1.125	0.751 – 1.498	0.969	×
freshwater	13	2.332	2.055 – 2.609	0.287	0.015 – 0.560	1.005	0.373 – 1.637	0.927	×
marine	10	3.601	3.152 – 4.050	0.522	0.050 – 0.994	0.819	0.330 – 1.308	0.955	×
variable	19	3.228	2.889 – 3.567	0.249	0.052 – 0.446	1.186	0.820 – 1.551	0.970	×

IV.S10 – TR	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	136	-2.305	-2.557 – -2.053	0.048	-0.137 – 0.233	0.851	-0.703 – 2.405	0.298	×
fissipeds	129	-1.865	-2.584 – -1.147	0.414	-0.308 – 1.137	0.232	-0.131 – 0.696	0.451	✓ (<i>D</i> =0)
Family									
Canidae	17	-	-	-	-	-	-	-	n.c.
Mustelidae	32	-2.104	-2.417 – -1.790	0.184	-0.142 – 0.510	0.563	-0.215 – 1.340	0.628	×
Procyonidae	7	-	-	-	-	-	-	-	n.c.
Ursidae	7	-	-	-	-	-	-	-	n.c.
Felidae	26	-2.255	-2.438 – -2.073	0.084	-0.070 – 0.239	1.167	0.073 – 2.261	0.768	×
Herpestidae	11	-	-	-	-	-	-	-	n.c.
Eupleridae	5	-	-	-	-	-	-	-	n.c.
Viverridae	14	-2.366	-2.502 – -2.230	0.130	-0.030 – 0.290	0.701	-0.225 – 1.628	0.794	×
Locomotor type									
arboreal	7	-	-	-	-	-	-	-	n.c.
semiarboreal	10	-2.302	-2.496 – -2.108	0.125	-0.075 – 0.325	1.246	-0.029 – 2.522	0.907	×
scansorial	45	-2.071	-2.333 – -1.810	0.198	-0.061 – 0.457	0.645	0.082 – 1.207	0.756	×
terrestrial	48	-	-	-	-	-	-	-	n.c.
semifossorial	7	-1.894	-2.766 – -1.023	0.438	-0.485 – 1.360	0.195	-0.307 – 0.698	0.976	✓ (<i>D</i> =0)
semiaquatic	11	-2.155	-2.482 – -1.828	0.143	-0.203 – 0.490	0.733	-0.759 – 2.225	0.665	×
aquatic	8	-	-	-	-	-	-	-	n.c.
Preferred habitat									
forest	38	-2.181	-2.399 – -1.563	0.103	-0.078 – 0.284	0.945	0.046 – 1.845	0.677	×
mosaic	39	-1.903	-3.319 – -0.487	0.453	-1.028 – 1.934	0.193	-0.454 – 0.839	0.481	✓ (<i>D</i> =0)
open	17	-	-	-	-	-	-	-	n.c.
freshwater	13	-2.135	-2.612 – -1.658	0.209	-0.298 – 0.715	0.647	-0.769 – 2.063	0.598	×
marine	10	-	-	-	-	-	-	-	n.c.
variable	19	-2.038	-3.831 – -0.244	0.376	-1.548 – 2.300	0.179	-0.864 – 1.222	0.438	n.s.
IV.S11 – L_c									
whole sample	85	4.518	4.363 – 4.672	0.149	0.082 – 0.215	1.359	1.153 – 1.565	0.962	✓ (<i>D</i> >1)
fissipeds	84	4.531	4.377 – 4.684	0.220	0.136 – 0.305	1.204	1.024 – 1.383	0.964	✓ (<i>D</i> >1)
Family									
Canidae	19	4.089	3.859 – 4.319	0.434	0.193 – 0.675	0.955	0.539 – 1.371	0.943	×
Mustelidae	15	3.475	3.262 – 3.688	0.436	0.196 – 0.676	0.812	0.477 – 1.148	0.961	×
Procyonidae									
Ursidae	5	4.530	3.650 – 5.409	0.424	-0.599 – 1.447	0.722	-3.029 – 4.473	0.887	×
Felidae	21	4.533	4.415 – 4.651	0.334	0.216 – 0.453	0.971	0.748 – 1.193	0.984	×
Herpestidae									
Eupleridae									
Viverridae	9	3.529	3.324 – 3.733	0.339	0.092 – 0.586	0.775	0.190 – 1.361	0.952	×
Locomotor type									
arboreal	6	3.634	3.298 – 3.969	0.452	-0.068 – 0.972	0.608	-0.840 – 2.057	0.973	×
semiarboreal	5	3.379	3.016 – 3.742	0.255	-0.234 – 0.744	1.164	-0.745 – 3.073	0.975	×
scansorial	35	4.389	4.253 – 4.525	0.171	0.080 – 0.261	1.340	1.045 – 1.635	0.970	✓ (<i>D</i> >1)
terrestrial	30	4.625	4.312 – 4.938	0.269	0.107 – 0.430	1.134	0.872 – 1.395	0.963	×
semifossorial									
semiaquatic	6	-	-	-	-	-	-	-	n.c.
aquatic									
Preferred habitat									
forest	23	4.187	3.989 – 4.384	0.312	0.153 – 0.472	1.002	0.726 – 1.279	0.965	×
mosaic	27	4.270	4.095 – 4.445	0.173	0.078 – 0.268	1.371	1.084 – 1.658	0.969	✓ (<i>D</i> >1)
open	13	4.595	4.305 – 4.885	0.370	0.126 – 0.615	1.028	0.664 – 1.391	0.980	×
freshwater	7	-	-	-	-	-	-	-	n.c.
marine									
variable	13	4.428	4.056 – 4.799	0.210	0.001 – 0.420	1.218	0.754 – 1.682	0.968	×

IV.S12 – r	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	85	4.341	4.188 – 4.493	0.184	0.112 – 0.257	1.274	1.094 – 1.453	0.969	✓ (<i>D</i> > 1)
fissipeds	84	4.340	4.190 – 4.491	0.261	0.172 – 0.349	1.137	0.979 – 1.295	0.970	×
Family									
Canidae	19	3.874	3.631 – 4.117	0.473	0.217 – 0.730	0.937	0.534 – 1.339	0.946	×
Mustelidae	15	3.239	3.035 – 3.444	0.445	0.215 – 0.675	0.820	0.505 – 1.135	0.966	×
Procyonidae									
Ursidae	5	<i>4.352</i>	<i>3.212 – 5.492</i>	<i>0.450</i>	<i>-0.848 – 1.748</i>	<i>0.648</i>	<i>-3.407 – 4.702</i>	<i>0.858</i>	n.s.
Felidae	21	4.268	4.108 – 4.429	0.328	0.172 – 0.485	1.043	0.740 – 1.347	0.974	×
Herpestidae									
Eupleridae									
Viverridae	9	3.301	3.108 – 3.494	0.400	0.163 – 0.637	0.710	0.244 – 1.175	0.967	×
Locomotor type									
arboreal	6	–	–	–	–	–	–	–	n.c.
semiarboreal	5	3.093	2.724 – 3.461	0.262	-0.235 – 0.760	1.146	-0.739 – 3.030	0.975	×
scansorial	35	4.190	4.049 – 4.330	0.218	0.115 – 0.320	1.232	0.974 – 1.490	0.975	×
terrestrial	30	4.438	4.131 – 4.746	0.302	0.136 – 0.467	1.092	0.854 – 1.329	0.966	×
semifossorial									
semiaquatic	6	–	–	–	–	–	–	–	n.c.
aquatic									
Preferred habitat									
forest	23	4.012	3.797 – 4.227	0.378	0.195 – 0.562	0.927	0.668 – 1.187	0.965	×
mosaic	27	4.050	3.885 – 4.214	0.215	0.115 – 0.314	1.260	1.019 – 1.500	0.975	✓ (<i>D</i> > 1)
open	13	4.331	4.049 – 4.613	0.369	0.134 – 0.604	1.040	0.688 – 1.392	0.982	×
freshwater	7	–	–	–	–	–	–	–	n.c.
marine									
variable	13	4.216	3.862 – 4.570	0.228	0.024 – 0.432	1.196	0.780 – 1.611	0.973	×

IV.S13 – d_{sc}	n	<i>ln A</i>	95% CI_{<i>ln A</i>}	<i>C</i>	95% CI_{<i>C</i>}	<i>D</i>	95% CI_{<i>D</i>}	<i>R</i>	<i>D</i> ≠ 1
whole sample	85	3.706	3.520 – 3.891	0.256	0.151 – 0.360	1.117	0.935 – 1.299	0.962	×
fissipeds	84	3.775	3.592 – 3.959	0.397	0.266 – 0.528	0.937	0.791 – 1.083	0.967	×
Family									
Canidae	19	3.142	2.772 – 3.511	0.585	0.186 – 0.984	0.784	0.308 – 1.259	0.912	×
Mustelidae	15	2.549	2.326 – 2.772	0.419	0.171 – 0.666	0.860	0.494 – 1.225	0.958	×
Procyonidae									
Ursidae	5	3.743	2.870 – 4.617	0.473	-0.586 – 1.532	0.886	-3.255 – 5.026	0.897	×
Felidae	21	3.572	3.400 – 3.743	0.404	0.229 – 0.580	0.918	0.650 – 1.187	0.974	×
Herpestidae									
Eupleridae									
Viverridae	9	2.554	2.408 – 2.699	0.363	0.185 – 0.540	0.737	0.350 – 1.125	0.977	×
Locomotor type									
arboreal	6	–	–	–	–	–	–	–	n.c.
semiarboreal	5	2.456	2.101 – 2.812	0.369	-0.108 – 0.845	0.828	-0.358 – 2.015	0.983	×
scansorial	35	3.595	3.450 – 3.741	0.349	0.222 – 0.477	0.971	0.782 – 1.160	0.981	×
terrestrial	30	3.839	3.482 – 4.195	0.435	0.205 – 0.666	0.919	0.695 – 1.144	0.954	×
semifossorial									
semiaquatic	6	–	–	–	–	–	–	–	n.c.
aquatic									
Preferred habitat									
forest	23	3.268	2.982 – 3.553	0.440	0.172 – 0.708	0.797	0.480 – 1.114	0.940	×
mosaic	27	3.421	3.254 – 3.589	0.300	0.181 – 0.419	1.085	0.882 – 1.287	0.978	×
open	13	3.655	3.321 – 3.989	0.444	0.144 – 0.744	0.937	0.569 – 1.304	0.976	×
freshwater	7	–	–	–	–	–	–	–	n.c.
marine									
variable	13	3.576	3.193 – 3.959	0.357	0.085 – 0.628	0.975	0.628 – 1.323	0.971	×

IV.S14 – d_{tc}	n	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R	D ≠ 1
whole sample	85	3.058	2.835 – 3.282	0.312	0.173 – 0.451	1.024	0.829 – 1.218	0.952	×
fissipeds	84	2.905	2.696 – 3.114	0.317	0.179 – 0.456	1.018	0.820 – 1.215	0.948	×
Family									
Canidae	19	2.252	1.988 – 2.516	0.361	0.091 – 0.632	1.052	0.475 – 1.629	0.909	×
Mustelidae	15	1.783	1.519 – 2.047	0.419	0.123 – 0.716	0.819	0.386 – 1.251	0.939	×
Procyonidae									
Ursidae	5	–	–	–	–	–	–	–	n.c.
Felidae	21	2.825	2.623 – 3.026	0.374	0.169 – 0.579	0.937	0.597 – 1.277	0.961	×
Herpestidae									
Eupleridae									
Viverridae	9	1.940	1.833 – 2.047	0.504	0.371 – 0.637	0.513	0.333 – 0.692	0.994	✓ (<i>D</i> <1)
Locomotor type									
arboreal	6	–	–	–	–	–	–	–	n.c.
semiarboreal	5	–	–	–	–	–	–	–	n.c.
scansorial	35	2.695	2.465 – 2.925	0.235	0.056 – 0.414	1.146	0.735 – 1.557	0.934	×
terrestrial	30	3.051	2.701 – 3.400	0.396	0.177 – 0.615	0.949	0.714 – 1.184	0.954	×
semifossorial									
semiaquatic	6	–	–	–	–	–	–	–	n.c.
aquatic									
Preferred habitat									
forest	23	2.680	2.437 – 2.923	0.517	0.283 – 0.751	0.760	0.527 – 0.992	0.964	✓ (<i>D</i> <1)
mosaic	27	2.399	2.198 – 2.601	0.119	0.026 – 0.211	1.535	1.126 – 1.944	0.948	✓ (<i>D</i> >1)
open	13	2.948	2.504 – 3.392	0.555	0.116 – 0.994	0.795	0.375 – 1.215	0.960	×
freshwater	7	–	–	–	–	–	–	–	n.c.
marine									
variable	13	2.689	2.229 – 3.150	0.274	-0.031 – 0.578	1.051	0.540 – 1.562	0.948	×

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Scaling and mechanics of the felid calcaneus: Geometric similarity without differential allometric scaling



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Abstract

Six mechanically significant skeletal variables were measured on the calcanei from 60 Felidae specimens (22 species) to determine whether these variables were scaled to body mass, and to assess whether differential scaling exists. The power equation ($y = a \cdot x^b$) was used to analyze the scaling of the six variables to body mass; we compared traditional regression methods (standardized major axis) to phylogenetically independent contrasts. In agreement with previous studies that compared these methodologies, we found no significant differences between methods in the allometric coefficients (b) obtained. Overall, the scaling pattern of the felid calcaneus conformed to the predictions of the geometric similarity hypothesis, but not entirely to those of the elastic similarity hypothesis. We found that the moment arm of the ankle extensors scaled to body mass with an exponent not significantly different from 0.40. This indicated that the *tuber calcanei* scaled to body mass faster than calcaneus total length. This explained why the effective mechanical advantage of the ankle extensors increased with body mass, despite the fact that limb posture does not change in felid species. Furthermore, this finding was consistent with the hypothesis of the isometric scaling of ground reaction forces. No evidence for differential scaling was found in any of the variables studied. We propose that this reflected the similar locomotor pattern of all felid species. Thus, our results suggested that the differences in allometric coefficients for “large” and “small” mammals were in fact caused by different types of locomotion among the species included in each category.

Keywords: biomechanics; calcaneus; Felidae; scaling; effective mechanical advantage; differential scaling; phylogenetically independent contrasts

Introduction

The calcaneus is the largest tarsal bone in mammals; it consists of an anterior portion, where the astragalus articulates, and a posterior portion, the *tuber calcanei*, where the Achilles tendon inserts (Lessertisseur & Saban, 1967). The calcaneus forms a lever for the calf muscles because the Achilles tendon is shared by the gastrocnemius and soleus, the ankle extensors. The length of this lever arm determines the moment of the force produced by the limbs as they push against the ground, which causes the body to rise and advance during forward locomotion (Alexander, 1983). Furthermore, the length of the *tuber calcanei* is related to the muscle mechanical advantage at the ankle, which counteracts the moment exerted on the joint by the ground reaction force (Biewener, 1989, 2003).

The shape of the calcaneus is variable in mammals. It has been proposed that, given its important role in the mechanics of locomotion, this variability would probably be related to locomotor specialization (Lessertisseur & Saban, 1967). However, size is another factor that must be taken into account (i.e., scaling). The main biomechanical consequences of scaling have been described in broadly comparative studies, and several hypotheses have been proposed to understand how increasing size affects animal design (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2005). These hypotheses, often referred to as similarity hypotheses, have been used to predict how anatomical structures and locomotion patterns would be affected by increasing body size. The hypothesis of geometric similarity, already supported by Hill (1950), states that two organisms are geometrically similar if their linear dimensions can be made equal by multiplying those of one of them by a constant (c). Thus, their surfaces could be made equal by multiplying by c^2 , whereas volumes should be multiplied by c^3 . Assuming a constant density (ρ), which would be logical if both organisms are made of the same materials, body mass would also be proportional to c^3 ($M_b = \rho V = \rho c^3$). Then, geometrically similar animals made of the same materials should present linear dimensions proportional to body mass^{1/3}. The hypothesis of elastic similarity, proposed by McMahon (1975), is based in the assumption that different-sized organisms have evolved to resist buckling and bending loads similarly (Schmidt-Nielsen, 1984). In order to maintain this similar elastic recovery, and assuming again a constant density, diameters must scale to body mass^{3/8}, and lengths to body mass^{1/4}. Nevertheless, none of those hypotheses appears to provide a universal explanation for the effects of size. For instance, mammalian linear dimensions typically conform to geometric similarity (Alexander et al., 1979), but in Bovidae, limb bone lengths appear to follow elastic similarity (McMahon,

1975). Another important point in scaling studies is whether general allometric calculations are applicable to a large range of variations in body size. Some studies on the scaling of skeletal elements appear to indicate otherwise. Economos (1983) predicted that, because volume increases faster than surface area, the pattern for scaling cross-sectional bone areas in large mammals (over 20 kg of body mass) should be different from that used in small mammals. This hypothesis of differential scaling was somewhat confirmed on mammalian long bones, mainly in carnivores (Bertram & Biewener, 1990; Christiansen, 1999*a, b*), and on mammalian body length (Silva, 1998). Thus, the first aim of this study was to determine the scaling pattern of the calcaneus bone, and to assess whether differential scaling could be found in this pattern.

As pointed out by Bou et al. (1987), similarity hypotheses imply adaptive neutrality, or at least independence of the locomotor type of the species that are compared. Therefore, samples with extreme locomotor patterns should show large deviations from predicted relationships. In fact, as stated by Day & Jayne (2007), phylogenetic diversity among different-sized samples might obscure the effect of size alone. To avoid this problem, we chose Felidae as our study group, because they comprise a well-defined, phylogenetically narrow clade (Mattern & McLennan, 2000; Johnson et al., 2006) with substantial differences in body size (Wilson & Mittermeier, 2009). The sizes of different Felidae species span two orders of magnitude and bracket the suggested 20-kg body mass change point for allometric relationships (Economos, 1983). Furthermore, they have similar locomotor patterns (Day & Jayne, 2007; Wilson & Mittermeier, 2009).

We also wondered whether the scaling pattern of the felid calcaneus would be influenced by ankle mechanics. On one hand, broadly comparative studies have shown that larger animals tend to run with more erect limb postures; this reduces the magnitude of the joint moments produced by the ground reaction force (\mathbf{F}_g), and thus, reduces the stresses acting on the bones (for a review, see Biewener, 2005). Consequently, the effective mechanical advantage (**EMA**), defined as the ratio of the extensor muscle moment arm to the \mathbf{F}_g moment arm (Fig. V.1a), scales to body mass with positive allometry (e.g. $\mathbf{EMA}_{\text{ankle}} = \mathbf{M}_b^{0.169}$ for a large sample of mammals; Biewener, 1989). On the other hand, Day & Jayne (2007) showed that large felids do not have more upright limbs than small felids. Thus, the angle of the ankle at footfall or midstance was not significantly correlated to body mass in felids. Although they could not definitively exclude the possibility that **EMA** increased with size in felids, the authors suggested that it would be very unlikely, because the \mathbf{F}_g orientation changed very little, even among phylogenetically diverse taxa (Biewener,

2005). Therefore, to support that theory, the muscle moment arms would have to increase with strong positive allometry in felids. Nevertheless, Alexander et al. (1981) have shown that muscle moment arms in mammals scaled to body mass with an exponent of 0.40 ($M_b^{0.40}$); this value was substantially higher than the exponents proposed for length scaling by similarity hypotheses (geometric similarity: $M_b^{0.33}$; elastic similarity: $M_b^{0.25}$). The muscle moment arm scaling factor ($b = 0.40$) was later supported by the work of Castiella & Casinos (1990) in insectivores and rodents. Thus, our second aim was to determine whether the moment arm of ankle extensors in felids scaled to body mass with the expected value of 0.40; this would provide evidence that **EMA** increased with body size in felids even though limb posture remained more or less constant. We chose the calcaneus bone, because it was assumed to have high mechanical significance.

Materials and methods

We studied 60 calcanei from 22 species of Felidae (Table V.1) by measuring the total length (L), the moment arm of the ankle extensors (r), and the sagittal and transverse diameters (d_s and d_t , respectively) just distal to the calcaneus-astragalus articulation (Fig. V.1b, c). The moment arm of a muscle is defined as the perpendicular distance from the centre of rotation of the joint to the line of action of the muscle (Fig. V.1a); thus, it depends upon the configuration of the limb segments. As proposed by Biewener (1989), the distance from the midpoint of the calcaneus-astragalus articulation to the posterior end of the *tuber calcanei* was taken as an approximation of the moment arm of the calf muscles (r) (Fig. V.1c). In the case of the generalized carnivore standing limb posture, this

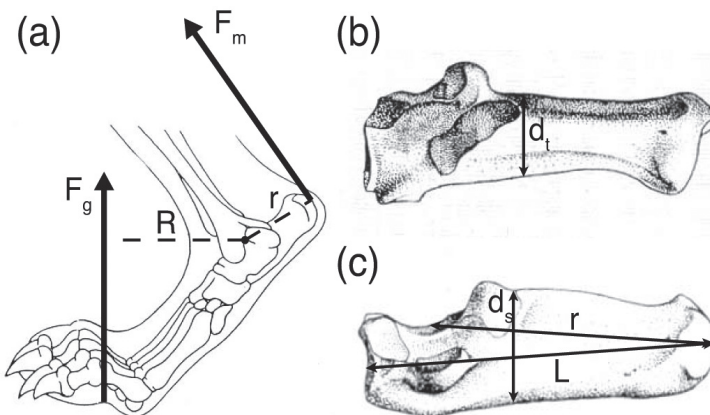


Figure V.1. Ankle anatomy and mechanics. (a) Lateral view of the distal skeletal elements of the felid hind limb and the forces acting at the ankle with their corresponding moment arms. (b) Dorsal view of the calcaneus of *Panthera sp.* (c) Medial view of the calcaneus of *Panthera sp.* Images modified from Lessertisseur & Saban (1967). Abbreviations: d_s , sagittal diameter; d_t , transverse diameter; F_g , ground reaction force; F_m , ankle extensors muscle force; L , calcaneus total length; R , moment arm of the ground reaction force; r , moment arm of the ankle extensors.

Table V.1. Measured specimens. Body mass values were obtained from Frandsen (1993), Grzimek (1988), and MacDonald (1984). Abbreviations: M_b , average body mass for the indicated species; n, number of specimens measured.

Species	abbreviation	n	Average M_b (kg)
<i>Acinonyx jubatus</i>	Aju	2	49.0
<i>Caracal caracal</i>	Cca	3	11.5
<i>Felis silvestris</i>	Fsi	4	4.5
<i>Leopardus colocolo</i>	Lco	1	4.3
<i>Leopardus geoffroyi</i>	Lge	2	4.5
<i>Leopardus pardalis</i>	Lpa	2	11.2
<i>Leopardus tigrinus</i>	Lti	1	2.5
<i>Leopardus wiedii</i>	Lwi	1	5.4
<i>Leptailurus serval</i>	Lse	6	11.0
<i>Lynx canadensis</i>	Lca	1	13.6
<i>Lynx lynx</i>	Lly	2	21.3
<i>Lynx pardinus</i>	Lpd	4	10.2
<i>Lynx rufus</i>	Lru	1	11.1
<i>Panthera leo</i>	Ple	5	158.4
<i>Panthera onca</i>	Pon	2	70.5
<i>Panthera pardus</i>	Ppa	6	48.5
<i>Panthera tigris</i>	Pti	6	151.2
<i>Panthera uncia</i>	Pun	3	41.7
<i>Prionailurus viverrinus</i>	Pvv	1	9.4
<i>Profelis aurata</i>	Pau	1	13.2
<i>Puma concolor</i>	Pco	4	49.1
<i>Puma yagouaroundi</i>	Pya	2	6.2

approximation will not diverge substantially from the actual moment arm. Furthermore, it was previously demonstrated that limb posture in Felidae was not affected by size (Day & Jayne, 2007). This study included specimens that belonged to collections housed in the Muséum National d'Histoire Naturelle of Paris (the former laboratories of Anatomie Comparée and Mammalogie), the Museu de Ciències Naturals de la Ciutadella of Barcelona, the Museo Nacional de Ciencias Naturales of Madrid, the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” of Buenos Aires, and the Museo de La Plata.

The corresponding transverse second moment of area (I) was calculated from the diameters measured with the following formula (Alexander, 1983):

$$I = \frac{\pi \cdot \left(\frac{d_s}{2}\right)^3 \cdot \frac{d_t}{2}}{4} \quad (1)$$

This formula assumed that the sagittal plane was the major axis of flexion during quadruped locomotion (Cubo & Casinos, 1998a).

The ratio r/L was also calculated for each specimen. This non-dimensional index reflected the relative length of the calf moment arm with respect to the total length of the calcaneus. Non-dimensional indexes are typically independent of body size, which allows comparisons among specimens independent of scale. Nevertheless, we expected r to be proportional to $M_b^{0.40}$, which is a higher value than that expected for the scaling of L ($M_b^{0.33}$ or $M_b^{0.25}$, according to geometric and elastic similarity, respectively). Therefore, this index should scale with positive allometry to body mass (i.e., $M_b^{0.40 - 0.33} = M_b^{0.07}$ or $M_b^{0.40 - 0.25} = M_b^{0.15}$, for geometric and elastic similarity, respectively).

Since the number of specimens per species was diverse (Table V.1), and we used a standard body mass for each species (based on values obtained from the literature), we used average values for variables other than body mass for every species.

We used regression methods to relate the following variables to body mass (M_b): L , r , d_s , d_t , r/L , and I . All regressions were calculated with the standardized major axis method (SMA), because we were primarily interested in the regression slopes. In contrast, common least squares regression methods tend to underestimate the slope of the line-of-best-fit, because it is calculated to fit the predicted y values as closely as possible to the observed y values (Warton et al., 2006). We assumed the power equation:

$$y = a \cdot x^b \quad (2)$$

and 95% confidence intervals were calculated for both a and b .

Many studies (e.g. Felsenstein, 1985; Grafen, 1989; Harvey & Pagel, 1991; Christiansen, 1999a, b, 2002a, b) have discussed that, in interspecific analyses, the error terms are correlated, because species are not independent of each other, but rather can be arranged in a hierarchical sequence (phylogenetic tree). Thus, a phylogenetic signal is introduced into the analysis, and the individual points cannot be considered truly independent. Alternatively, the method of phylogenetically independent contrasts (PIC; Felsenstein, 1985) takes into account this phylogenetic signal in regressions on interspecific data; therefore, we also calculated SMA regression slopes for PIC with the PDAP: PDTREE module of Mesquite (Maddison & Maddison, 2010; Midford et al., 2010). These PIC slopes were then compared to those obtained by traditional regression analysis with an F-test ($\alpha <$

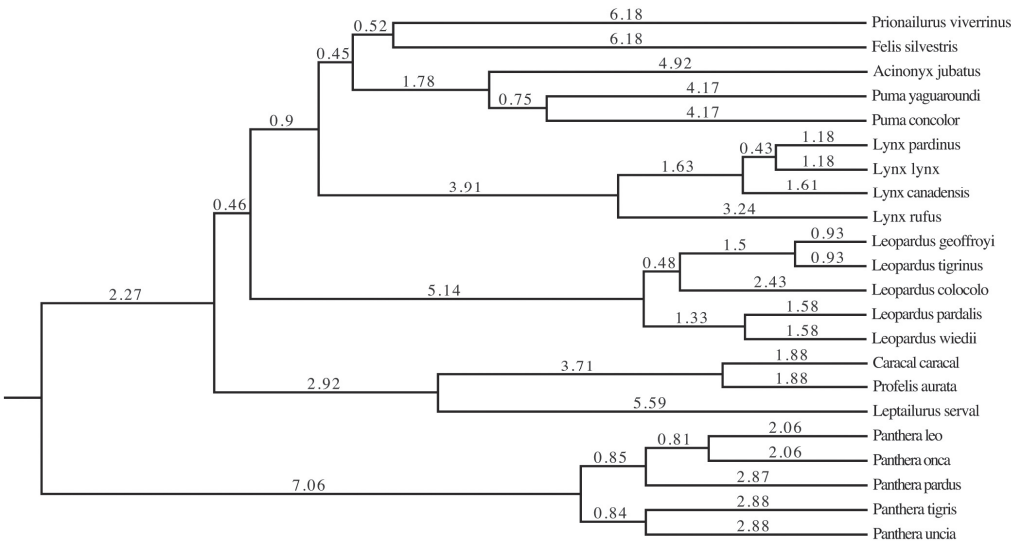


Figure V.2. Phylogenetic relationships between the 22 species of Felidae used in this study (modified from Johnson et al., 2006). The taxonomy shown is that presented by Wozencraft (2005), but with *Panthera uncia* instead of *Uncia uncia*, as proposed by Johnson et al. (2006) and Wilson & Mittermeier (2009).

0.01) to assess whether this phylogenetic signal had any effect on our results. The structure of the phylogenetic tree for the included species was that described by Johnson et al. (2006) and is shown in Figure V.2.

Finally, we tested for the presence of differential scaling in the felid calcaneus with the model proposed by Jolicoeur (1989). This model would detect the presence of complex allometry in our sample (i.e., variables that are not proportional to each other, as in simple allometry):

$$\ln y = \ln A - C \cdot (\ln x_{\max} - \ln x)^D, \quad (3)$$

where A is a constant (corresponding to a in Eq. 2), C is the allometry exponent, x_{\max} is the maximum observed value of the independent variable (i.e., body mass, \mathbf{M}_b), and D is the exponent of complex allometry, a time-scale factor. In our case, $D > 1$ indicated faster relative growth in small individuals, and $D < 1$ indicated that relative growth increased with size. The complex allometry hypothesis was thus accepted when D was significantly different from 1 ($p < 0.05$). Equation 3 was fitted with SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), and 95% confidence intervals were calculated for all parameters.

Results

The coefficients for the allometric equations obtained with both traditional regression analysis and phylogenetically independent contrasts (PIC) are shown in Table V.2. No branch length transformations were necessary for PIC regressions, except in the case of the ratio $\mathbf{r/L}$. For all other variables, the absolute values of the standardized contrasts were not significantly correlated to the corresponding standard deviations (Fig. V.3). Consequently, we used the Rho transformation proposed by Grafen (1989) in the case of $\mathbf{r/L}$.

Overall, the correlation coefficients (R) from the PIC analysis were lower than those from traditional regression (Table V.2). This was consistent with previous studies that indicated a higher risk of type I errors (i.e., indicating a significant correlation between two variables when there was none) when the correlation analysis neglected the effect of phylogeny (Grafen, 1989; Christiansen, 2002a). This could explain the different findings for the ratio $\mathbf{r/L}$ (traditional regression: $R = 0.558$; $p = 0.011$; PIC: $R = 0.358$; $p = 0.132$; Table V.2). In all cases, zero was not included in the 95% confidence interval for the slope (b) (Table V.2). However, in both methodologies, the value predicted by geometric similarity ($\mathbf{M}_b^{0.07}$) was included in the 95% confidence interval, but not the value predicted by elastic

Table V.2. Regression coefficients obtained from traditional regression analysis and from phylogenetically independent contrasts (PIC). All variables were plotted against body mass. The allometric coefficients (b) obtained with traditional regression analysis were not significantly different from those obtained with PIC (p -value > 0.01 for all comparisons). Values shown in italics indicate a non-significant regression. Abbreviations: 95% CI_a, 95% confidence interval for the coefficient (a); 95% CI_b, 95% confidence interval for the allometric coefficient (b); d_s , sagittal diameter; d_t , transverse diameter; I , second moment of area; L , calcaneus total length; r , moment arm of the ankle extensors; R , correlation coefficient.

	traditional regression				PIC			
	a	95% CI _a	b	95% CI _b	R	b	95% CI _b	R
L	17.911	15.284 – 20.989	0.323	0.270 – 0.375	0.936	0.384	0.258 – 0.510	0.716
r	11.784	9.834 – 14.120	0.360	0.300 – 0.420	0.933	0.429	0.293 – 0.565	0.734
d_t	2.833	2.299 – 3.492	0.349	0.280 – 0.419	0.904	0.392	0.252 – 0.532	0.647
d_s	5.450	4.442 – 6.687	0.364	0.296 – 0.432	0.916	0.452	0.297 – 0.607	0.683
r/L	0.617	0.575 – 0.662	0.060	0.037 – 0.084	0.558	<i>0.095</i>	<i>0.053 – 0.137</i>	<i>0.358</i>
I	23.678	10.611 – 52.837	1.427	1.160 – 1.695	0.916	1.739	1.140 – 2.338	0.677

similarity ($M_b^{0.15}$). Thus, although phylogeny appeared to account for most of the correlation between variables, the ratio r/L showed, as expected, a positive allometry to body mass. This indicated that the moment arm of the ankle extensors (r) provided stronger scaling than calcaneus length (L) (see below).

For variables other than the ratio r/L , the allometric coefficients (b) obtained with traditional regression analysis were not significantly different from those obtained with PIC (Table V.2; Fig. V.4). This was consistent with previous studies that compared these

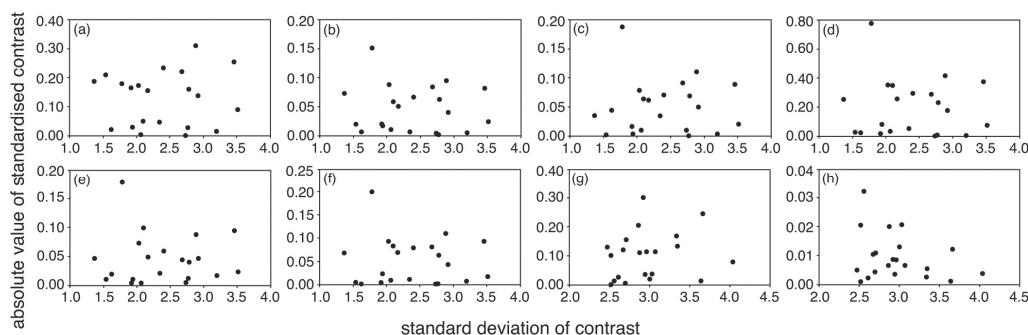
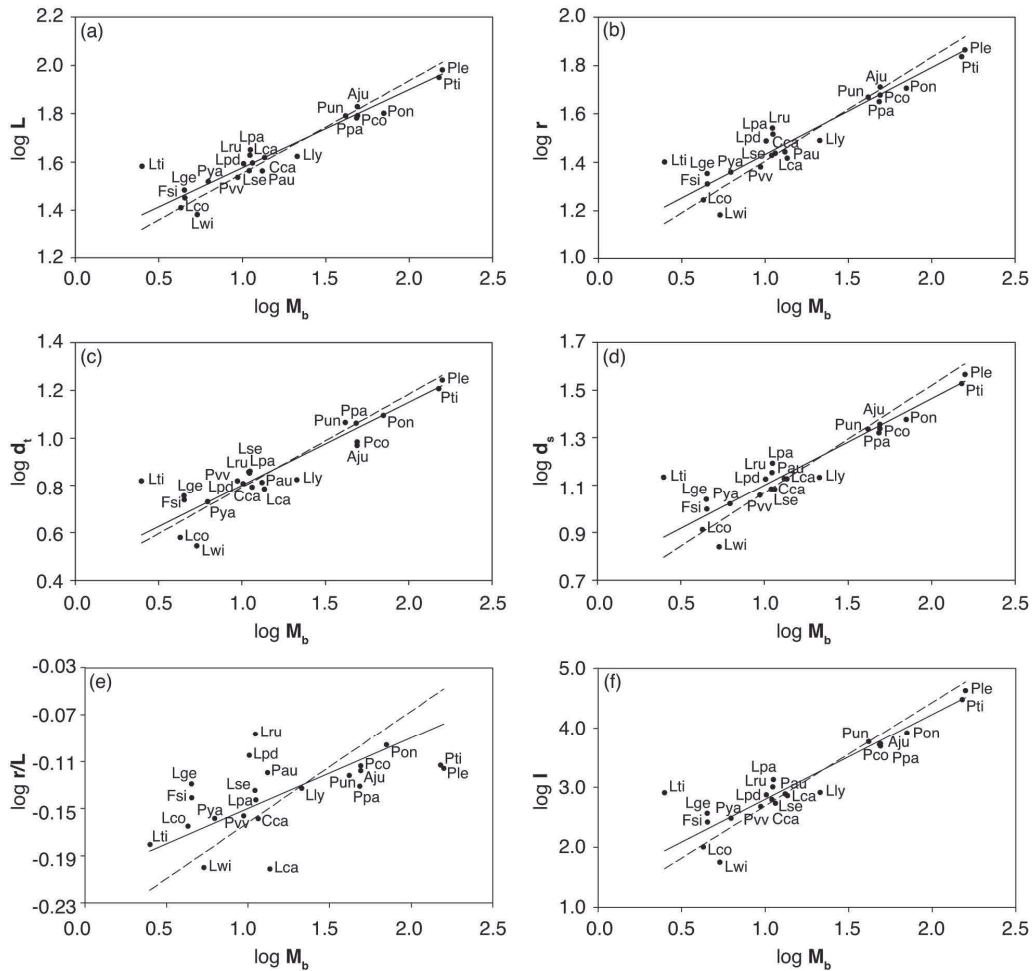


Figure V.3. Plots of standardized contrasts vs. their standard deviations. (a) body mass, M_b ($p = 0.857$); (b) calcaneus total length, L ($p = 0.782$); (c) moment arm of the ankle extensors, r ($p = 0.986$); (d) second moment of area, I ($p = 0.785$); (e) transverse diameter, d_t ($p = 0.921$); (f) sagittal diameter, d_s ($p = 0.806$); (g) body mass, M_b , after rho transformation ($p = 0.430$); (h) ratio r/L after rho transformation ($p = 0.224$). The p values are consistent with the hypothesis that the standardized contrasts were not significantly related to their corresponding standard deviations.

Figure V.4. Scaling by traditional regression analysis compared to scaling by phylogenetically independent contrasts.

Logarithmically transformed study variables were plotted against body mass (M_b). Traditional regression results are shown with a continuous line, while phylogenetically independent contrasts are shown with a broken line. (a) calcaneus total length, L ; (b) moment arm of the ankle extensors, r ; (c) transverse diameter, d_t ; (d) sagittal diameter, d_s ; (e) ratio r/L ; (f) second moment of area, I . Species abbreviations are shown in Table V.1.



methodologies (Christiansen, 1999a, b, 2002b). This indicated that the scaling of our variables with body mass was not dependent on the phylogenetic relationships within our sample. We also found that the 95% confidence interval for the allometric coefficient (b) of the regressions for calcaneus total length (L) included 0.33, the expected value for geometrically similar animals, but not 0.25, the value proposed for elastic similarity (Schmidt-Nielsen, 1984) (Table V.2). On the other hand, for both diameters (d_t , d_s), the 95% confidence intervals included the values predicted by both geometric (0.33) and elastic (0.375) similarities. As expected, neither method produced a slope for the moment arm of the ankle extensors (r) that was significantly different from the predicted value for muscle moment arms (0.40; Alexander et al., 1981; Castiella & Casinos, 1990). Finally, the scaling exponent of the second moment of area (I) was not significantly different from either 1.33

or 1.50, the values expected in geometrically and elastically similar animals, respectively (Cubo & Casinos, 1998*b*). Overall, the scaling pattern of the felid calcaneus conformed to the predictions of geometric similarity, but not entirely to those of elastic similarity.

Results of the tests for complex allometry are shown in Table V.3. In all cases, the 95% confidence interval for the exponent of complex allometry (D) included 1. Thus, no evidence for differential scaling was found in any of our variables.

Discussion

Our results showed that the scaling pattern of the felid calcaneus fit the predictions of the geometric similarity hypothesis better than the elastic similarity hypothesis. This finding was consistent with previous studies on the scaling of long bone dimensions in carnivores (Bertram & Biewener, 1990; Christiansen, 1999*a*). The work of Silva (1998) on the scaling of body length on a big sample of mammals also reported similar results, especially when considering “terrestrial non-volant mammals”, “terrestrial carnivores”, and felids. Furthermore, our findings supported previous studies that described elastic similarity as an atypical scaling pattern found mostly in large bovids (Alexander, 1977; Alexander et al., 1979; Biewener, 1983; Christiansen, 1999*b*; Rocha-Barbosa & Casinos, 2011). Also, consistent with previous studies (Christiansen, 1999*a, b*, 2002*b*), the phylogenetic signal had no significant effect on the scaling pattern, because we obtained similar values for the allometric coefficients (b), regardless of whether phylogeny was taken into account.

	ln A	95% CI_{ln A}	C	95% CI_c	D	95% CI_D	R
ln L	4.569	4.348 – 4.791	0.425	0.187 – 0.663	0.782	0.447 – 1.118	0.943
ln r	4.304	4.053 – 4.554	0.423	0.161 – 0.686	0.850	0.470 – 1.231	0.937
ln d_t	2.881	2.575 – 3.188	0.503	0.166 – 0.839	0.712	0.323 – 1.101	0.915
ln d_s	3.625	3.329 – 3.922	0.533	0.207 – 0.858	0.707	0.353 – 1.062	0.927
ln r/L	-0.246	-0.326 – -0.165	0.019	-0.046 – 0.084	1.417	-0.885 – 3.719	0.578
ln I	10.741	9.577 – 11.906	2.099	0.822 – 3.376	0.709	0.356 – 1.062	0.928

Table V.3. Results of the complex allometry test. None of the exponents of complex allometry (D) deviated from 1; thus, none of our variables deviated from simple allometry. Abbreviations: 95% CI_c, 95% confidence interval for the coefficient (C); 95% CI_D, 95% confidence interval for the exponent of complex allometry (D); 95% CI_{ln A}, 95% confidence interval for ln A ; d_s , sagittal diameter; d_t , transverse diameter; I , second moment of area; L , calcaneus total length; r , moment arm of the ankle extensors; R , correlation coefficient.

Biomechanical consequences of moment arm scaling

Our results supported the notion that muscle moment arms (\mathbf{r}) scale to body mass as $\mathbf{M}_b^{0.40}$ (Alexander et al., 1981; Castiella & Casinos, 1990). This indicated that a larger body mass corresponded to a longer *tuber calcanei* (relative to the total length of the calcaneus, which scaled to body mass as $\mathbf{L} \propto \mathbf{M}_b^{0.33}$). In turn, this allows the effective mechanical advantage of the ankle extensors to increase with body mass (Biewener, 1989) without requiring a change in the limb posture of felid species (Day & Jayne, 2007), given that the segment lengths (i.e., distances between joints) and joint angles remain unaffected by the length of the muscle moment arms.

As mentioned above, the effective mechanical advantage is defined as the ratio of the extensor muscle moment arm (\mathbf{r}) to the moment arm of the ground reaction force (\mathbf{R}). This assumes that the force exerted by the extensor muscles (\mathbf{F}_m) confers a mechanical advantage that counteracts the mechanical moment exerted by the ground reaction force (\mathbf{F}_g) (Biewener, 2003). Biewener (1989) found that, for mammalian ankle extensors, the effective mechanical advantage scaled to body mass with an exponent of 0.169 (± 0.046):

$$\frac{r}{R} \propto M_b^{0.169} \quad (4)$$

When \mathbf{r} in (4) is substituted with the assumed proportionality for muscle moment arms ($\mathbf{r} \propto \mathbf{M}_b^{0.40}$), we can derive a hypothesis about the scaling of the moment arm of \mathbf{R} :

$$R \propto \frac{r}{M_b^{0.169}} \propto \frac{M_b^{0.40}}{M_b^{0.169}} \propto M_b^{0.231} \quad (5)$$

Under equilibrium conditions, the moments acting on a joint must be balanced; that is, the moments of the muscle forces acting on the joint must equal the moment of the ground reaction force:

$$F_m \cdot r = F_g \cdot R \quad (6)$$

According to Alexander (1983), muscle force (\mathbf{F}_m) is equivalent to:

$$F_m = S \cdot \sigma \quad (7)$$

where \mathbf{S} is the cross-sectional area of the muscle and σ is the maximum isometric stress (250-300 kPa). Because σ is a constant, the following equation holds:

$$F_m \propto S \propto \frac{V}{l_f} \propto \frac{m \cdot \rho}{l_f} \quad (8)$$

where \mathbf{V} is the volume of the muscle, \mathbf{l}_f the mean fibre length, \mathbf{m} the muscle mass, and ρ the muscle density (1060 kg m⁻³). In the case of pennated muscles, a correction factor equal to the cosine of the pennation angle should be added to \mathbf{l}_f , but this angle can be assumed to be constant for each muscle; thus, we can disregard it with the other constants in this

proportionality. Once constants have been removed, (8) can be written as:

$$F_m \propto \frac{m}{l_f} \quad (9)$$

Castiella & Casinos (1990) found that, for a large sample of mammals, muscle mass scaled to body mass as $\mathbf{m} \propto \mathbf{M}_b^{1.06}$, and the mean fibre length scaled to body mass as $\mathbf{l}_f \propto \mathbf{M}_b^{0.20}$. By substituting these values in (9), the scaling of muscle force to body mass can be hypothesised:

$$F_m \propto \frac{M_b^{1.06}}{M_b^{0.20}} \propto M_b^{0.86} \quad (10)$$

Then substituting (5) and (10) into (6):

$$M_b^{0.86} \cdot M_b^{0.40} \propto F_g \cdot M_b^{0.231} \quad (11)$$

And finally:

$$F_g \propto \frac{M_b^{0.86} \cdot M_b^{0.40}}{M_b^{0.231}} \propto M_b^{1.029} \quad (12)$$

This supports the hypothesis proposed by Alexander et al. (1977) that the scaling of the ground reaction force is isometric, since the derived exponent of 1.029 is not significantly different from 1.

Differential scaling

To date, most studies on differential scaling have focused on comparing a sample of “large” mammals to a sample of “small” mammals (e.g. Economos, 1983; Christiansen, 1999*b*, 2002*a*). One problem with that approach is that it depends on a “threshold” body mass value that is rather arbitrarily chosen for separating “large” from “small” mammals. Furthermore, this threshold varies depending on the group under consideration (i.e., 20 kg might be appropriate for mammals as a whole, but not for scaling among bovids). Two alternate solutions to this problem have been proposed: first, a quadratic regression can be used to test for non-linear trends in log-transformed data (Bertram & Biewener, 1990); or second, a Gompertz-derived model can be fit to bivariate data in order to quantify the deviation from simple allometry (Jolicoeur, 1989). Both methodologies can determine whether relative growth increases or decreases with size. We chose the model proposed by Jolicoeur (1989), because it was equivalent to the power equation (used to describe simple allometry) when D was not different from 1, and it was equivalent to quadratic regression (used by Bertram & Biewener, 1990) when D was not different from 2.

As mentioned above, we found no evidence of differential scaling in the felid calcaneus, despite the wide range of body masses that spanned two orders of magnitude. This result suggested that, at least in the particular case of Felidae, similarity in allometric scaling was

a consequence of the similar locomotor requirements of all felid species (Day & Jayne, 2007; Wilson & Mittermeier, 2009). Another possible explanation would be a phylogenetic constraint; however, this seems unlikely, because the recent origin of this family has not prevented wide variations in felid size, for example, from the tiny *Felis nigripes* Burchell 1824 (around 1.5 kg) to well over 250 kg in the tiger (*Panthera tigris* Linnaeus, 1758) and in other species evidenced in fossils. Assuming that the similarity in allometric scaling was a consequence of the similarity in locomotor requirements, we would expect that other skeletal variables with mechanical significance would also show similar allometric scaling among felids. To investigate this, we revisited the data of previous scaling studies that included felid species and tested for complex allometry in skeletal variables. In particular, we reanalyzed the data of Bertram & Biewener (1990) and that of Christensen (1999*b*). As expected, we found no evidence for complex allometry in the scaling of sagittal diameter, transverse diameter, or bone circumference to bone length, or in the scaling of those four variables to body mass. This was consistent for all the long bones measured (humerus, radius, femur, tibia; Tables V.S1, V.S2). Nevertheless, like in the original studies (Bertram & Biewener, 1990; Christensen, 1999*b*) and others dealing with differential scaling (Economos, 1983; Silva, 1998), we found evidence for complex allometry when we included a large sample of carnivores in the analysis, and when we included the whole sample studied by Christiansen (1999*b*), which included species from several orders of mammals (Tables V.S1, V.S2). In those cases, the samples included species with different types of locomotion (Van Valkenburgh, 1985, 1987; Wilson & Mittermeier, 2009). In light of these results, we propose that the differences found in allometric coefficients (*b*) between “large” and “small” mammals of different species (i.e., differential scaling) must be more related to differences in locomotor requirements, rather than differences in body mass. This hypothesis requires further scaling studies to investigate whether there are grade shifts (different slopes) that correspond to different types of locomotion among different species.

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Supplementary material

The equations derived from the reanalyzed data of Bertram & Biewener (1990) and of Christensen (1999*b*) are presented as supplementary material.

O. CARNIVORA	ln A	95% CI _{ln A}	C	95% CI _C	D	95% CI _D	R
ln L = ln A - C · (ln d_{s,max} - ln d_s)^D							
humerus	5.906	5.776 - 6.035	0.724	0.597 - 0.850	1.109	0.980 - 1.238	0.979
radius	5.608	5.459 - 5.756	0.620	0.476 - 0.763	1.371*	1.070 - 1.246	0.956
femur	6.104	6.015 - 6.192	0.867	0.778 - 0.956	1.099*	1.170 - 1.571	0.990
tibia	5.676	5.579 - 5.744	0.440	0.355 - 0.525	1.481*	1.114 - 1.421	0.976
ln L = ln A - C · (ln d_{t,max} - ln d_t)^D							
humerus	5.887	5.803 - 5.971	0.705	0.624 - 0.787	1.158*	1.018 - 1.180	0.989
radius	5.662	5.532 - 5.791	0.568	0.449 - 0.686	1.267*	1.070 - 1.246	0.974
femur	6.033	5.947 - 6.120	0.782	0.697 - 0.868	1.158*	1.323 - 1.640	0.987
tibia	5.750	5.662 - 5.838	0.573	0.490 - 0.655	1.275*	1.162 - 1.388	0.985
ln L = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	5.815	5.684 - 5.946	0.182	0.116 - 0.248	1.305*	1.133 - 1.477	0.971
radius	5.568	5.421 - 5.715	0.101	0.050 - 0.152	1.630*	1.383 - 1.877	0.952
femur	5.945	5.821 - 6.069	0.165	0.106 - 0.223	1.368*	1.199 - 1.537	0.973
tibia	5.575	5.465 - 5.685	0.069	0.035 - 0.102	1.729*	1.486 - 1.971	0.956
ln d_s = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	3.780	3.607 - 3.952	0.302	0.199 - 0.404	1.140	0.984 - 1.296	0.972
radius	3.011	2.833 - 3.189	0.265	0.162 - 0.367	1.171	0.991 - 1.351	0.964
femur	3.427	3.294 - 3.560	0.227	0.154 - 0.299	1.223*	1.072 - 1.373	0.978
tibia	3.595	3.436 - 3.753	0.277	0.184 - 0.371	1.152	0.997 - 1.307	0.973
ln d_t = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	3.585	3.437 - 3.732	0.298	0.210 - 0.386	1.138*	1.003 - 1.273	0.979
radius	3.425	3.222 - 3.629	0.250	0.145 - 0.356	1.276*	1.078 - 1.475	0.961
femur	3.617	3.468 - 3.767	0.281	0.192 - 0.371	1.136	0.990 - 1.281	0.975
tibia	3.315	3.177 - 3.453	0.183	0.116 - 0.249	1.348*	1.175 - 1.521	0.971
Fam. FELIDAE	ln A	95% CI_{ln A}	C	95% CI_C	D	95% CI_D	R
ln L = ln A - C · (ln d_{s,max} - ln d_s)^D							
humerus	5.668	5.543 - 5.793	0.721	0.574 - 0.868	1.012	0.757 - 1.267	0.979
radius	5.481	5.229 - 5.733	0.617	0.316 - 0.918	1.109	0.487 - 1.731	0.915
femur	5.897	5.758 - 6.037	0.835	0.676 - 0.994	1.045	0.804 - 1.286	0.987
tibia	5.706	5.530 - 5.881	0.657	0.454 - 0.860	1.106	0.719 - 1.492	0.969
ln L = ln A - C · (ln d_{t,max} - ln d_t)^D							
humerus	5.698	5.547 - 5.849	0.835	0.663 - 1.007	0.956	0.685 - 1.226	0.979
radius	5.518	5.247 - 5.790	0.655	0.335 - 0.975	1.040	0.481 - 1.598	0.939
femur	5.836	5.702 - 5.970	0.835	0.681 - 0.988	1.079	0.812 - 1.346	0.981
tibia	5.665	5.530 - 5.800	0.713	0.558 - 0.869	1.065	0.750 - 1.380	0.971
ln L = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	5.741	5.532 - 5.949	0.362	0.159 - 0.566	0.867	0.555 - 1.180	0.952
radius	5.572	5.296 - 5.849	0.336	0.067 - 0.605	0.880	0.433 - 1.327	0.910
femur	5.865	5.658 - 6.072	0.312	0.118 - 0.506	0.972	0.614 - 1.329	0.951
tibia	5.692	5.487 - 5.898	0.248	0.060 - 0.435	1.026	0.584 - 1.468	0.934
ln d_s = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	3.680	3.465 - 3.895	0.484	0.274 - 0.693	0.884	0.642 - 1.125	0.972
radius	2.942	2.702 - 3.182	0.488	0.255 - 0.722	0.878	0.612 - 1.145	0.965
femur	3.354	3.151 - 3.557	0.382	0.189 - 0.575	0.939	0.652 - 1.226	0.965
tibia	3.456	3.203 - 3.709	0.403	0.161 - 0.644	0.929	0.589 - 1.270	0.951
ln d_t = ln A - C · (ln M_{b,max} - ln M_b)^D							
humerus	3.332	3.136 - 3.528	0.396	0.210 - 0.583	0.935	0.668 - 1.202	0.969
radius	3.279	3.068 - 3.489	0.409	0.213 - 0.605	0.994	0.717 - 1.270	0.971
femur	3.406	3.226 - 3.587	0.370	0.199 - 0.541	0.948	0.685 - 1.212	0.971
tibia	3.340	3.116 - 3.565	0.378	0.165 - 0.591	0.949	0.627 - 1.270	0.958

Table V.S1. Results of the complex allometry test. Data from Bertram & Biewener (1990) was reanalysed. The total sample included 100 carnivore species (O. Carnivora) with 28 felid species (Fam. Felidae). An asterisk indicates that the exponent of complex allometry (D) was significantly different from 1, indicating a significant deviation from simple allometry. Abbreviations: A , proportionality constant; 95% CI_C, 95% confidence interval for the coefficient (C); 95% CI_D, 95% confidence interval for the exponent of complex allometry (D); 95% CI_{ln A}, 95% confidence interval for $\ln A$; d_s , sagittal diameter; d_t , transverse diameter; L , bone length; R , correlation coefficient.

Table V.S2. Results of the complex allometry test.

Data from Christiansen (1999b) was reanalyzed. The total sample included 188 mammalian species; this was later reduced to 78 carnivore species, which included 24 felid species. An asterisk indicates that the exponent of complex allometry (D) was significantly different from 1, indicating a significant deviation from simple allometry. Abbreviations: A , proportionality constant; O , bone circumference; 95% CI_C , 95% confidence interval for the coefficient (C); 95% CI_D , 95% confidence interval for the exponent of complex allometry (D); 95% $CI_{\ln A}$, 95% confidence interval for $\ln A$; d_s , sagittal diameter; d_t , transverse diameter; L , bone length; R , correlation coefficient.

WHOLE SAMPLE	$\ln A$	95% $CI_{\ln A}$	C	95% CI_C	D	95% CI_D	R
$\ln L = \ln A - C \cdot (\ln O_{\max} - \ln O)^D$							
humerus	6.419	6.287 – 6.552	0.666	0.542 – 0.790	1.090	0.965 – 1.216	0.974
radius	6.038	5.939 – 6.137	0.632	0.524 – 0.739	1.142*	1.006 – 1.279	0.957
femur	6.498	6.395 – 6.601	0.612	0.515 – 0.709	1.238*	1.119 – 1.357	0.978
tibia	6.128	6.041 – 6.215	0.340	0.266 – 0.415	1.658*	1.473 – 1.843	0.964
$\ln L = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	6.464	6.276 – 6.651	0.213	0.120 – 0.305	1.119	0.944 – 1.293	0.956
radius	6.180	6.000 – 6.360	0.085	0.031 – 0.139	1.536*	1.262 – 1.810	0.934
femur	6.585	6.424 – 6.746	0.170	0.100 – 0.240	1.231*	1.063 – 1.400	0.964
tibia	6.124	5.994 – 6.255	0.036	0.010 – 0.061	1.865*	1.551 – 2.178	0.933
$\ln O = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	5.844	5.662 – 6.026	0.342	0.244 – 0.440	1.036	0.924 – 1.149	0.979
radius	5.287	5.101 – 5.474	0.164	0.096 – 0.233	1.372*	1.196 – 1.548	0.966
femur	5.809	5.637 – 5.981	0.349	0.254 – 0.445	1.006	0.900 – 1.113	0.980
tibia	5.563	5.384 – 5.742	0.279	0.189 – 0.369	1.096	0.968 – 1.224	0.975
O. CARNIVORA							
$\ln L = \ln A - C \cdot (\ln O_{\max} - \ln O)^D$							
humerus	5.889	5.707 – 6.070	0.614	0.429 – 0.800	1.301*	1.028 – 1.574	0.960
radius	5.700	5.520 – 5.880	0.591	0.401 – 0.781	1.389*	1.074 – 1.704	0.953
femur	6.150	5.983 – 6.317	0.813	0.638 – 0.989	1.198	0.997 – 1.400	0.976
tibia	5.781	5.632 – 5.930	0.586	0.429 – 0.743	1.374*	1.098 – 1.650	0.959
$\ln L = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	5.846	5.692 – 6.001	0.200	0.106 – 0.295	1.263*	1.021 – 1.504	0.956
radius	5.741	5.533 – 5.949	0.195	0.071 – 0.318	1.291	0.965 – 1.617	0.926
femur	6.017	5.858 – 6.177	0.229	0.127 – 0.331	1.206	0.980 – 1.432	0.958
tibia	5.683	5.514 – 5.853	0.110	0.027 – 0.193	1.496*	1.099 – 1.893	0.914
$\ln O = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	4.811	4.660 – 4.963	0.342	0.232 – 0.453	1.051	0.893 – 1.208	0.973
radius	4.366	4.187 – 4.545	0.312	0.187 – 0.438	1.099	0.900 – 1.298	0.961
femur	4.679	4.563 – 4.794	0.294	0.212 – 0.376	1.073	0.935 – 1.211	0.980
tibia	4.498	4.365 – 4.631	0.247	0.159 – 0.335	1.166	0.987 – 1.345	0.972
Fam. FELIDAE							
$\ln L = \ln A - C \cdot (\ln O_{\max} - \ln O)^D$							
humerus	5.619	5.404 – 5.833	0.649	0.402 – 0.897	1.111	0.601 – 1.621	0.939
radius	5.396	5.199 – 5.593	0.469	0.231 – 0.707	1.526	0.762 – 2.291	0.926
femur	5.923	5.756 – 6.090	0.851	0.662 – 1.039	1.060	0.762 – 1.358	0.979
tibia	5.739	5.591 – 5.888	0.677	0.507 – 0.846	1.179	0.825 – 1.533	0.972
$\ln L = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	5.757	5.548 – 5.966	0.337	0.146 – 0.528	0.927	0.608 – 1.246	0.958
radius	5.647	5.343 – 5.951	0.358	0.076 – 0.640	0.885	0.447 – 1.323	0.917
femur	5.886	5.642 – 6.130	0.289	0.078 – 0.500	1.061	0.634 – 1.487	0.948
tibia	5.722	5.976 – 5.968	0.202	0.003 – 0.401	1.196	0.601 – 1.791	0.927
$\ln O = \ln A - C \cdot (\ln M_{b, \max} - \ln M_b)^D$							
humerus	4.644	4.283 – 5.005	0.449	0.117 – 0.781	0.912	0.498 – 1.327	0.930
radius	4.241	3.956 – 4.527	0.435	0.181 – 0.690	0.987	0.652 – 1.323	0.961
femur	4.563	4.325 – 4.801	0.371	0.158 – 0.584	0.980	0.651 – 1.308	0.961
tibia	4.451	4.174 – 4.728	0.335	0.094 – 0.576	1.050	0.631 – 1.468	0.949

Section D: Scapula

Journal Reference

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Evolution of scapula size and shape in Carnivora: locomotor adaptations and differential shape scaling



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Abstract

The effect of size, phylogeny, and locomotor pattern, on shape was tested in 213 scapulas from 101 carnivoran species, digitizing 34 3D-landmarks and using geometric morphometric methods. The sampled species spanned the whole size range and locomotor patterns in Carnivora. The results of the present study indicate that, in this order, scapula shape responds to the complex interaction of allometric, phylogenetic, and functional effects. Furthermore, evidence for differential scaling in the shape of the carnivoran scapula was found, which would probably be caused by scaling differences among carnivoran families. Additionally, most allometric shape variation in the carnivoran scapula was related to size changes along phyletic lines. Locomotor-related shape differences were assessed using canonical variate analysis and discriminant function analysis (DFA). Most locomotor habits could be significantly separated from each other based on scapula shape, although high DFA misclassification rates were obtained when comparing semiarboreal and semifossorial carnivorans to other locomotor types. Locomotor adaptations in the scapula shape of extant carnivorans seemed independent of size or shared ancestry and could be related to muscular function. These locomotor adaptations were then used to infer the locomotor habits of several internal nodes of the carnivoran phylogeny, whose scapular size and shape was reconstructed using weighted square-change parsimony. According to scapula size and shape, the carnivoran ancestor was a medium-sized scansorial animal (i.e., it spent most of its time on the ground, but was a good climber).

Keywords: Carnivora; geometric morphometrics; locomotor type; morphological evolution; scapula

Introduction

The therian scapula consists of a slightly concavoconvex bone plate (scapular blade) whose lateral surface is divided by the scapular spine in two fossae (supraspinous and infraspinous). The medial surface of the scapular blade is known as subscapular fossa. The scapular spine is a roughly flat plate of bone extending almost perpendicularly to the scapular blade. The spine broadens distally into the acromion, which can present a ventral projection (hamatus process) and a caudal extension (suprahamatus process or metacromion). The scapula articulates distally with the proximal humerus at the glenoid cavity, which is separated from the rest of the scapular blade by a strangulation known as scapular neck. Finally, in some species a coracoid process may arise cranially to the glenoid. As stated by Monteiro & Abe (1999), the therian scapula is a complex morphological structure (Atchley & Hall, 1991), since it derives from two ossification centers with different ontogenetic origin: the scapular plate and the coracoid plate (Goodrich, 1930).

Scapular morphology arises from the combination of phylogenetic history and functional requirements. The scapula is both an element of the thoracic girdle, providing insertion to the muscles connecting the forelimb to the rest of the body (Lessertisseur & Saban, 1967), and a functional element of the forelimb, being the most propulsive segment during locomotion (Fischer et al., 2002). Thus, its functional requirements include both shoulder stabilization and scapular mobility. The relative importance of those functions, however, surely varies among specialized locomotor patterns. For instance, a slow arboreal species would require stronger stabilization to avoid shoulder dislocation while navigating the three-dimensional pathways of the canopy, whereas larger scapular mobility in the parasagittal plane would increase the performance of a fast cursorial species (*sensu* Stein & Casinos, 1997) by allowing larger strides. Furthermore, differences in body size are expected to also influence scapular morphology, since body size plays a major role determining the biomechanics of locomotion (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003). Thus, the scapula is considered particularly suited for studies on ecomorphology and morphological evolution (Astúa, 2009).

Most of the previous ecomorphological studies on the therian scapula focus on functional anatomy, relating sets of anatomical characters to particular locomotor habits in the studied groups (Davis, 1949; Smith & Savage, 1956; Lehmann, 1963; Ashton et al., 1965; Müller, 1967; Oxnard, 68; Roberts, 1974; Taylor, 1974; English, 1977; Taylor, 1997;

Argot, 2001; Seckel & Janis, 2008). The development of geometric morphometrics (GM) methods in the 1990s allowed the separate analysis of shape and size in morphological studies. To date, scapular shape has been studied in rodents (Swiderski, 1993; Morgan, 2009), dolphins (Smith et al., 1994), xenarthrans (Monteiro & Abe, 1999; Monteiro, 2000), primates (Young, 2004; Taylor & Slice, 2005; Young, 2008), and didelphids (Astúa, 2009). According to these studies, scapular shape is heavily influenced by phylogeny, while the amount of scapular shape variation that can be attributed to locomotor differences varies among groups. Regarding size, a significant allometric effect on scapular shape was found in didelphids (Astúa, 2009), but not in xenarthrans (Monteiro & Abe, 1999) or caviomorph rodents (Morgan, 2009).

The order Carnivora currently comprises over 280 species in 16 families, and constitutes a well-defined monophyletic group (Wilson & Mittermeier, 2009; Nyakatura & Bininda-Emonds, 2012). Carnivorans present one of the widest locomotor diversities among mammals, which makes them perfect subjects for ecomorphological studies (e.g. Oxnard, 1968; Taylor, 1974; Van Valkenburgh, 1985, 1987; Iwaniuk et al., 1999). Furthermore, they span a size range of four orders of magnitude (from less than 0.1 kg in the least weasel (*Mustela nivalis*) to well over two tonnes in elephant seals (*Mirounga sp.*)), which provides a solid base from which to test for allometric effects. Recently, several workers have analyzed bone shape in Carnivora using GM methods, particularly on the cranium and mandible (e.g. Goswami, 2006; Meloro et al., 2008; Figueirido et al., 2010) and, to a lesser extent, the long bones of the limbs (Schutz & Guralnick, 2007; Walmsley et al., 2012; Fabre et al., 2013*a,b*; Martín-Serra et al., 2014). However, despite the remarkable shape variability of the scapula and its substantial biomechanical importance, only the work of Martín-Serra et al. (2014) paid any attention to this bone, and then only to the distalmost scapula (acromion and coracoglenoid region) plus teres major process.

Thus, the first aim of the present study is to explore the shape variability of the carnivoran scapula, and to quantify to what extent, if any, phylogenetic history and size differences affect scapula shape. The second aim is to assess whether adaptations to particular locomotor habits (e.g. climbing, swimming) can be observed in the carnivoran scapula, and to characterize them in case they do. Finally, should these locomotor adaptations exist, the locomotor type of the carnivoran ancestor could be inferred according to the reconstructed evolution of scapula shape in this clade.



Figure VI.1. Phylogenetic relationships among the species of Carnivora used in this study. The time-scale represents divergence times in millions of years. The phylogeny shown was modified after Nyakatura & Bininda-Emonds (2012), as described in Chapter III.

Material and Methods

The sample consisted of 213 scapulas from 101 species of Carnivora (Table VI.1), representing all extant families but Odobenidae and Prionodontidae (Wozencraft, 2005; Wilson & Mittermeier, 2009). Furthermore, the sampled species spanned the whole size range of the order, and also covered all locomotor habits in Carnivora. As described elsewhere (Chapter II), each species was assigned a locomotor type category based on the literature (Table VI.2). The phylogeny proposed by Nyakatura & Bininda-Emonds (2012) was used, although slightly modified (see Chapter III for a detailed description) (Fig. VI.1).

Specimens studied are housed in the collections of the Museu de Ciències Naturals de la Ciutadella (Barcelona, Spain), the Muséum National d'Histoire Naturelle (Paris, France), the

Table VI.1. Measured species. See legend on next page.

species	abbr.	n	loctyp	species	abbr.	n	loctyp
Canidae							
<i>Canis aureus</i>	Cau	1	terrestrial	<i>Lycaon pictus</i>	Lpi	2	terrestrial
<i>Canis lupus</i>	Clu	4	terrestrial	<i>Vulpes chama</i>	Vch	1	terrestrial
<i>Chrysocyon brachyurus</i>	Cbr	2	terrestrial	<i>Vulpes vulpes</i>	Vvu	11	terrestrial
<i>Lycalopex culpaeus</i>	Lcu	1	terrestrial	<i>Vulpes zerda</i>	Vze	1	terrestrial
<i>Lycalopex gymnocercus</i>	Lgy	2	terrestrial				
Mustelidae							
<i>Eira barbara</i>	Eba	1	semiarboreal	<i>Martes martes</i>	Mma	3	semiarboreal
<i>Enhydra lutris</i>	Elu	1	aquatic	<i>Martes zibellina</i>	Mzi	1	scansorial
<i>Galictis cuja</i>	Gcu	2	terrestrial	<i>Meles meles</i>	Mme	3	semifossorial
<i>Galictis vittata</i>	Gvi	1	terrestrial	<i>Mellivora capensis</i>	Mca	1	semifossorial
<i>Gulo gulo</i>	Ggu	1	scansorial	<i>Melogale moschata</i>	Mmo	1	terrestrial
<i>Ictonyx striatus</i>	Ist	1	terrestrial	<i>Mustela erminea</i>	Mer	2	terrestrial
<i>Lontra felina</i>	Lfe	2	semiaquatic	<i>Mustela eversmannii</i>	Mev	1	terrestrial
<i>Lontra longicaudis</i>	Llo	1	semiaquatic	<i>Mustela lutreola</i>	Mlu	1	semiaquatic
<i>Lontra provocax</i>	Lpr	2	semiaquatic	<i>Mustela nivalis</i>	Mni	2	terrestrial
<i>Lutra lutra</i>	Llu	3	semiaquatic	<i>Mustela putorius</i>	Mpu	2	terrestrial
<i>Lyncodon patagonicus</i>	Lpt	2	terrestrial	<i>Mustela vison</i>	Mvi	2	semiaquatic
<i>Martes americana</i>	Mam	1	semiarboreal	<i>Pteronura brasiliensis</i>	Pbr	1	semiaquatic
<i>Martes foina</i>	Mfo	18	scansorial				
Mephitidae							
<i>Conepatus chinga</i>	Cch	2	semifossorial	<i>Spilogale gracilis</i>	Sgr	2	terrestrial
Otariidae							
<i>Arctocephalus australis</i>	Aau	1	aquatic	<i>Otaria flavescens</i>	Ofl	2	aquatic
<i>Arctocephalus gazella</i>	Aga	1	aquatic	<i>Zalophus californianus</i>	Zca	2	aquatic
Phocidae							
<i>Hydrurga leptonyx</i>	Hle	1	aquatic	<i>Phoca vitulina</i>	Pvi	2	aquatic
<i>Mirounga leonina</i>	Mle	1	aquatic				
Ailuridae							
<i>Ailurus fulgens</i>	Afu	7	scansorial				
Procyonidae							
<i>Bassaricyon gabbii</i>	Bga	1	arboreal	<i>Potos flavus</i>	Pfl	2	arboreal
<i>Bassariscus astutus</i>	Bas	1	scansorial	<i>Procyon cancrivorus</i>	Pca	2	scansorial
<i>Nasua narica</i>	Nnr	4	scansorial	<i>Procyon lotor</i>	Plo	3	scansorial
<i>Nasua nasua</i>	Nna	2	scansorial				
Ursidae							
<i>Ailuropoda melanoleuca</i>	Ame	1	scansorial	<i>Ursus arctos</i>	Uar	4	scansorial
<i>Tremarctos ornatus</i>	Tor	1	scansorial	<i>Ursus maritimus</i>	Uma	3	terrestrial
<i>Ursus americanus</i>	Uam	1	scansorial				
Viverridae							
<i>Arctictis binturong</i>	Abi	3	arboreal	<i>Paradoxurus hermaphroditus</i>	Phe	2	arboreal
<i>Arctogalidia trivirgata</i>	Atr	2	arboreal	<i>Poiana richardsoni</i>	Pri	1	semiarboreal
<i>Civettictis civetta</i>	Cci	2	terrestrial	<i>Viverra zibetha</i>	Vta	3	terrestrial
<i>Genetta genetta</i>	Gge	6	scansorial	<i>Viverra zibetha</i>	Vzi	2	terrestrial
<i>Genetta maculata</i>	Gma	3	semiarboreal	<i>Viverricula indica</i>	Vin	3	scansorial

species	abbr.	n	loctyp	species	abbr.	n	loctyp
Herpestidae							
<i>Atilax paludinosus</i>	Apa	1	semiaquatic	<i>Herpestes ichneumon</i>	Hic	3	terrestrial
<i>Crossarchus obscurus</i>	Cob	1	terrestrial	<i>Herpestes javanicus</i>	Hja	1	terrestrial
<i>Galerella sanguinea</i>	Gsa	1	terrestrial	<i>Ichneumia albicauda</i>	Ial	1	terrestrial
<i>Herpestes edwardsii</i>	Hed	2	terrestrial	<i>Suricata suricatta</i>	Ssu	2	semifossorial
Eupleridae							
<i>Cryptoprocta ferox</i>	Cfe	2	semiarboreal	<i>Mungotictis decemlineata</i>	Mde	1	scansorial
<i>Fossa fossa</i>	Ffo	1	terrestrial	<i>Salanoia concolor</i>	Sco	2	scansorial
<i>Galidia elegans</i>	Gel	2	scansorial				
Hyaenidae							
<i>Crocuta crocuta</i>	Ccr	1	terrestrial	<i>Proteles cristatus</i>	Pcr	1	terrestrial
<i>Hyaena hyaena</i>	Hhy	1	terrestrial				
Felidae							
<i>Acinonyx jubatus</i>	Aju	2	scansorial	<i>Lynx rufus</i>	Lru	1	scansorial
<i>Felis silvestris</i>	Fsi	2	scansorial	<i>Panthera leo</i>	Ple	2	scansorial
<i>Leopardus colocolo</i>	Lco	1	scansorial	<i>Panthera onca</i>	Pon	2	scansorial
<i>Leopardus geoffroyi</i>	Lge	2	scansorial	<i>Panthera pardus</i>	Ppa	3	scansorial
<i>Leopardus pardalis</i>	Lpa	1	scansorial	<i>Panthera tigris</i>	Pti	3	scansorial
<i>Leopardus tigrinus</i>	Lti	1	scansorial	<i>Panthera uncia</i>	Pun	2	scansorial
<i>Leptailurus serval</i>	Lse	2	scansorial	<i>Profelis aurata</i>	Pau	1	scansorial
<i>Lynx lynx</i>	Lly	1	scansorial	<i>Puma concolor</i>	Pco	2	scansorial
<i>Lynx pardinus</i>	Lpd	4	scansorial	<i>Puma yaguaroundi</i>	Pya	1	scansorial
Nandiniidae							
<i>Nandinia binotata</i>	Nbi	4	semiarboreal				

Table VI.1. Measured species. (cont.) For each species, the table shows the abbreviation used in the text and figures (abbr.), the number of measured specimens (n), and the assigned locomotor type category (loctyp). See Table VI.2 for a description of locomotor type categories.

Museo Nacional de Ciencias Naturales (Madrid, Spain), the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (Buenos Aires, Argentina), and the Museo de La Plata (La Plata, Argentina). Only adult specimens (judged by epiphyseal fusion) were sampled and, where possible, only the left scapula was measured.

To describe scapula shape, the three-dimensional coordinates of 34 landmarks (15 true landmarks and 17 semilandmarks) were recorded using a Microscribe G2X digitizer

Locomotor type	Description
arboreal	species that spend most of their life in trees (over 75%), rarely descending to the ground
semiarboreal	species that spend a large amount of their time in the trees (between 50% and 75%), both foraging and resting, but also on ground surface
scansorial	species that, although mostly terrestrial (over half their time is spent on the ground), can climb well and will readily do so to chase arboreal prey or escape, and might nest in trees for protection against terrestrial predators
terrestrial	species that rarely or never climb or swim, and that might dig to modify a burrow but not regularly for food
semifossorial	species that dig regularly for both food and shelter, but that still show considerable ability to move around on the surface
semiaquatic	species that forage regularly underwater and usually plunge into the water to escape, but must spend time ashore to groom,...
aquatic	species that carry out most of their life cycle in water, although some part of this cycle can be confined to land (parturition, mating, rearing the young)

Table VI.2. Description of the locomotor type categories. Locomotor type categories were adapted from previous works on the relationship between locomotor behavior and forelimb morphology (Eisenberg, 1981; Van Valkenburgh, 1985, 1987).

Table VI.3. Description of the scapular landmarks used in this study.

Landmark	Definition
1	Intersection between scapular spine and vertebral border.
2 – 5	Semilandmarks along caudal part of vertebral border.
6	Caudal angle.
7 – 10	Semilandmarks along caudal border.
11	Point of maximum curvature along caudal scapular neck margin.
12	Caudalmost point on lip of glenoid cavity.
13	Cranialmost point on lip of glenoid cavity.
14	Point of maximum curvature along cranial scapular neck margin.
15	Ventral end of cranial border.
16 – 18	Semilandmarks along cranial border.
19	Cranial angle.
20 – 22	Semilandmarks along cranial part of vertebral border.
23	Limit between acromion and scapular spine.
24 – 26	Semilandmarks along edge of scapular spine.
27 – 28	Semilandmarks along base of scapular spine.
29	Ventralmost point of scapular spine base.
30	Cranialmost point of tip of acromion.
31	Caudalmost point of tip of acromion.
32	Point of maximum curvature between acromion and metacromion.
33	Ventralmost point of tip of metacromion.
34	Dorsalmost point of tip of metacromion.

(Immersion Corporation; San Jose, California, US) (Fig. VI.2; Table VI.3). After digitalization, semilandmark coordinates were recalculated with RESAMPLE (Raaum, 2006), which uses weighted linear interpolation to evenly space semilandmarks along the curve they define.

Measurement error (ME) was quantified using partial superimposition (von Cramon-Taubadel et al., 2007). For that, the landmark configurations of five specimens belonging to five different-sized species were digitized five times (Aju, Pco, Plo, Mfo, Vvu; see Table VI.1 for species names abbreviations). Landmarks 1, 6 and 29 were used as the baseline. The mean measurement error for any given landmark ranged between 0.24 and 0.48 mm (i.e., close to once and twice the accuracy of the digitizer, ± 0.23 mm, respectively). The highest ME values corresponded to landmarks 18 and 19, which reflected the difficulty of precisely locating the cranial angle in some species.

Prior to any further analyses, all non-shape information (i.e., size, location and orientation) was removed performing a Generalized Procrustes Superimposition (GPS) on all landmark configurations. Briefly, this procedure first standardizes size by equaling centroid size (CS; the squared root of the sum of the squared distances of each landmark to the centroid of the configuration) to unit in each configuration, then shifts all configurations so that their centroid is located at the same position, and finally aligns the

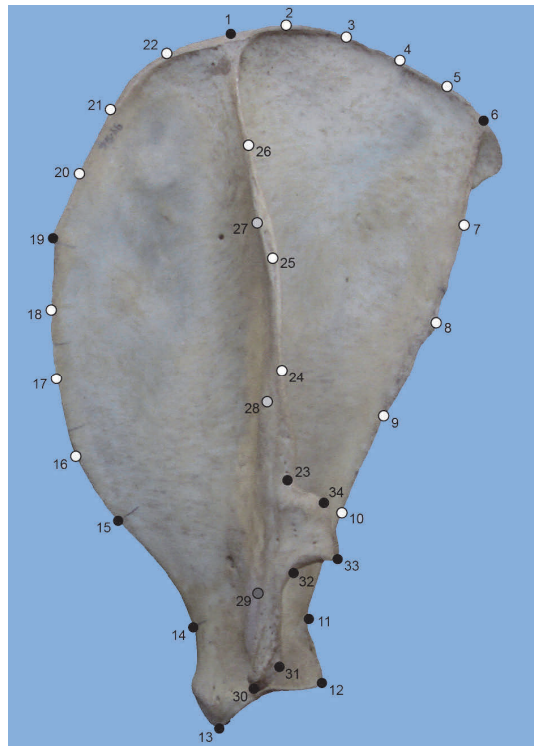


Figure VI.2. Left scapula of *Acinonyx jubatus* showing position of landmarks used in this study. Black dots represent true landmarks, while white dots correspond to semilandmarks. Landmark 29 and semilandmarks 27 and 28 are greyed out because their anatomical position can not be observed directly on the picture. See Table VI.3 for definition of landmarks.

configurations by iteratively minimizing the sum of squared distances between corresponding landmarks of each configuration. The scaling of CS to unit only removes isometric size effects, retaining both shape variation unrelated to size and allometric shape variation. A more detailed explanation of this procedure and its computation can be found elsewhere (Bookstein, 1991; Dryden & Mardia, 1998; Zelditch et al., 2004). After the GPS, the aligned landmark configurations (Procrustes coordinates) were averaged by species to eliminate the possible effect of static allometry and sexual shape dimorphism.

The allometric effect on scapula shape was quantified by regressing the Procrustes coordinates (shape variables) onto CS. Due to the large variation of body sizes in the species sampled, the regression was performed using both raw CS values and log-transformed centroid size (log CS). Since the latter magnifies shape changes at small sizes, differences between both regressions would suggest that the allometric effect is not constant over the studied size range. This is known as differential scaling and it has been previously documented for several linear measurements in Carnivora (Bertram & Biewener, 1990; Chapters III & IV).

The presence of a phylogenetic signal in the shape of the carnivoran scapula was tested using a permutation test (Klingenberg & Gidaszewski, 2010). In this test, the null

hypothesis of complete absence of a phylogenetic signal is simulated by randomly permuting the Procrustes coordinates among the terminal taxa and calculating the total amount of squared change summed over all branches of the tree. Then, these summed squared changes are compared to the value calculated for the original data, and an empirical p-value is thus defined as the proportion of permuted data sets with sums lower or equal than the original.

In addition, a MANOVA by locomotor type was carried out on the Procrustes coordinates to determine whether locomotor differences had a significant effect on scapula shape in Carnivora.

Shape variation in the carnivoran scapula was first explored using a principal components analysis (PCA) of the shape variables. The number of principal components (PCs) to be further analyzed was determined using the broken-stick model (Frontier, 1976), according to which a PC can be interpreted if its observed eigenvalue exceeds the value expected under a random distribution of total variance amongst all PCs. Then, the effect of size, phylogeny and function (locomotor type) was evaluated in each of those PCs individually. The former was quantified regressing the PC scores onto CS (and log CS), while one-way ANOVAs were used to assess the effect of the other two factors. Additionally, the reconstructed ancestral shapes (see below) were plotted onto the shape spaces defined by the PCs and then connected by the branches of the tree in Figure VI.1. The resulting phylomorphospaces allow the assessment of the evolutionary history of shape changes (Klingenberg & Gidaszewski, 2010).

Although PCA identifies the major axes of shape variation and the related ordination of specimens, it is not intended to separate those specimens into groups. Thus, a canonical variates analysis (CVA) was performed on the shape variables in order to determine whether species with similar locomotor habits shared similarly shaped scapulae. Furthermore, this would allow the identification of morphological adaptations for each locomotor type with a distinct scapular shape. As with PCA, the CV scores were regressed onto CS (and log CS) to quantify the effect of size on group separation. Since group means were the main target of this comparison, differences between groups should be tested based on the Mahalanobis distances between them (Klingenberg & Monteiro, 2005). However, the presence of anisotropic shape variation (results not shown), together with unequal group sizes, could violate the assumption of identical within-group covariation matrixes. Thus, discriminant function analyses (DFAs) were preferred for the intergroup comparison, and its significance was determined using permutation tests based on

Procrustes distances. Furthermore, since DFA tends to over-estimate differences between groups when sample size is small compared to the number of dimensions (i.e., landmarks), the reliability of the discrimination was assessed using leave-one-out cross-validation (Lachenbruch, 1967).

Finally, hypothetical scapular sizes and shapes were reconstructed for each node of the phylogeny, using squared-change parsimony weighted by branch lengths (Maddison, 1991). This procedure minimizes the sum of squared-changes along the branches of the phylogeny in order to reconstruct the value of continuous characters at ancestral nodes. Changes on longer branches are considered less costly because they are weighted using branch lengths (Maddison, 1991). Although this methodology has been criticized for producing wide confidence intervals for the reconstructed values, its accuracy can be increased by including fossil taxa or increasing taxon sampling (Finarelli & Flynn, 2006). Here, the second option was preferred, since whole scapulae are scarce in the fossil record due to the thinness of the scapular blade. Once the ancestral scapular sizes and shapes were reconstructed, the scapular morphology of living species was used to infer locomotor type at several nodes.

All analyses were performed using the software package MorphoJ (Klingenberg, 2011), except for the ANOVAs and MANOVAs, which were carried out with SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA).

Results

The shape variation of the carnivoran scapula is significantly influenced by both size and phylogeny. The regressions of the shape variables (Procrustes coordinates) onto CS and log CS produced similar results, indicating that about 17% of scapular shape variation is caused by size differences among species (CS: 16.71% / log CS: 17.18%; $p < 0.0001$ in both cases) (Fig. VI.S1). Furthermore, the permutation test revealed a strong phylogenetic signal in scapular shape ($p < 0.0001$). Together with the MANOVA performed on the Procrustes coordinates, which revealed significant shape differences between locomotor types ($p < 0.0001$), these results indicate that scapular morphology responds to the complex interaction of allometric, phylogenetic, and functional effects.

Shape variability

The broken-stick model suggested that the first eleven PCs could be interpreted. Table

Table VI.4. Effect of size, phylogeny and locomotor type in the first principal components. The allometric

effect on each principal component (PC) was determined using regression methods, which allows the shape variation explained by size changes to be expressed as a percentage of the total. Non-significant results (i.e., p-value > 0.05) are presented in *grey bold italics*. Abbreviations: % acc., accumulated percentage of explained shape variance; % var., percentage of shape variance explained by each PC; CS, centroid size.

	% var.	% acc.	allometric effect		phylogeny	locomotor type
			CS	log CS		
PC1	37.42%	37.42%	p < 0.0001 (35.13%)	p < 0.0001 (32.81%)	p < 0.0001	p < 0.0001
PC2	16.38%	53.80%	p = 0.0003 (11.94%)	p < 0.0001 (20.89%)	p < 0.0001	p = 0.0036
PC3	9.50%	63.30%	<i>p = 0.0968</i> <i>(2.74%)</i>	p = 0.0336 (4.47%)	p < 0.0001	p < 0.0001
PC4	8.28%	71.59%	p = 0.0058 (7.03%)	p = 0.0438 (3.98%)	p < 0.0001	p < 0.0001
PC5	5.98%	77.56%	<i>p = 0.0837</i> <i>(3.03%)</i>	p = 0.0434 (3.89%)	p < 0.0001	<i>p = 0.0774</i>
PC6	4.06%	81.62%	p = 0.0019 (9.36%)	p = 0.0034 (7.77%)	p < 0.0001	<i>p = 0.1093</i>
PC7	3.24%	84.86%	<i>p = 0.1285</i> <i>(2.31%)</i>	<i>p = 0.2438</i> <i>(1.37%)</i>	p < 0.0001	<i>p = 0.3915</i>
PC8	2.05%	86.91%	<i>p = 0.4314</i> <i>(0.62%)</i>	<i>p = 0.5667</i> <i>(0.32%)</i>	p < 0.0001	p = 0.0032
PC9	1.94%	88.85%	<i>p = 0.6798</i> <i>(0.16%)</i>	<i>p = 0.4905</i> <i>(0.49%)</i>	<i>p = 0.5244</i>	<i>p = 0.0606</i>
PC10	1.36%	90.21%	<i>p = 0.0915</i> <i>(2.85%)</i>	p = 0.0467 (3.83%)	<i>p = 0.1719</i>	p = 0.0116
PC11	1.26%	91.47%	<i>p = 0.8201</i> <i>(0.05%)</i>	<i>p = 0.3289</i> <i>(1.00%)</i>	p = 0.0002	<i>p = 0.6582</i>

VI.4 shows the results for the allometric regressions and the ANOVAs by family and locomotor type for each of those PCs. Each of the first four PCs was significantly related to size, phylogeny and locomotor type (Table VI.4). On the other hand, PC5 through PC11 showed a varied relationship with these factors (Table VI.4), being significantly related either to one, two, or none of them.

The first PC explained 37.42% of the shape variation of the carnivoran scapula, clearly separating pinnipeds and fissipeds (Fig. VI.3). Extreme negative PC1 scores corresponded to short and wide scapulae with large fossae, a broad neck, and a poorly developed acromion. On the other hand, extreme positive PC1 scores were associated to long and narrow scapulae, with well-developed hamatus and suprahamatus processes, a high scapular spine, and an extremely reduced anterior part of the vertebral border.

The shape changes associated to PC2 (16.38%) were mainly related to the relative development of the fossae. Species with the lowest PC2 scores had an expanded infraspinous fossa and a smaller supraspinous fossa, while the opposite was true for those with high PC2 scores (Fig. VI.3). Furthermore, the expansion of the supraspinous fossa along PC2 was accompanied by its flattening. The dorsal end of the spine displaced

caudally as the cranial part of the vertebral border expanded and the caudal part contracted. Finally, as in PC1, the acromion processes were poorly developed at the negative end and clearly distinct at the positive end.

Together, PC3 and PC4 accounted for 17.78% of shape variation (Table VI.4). Increasing PC3 scores resulted in the expansion of the caudal part of the vertebral border and the contraction of the cranial part, which resulted in the cranial displacement of the dorsal spine (Fig. VI.3). Furthermore, both the cranial and caudal borders expanded, increasing scapular width. The well-developed acromion became larger and wider, and twisted its orientation relative to the scapular blade. Regarding PC4, the cranial border expanded with increasing PC4 scores, reducing the cranial part of the vertebral border and enlarging the supraspinous fossa (Fig. VI.3). On the other hand, the caudal part of the vertebral border shifted distally at the caudal angle, while the glenoid cavity displaced caudally, which

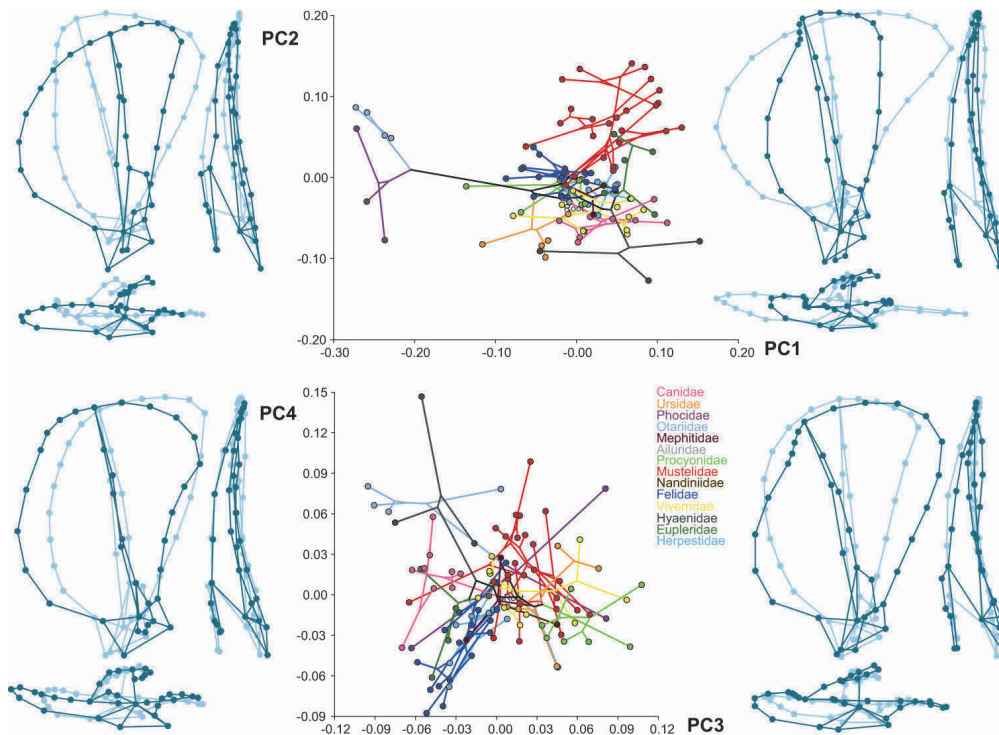


Figure VI.3. Principal components analysis of the shape variation of the carnivoran scapula. Phylomorphospaces defined by the first four principal components (PCs), which explained over 70% of shape variation. The tree topology projected on each phylomorphospace corresponds to the phylogeny presented in Figure VI.1. The shape change associated to each PC is represented using wire-frames, from the most negative values (light) to the most positive ones (dark). For each PC, a set of three pairs of wire-frames is presented so that shape changes can be observed in lateral (x-y; left), dorsal (x-z; bottom), and caudal (y-z; right) views.

resulted in a short and concave caudal border. Furthermore, the acromion processes shrank and the scapular blade increased its curvature.

No clear phylogenetic pattern could be observed in the phylomorphospace defined by those pairs of PCs (other than the pinniped/fissiped separation; Fig. VI.3), nor any clustering of locomotor types became apparent using those axes (Fig. VI.S2). This is probably related to those PCs being significantly affected by size, phylogeny and function at the same time, and again suggests that scapular morphology in Carnivora results from the complex interaction of those factors.

Allometric effect

Although the regressions of shape onto CS and log CS produced similar results, several observations could be made from the scatter plots (Fig. VI.S1). First, pinnipeds were placed well above the main regression line (i.e. present higher shape values than similar-sized fissipeds), which could be affecting the regression results. Indeed, repeating the regressions on a subsample excluding Pinnipedia (i.e., fissiped subsample) revealed that the allometric effect decreased to 11.78% and 14.40% when using CS and log CS, respectively. Second, the allometric effect seemed to vary in the different carnivoran families (see 95% confidence ellipses in Fig. VI.S1). And third, log-transforming centroid size did not linearize the relationship of shape and size, which in bivariate scaling studies suggests the presence of differential scaling (Bertram & Biewener, 1990; Chapters III & IV).

Regarding the allometric effect on the different PCs, the regressions on CS and log CS produced different result in several cases. In the case of PC2 size explained about 12% of shape variation when using raw CS data, but close to 21% when using log CS. Similarly, the regression on log CS for PC3, PC5 and PC10 were significant but not those using raw CS data (Table VI.4). This would suggest that the shape changes described by those PCs are more strongly affected by size in small species than in large carnivorans. On the other hand, the shape changes described by PC4 should be more accentuated in large species, since the magnitude of the allometric effect almost halves and is barely significant when using log CS (Table VI.4).

In light of these results, the effect of size on scapular shape was further explored, separately, in the different carnivoran families and locomotor types studied (Table VI.S1). Overall, the regressions on CS and log CS produced similar results, which suggested that the differential scaling observed in scapular shape is a consequence of scaling differences among carnivoran families and/or among locomotor types, not among different-sized

species. For instance, the allometric effect detected in Felidae, Mustelidae, and scansorial carnivorans, was consistent, no matter the size variable used, despite the wide size ranges of those groups. A significant allometric effect was found in Mustelidae, Felidae, and Herpestidae, and in scansorial, terrestrial, semifossorial, and semiaquatic carnivorans (Table VI.S1). It is interesting to note that, although the amount of shape variation explained by size differences was large in Ursidae, Procyonidae, and Eupleridae, the regressions were not significant, probably due to the small sample size of those families.

In order to further explore the relationship between shape, size and phylogeny, the regression of shape variables on log CS was repeated using phylogenetically independent contrasts (PIC). This methodology incorporates the phylogenetic structure of the sampled species into the analysis, and thus accounts for the potential correlation of the error terms that could arise due to the lack of independence among species (Felsenstein, 1985). The allometric effect was still significant when taking into account the phylogenetic signal in the studied dataset, but the amount of shape variation explained by size dropped to 5.31% (5.75% in the fissiped subsample). These results suggest that most of the allometric shape differences found in the carnivoran scapula are related to size changes along phyletic lines. Finally, when studying the effect of size on scapular shape in the different families and locomotor types, PIC regressions only showed a significant allometric effect in Mustelidae, Herpestidae, and scansorial carnivorans (Table VI.S1). Furthermore, the amount of scapular shape variation explained by size was greatly reduced in all subsamples but herpestids. These results also indicate that, in the rest of subsamples for which a significant allometric effect was reported above, allometric shape differences were related exclusively to size changes along phyletic lines.

Summarizing, the results of the present study suggest that there is evidence for differential scaling in the shape of the carnivoran scapula, which is mainly caused by differences among carnivoran families. In fact, although size explains about 17% of scapular shape variation in Carnivora, only 5.3% of this allometric shape variation is not related to size changes along phyletic lines.

Shape and locomotion

The CVA on shape variables grouping species by locomotor type produced six non-zero CVs. The first two accounted for 82.37% of shape variation (Table VI.5), and defined a shape space in which all groups were clearly separated (Fig. VI.4). However, DFs were not able to significantly separate either between semifossorial and semiarboreal, scansorial and

Table VI.5. Canonical variates analysis of scapular shape by locomotor type. The allometric effect on each canonical variate (CV) was determined using regression methods, which allows the shape variation explained by size changes to be expressed as a percentage of the total. Non-significant results (i.e., p-value > 0.05) are presented in *grey bold italics*. Abbreviations: % acc., accumulated percentage of explained shape variance; % var., percentage of shape variance explained by each CV; CS, centroid size.

	% var.	% acc.	allometric effect	
			CS	log CS
CV1	63.58%	63.58%	p < 0.0001 (23.30%)	p < 0.0001 (17.67%)
CV2	18.79%	82.37%	<i>p = 0.6808</i> (0.17%)	<i>p = 0.4004</i> (0.70%)
CV3	11.94%	94.31%	<i>p = 0.1804</i> (1.82%)	<i>p = 0.1813</i> (1.78%)
CV4	2.98%	97.29%	<i>p = 0.5060</i> (0.48%)	<i>p = 0.5352</i> (0.39%)
CV5	1.88%	99.16%	<i>p = 0.6879</i> (0.17%)	<i>p = 0.5420</i> (0.37%)
CV6	0.84%	100.0%	p = 0.0021 (8.70%)	p = 0.0007 (10.87%)

terrestrial carnivorans, or between semiarboreal and terrestrial carnivorans (Table VI.6). Small sample sizes probably affected the resolution of DFs, as probably the rather broad definition of the terrestrial category did.

Since the previous analyses suggested a strong interaction between phylogeny and size in scapular shape (see above), the CVA and DFAs were repeated on the residuals of the PIC regression of shape variables onto log CS. The results of these size- and phylogeny-corrected analyses were practically identical to those of the original dataset (results not shown), suggesting that locomotor adaptations in scapular shape are independent of size or shared ancestry in Carnivora. Thus, only the results of the uncorrected analyses are further discussed, since they provide a more realistic comparison for reconstructed ancestral shapes.

	arb	sarb	scan	terr	sfos	saq	aq
arb	-	33.3% / 33.3%	16.7% / 8.3%	33.3% / 6.1%	16.7% / 25%	33.3% / 12.5%	0% / 25%
sarb	0.0050	-	50% / 19.4%	66.7% / 33.3%	66.7% / 50%	16.7% / 12.5%	0% / 25%
scan	< 0.0001	0.0170	-	22.2% / 18.2%	8.3% / 75%	0% / 25%	0% / 12.5%
terr	< 0.0001	0.3560	< 0.0001	-	15.2% / 75%	33.3% / 37.5%	0% / 37.5%
sfos	0.0090	0.1680	0.3440	0.4150	-	0% / 12.5%	0% / 12.5%
saq	< 0.0001	0.0160	< 0.0001	0.0030	0.0190	-	12.5% / 25%
aq	0.0020	0.0010	< 0.0001	< 0.0001	0.0010	< 0.0001	-

Table VI.6. Shape differences between locomotor types. Each pair of locomotor types was compared using discriminant function analysis based on Procrustes distances. The p-value for each of the pairwise comparisons appears under the diagonal, whereas values over that line represent misclassification rates of the cross-validation procedure. The first percentage indicates the amount of row-group species misclassified as column-group carnivorans, while the second percentage corresponds to column-groups species incorrectly placed into the row-group. Results of non-significant pairwise comparisons are presented in *grey bold italics*. Abbreviations: aq, aquatic; arb, arboreal; saq, semiaquatic; sarb, semiarboreal; scan, scansorial; sfos, semifossorial; terr, terrestrial.

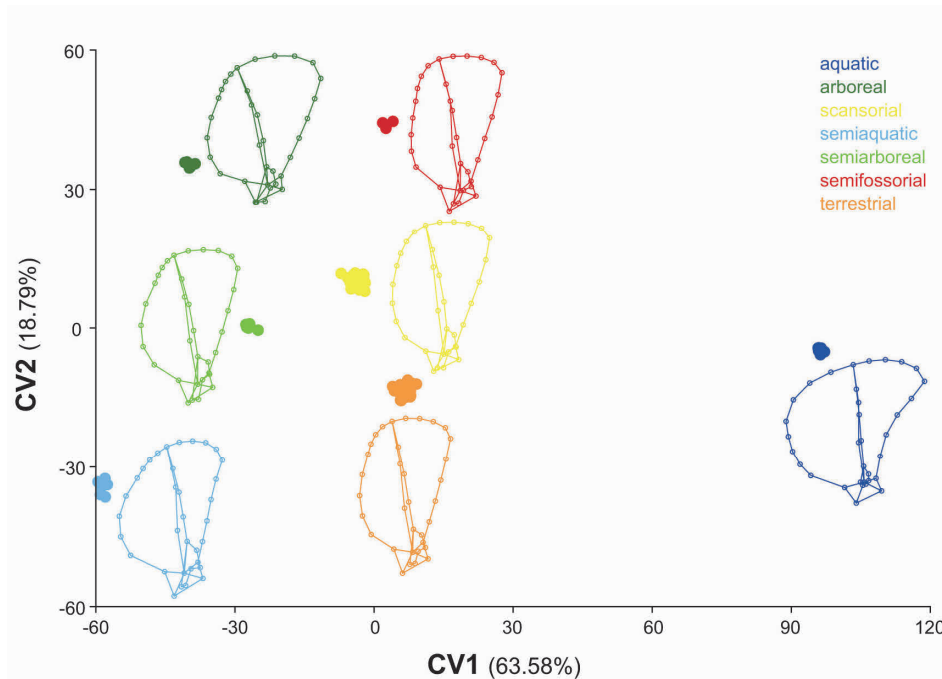


Figure VI.4. Canonical variates analysis of the shape variation of the carnivoran scapula, grouped by locomotor type.

Percentages express the amount of shape variance explained by each canonical variate (CV). The mean shape of each locomotor type categories is also presented (lateral view).

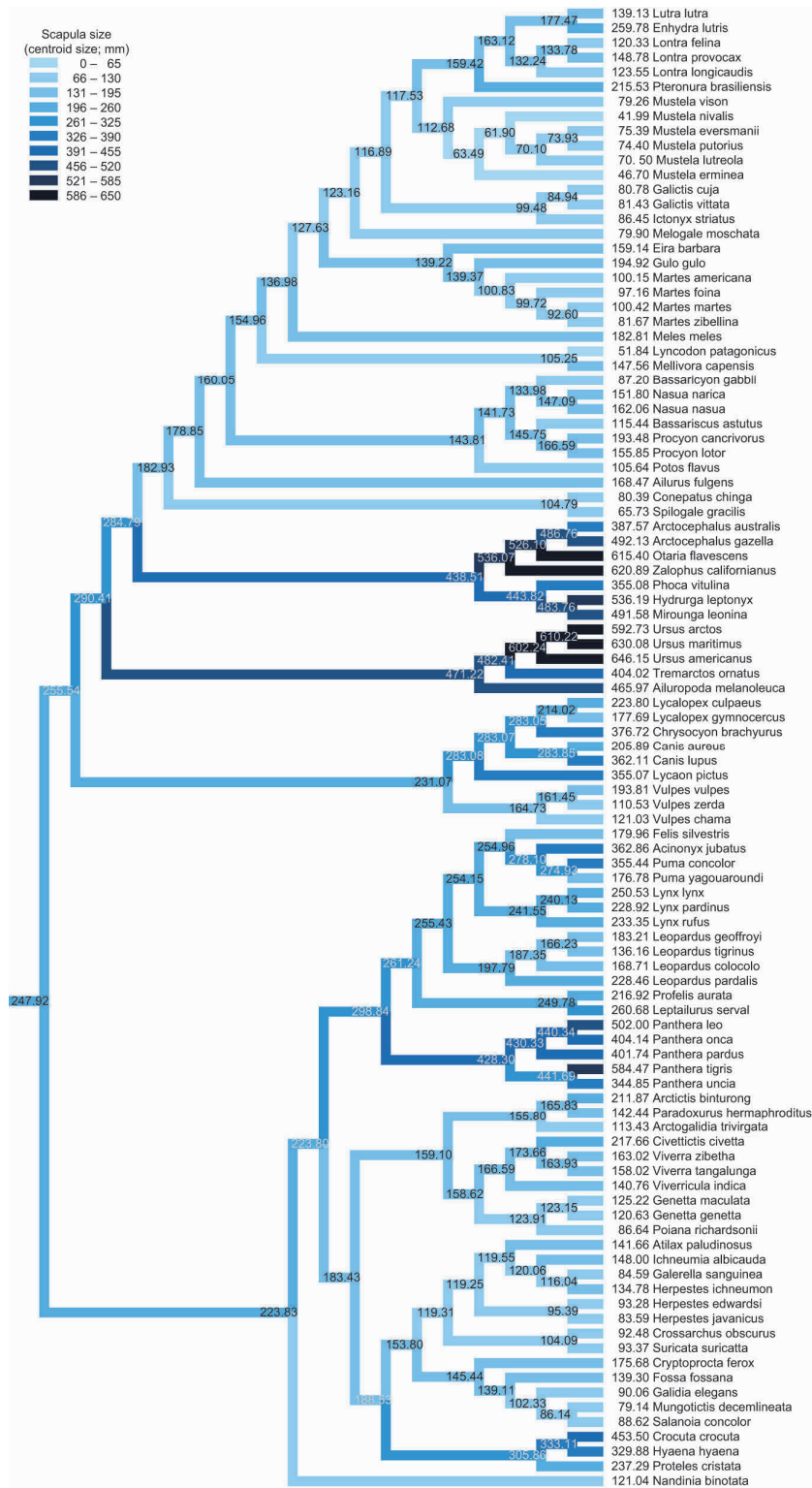
The first CV explained 63.58% of scapular shape variation and was significantly affected by size (Table VI.5). CV1 clearly separated aquatic carnivorans on one extreme and semiaquatic species on the other, while the other locomotor type categories occupied an intermediate position with increasing CV1 scores as arboreality decreased (Fig. VI.4). The shape changes associated to CV1 corresponded to an expansion of the vertebral border and a flattening of the scapular blade, coupled with a reduction and reorientation of the acromion processes. Furthermore, the scapular neck narrowed and the spine straightened from a cranially bent position.

The highest and lowest CV2 scores corresponded, respectively, to semifossorial and semiaquatic carnivorans (Fig. VI.4). CV2 described a reorientation of the glenoid cavity and the acromion, the former aligning with the scapular blade from a medially oriented position and the latter shifting cranio-laterally. Furthermore, the infraspinous fossa expanded and the supraspinous fossa slightly contracted.

Ancestral state reconstruction

Reconstructed ancestral states for scapular size and shape are presented, respectively, in Figures VI.5 and VI.6. The basal carnivoran had a centroid size of 247.92 mm, which corresponds to the size of the scapula of some extant medium-sized species (e.g. most

Figure VI.5. Ancestral states reconstruction of scapular size. Values at terminal nodes represent mean centroid size of the scapula (CS) for each species, while values at internal nodes correspond to estimated ancestral sizes. Branch shading corresponds to estimated CS values, and is maintained for cross-reference with Figure VI.6. To ease the visualization of the results, branch lengths are not drawn at their proportional length (see Fig. VI.1 for actual branch lengths).



lynxes (*Lynx sp.*), the larger otters (*Enhydra, Pteronura*), and the aardwolf (*Proteles*). In caniform carnivorans, scapula size first increased, leading to increasingly larger clades (Canidae, Ursidae, Pinnipedia), and then decreased in the musteloid clades (Fig. VI.5). On the other hand, scapula size decreased during the evolution of most feliform clades, increasing only in Felidae and Hyaenidae (Fig. VI.5).

The scapula shape reconstructed for the carnivoran ancestor did not resemble any of the shapes of the extant species (Fig. VI.6A). The shape of its scapular blade roughly corresponded to that of some genets and mongooses, but in the former both the insertion of *m. levator scapulae* and the acromion processes were shorter, while in the latter the vertebral border was more dorsally extended and the spine and acromion had a rather different shape. The ancestral shape did closely match the mean shape of scansorial carnivorans (Figs. VI.4, VI.6A), however, suggesting that the carnivoran ancestor was a good climber but spent most of its time on the ground. The main differences between both shapes were a slightly larger infraspinous fossa in the carnivoran ancestor than in the mean scansorial shape, and an acromion similar to the mean terrestrial shape, although more cranially oriented (as in scansorial species) (Figs. VI.4, VI.6A). The former differences indicate a higher degree of arboreality than in extant scansorial carnivorans, while the latter could be interpreted as a different solution for the same problem (moderate degree of arboreality).

From this ancestral shape, the carnivoran scapula suffered several major shape changes along the branches leading to the extant families. Thus, the evolution of the carnivoran scapula is more deeply addressed in the discussion of these results.

Discussion

Morphological variation in the carnivoran scapula

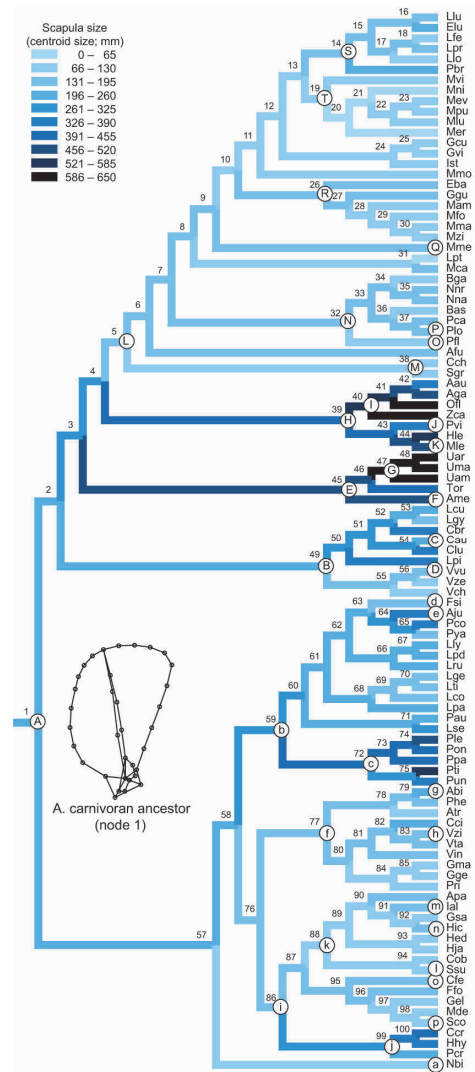
According to previous studies, the shape of the mammalian scapula is strongly linked to shared evolutionary history and, within each lineage, shape variability can be attributed either to size differences between closely related species (Didelphidae, Astúa, 2009), or to different functional requirements (Xenarthra, Monteiro & Abe, 1999; Caviomorpha, Morgan, 2009; Anthropoidea, Young, 2008). However, the results of the present study suggest that, in Carnivora, scapula shape reflects the complex interaction of historical, allometric and functional effects. Not only can none of these factors alone explain the high shape variability of the carnivoran scapula (Figs. VI.3, VI.S1, VI.S2), but also this shape

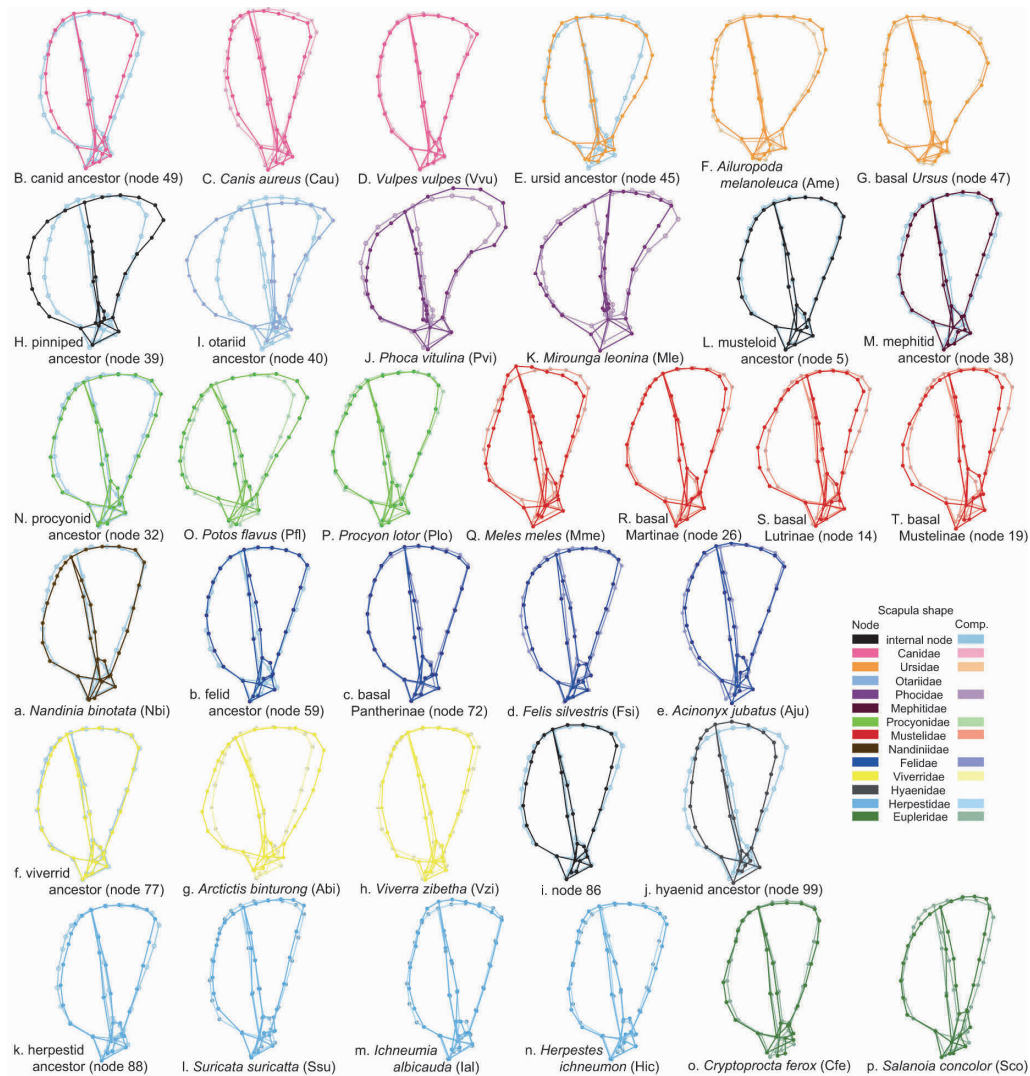
Figure VI.6. Ancestral states reconstruction of scapular shape. (double page)

Wire-frames correspond to either selected estimated internal nodes or to mean scapular shapes of extant species. For clarity, only the most significant nodes are shown. The shape of the carnivoran ancestor (A) and those of Caniformia are labeled with upper case letters (B, C,...), while Feliformia uses lower case letters (a, b,...). Internal nodes common to several families (H, L, i), plus the ancestor of each family (e.g. B, b), are compared to the estimated shape of the carnivoran ancestor (node A). Terminal taxa (e.g. C, d) and internal nodes within families (e.g. G, c) are compared to the ancestor of their family instead (e.g. C to B). All scapular shapes are presented in lateral view. Branch shading in the phylogenetic tree corresponds to estimated CS values, and is maintained for cross-reference with Figure VI.5. To ease the visualization of the results, branch lengths are not drawn at their proportional length (see Fig. VI.1 for actual branch lengths). Legend: "Node" denotes the main color used on the wire-frames of each family, while "Comp." is the color used on the comparative wire-frames. See Table VI.1 for species names abbreviations.

variability is highly correlated to all of those factors, considering either scapula shape as a whole (Procrustes coordinates, see Results) or the main axes of shape variation separately (PC1 to PC4, Table VI.4). Previous studies on forelimb long bones have reported a similar strong interaction between size, phylogeny and function in Carnivora (Walmsley et al., 2012; Fabre et al., 2013a).

The principal components analysis not only defined the main axes of shape variation, but it also identified the scapular regions in which most of this variation occurred. That is, while the shape changes of most scapular regions were characterized by one or few PCs (e.g. PC2 and PC4 defined the angle between the spine and the glenoid cavity), those of some other regions were described by most PCs, suggesting that they represent most of the shape variability of the carnivoran scapula. One of these regions was the vertebral border, in which the serratus ventralis muscle (= *m. serratus anterior sensu lato*) inserts. This muscle can be subdivided into an anterior part (*m. levator scapulae*), which inserts on the cranial part of the vertebral border, and a posterior part (*m. serratus anterior sensu stricto*), inserting on the caudal part of the vertebral border. The former protracts the forelimb, while the latter retracts it (Smith & Savage, 1956; Argot, 2001). The major shape changes





observed in the vertebral border were its overall expansion/contraction, the relative length of its cranial and caudal parts, and the angulation between these parts (Fig. VI.3). All of these features determine the size and moment arms of mm. levator scapulae and serratus anterior *s. s.*, and have already been related to several locomotor specializations (Oxnard, 1968; Taylor, 1974; English, 1977; Argot, 2001; Astúa, 2009; Morgan, 2009). A second region of high shape variability were the fossae, which varied mainly in their overall extension and in their relative development (i.e. whether the supraspinous or infraspinous fossa was larger) (e. g. PC1–PC3; Fig. VI.3). Larger scapular fossae reflect enlarged supraspinous and infraspinous muscles (Roberts, 1974). Besides its main function as shoulder stabilizers, these muscles play an important role in shoulder mobility (Argot,

2001): *m. supraspinatus* protracts the humerus, while *m. infraspinatus* rotates it. Furthermore, both support humeral abduction. Thus, the relative development of the fossae indicates whether greater forelimb protraction or rotation is required during locomotion. Finally, another common feature of most PCs was the degree of development of the hamatus and suprahamatus processes (e.g. PC1, PC2, PC4; Fig. VI.3). The former provides insertion to the acromiodeltoid muscle, the main abductor of the forelimb, while the acromiotrapezius and omotransversarius muscles attach to the latter and move the scapula cranially (Larson, 1993; Argot, 2001). Furthermore, the orientation of the processus hamatus has been related to several locomotor adaptations (Smith & Savage, 1956; Lehmann, 1963; Roberts, 1974; Taylor, 1974; Argot, 2001).

The fact that most shape variation in the carnivoran scapula occurs in the vertebral border, fossae, and acromion, would explain the different results obtained here and in a previous study (Martín-Serra et al., 2014). In that study, the authors concluded that the main axis of shape variation in the carnivoran scapula (their PC1) corresponded to the transition “from the long and slender scapula of canids and procyonids [...] to the wide and robust one of bears” (Martín-Serra et al., 2014). However, landmark selection in that study was restricted to the distal scapula (acromion, scapular neck and glenoid) plus two landmarks encompassing the origin of the teres muscle (caudal border), and thus largely omitted the major regions of shape variation characterizing scapula length and width (vertebral border, fossae). In fact, according to the landmarks sampled in that study, decreasing scores of their PC1 corresponded to an expansion of the scapular neck and the acromion and a dorsocaudal displacement of the caudal angle (see Figures 1A and 7A in Martín-Serra et al., 2014). Thus, their conclusion was probably a misinterpretation of the 3D models used to visualize shape changes. Another argument against the aforementioned conclusion is that procyonids do not present long and slender scapulae (compare the shapes of *Procyon lotor*, Plo, and *Canis aureus*, Cau, in Figure VI.6C, P).

Further discrepancies between the results of the present study and those of Martín-Serra et al. (2014) were the amount of scapula shape variation explained by the allometric effect (significantly higher in the present study), and the evolutionary history of shape changes in the carnivoran scapula (the previous study found that the different carnivoran families occupied well-differentiated portions of the morphospaces, while in the present study consistent overlapping between families was observed). Both of these discrepancies could be related to the different species composition of both studies. While in the present study the sampling effort was put in representing accurately the living diversity of

Carnivora, Martín-Serra et al. (2014) focused on reconstructing the evolutionary history of the large-bodied families, including both living and extinct species of those families. The usually higher percentages of allometric shape variation obtained in the present study when using log-transformed centroid size (which magnify changes at small sizes) suggest that size has a larger effect on the shape of the scapula in small carnivorans. Thus, a lower allometric effect would be expected in a sample consisting mainly of large species, as that of Martín-Serra et al. (2014). In fact, removing from the sample the species not measured in the previous study resulted in the allometric effect explaining around 10% of scapula shape variation, very close to the value reported by Martín-Serra et al. (2014). Another possible explanation would be that the shape of the fossae and spine was more heavily influenced by size differences than that of the acromion or coracoglenoid regions. However, this explanation is unlikely, since shape variation between the scapular blade and the acromion is highly integrated (Young, 2004). Furthermore, the regression of shape on size in a subsample consisting only of landmarks measured on the scapular blade and spine produced similar results to that performed on a subsample including only acromion and glenoid landmarks (results not shown). Finally, regarding phylomorphospace occupation, if only the living species measured by Martín-Serra et al. (2014) are represented in the morphospaces shown in Figure VI.3, most remaining families are confined to separate regions of the morphospace, mirroring the results of the previous study.

Differential scaling on scapula shape in Carnivora

The results of the present study strongly support the presence of differential scaling in the shape of the carnivoran scapula. That is, the amount of shape variation explained by size differences varies with increasing size.

One of the arguments favoring differential shape scaling are the higher shape values found in pinnipeds relative to similar-sized fissipeds (Fig. VI.S1). In fact, differences in centroid size explain 19.32% of scapula shape variation in pinnipeds (21.06% using log CS), whereas the allometric effect accounts for 11.78% or 14.40% of this variation in fissipeds (CS or log CS, respectively). Since size changes along phyletic lines account for most of the allometric effect on scapula shape in Carnivora, it could be argued that the scaling differences between fissipeds and pinnipeds would have a similar explanation. However, PIC regressions of shape on size also show a higher allometric effect in pinnipeds than in fissipeds (8.69% and 5.75%, respectively), confirming the scaling differences between both

groups.

Further evidence for differential shape scaling in the carnivoran scapula is provided by the different percentages obtained in fissipeds when using CS and log CS as the size variable, which suggest that the allometric effect is larger in small fissipeds (since using log CS emphasizes shape changes at small sizes). In agreement with this, Martín-Serra et al. (2014) found a lower allometric effect in the shape of the carnivoran scapula using a sample of mostly large-sized fissipeds (a result that could be replicated in the present study reducing the sample to include only the species measured in the previous study, see above). Additionally, the results obtained for the different family and locomotor type subsamples also support differential shape scaling in fissipeds, since the allometric effect decreased in the groups including progressively larger species (Herpestidae > Mustelidae > Felidae; semifossorial > semiaquatic > scansorial, terrestrial; Table VI.S1).

Summarizing, the allometric effect on scapula shape is stronger in pinnipeds than in fissipeds and, within the latter, the effect of size is more pronounced in small species. Astúa (2009) reported a similar result in Didelphidae. However, in this group scapula shape variation was more heavily influenced by size in large species, since shape differences between locomotor habits could be observed in large didelphids but all small species had similarly shaped scapulae.

Locomotor adaptations in the carnivoran scapula

Swimming

The biomechanical demands of locomotion in water are highly different from those of overland locomotion (Alexander, 2002; Biewener, 2003). Water is denser and more viscous than air, which increases drag significantly. On the other hand, gravitational forces are the main factor to overcome in overland locomotion. Thus, it was not surprising that aquatic carnivorans exhibited the most characteristic scapula shape, clearly separated from all other locomotor types by CV1 (Fig. VI.4). As previously described for aquatic mammals (Smith & Savage, 1956), aquatic carnivorans presented the relatively shortest and widest scapulae, with a greatly expanded vertebral border (especially its cranial portion) (Figs. VI.4, VI.S3). The wide vertebral border is associated with strong mm. levator scapulae and serratus anterior *s. s.*, reflecting powerful forelimb protraction and retraction. These adaptations would be expected in pectoral oscillators such as otariids, which produce forward thrust beating their enlarged foreflippers (Alexander, 2002; Pierce et al., 2011). In

these animals, the powerful *m. levator scapulae* helps overcome water drag while protracting the forelimb during the recovery phase (upstroke), while the *m. serratus anterior s. s.* retracts the forelimb during the downstroke, pushing the water downward and generating forward thrust. However, phocids swim by pelvic oscillation, generating thrust with horizontal undulations of the spine combined with hindflipper paddling (Williams, 1989; Pierce et al., 2011). Thus, aquatic locomotion cannot explain these enlarged muscles. In phocids, these muscles are probably related to terrestrial locomotion, since on land the forelimbs are used to drag the heavy body, helped by axial movements. The expansion of the vertebral border, particularly its caudal portion, has also been related to an increased attachment area for the *mm. teres major* and *deltoideus* in otariids (English, 1977). In this group, the deltoid muscle consists of a single mass originating from the vertebral border near the caudal angle, extending distally along the ridge of the scapular spine into the acromion, and inserting in the deltoid tuberosity of the humerus (English, 1977). Furthermore, the caudal border of aquatic carnivorans was concave, resulting in a particularly protruding caudal angle (Figs. VI.4, VI.S3), which has previously been related to an increased moment arm of the *teres major* muscle (Smith & Savage, 1956; Monteiro & Abe, 1999). All these adaptations indicate strong *teres major* and deltoid muscles, reflecting powerful humeral adduction and abduction, respectively. In otariids, the forelimb is abducted during the upstroke and adducted during the propulsive downstroke (English, 1977). In phocids, the forelimbs provide directional control (Pierce et al., 2011), which would also involve powerful humeral abduction and adduction, not only to orient the forelimbs, but also to resist the water drag.

In agreement with previous observations on aquatic mammals (Smith & Savage, 1956), the mean scapula shape of aquatic carnivorans was the only one in which the acromion processes were completely absent (Figs. VI.4, VI.S3). This is probably related to the lack of differentiation of the *m. deltoideus* into the *spinodeltoid* and *acromiodeltoid* muscles in pinnipeds, the latter of which originates on the hamatus process (sometimes also on the ventral lip of the *suprahamatus* process; English, 1977).

Finally, as previously described for otariids (English, 1977), aquatic carnivorans presented greatly expanded and flat supraspinous and infraspinous fossae, particularly the former, and a low scapular spine. As stated above, broad fossae indicate a greater development of *mm. supraspinatus* and *infraspinatus*, and thus reflect powerful shoulder stabilization but also enhanced mobility at the glenohumeral joint (Roberts, 1974; Argot, 2001; Morgan, 2009). This increase in shoulder stabilization is probably related to the

greater development of humeral abductors and adductors (i.e., mm. teres major and deltoideus, see above).

Semiaquatic carnivorans shared some scapular features with aquatic species, namely a short scapular blade, a wide and flat supraspinous fossa, a markedly convex vertebral border, and a slightly concave caudal border (Figs. VI.4, VI.S3). Some of these shape features were also described in the semiaquatic marsupial *Chironectes* (Astúa, 2009). However, contrary to aquatic carnivorans, semiaquatic species presented a reduced vertebral border (particularly the cranial portion), a high scapular spine with the acutest angulation relative to the scapular blade, the smallest infraspinous fossa, and well-developed acromion processes (especially the suprahamatus process) (Figs. VI.4, VI.S3). The reduced insertion for m. levator scapulae would suggest weak forelimb protraction in semiaquatic carnivorans, but the action of this muscle is probably supported by the enlarged m. supraspinatus and mm. acromiotrapezius and omotransversarius (indicated, respectively, by the wide supraspinous fossa and the enlarged suprahamatus process). Other scapular features of semiaquatic carnivorans indicate strong humeral retraction and abduction thanks to enlarged mm. teres major and acromiodeltoid (e.g. marked caudal angle, concave caudal border, long hamatus process). Unfortunately, a more detailed explanation of the role of these muscles in the locomotion of semiaquatic carnivorans was not possible due to the varying degree of forelimb usage in the studied species (e.g. minks use their forelimbs for both aquatic and overland locomotion, while otters can be considered pelvic oscillators (see above); Williams, 1983; Williams et al., 2002).

Climbing

Several shape change trends could be observed in the carnivoran scapula as arboreality increased. Overall, the scapular blade became shorter and wider (Figs. VI.4, VI.S3). The increase in width was mainly effected by an expansion of the infraspinous fossa, since the width of the supraspinous fossa remained more or less constant except for arboreal species, in which the supraspinous fossa was also enlarged (due to an expansion of the cranial border) (Figs. VI.4, VI.S3). Furthermore, the medio-lateral curvature of the supraspinous fossa decreased with increasing arboreality. An expansion of the infraspinous fossa in arboreal species was also described in didelphids (Argot, 2001; Astúa, 2009), while arboreal xenarthrans were characterized by an enlarged supraspinous fossa (Monteiro & Abe, 1999). Additionally, arboreal primates also present large scapular fossae, which have been related to greater shoulder stabilization, relatively heavy limbs, powerful limb

movements, and forelimbs used in an extreme protracted or retracted position (Roberts, 1974). As stated above, enlarged fossae are an indication of larger *m. supraspinatus* and *m. infraspinatus*. The main function of these muscles is shoulder stabilization, but they also provide enhanced mobility of the glenohumeral joint (Roberts, 1974; Argot, 2001), which helps reaching for support in the three-dimensional canopy (Monteiro & Abe, 1999).

Regarding the vertebral border, its cranial portion remained more or less constant, while its caudal portion expanded with increasing arboreality (Figs. VI.4, VI.S3). Thus, the *serratus anterior s. s.* would be larger in arboreal species, providing stronger forelimb retraction, but forelimb protraction would be similar regardless of the degree of arboreality, since the insertion area of the *m. levator scapulae* remained fairly constant. While the former was expected, since larger forelimb retractors produce larger tensile forces for protracting the body while climbing (Argot, 2001; Astúa, 2009), the latter seemed quite counterintuitive because reaching for a support during arboreal locomotion normally involves extreme forelimb protraction (Roberts, 1974; Monteiro & Abe, 1999). Arboreal didelphids, for instance, also presented enlarged vertebral borders (Argot, 2001), but this was mainly caused by an expansion of its cranial portion instead (i.e., increased forelimb protraction), which was short and angular in terrestrial species. However, the action of enlarged *m. supraspinatus* of arboreal carnivorans must also be taken into account, since it also acts as a humeral protractor and thus supports the movements of the scapula when reaching for a support. In agreement with this, arboreal didelphids presented relatively smaller supraspinous fossae than terrestrial species (Argot, 2001), since the extra forelimb protraction was not necessary. It is worth noting, however, that Taylor (1974) found differences related to arboreality in the insertion and angulation of the *m. levator scapulae* of “viverrid-like” carnivorans. Thus, although the general trend in arboreal carnivorans is not to modify this muscle, it has been nonetheless changed in some phyletic lines within Carnivora.

The shape changes of the vertebral border were associated with a cranial displacement of the dorsal end of the scapular spine, especially in arboreal species, in which resulted in a marked curvature of the spine along the dorso-ventral axis (Figs. VI.4, VI.S3). This increased curvature results in a longer moment arm for the spinodeltoid muscle, which allows a stronger flexion of the shoulder. Similarly, the expansion of the caudal portion of the vertebral border and of the infraspinous fossa also resulted in an increased moment arm of *m. teres major* (Smith & Savage, 1956; Monteiro & Abe, 1999), one of the major humeral adductors. Both powerful flexion and adduction of the humerus are important in

arboreal mammals, since they help pulling the trunk while climbing (Taylor, 1974; Argot, 2001; Astúa, 2009).

The acromion processes became coplanar with increasing arboreality. Furthermore, as observed in arboreal didelphids (Argot, 2001; Astúa, 2009), the hamatus process both lengthened and shifted cranially, ending up surpassing the glenoid cavity (Figs. VI.4, VI.S3). A longer hamatus process increases the moment arm of *m. acromiodeltoid*, which results in a more powerful yet controlled abduction of the shoulder (Taylor, 1974; Argot, 2001). In parallel, a cranially oriented hamatus process both changes the line of action of the *acromiodeltoid* (so that it contributes to forelimb extension instead of shoulder flexion) and permits abduction of the humerus without colliding with the acromion (Roberts, 1974). It is worth noting that the hamatus process was relatively shorter in arboreal species, since the whole scapula was shortened, but it still extended beyond the glenoid. The shape and orientation of the suprahamatus process remained more or less constant, suggesting that the function of *mm. acromiotrapezius* and *omotransversarius* is not affected by arboreality in carnivorans (cf. other forelimb protractors: *mm. levator scapulae* and *supraspinatus*).

Finally, the glenoid cavity shifted medially and became more cranially adducted in arboreal carnivorans (Figs. VI.4, VI.S3). This shift of the glenohumeral joint places the humerus in a more adducted position, placing the lower arm under the body, which has been shown to increase stability when moving on narrow supports (Schmitt, 2003; Gálvez-López et al., 2011).

Digging

The mean scapula shape of semifossorial carnivorans was not statistically significant from that of semiarboreal, scansorial or terrestrial species (Table VI.6, Fig. VI.4). This could probably be related to the small number of semifossorial species in our sample, since semifossorial carnivorans can be significantly distinguished from other locomotor types using other forelimb elements (Van Valkenburgh, 1987; Bertram & Biewener, 1990). Nevertheless, some features distinguished the scapulae of semifossorial carnivorans. Relative to the terrestrial mean shape, semifossorial species presented a larger infraspinous fossa, a slightly narrower supraspinous fossa (due to the contraction of the cranial border), a lower spine, a more cranially oriented hamatus process, a larger suprahamatus process, and a medially oriented glenoid cavity (Figs. VI.4, VI.S3). In their study on locomotor adaptations in mammals, Smith & Savage (1956) stated that fossorial

species presented a wide and short scapular blade, a high scapular spine, and a long acromion overhanging the glenoid cavity. None of these adaptations were found in semifossorial carnivorans in the present study. A latter study on fossoriality in rodents (Lehmann, 1963) also reported high scapular spines and, most significantly, the presence of a teres major process at the caudal angle. Similarly, Monteiro & Abe (1999) reported that the shape of the scapula in fossorial xenarthrans (armadillos) was characterized by an expansion of the infraspinous fossa at the origin of the teres major muscle (i.e., at the caudal angle) and also by a relatively longer caudal border. These adaptations relate to an enlarged m. teres major (wide origin) with a long moment arm (caudal border) and, thus, to the powerful limb retraction required for digging with the forelimbs (Hildebrand, 1985). As stated above, semifossorial carnivorans presented similar adaptations of the infraspinous fossa.

The evolution of scapular morphology in Carnivora

The reconstruction of the ancestral scapula size and shape suggested that extant carnivorans evolved from a medium-sized scansorial ancestor with a scapula similar in shape to that of some genets and mongooses (Figs. VI.5, VI.6). In a previous study, Gálvez-López (Chapter II) analyzed the residual means of several morphological variables measured on the appendicular skeleton of a large sample of carnivorans, and arrived to a similar conclusion. The author proposed that the carnivoran ancestor was a forest-dwelling animal, with a similar limb morphology to extant “viverrid-like” taxa (i.e. viverrids, herpestids,...) and mixing terrestrial and arboreal adaptations (Chapter II). Both studies are congruent with the placement of “miacids” at the branch leading to extant Carnivora, since recent studies have described a mixed set of adaptations to arboreality and high-speed running in these fossil species (Wesley-Hunt & Flynn, 2005; Spaulding & Flynn, 2009). Other previous studies have proposed that ambulatory species represent the ancestral and unspecialized morphotype in Carnivora (Taylor, 1989; Schutz & Guralnick, 2007). However, comparison with these studies is beyond the scope of the present work, since a proper distinction between generalized and cursorial (*sensu* Stein & Casinos, 1997) carnivorans would require measuring lateral displacements of the limbs during locomotion (e.g. Jenkins, 1971).

Caniformia

Regarding the evolution of the carnivoran scapula, the shape of the ancestral caniform

(node 2; Fig. VI.6) was almost identical to that of the carnivoran ancestor (node 1; Fig. VI.6A), although scapula size was slightly larger (Fig. VI.5). During caniform evolution, the scapula became larger and wider (nodes 3, 4; Fig. VI.6), acquiring the basal size and shape from which the ancestors of the large-bodied ursids and pinnipeds diverged (nodes 45 and 39, respectively; Fig. VI.6E, H). The large scapula sizes reconstructed for basal caniforms agree with the large body mass values estimated by Flynn et al. (2005) for those nodes. However, Finarelli & Flynn (2006) shown that the large ancestral body size of Caniformia was an artifact caused by sampling extant species exclusively. When these authors reconstructed ancestral body sizes including fossil carnivorans in the sample, a small-sized ancestor to Caniformia was the most parsimonious result (Finarelli & Flynn, 2006). Thus, the reconstructed values for ancestral scapula size obtained in the present study must be considered cautiously, since only extant species were measured (due to the scarcity of complete scapulae in the fossil record).

The scapular blade narrowed and lengthened considerably along the branch leading to the ancestor of extant canids (node 49; Fig. VI.6B), while the cranial edge of the supraspinous fossa bent laterally towards the cranial border and the acromion processes were significantly reduced. All these changes suggest that the canid ancestor was already adapted for running efficiently, as previously suggested by Wang (1993). Similar shape changes occurred during the evolution of the Canini tribe (node 50 onwards), producing even narrower and relative longer scapulae (e.g. *Canis aureus*, Cau; Fig. VI.6C). A notable deviation from this trend was the re-acquisition of separate hamatus and suprahamatus processes in *Lycalopex* (node 53). On the other hand, shape changes in the scapulae of the Vulpini tribe (node 55 onwards) were small and mostly occurred along the terminal branches. A characteristic feature of vulpine species was a caudal angle projected caudad (e.g. *Vulpes vulpes*, Vvu; Fig. VI.6D), which increased the moment arm of *m. teres major*. As explained above, some authors have related this scapular feature to fossoriality (Lehmann, 1963; Monteiro & Abe, 1999). The fact that foxes often bury their captures for latter consumption supports this finding (Wilson & Mittermeier, 2009).

According to its reconstructed scapula size, the ursid ancestor had a similar size than extant pandas (*Ailuropoda melanoleuca*; Fig. VI.5). However, this must be considered cautiously, since the fossil record suggests that early ursids were small- to medium-sized animals (McLellan & Reiner, 1994; Finarelli & Flynn, 2009). The expanded caudal border of the scapula shape reconstructed for the ursid ancestor (node 45; Fig. VI.6E) suggests that the enlarged postscapular fossa was already developed. Similarly, the scapula of the ursid

ancestor presented an almost rectangular scapular blade and a broad neck. All these scapular features have been previously described by Davis (1949) as characters distinguishing bears from other carnivorans. The scapula shape of the ursid ancestor was characterized by a relatively short and wide scapular blade, an expanded vertebral border (particularly in its caudal portion), and a wide and cranially-oriented acromion extending beyond the glenoid cavity (Fig. VI.6E). All these scapular features are typical of arboreal carnivorans (see *Climbing*, above), which suggests that the ancestor of extant ursids had a higher degree of arboreality than extant species, as already suggested by Oxnard (1968). All these arboreal features were further developed in the ailurine line, resulting in the extreme scapula shape of the giant panda (*Ailuropoda melanoleuca*, Ame; Fig. VI.6F). The spectacled bear (*Tremarctos ornatus*, Tor), the only living representative of the tremarctine subfamily, is one of the most arboreal of extant ursids and presents a scapula shape almost identical to the ursid ancestor, although with a longer and more ventrally-oriented acromion (shape not shown). The high degree of arboreality of basal ursids and modern tremarctine bears (Tor) suggests that the alleged adaptations for endurance running of the larger tremarctine species (e.g. *Arctodus*; Matheus, 1997) probably represent an evolutionary dead-end in this lineage. Finally, all ursine bears shared a similar scapula size and shape (node 47 onwards; Figs. VI.5, VI.6G), mainly characterized by an extremely convex vertebral border with a marked angulation between its cranial and caudal portions. This scapular feature indicates a clear functional division of the two parts of *m. serratus ventralis* in protraction and retraction of the forelimb (Smith & Savage, 1956), and is probably related to the large force required in the particular climbing style of these bears (i.e., “bracing”; Davis, 1949). When “bracing” climbing, the bear first grips the trunk with both forelimbs and pulls the body through the forelimbs (using the forelimb retractors, i.e. *m. serratus ventralis s. s.*) and then secures the hind limbs upper on the trunk while most of the body weight is suspended by the forelimbs (using the forelimb protractors, i.e. *m. levator scapulae*).

The reconstructed scapula shape for the pinniped ancestor was similar to the mean scapula shape of aquatic carnivorans (node 39; Figs. VI.4, VI.S3, VI.6H), supporting the hypothesis that the transition to an aquatic lifestyle occurred shortly after this phyletic line diverged from their shared ancestor with musteloid carnivorans (Arnason et al., 2006; Rybczynski et al., 2009). The main difference between the scapula shape of the pinniped ancestor and the mean shape of aquatic carnivorans was a dorsocaudal expansion of the vertebral border, which is also the scapular feature common to all the oldest pinniped

fossils (i.e., *Puijila*, *Potamotherium*, *Enaliarctos*; Rybczynski et al., 2009). It is also interesting to note that, in the phylomorphospace defined by PC1 and PC2, the branch leading to Pinnipedia extended almost perpendicularly to the latter at null PC2 scores (Fig. VI.3), indicating that both fossae were enlarged simultaneously prior to the Phocidae/Otariidae split. Then, after the split, otariids expanded towards positive PC2 scores (i.e., enlarged supraspinous fossa) and phocids towards negative PC2 scores (i.e., enlarged infraspinous fossa). Otariids swim using their forelimbs for propulsion (pectoral oscillators), while in phocids forward thrust is generated with axial undulation and hind limb paddling (pelvic oscillators; see *Swimming*, above). Thus, the expansion of the supraspinous and infraspinous fossae could be related to swimming using the forelimbs or hind limbs, respectively. This finding seems congruent with the hypothesis that early pinnipeds swam quadrupedally using both the forelimbs and the hindlimbs for propulsion (Rybczynski et al., 2009), since both fossae were enlarged simultaneously during the early evolution of this clade. The reconstructed ancestral shapes for the internal nodes of Otariidae and Phocidae further support this interpretation of the phylomorphospace: an expansion of the supraspinous fossa was characteristic of the otariid ancestor (node 40; Fig. VI.6I), while the infraspinous fossa was enlarged in basal phocids (nodes 43, 44; Fig. VI.6J). Additionally, a secondary expansion of the supraspinous fossa was observed in the elephant seal (*Mirounga leonina*, Mle; Fig. VI.6K), probably reflecting the need of powerful forelimb protractors to drag their heavy body on land. Finally, it is worth noting that no significant shape changes occurred during otariid evolution, as it would be expected given the recent radiation of this clade (Nyakatura & Bininda-Emonds, 2012; Fig. VI.1).

According to its reconstructed scapula size and shape, the musteloid ancestor was a medium-sized scansorial mammal (node 5; Figs. VI.5, VI.6L). Its scapula shape was very similar to the carnivoran ancestor (node 1; Fig. VI.6A), but with a slightly expanded cranial border and a dorsally extended acromion. It also matched closely the mean shape of scansorial carnivorans (Figs. VI.4, VI.S3), although the musteloid ancestor had a wider scapular blade and neck. Unfortunately, the fossil record for the Musteloidea is incomplete for most lineages, especially regarding the postcranium (Kurtén & Anderson, 1980; Wolsan, 1993). Thus, a direct comparison between the locomotor type inferred from the reconstructed scapula shape and that of early musteloid fossils could not be made. Fabre et al. (2013*b*) conducted a similar study on extant musteloids focusing on the shape of the forelimb long bones, but they reported equivocal results when trying to infer the locomotor type of the musteloid ancestor. The reconstructed centroid size of the musteloid

ancestor was 182.93 mm, which corresponded to extant carnivorans in the 4.5 – 9.5 kg body mass range. These values are intermediate between the body mass estimate produced by Finarelli & Flynn (2006) using only extant species and that recovered in the same study after including fossils in the sample. No significant shape changes occurred in the internal nodes representing the divergence of the musteloid families (nodes 5-7; Fig. VI.6), while reconstructed centroid size values decreased, but remained within the same body mass range (Fig. VI.5).

The mephitid ancestor presented a particular scapula shape that could not be matched to any of the locomotor type mean shapes (node 38; Figs. VI.4, VI.S3, VI.6M). However, it did present several scapular features associated with fossoriality, namely an enlarged infraspinous fossa, a low scapular spine, and a large acromion (particularly the suprahamatus process) (see *Digging*, above). Up to date, no postcranial elements of early mephitids have been found, and thus nothing is known of their locomotor habits. Regarding scapula size, the reconstructed value suggested a marten-like size for this ancestor (Fig. VI.5), which is somewhat higher to previous body mass estimations for early mephitids (Finarelli & Flynn, 2009). Finally, it must be noted that only two mephitid species were measured in the present study (Table VI.1), and thus the reconstructed ancestral scapula size and shape for this clade should be considered cautiously.

Previous studies have suggested an arboreal origin for Procyonidae (Romer, 1966; Baskin, 1982; Fabre et al., 2013b), which is strongly supported in the present study. The scapula shape reconstructed for the procyonid ancestor was similar to the mean shape of arboreal carnivorans, but presented even longer and wider acromion processes and a larger scapular blade (node 32; Figs. VI.4, VI.S3, VI.6N). The scapular features related to arboreality (e.g. wide and short scapular blade, long and cranially-oriented acromion) were further developed in the most arboreal extant species: the kinkajou (*Potos flavus*, Pfl) and the olingo (*Bassaricyon gabbii*, Bga) (Fig. VI.6O). Since the kinkajou line diverged early from the procyonid ancestor and the olingos are currently considered sister-taxa to the coatis (*Nasua sp.*; Koepfli et al., 2007), these shape changes must have occurred twice, being more pronounced in the former line. Additionally, in the olingo/coati line the acromion processes were widened (particularly the suprahamatus process) (node 34 onwards; Fig. VI.6). On the other hand, during the evolution of the raccoon line the scapula became slightly longer and narrower, probably reflecting the less arboreal habits of this clade (node 36 onwards; Fig. VI.6P).

The reconstructed scapula size and shape for the mustelid ancestor (node 8; Fig. VI.6)

were very similar to that of the musteloid ancestor (node 5; Figs. VI.5, VI.6L), indicating that it would also have been a scansorial animal. These results agree with the arboreal habits attributed to *Plesictis*, one of the oldest fossil mustelid, based on its cranial morphology (Palmer, 1999), and also agree with a previous locomotor reconstruction based on extant taxa (Fabre et al., 2013b). Both badgers (i.e., *Meles meles*, Mme, and *Mellivora capensis*, Mca) presented highly modified scapula shapes, probably due to their early divergence from the mustelid stem (Fig. VI.6Q). Both species were considered semifossorial, and as such presented several adaptations to digging (e.g. wide infraspinous fossa, medially oriented glenoid cavity). The rest of the mustelid subfamilies arose in a diversification burst between the middle and late Miocene (Koepfli et al., 2008), which in terms of scapula shape corresponded principally to a reduction of the infraspinous fossa and a shift of the acromion to a more vertically oriented position (nodes 10–13; Fig. VI.6). Both of these shape changes could be related to a decrease in arboreality (see *Climbing*, above), which would suggest that the arboreal habits were reacquired during the evolution of Martinae (node 26 onwards; Fig. VI.6R). Indeed, in the internal nodes leading to the extant martens, the hamatus process became progressively longer and more cranially oriented, and the infraspinous fossa expanded again. Another subfamily appearing in this diversification burst was Lutrinae (node 14 onwards; Fig. VI.6S). However, the shape changes associated to their evolution will not be discussed, since the scapulae in this clade closely matched the mean shape described for semiaquatic carnivorans (Figs. VI.4, VI.S3), probably because most species in this category were lutrines (Table VI.1). The shape changes described for the diversification burst were particularly evident in galictine (node 24 onwards; Fig. VI.6) and musteline species (node 19 onwards; Fig. VI.6T), in which also an expansion of the cranial border was observed. Overall, the scapula shape of these terrestrial mustelids was quite different to that of other terrestrial carnivorans, and presented features associated with both over ground locomotion (e.g. reduced infraspinous fossa, ventrally directed acromion) and arboreality (e.g. expanded supraspinous fossa, enlarged acromion processes). Schutz & Guralnick (2007) found similar difficulties when trying to infer the locomotor type of *Trigonictis*, a basal mustelid probably related to galictine species, using long bone shape. It could be argued that their characteristic body plan (short legs and long body) would constraint their locomotor performance and that this particular appendicular morphology would be a consequence of it. However, this seems an unlikely explanation, since Horner & Biknevicius (2010) shown that locomotion in terrestrial mustelids is similar to that of other small mammals. On the other hand, their

small size could explain these mixed adaptations. As suggested by Astúa (2009), all small mammals could be considered functionally “scansorial” because, for those species, overland and arboreal locomotion pose similar challenges, as some climbing is usually necessary to surpass most obstacles.

Feliformia

The earliest feliform fossils belong to the late Eocene and early Oligocene, and already can be ascribed to either the felid or the “viverrid-like” lines (Rose, 2006). Thus, nothing is known of the early evolution of Feliformia, during which the *Nandinia* line and the felid lineage split from the feliform stem (Johnson et al., 2006; Nyakatura & Bininda-Emonds, 2012; Fig. VI.1). The reconstructed scapula shapes for basal feliforms (nodes 57, 58; Fig. VI.6) were practically identical to that of the carnivoran ancestor (node 1; Fig. VI.6A), but with a slightly larger and more cranially directed acromion. According to this, basal feliforms probably would also be scansorial animals, although slightly more arboreal than the earliest carnivorans. On the other hand, scapula size decreased to *c.* 223 mm, which corresponds to the centroid sizes of several extant feliforms in the 10 – 12 kg body mass range (e.g. ocelot, *Leopardus pardalis*; Fig. VI.5). Thus, it would seem that a size reduction associated with increasing arboreal habits was the main evolutionary trend during early feliform evolution. This trend was probably maintained in the nandiniid line, judging for the scapula size and shape of its small and arboreal lone living representative, the African palm civet (*Nandinia binotata*, Nbi; Fig. VI.6a).

In agreement with the trend of increasing arboreality proposed for basal Feliformia, the oldest felid, *Proailurus*, was an ocelot-sized carnivoran of the late Oligocene, probably arboreal, since its appendicular skeleton suggests that it was a better climber than most extant species (Agustí & Antón, 2002). Subsequently, felid evolution shifted towards increasingly larger and less arboreal species, a transition that can be observed in the different species of *Pseudaelurus*, a probable descendant of *Proailurus*. The oldest members of *Pseudaelurus* were cat-sized and arboreal, while younger species attained the size of a puma (*Puma concolor*) and were considered more terrestrial (Agustí & Antón, 2002). The reconstructed scapula shape of the ancestor of extant felids suggested a similar locomotor habit, since it was similar to the mean shape of scansorial carnivorans but with a dorsally expanded vertebral border (node 59; Figs. VI.4, VI.S3, VI.6b). Additionally, although none of the sampled species presented a similar scapula size than the felid ancestor, the closest values belonged to carnivorans in the puma size range (e.g. *Hyaena*

hyaena, Hhy; Fig. VI.5), and are thus similar-sized to the youngest species of *Pseudaelurus*. According to recent molecular phylogenetic analyses (Johnson et al., 2006), all extant felid species share a common ancestor dating back the late Miocene, which would explain the low shape variability in the scapulae of extant felids (Fig. VI.6b–e). Nevertheless, significant shape changes could be observed in the scapula during felid evolution, particularly when comparing the two subfamilies. The evolution of pantherine cats was characterized by a ventral displacement of the caudal angle and a dorsal expansion of the vertebral border at its insertion with the scapular spine, which resulted in an increased angulation of the caudal and cranial portions of the vertebral border (node 72 onwards; Fig. VI.6c). This scapular feature has been related to the functional division of the two parts of *m. serratus ventralis* in protraction and retraction of the forelimb (Smith & Savage, 1956). Further shape changes observed in Pantherinae were a reduction of the acromion processes and a caudal expansion of the neck and glenoid region. Similar scapular features developed during the evolution of Ursidae (Fig. VI.6E, G), suggesting that these might be allometric shape changes. On the other hand, during the evolution of feline cats the caudal portion of the vertebral border expanded dorsally, the scapular neck narrowed, and the acromion processes became larger (e.g. *Felis silvestris*, Fsi; Fig. VI.6d). Additionally, some shape changes were observed in the terminal taxa of both subfamilies, for instance, an expansion of the fossae at the cranial and caudal angles, and several reorientations of the acromion processes. Finally, it is worth noting that, as specialized runners, both the cheetah and the canids converged in a similar scapula shape (compare *Acinonyx jubatus*, Aju, Fig. VI.6e, with canids, Fig. VI.6C, D). To produce such convergence, several shape changes occurred along the branch leading to the cheetah, including a reduction of the supraspinous fossa, a lengthening of the scapular blade and glenoid region, and a ventral shift of the hamatus process.

The remaining extant “viverrid-like” feliforms share a common ancestor dating back to the early Oligocene (Nyakatura & Bininda-Emonds, 2012; Fig. VI.1). The reconstructed scapula size and shape of this common ancestor (node 76; Figs. VI.5, VI.6) suggest that the early evolution of “viverrid-like” carnivorans followed the feliform trend of increasing arboreality and decreasing size. This trend was further continued in the early evolution of Viverridae, since the reconstructed scapula size and shape of the viverrid ancestor indicated that it was civet-sized and semiarboreal (node 77; Figs. VI.5, VI.6f). However, along the line leading to extant herpestids, euplerids and hyaenids, the trend shifted towards decreasing arboreality, as suggested by the longer and narrower scapula shape

reconstructed for their common ancestor (node 86; Fig. VI.6i).

The scapula shape of the viverrid ancestor was similar to the mean shape of semiarboreal carnivorans, presenting a wide infraspinous fossa, a cranially oriented acromion, and the characteristic cranial displacement of the dorsal end of the scapular spine (accompanied by the contraction of the cranial portion of the vertebral border, and the expansion of its caudal portion) (node 77; Figs. VI.4, VI.S3, VI.6f). These scapular features were further developed in Genettinae (node 84 onwards) and, especially, in Paradoxurinae (node 78 onwards), which includes the most arboreal viverrid species (Taylor, 1974; Wilson & Mittermeier, 2009). It is interesting to note the high degree of convergence in scapula shape between the arboreal paradoxurines (e.g. *Arctictis binturong*, Abi; Fig. VI.6g) and the arboreal procyonids (Fig. VI.6O). The evolution of Viverrinae involved a rather different set of shape changes in the scapula. Civets are mostly terrestrial viverrids and thus their scapula shape changed accordingly (e.g. *Viverra zibetha*; Fig. VI.6h): the supraspinous fossa became smaller and bended laterally, the scapular spine straightened, and the acromion processes ceased to be coplanar (see *Climbing*, above). The earliest viverrid fossils belong to the early Miocene of Eurasia (e.g. *Semigenetta*; Veron, 2010), and have been described as small- to medium-sized scansorial carnivorans (Agustí & Antón, 2002; Morlo et al., 2010). These fossils probably represent basal members of the Genettinae + Viverrinae clade (Veron, 2010), which would explain their less arboreal habits (particularly if they were more related to Viverrinae).

As stated above, herpestids, euplerids and hyaenids share a common ancestor whose scapula shape suggested a more terrestrial habit than basal “viverrid-like” carnivorans (node 86; Figs. VI.4, VI.S3, VI.6i). A very similar scapula shape was recovered for the common ancestor of herpestids and euplerids (node 87). Besides being longer and narrower than in previous nodes, the scapulae of these internal nodes presented reduced acromion processes and a more laterally curved supraspinous fossa, which are further indicators of decreased arboreality (see *Climbing*, above). Regarding size, although the reconstructed centroid size decreased between these two internal nodes, it was similar to that of several extant carnivorans in the 4 – 11 kg body mass range in both nodes (Fig. VI.5). The oldest fossils of the Hyaenidae + (Eupleridae + Herpestidae) clade date from the middle Miocene and can already be ascribed to Hyaenidae (*Protictitherium*; Agustí & Antón, 2002). Thus, the reconstructed values for nodes 86 and 87 cannot be compared to the fossil record. However, the fact that similar values of both body size (3 – 10 kg; Morlo et al., 2010) and locomotor habits (generalized terrestrial, Morlo et al., 2010; semiarboreal,

Agustí & Antón, 2002) were inferred for *Protictitherium* supports the validity of the present reconstruction.

The early evolution of Hyaenidae is characterized by an increase in both size and terrestrial habits, as evidenced by the sequence *Protictitherium* – *Plioviverrops* – *Thalassictis* (Agustí & Antón, 2002), the latter of which was fully terrestrial and in the 20 kg body mass range (Finarelli & Flynn, 2009). This is congruent with the reconstructed scapula size and shape for the ancestor of extant hyaenids (node 99; Figs. VI.5, VI.6j), which suggested that it was terrestrial and somewhat smaller than a striped hyaena (*Hyaena hyaena*, Hhy). Additionally, as observed in canids and the cheetah (Fig. VI.6C, D, e), the scapula shape of the hyaenid ancestor presented all the scapular features previously described as adaptations to running efficiently (Fig. VI.6j): long and narrow scapula, reduced fossae with laterally curved margins, highly reduced acromion processes, and a marked angulation between the cranial and caudal portions of the vertebral margin. All these scapular features were further developed in extant hyaenids.

The reconstructed scapula shape of the ancestor of extant herpestids was similar to the mean shape of terrestrial carnivorans (node 88; Figs. VI.4, VI.S3, VI.6k). However, the caudal angle was significantly expanded caudad, which indicates well-developed digging abilities (see *Digging*, above). This semifossorial habit was further developed during the evolution of social mongooses (Mungotinae, e.g. *Suricata suricatta*, Ssu; Fig. VI.6l), since the main shape changes observed in the scapula in this clade were an elongation of both the moment arm of m. teres major (expanded caudal border, dorsally projected caudal angle) and the acromion processes (especially the suprahamatus process). According to previous phylogenetic studies (Nyakatura & Bininda-Emonds, 2012), solitary mongooses underwent a large adaptive radiation at the base of the clade (Fig. VI.1). Thus, most of the internal nodes for Herpestinae (nodes 88 – 91) presented an almost identical scapula shape, which in turn was very similar to that of the herpestid ancestor. On the other hand, several evolutionary trends could be observed in the terminal herpestine taxa. Both the slender mongoose (*Galerella sanguinea*, Gsa) and the Asian members of *Herpestes* (*H. edwardsi*, Hed, and *H. javanicus*, Hja) presented similar fossorial adaptations as social mongooses (e.g. increased moment arm of m. teres major). Due to its long limbs and proximally located limb musculature, the white-tailed mongoose (*Ichneumia albicauda*, Ial; Fig. VI.6m) is considered the “most cursorial” herpestid (e.g. Taylor, 1974). Accordingly, its scapula shape was highly convergent with that of other carnivorans adapted to running efficiently (hyaenids, canids,...; Fig. VI.6C, D, e, j). Finally, the largest herpestine species

presented similar-shaped scapulae (e.g. *Herpestes ichneumon*, Hic; Fig. VI.6n), suggesting that these might be allometric shape changes. Regarding scapula size, the reconstructed centroid size of the herpestid ancestor was similar to that of several extant “viverrid-like” taxa weighting about 2 kg (Fig. VI.5). As a final remark, no comparison with the fossil record was possible for Herpestidae, since the fossil remains of early herpestids consist mostly of teeth and skull fragments (Agustí & Antón, 2002).

According to its scapula shape, the common ancestor of extant Malagasy carnivorans was very similar to early members of the clade Hyaenidae + (Herpestidae + Eupleridae) (nodes 86–87; Fig. VI.6i). However, it probably was slightly smaller, since its reconstructed centroid size is similar to that of extant carnivorans in the 2 – 9 kg body mass range (Fig. VI.5). This small terrestrial ancestor with some climbing abilities arrived to Madagascar from Africa, probably by rafting, which was followed by an adaptive radiation to occupy different niches on the island (Wilson & Mittermeier, 2009). This adaptive radiation is clearly reflected in the variation of scapula shape within this clade. Arboreality was regained along the branch leading to the fossa (*Cryptoprocta ferox*, Cfe; Fig. VI.6o), which specializes in lemur predation. Consequently, several scapular features related to increased arboreality were developed (e.g. enlarged scapular fossae, shorter scapula, enlarged acromion processes). However, some of these convergent scapular features were brought about by shape changes different than those occurring in most other arboreal carnivorans. For instance, the infraspinous fossa was enlarged mainly by an expansion of the caudal border, while the vertebral border remained practically unchanged. Similarly, the scapula was shortened particularly at the neck and glenoid region, not the scapular blade. These differences could be related to the fact that most other arboreal carnivorans originated from an evolutionary trend towards increased arboreality (e.g. procyonids, viverrids), while the opposite seems to be the case for the clade Hyaenidae + (Herpestidae + Eupleridae). In another euplerid line, now represented by the Malagasy civet (*Fossa fossana*, Ffo), arboreality was further reduced, as evidenced by its long and narrow scapula, convergent with that of other terrestrial carnivorans (shape not shown). Finally, the evolution of Malagasy mongoose was characterized by similar shape changes to those described for true mongooses (Herpestidae): an elongation of the acromion processes (especially the suprahumeral), an expansion of the caudal border, and a dorsal projection of the caudal angle (e.g. *Salanoia concolor*, Sco; Fig. VI.6p). As in Herpestidae, the reconstructed values for ancestral euplerid nodes could not be compared to the fossil record, since there are no fossil remains of early Malagasy carnivorans (Veron, 2010).

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Supplementary Material

	n	CS	log CS	PIC
Canidae	9	<i>p = 0.8013</i> (6.78%)	<i>p = 0.7463</i> (7.33%)	<i>p = 0.4993</i> (8.11%)
Ursidae	5	<i>p = 0.2128</i> (33.67%)	<i>p = 0.2182</i> (33.11%)	<i>p = 0.9577</i> (9.32%)
Procyonidae	7	<i>p = 0.1076</i> (31.43%)	<i>p = 0.0648</i> (33.75%)	<i>p = 0.0961</i> (28.59%)
Mustelidae	25	p < 0.0001 (20.58%)	p = 0.0001 (20.93%)	p = 0.0198 (11.41%)
Felidae	18	p = 0.0009 (19.93%)	p = 0.0019 (18.83%)	<i>p = 0.1519</i> (9.04%)
Viverridae	10	<i>p = 0.3793</i> (10.50%)	<i>p = 0.3658</i> (10.80%)	<i>p = 0.4404</i> (9.94%)
Eupleridae	5	<i>p = 0.0941</i> (40.39%)	<i>p = 0.0727</i> (40.96%)	<i>p = 0.6280</i> (17.26%)
Herpestidae	8	p = 0.0373 (27.62%)	p = 0.0350 (26.99%)	p = 0.0454 (23.67%)
arboreal	6	<i>p = 0.9064</i> (8.78%)	<i>p = 0.8517</i> (9.73%)	<i>p = 0.3414</i> (24.81%)
semiarboreal	6	<i>p = 0.6771</i> (14.83%)	<i>p = 0.6784</i> (14.36%)	<i>p = 0.4283</i> (14.45%)
scansorial	36	p < 0.0001 (19.37%)	p < 0.0001 (21.68%)	p = 0.0084 (8.23%)
terrestrial	33	p = 0.0001 (20.09%)	p < 0.0001 (28.40%)	<i>p = 0.1267</i> (5.79%)
semifossorial	4	p = 0.0410 (50.30%)	p = 0.0431 (50.03%)	<i>p = 0.3318</i> (51.94%)
semiaquatic	8	p = 0.0220 (27.76%)	p = 0.0074 (29.05%)	<i>p = 0.2489</i> (19.43%)
aquatic	8	<i>p = 0.5356</i> (12.28%)	<i>p = 0.4327</i> (14.34%)	<i>p = 0.9417</i> (6.60%)

Table VI.S1. Regressions of shape variables on centroid size in the different subsamples. The allometric effect on each subsample was determined using regression methods, which allows the shape variation explained by size changes to be expressed as a percentage of the total. Furthermore, the presence of phylogenetic signal was tested on each subsample using permutation tests. See Table VI.2 for definition of the locomotor types. Non-significant results (i.e., p-value > 0.05) are presented in *grey bold italics*. Abbreviations: CS, results of the regression of shape onto centroid size; log CS, results of the regression of shape on log-transformed centroid size; n, sample size; phylogeny, significance of the permutation tests on phylogenetic signal; PIC, results of the regression of shape on size using phylogenetically independent contrasts.

Figure VI.S1. Regressions of shape variables on centroid size (CS). 95% Confidence ellipses are shown for each family except Ailuridae and Nandiniidae (monotypic families).

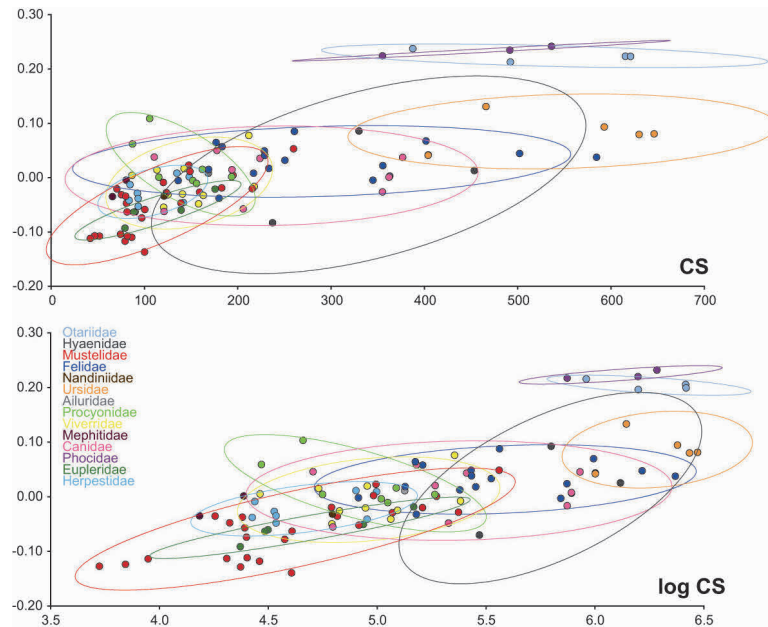
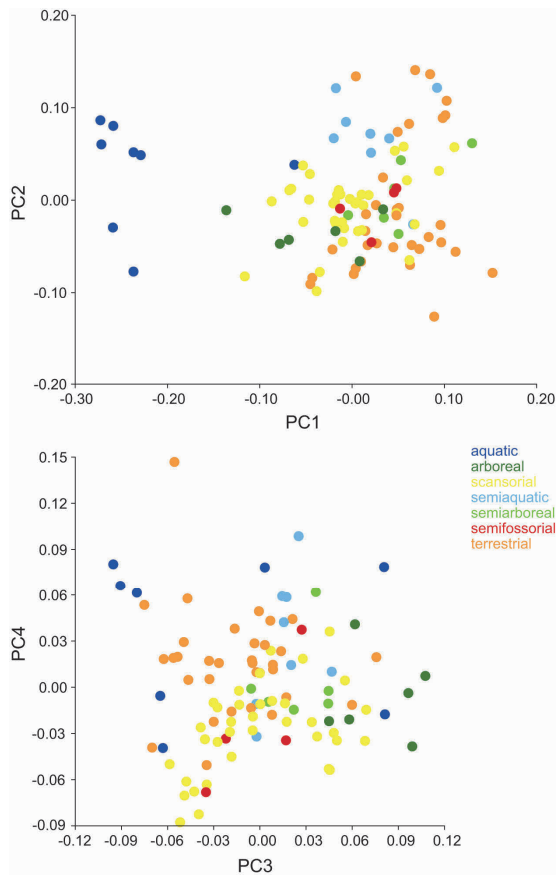


Figure VI.S2. Principal components analysis of the shape variation of the carnivoran scapula, colored by locomotor type. See Table VI.2 for definition of the locomotor types, and Figure VI.3 for the shape changes associated to each principal component.



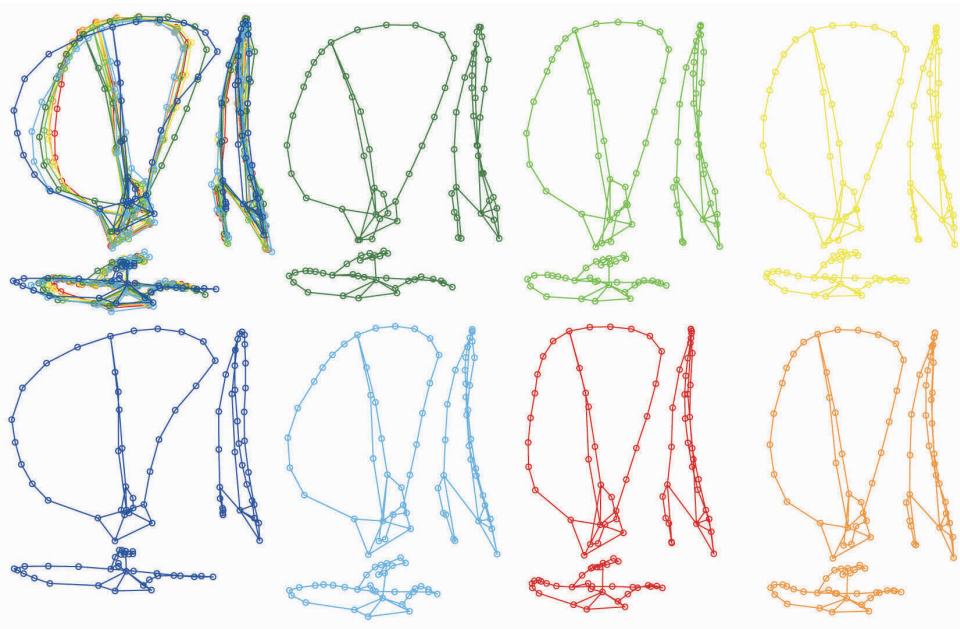


Figure VI.S3. Mean scapular shape by locomotor type.

For each locomotor type, a set of three wire-frames is presented so that scapular shape can be observed in lateral (left), dorsal (bottom), and caudal (right) views. Furthermore, a superimposition of all mean shapes is presented to ease comparison. See Table VI.2 for definition of the locomotor types.

Discussion & Conclusions

GENERAL DISCUSSION

Arboreal locomotion

The comparison between locomotion on narrow supports and overground locomotion (Chapter I) has demonstrated that a different locomotor strategy is employed on each substrate. Furthermore, the strategies employed by mammals with a different degree of arboreality, also differ between them. Arboreal mammals (e.g. most primates, some didelphids), for instance, present adaptations to moving and foraging in the canopy so marked that it makes their overground locomotion distinct from that of other mammals (e.g. prehensile extremities, more protracted arm postures at touch-down, diagonal-sequence gaits; Larson et al., 2000; Schmitt & Lemelin, 2002). On the other hand, terrestrial mammals lack the morphological adaptations necessary to avoid rolling and toppling from narrow supports (e.g. Cartmill, 1985). Thus, they move along these substrates at high speeds in order to gain dynamic stability, which is complemented by using asymmetrical coordination patterns and reducing whole-body aerial phases. Finally, both small and medium-sized mammals with an intermediate degree of arboreality (i.e., semiarboreal and scansorial species) use a common strategy to increase their stability when in an arboreal situation. This strategy consisted principally in the use of lower speeds and in changes in hand/foot placement. The former is associated with an increased stance phase duration and, according to Schmidt & Fischer (2010), it can only be accomplished if some grasping ability is retained (e.g. hook-like claws). The existence of these different locomotor strategies for arboreal locomotion associated to varying degrees of arboreality supports the use of locomotor categories when studying morphological adaptations in the appendicular skeleton. That is, since terrestrial, scansorial (plus semiarboreal) and arboreal species use different strategies for arboreal locomotion, it seems likely that they also require different morphological adaptations. This was later evidenced by the results of Sections C and D, in

which several differences in scaling and scapula shape were described among those locomotor groups. As a final remark on these different strategies, it is worth noting that, ultimately, they achieve the same result: reducing peak vertical forces, which minimizes the oscillations of both the center of mass and those of the support (Schmitt, 1999; Schmitt et al., 2006). Furthermore, a couple of factors common to all arboreal locomotor strategies were evidenced in Chapter I: a reduced swing phase duration and the use of a crouched posture. These common features emphasize that, when studying animal locomotion, arboreal locomotion should be separated from overground locomotion, even in species that are not strictly arboreal.

Regarding the kinematics and coordination of arboreal locomotion, diagonal-sequence gaits are of particular interest. This kind of gaits is characteristic of most primates (Hildebrand, 1967; Cartmill et al., 2002). Some authors have argued that support polygons resulting from diagonal-sequence walk improve balance on narrow supports, since they reduce yawing moments (Rollinson & Martin, 1981; Meldrum, 1991). Thus, these gaits would be an adaptation to arboreal locomotion. Others, however, considered that the ability to use these gaits is just a consequence of the greater cortical control of locomotion evolved by primates for reaching and grasping among fine branches (Vilensky & Larson, 1989). Since diagonal-sequence walking gaits have also been found in other mammals (woolly opossum, *Caluromys philander*, Schmitt & Lemelin, 2002; Lemelin et al., 2003; giant armadillo, *Priodontes maximus*, aardvark, *Oricteropus afer*, and kinkajou, *Potos flavus*, Hildebrand, 1967, 1980; although Cartmill et al. (2002) did not observe diagonal-sequence gaits on the kinkajou), the hypothesis proposed by Vilensky and Larson (1989) does not seem to hold. Whatever the hypothesis we accept to explain the origin of diagonal-sequence walking gaits, locomotion on narrow supports (fine branches) is always related to the use of these gaits in arboreal mammals (Schmitt & Lemelin, 2002; Lemelin et al., 2003). This way, it would have been expected to find diagonal-sequence gaits in the arboreal situation analyzed in Chapter I, but no such gait was observed either for cats or for dogs. It seems thus that, either locomotion on narrow supports is not enough to encourage the use of diagonal-sequence gaits, or that this kind of gaits has not evolved in our studied species. Maybe this kind of gaits have not even appeared in Carnivora, since the only carnivoran for which the use of diagonal-sequence walk has been ever documented is the kinkajou, and then only as an observation not supported by either the frequency of use of this gait or the conditions in which it was observed (Hildebrand, 1967, 1980; Cartmill et al., 2002). Another explanation for the lack of diagonal-sequence gaits in the arboreal

situations is that it requires training, maybe this kind of gaits only appears after the animals get used to the arboreal situation. Unfortunately, however, to determine which of these hypotheses is responsible for the lack of diagonal-sequence gaits in the studied arboreal situation was beyond the scope of that study (Chapter I). Diagonal-sequence gaits are not the sole adaptations of primates (and also of the woolly opossum) to arboreal locomotion. They also show highly protracted arm positions at forelimb touch-down, and relatively higher peak vertical forces on the hindlimbs compared to the forelimbs (Vilensky & Larson, 1989; Schmitt, 1999; Schmitt & Lemelin, 2002). Furthermore, primates present grasping hands and feet (Cartmill, 1974; Schmitt, 1999), which are also present in the woolly opossum but not in the grey short-tailed opossum (*Monodelphis domestica*), the first sharing the arboreal adaptations with primates, but not the second (Schmitt & Lemelin, 2002; Lemelin et al., 2003; Lammers & Biknevicius, 2004). Given that grasping extremities provide better control of pitching and rolling moments around the support axis (Cartmill, 1985), they could also be a part of the set of adaptations related to arboreal locomotion present in primates and some opossums. This way, since none of these adaptations is shown by the species studied in Chapter I, even in an arboreal situation, it seems that, along with the rest of convergences, diagonal-sequence gaits have evolved independently in both primates and some opossums in response to a similar selective pressure, and that they are not variants of a general motor program present in all mammals. Studies on the ontogeny of locomotion in the rhesus macaque (*Macaca mulatta*; Hildebrand, 1967) and the vervet monkey (*Chlorocebus aethiops*; Hurov, 2005) seem to support this idea, since they show that lateral-sequence walking gaits are predominant on the first days of life, and that they are progressively replaced by diagonal-sequence gaits in the following months. This way, if ontogeny reflects phylogeny, it could be argued that diagonal-sequence gaits originated later in the evolutionary history of mammals, maybe as an arboreal adaptation involving a change in the original motor program governing lateral-sequence gaits.

Finally, although this dissertation has shed some light in both the locomotor strategies and adaptations related to arboreality in Carnivora, further questions remain unanswered and could be explored in future studies. One of these questions is the locomotor strategy employed by arboreal carnivorans. To date, no study has focused on the locomotion of arboreal carnivorans. Cartmill et al. (2002) included some arboreal and semiarboreal species in their study, but only gaits and duty factors were analyzed. Furthermore, they mixed locomotor cycles filmed overground and on narrow supports. Thus, it would be

interesting to analyze the kinematics, dynamics, and coordination, of locomotion employed by arboreal carnivorans when moving on narrow supports. Comparison of these results with previous data on other arboreal mammals would help to confirm whether the locomotor strategies employed by arboreal mammals are truly universal. Both the binturong (*Arctictis binturong*) and the kinkajou (*Potos flavus*) would be the best candidates for such a study, since not only both are extremely arboreal species presenting prehensile tails, but they also have rather different body masses (around 3kg and 14kg, respectively) (e.g. Wilson & Mittermeier, 2009). Similarly, arboreal locomotion should also be studied in large non-arboreal carnivorans (e.g. bears, pantherine cats), which would allow to test whether the strategies described for small and medium-sized non-arboreal specialists are also employed by larger species. Finally, the results of Section D suggest that locomotor adaptations related to arboreality in carnivoran scapula shape consist mostly in the development of muscle attachment sites associated with climbing. Thus, it would be interesting to study the locomotion of both arboreal and non-arboreal carnivorans along inclined narrow supports and when climbing vertically. All the aforementioned supplementary studies would appreciate the use of cineradiographic and electromiographic techniques, since these methods would permit the better integration of locomotor variables and musculoskeletal adaptations.

Factors influencing limb bone morphology

Sections B to D have shown that limb bone morphology in Carnivora is determined by the interaction of size, phylogenetic history, and function. This interaction is complex, and varies from one variable to the next.

Overall, size seemed to be the major determinant of limb bone morphology in Carnivora, as shown by the results of Chapter II and the high correlation coefficients obtained throughout Section C. This was an expected result, since previous studies have shown a significant allometric effect on many properties of the musculoskeletal system, as well as in most variables describing the kinematic, dynamic, and coordination of locomotion (e.g. Alexander et al., 1979; Bertram & Biewener, 1990; Christiansen, 1999^{a,b}, 2002; Casinos et al., 2012). More surprising, however, was the fact that interspecific size differences within Carnivora led to artifactual differences when comparing taxonomic and functional groups (Chapter II). Usually, limb bone measurements of extant species are used to infer the ecomorphology of extinct species (e.g. Van Valkenburgh, 1987; Argot, 2001;

Fujiwara, 2009). Thus, if these limb bone measurements are not size-corrected, for instance, using regression residuals, any inference based on these measurements could be misleading. As an example, the ANOVAs and *post hoc* tests conducted on Chapter II indicated that aquatic carnivorans had longer limb bones than other locomotor groups. That way, if we were to find a new carnivoran fossil with exceptionally long limb bones, it would be logical to think of it as an aquatic species. However, performing the same analyses on regression residuals showed that this finding was an artifact caused by the larger body size of aquatic carnivorans, and that these species actually had the shortest limb bones (Chapter II). Consequently, that fossil species was probably not adapted to swimming (more probably to running efficiently; Hildebrand, 1985; Van Valkenburgh, 1987). As forced as this example might seem, a similar misinterpretation occurred in the early reconstructions of the posture of *Iguanodon*, whose much smaller forelimbs than hind limbs led to the belief that it was bipedal and dragged its tail on the ground (Norman, 1980). Several authors “avoid” this problem with size-related artifacts using ratios instead of direct limb bone measurements (e.g. Oxnard, 1968; Gonyea, 1976; Van Valkenburgh, 1987; Iwaniuk et al., 1999), since these non-dimensional indexes ought to be independent of body size. However, as pointed out by Aiello (1981), this is only true when both numerator and denominator in the ratio scale to body mass with the same exponent, which, as shown in Section C, is rarely the case. Regression residuals seem, thus, the most appropriate solution to size-related artifacts, although its use with fossil material would involve a prior estimation of its body mass from another skeletal element (e.g. cranial or dental characters when studying the appendicular skeleton), which would also incorporate uncertainty to any ecomorphological inference.

Several authors have suggested that Carnivora is an evolutionarily conservative group regarding locomotor type and limb morphology (e.g. Oxnard, 1968; Bertram & Biewener, 1990; Day & Jayne, 2007). That is, according to these authors, both locomotor habits and limb morphology are constrained by phylogeny in Carnivora. The former is unlikely because, as pointed out by Heinrich & Biknevicius (1998), carnivorans present one of the widest diversity of locomotor habits of all mammalian orders. Furthermore, significant differences in the limb posture and locomotor kinematics of several carnivoran species have been described (Jenkins, 1971; Jenkins & Camazine, 1977). Similarly, as shown in Chapter I, carnivorans employ different locomotor strategies depending on the substrate upon which they move and their degree of familiarity with this substrate. Regarding the aforementioned conservative design of carnivoran limbs, Bertram & Biewener (1990)

stated that morphological differences among terrestrial, scansorial, and arboreal carnivorans are mostly caused by size differences among these groups, whereas adaptations to swimming and digging should be independent of size. The results of this dissertation strongly refute this statement. For one thing, Chapter I revealed that size differences between locomotor groups created many artifactual differences in limb bone measurements, particularly between aquatic and non-aquatic carnivorans, and among the different groups defined by the degree of arboreality (i.e., scansorial, semiarboreal...). Additionally, the scaling pattern of the forelimb differed significantly both among locomotor types and between those and the whole order (Chapter III). The scaling pattern of the hind limb, however, did not differ significantly between locomotor types, probably due to the similar role of the hind limbs in all non-aquatic locomotor types (Chapter IV). Similar morphological differences between locomotor types in Carnivora had also been previously reported (e.g. Van Valkenburgh, 1987; Iwaniuk et al., 1999). Summarizing, neither locomotor type nor limb morphology in Carnivora can be described as “conservative” or be considered constrained by phylogeny.

Nevertheless, a strong phylogenetic signal was evidenced in most of the studied variables (Chapter II) and their scaling patterns (Chapters III–IV), and also in the shape of individual elements of the appendicular skeleton (Chapter VI; Walmsley et al., 2012; Fabre et al., 2013a). The youngest carnivoran families date back to the Late Oligocene / Early Miocene, corresponding to the split between Herpestidae and Eupleridae (18 – 24 Mya; Yoder et al., 2003; Nyakatura & Bininda-Emonds, 2012). Considering that the wide morphological and locomotor diversity of extant Mustelidae originated ca. 17 Mya (Nyakatura & Bininda-Emonds, 2012), it is safe to assume that all those millennia separating the evolution of the different carnivoran families produced a fair amount of morphological variability exclusive to each family. This would explain that most of the phylogenetic-related morphological variability in the carnivoran appendicular skeleton occurs at the family level (Chapter II). While discussing evolutionary time and morphological variability, Felidae deserves special consideration. Extant Felidae originated in a recent radiation ca. 11 Mya (Johnson et al., 2006), during which they developed a similar limb posture and locomotor habits (Day & Jayne, 2007; Wilson & Mittermeier, 2009). In addition, their scaling pattern is characterized by high correlation coefficients and narrow confidence intervals (Section C, esp. Chapter V), which would suggest reduced morphological variability (low dispersion around the regression line; Sokal & Rohlf, 1995). However, Felidae also presents one the widest body mass range of all extant carnivoran

families (only wider in extant Ursidae; Wilson & Mittermeier, 2009). It has been shown that larger animals present more erect limb postures to reduce the magnitude of the joint moments produced by the ground reaction force, which in turn reduces the stresses acting on the bones (Biewener, 2005). Since limb posture is fairly constant in extant Felidae, another strategy to reduce those stresses should exist. It was shown in Chapter V that, at the ankle, this is accomplished thanks to the faster scaling of the moment arm of the ankle extensors. A similar explanation can be derived from the elbow, since the length of the olecranon, the moment arm of the elbow extensors, scales significantly faster than ulna length (Chapter III). Furthermore, the olecranon angle also scales with size, further increasing the leverage of those muscles in large felids. Thus, limb posture can be maintained more or less constant in Felidae thanks to marked morphological changes in their appendicular skeleton. Another striking morphological change was observed in the felid scapula: although the cheetah (*Acinonyx jubatus*) diverged from the *Puma* lineage ca. 5 Mya ago (Johnson et al., 2006), the shape of its scapula is markedly different from that of other felids and shows convergent features with that of canids (Chapter VI). These findings indicate that limb morphology in extant Felidae is more varied than its recent radiation or scaling results suggested. Additionally, these insights on felid evolution also suggest that limb bone morphology is more easily altered during evolution than postural or locomotor properties. This might seem a logical conclusion, since changing a single element should be easier than changing how multiple elements interact. However, mammalian limbs are a highly integrated structure, and thus modifications to a single element cascade throughout the whole structure (Hallgrímsson et al., 2002; Young, 2004; Schmidt & Fischer, 2009). This way, quantifying the evolvability of morphological and locomotor traits would be an interesting topic for future studies (Kirschner & Gerhart, 1998; Hamrick, 2007).

Interestingly, in contrast with the morphological variability of limb bones, the relative lengths of the forelimb segments were quite constant in Carnivora (Chapter II). Similar results for this and other mammalian groups have been previously reported by Schmidt (2008) and Schmidt & Fischer (2009). This constancy of segment proportions could be explained by the interaction of several factors. On one hand, during limb development, the specification and patterning of the stylopodium or upper arm, the zeugopodium or forearm, and the autopodium or hand, is regulated by an expression gradient of the *HoxA* and *HoxD* gene complexes (Duboule, 1992; Rijli & Chambon, 1997; Wellik & Capecchi, 2003). However, the development of the scapula is regulated by a different set of genes, namely *Emx2* supported by *Pax1* and possibly *HoxC6* (Sharpe et al., 1988; Wilm et al.,

1998; Pellegrini et al., 2001). This would suggest that development of the proximal segment (scapula) is independent to that of the middle (upper arm) and distal (forearm). On the other hand, from a biomechanical point of view, it has been shown that the self-stability of crouched limbs is increased when relative segment lengths are identical (i.e., 33% – 33% – 33%; Fischer & Blickhan, 2006), while extended limbs require different segment proportions for self-stability (Seyfarth et al., 2001). Thus, some sort of mechanism controlling the proportions of all segments would be expected. Since the understanding of the regulation of developmental processes is still growing, it seems likely that this mechanism integrating all limb segments remains undiscovered. As an additional note on limb proportions, it has been found that relative segment lengths scale, although slowly, to body mass (Schmidt & Fischer, 2009; Chapter III). Thus, some of the observed low variability of limb proportions in Carnivora seems to be size-related. Crouched limbs are characteristic of small mammals (Jenkins, 1971; Fischer et al., 2002), while, as stated above, larger animals present more extended limbs (Biewener, 2005). Due to the different requirements for self-stability of both types of limbs, and considering that carnivorans span a wide range of body masses, it would be expected that small carnivorans showed similar relative segment lengths and that these became more dissimilar with increasing body mass. However, this is not the case, since limb proportions are fairly constant in carnivorans. A possible explanation to this could be that carnivorans evolved from an ancestor with extended limbs, and that small species had inherited its dissimilar limb proportions due to the constancy of these. Nevertheless, significant evidence for complex allometry was found in the scaling of relative segment lengths (Chapter III), which supports the notion of small and large carnivorans having different requirements for these variables.

As a final remark on the factors influencing limb morphology, it should be noted that the main question left unanswered by this dissertation are the causes of differential scaling. Originally, the scaling differences between small and large mammals were attributed to the fact that gravitational loading would result in structural problems only in large animals (Economos, 1983). This was later expanded to small and large mammals having different locomotor requirements (Bertram & Biewener, 1990; Christiansen, 1999*a*). Furthermore, since small mammals tended to conform to the geometric similarity hypothesis and large mammals seemed to scale elastically, Christiansen (1999*b*) suggested that animals maintained resistance to bending forces by evolving increasingly larger diaphysial diameters. Excluding Pinnipedia, the scaling of whose limb bones is probably

modified by the particular requirements of aquatic locomotion, the results of Section C support this hypothesis for the cause of differential scaling only in part. On one hand, differential scaling was found in several variables. Furthermore, Ursidae, which includes the largest non-aquatic carnivorans, tended to conform better to the elastic similarity. On the other hand, however, no evidence for differential scaling was found in any of the families spanning wide body mass ranges (i.e., Canidae, Felidae, Ursidae). In addition, only lengths scaled elastically in Ursidae, since their bone diameters (and also bone robusticities) tended to scale slower than in the rest of carnivoran families. Another argument against this hypothesis was the fact that differential scaling was found in some families with narrow body mass ranges, such as Viverridae. Bou et al. (1987) had suggested that the low conformity of some scaling relationships to either geometric or elastic similarity could be related to mixing species with different locomotor requirements, which was tested in Section C as an alternate hypothesis explaining differential scaling. According to this hypothesis, it would have been expected that differential scaling was never observed in the locomotor type subsamples, since these should not mix species with different locomotor requirements. However, that was not the case, since differential scaling was found for several variables in semiarboreal and scansorial carnivorans. In the latter case, small species were found to scale faster than larger species, which seems coherent with the fact that the low-scaling ursids are the largest scansorial carnivorans. However, no explanation could be found for the differential scaling of semiarboreal species, in which allometric exponents increased with size. In summary, neither size differences nor mixing locomotor requirements provide a universal explanation to the presence of complex allometry in scaling studies. Differential scaling, thus, could reflect a common response to multiple allometric problems.

Morphological evolution in Carnivora

The results of Chapters II and VI suggest that the carnivoran ancestor was a medium-sized, forest-dwelling, scansorial mammal. These results agree both with previous reconstructions of the locomotor habits of ancestral Carnivora (Schutz & Guralnick, 2007; Fabre et al., 2013*b*) and with inference driven from the fossil record (e.g. Agustí & Antón, 2002; Spaulding & Flynn, 2009). However, the size of the carnivoran ancestor was probably overestimated in the present dissertation, since Finarelli & Flynn (2006) showed that this is a common occurrence when reconstructing this trait based exclusively on data from extant

Carnivora.

According to scapula shape, a size reduction associated with increasing arboreal habits was the main evolutionary trend during early feliform evolution. Subsequently, arboreal habits were lost in the branch leading to hyaenids, herpestids, and Malagasy carnivorans, and the reacquired in the latter family. On the other hand, arboreal habits were lost multiple times during caniform evolution (e.g. Canidae, pinniped line, many mustelid lineages). Similarly, the adaptation to an aquatic lifestyle occurred at least twice in Carnivora (once in the pinniped line and another in the lutrine lineage), since the ancestral scansorial habit is retained in most of the intermediate internal nodes. Body size also increased independently in several carnivoran lineages (Canidae, Ursidae, Pinnipedia, pantherine cats, Hyaenidae). Finally, although convergent evolution should be expected in a highly speciose and locomotory diverse group such as Carnivora, the adaptation to cursoriality (*sensu* Stein & Casinos, 1997) was particularly remarkable. This locomotor adaptation occurred independently in Canidae, Hyaenidae, the cheetah, and some herpestids, in all cases resulting a strikingly similar scapula shape.

Finally, although the study of scapula shape has provided good insight on the locomotor evolution of Carnivora, it would be interesting to also reconstruct the morphology of the rest of limb elements. Hopefully, this would further support the findings of the present dissertation. Additionally, fossil material should be included in future studies, which should increase the accuracy of morphological reconstructions (Finarelli & Flynn, 2006).

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CONCLUSIONS

- 1 Both small and medium-sized non-arboreal mammals present a common locomotor strategy to move on narrow supports. This strategy relies on the use of low speeds, probably to reduce peak vertical forces, hence reducing vertical oscillations of the center of mass and those of the support.
- 2 The dog, a fully terrestrial mammal, uses high speeds to gain in dynamic stability when moving on narrow supports. Furthermore, it uses unsteady asymmetrical gaits, suggesting constant readjustments in limb coordination. Finally, vertical oscillations were reduced by reducing whole-body aerial phases.
- 3 Maximization of the contact time between the animal and the support, reduction of swing phase duration, and use of a crouched posture, were identified as common features to all mammals moving on narrow supports.
- 4 The morphology of the limb bones in Carnivora is determined by the interaction of size, phylogenetic history, and function. This interaction is complex, and varies among the different variables studied.
- 5 Size is the main factor affecting carnivoran limb morphology, and the allometric effect creates several artifactual differences among several locomotion-related categories, while also masking several actual differences among those groups.

6

Although there is a strong phylogenetic signal in the morphology of the appendicular skeleton, neither locomotor habits nor limb morphology are constrained by shared phylogenetic history in Carnivora.

7

Neither the elastic nor the geometric similarity hypotheses successfully predict the scaling pattern of the carnivoran forelimb. On the other hand, the hind limb scales geometrically in Carnivora. Overall, these results emphasize that similarity hypotheses are too simplistic and should be rebuilt from similarities in the scaling patterns of phylogenetically narrow samples of species with similar locomotor requirements.

8

Both phylogeny and adaptation cause significant deviations from the scaling pattern of the whole order in the carnivoran forelimb, but not in the hind limb. This is probably related to the fact that, the forelimbs are involved in both locomotion and prey capture/handling in Carnivora, while the hind limbs are merely locomotor.

9

In large non-aquatic carnivorans, the size-related increases in bone stresses associated with locomotion are compensated primarily by limb posture changes instead of by modifying limb bone scaling.

10

Contrary to previous studies comparing both methodologies, significant differences were found between the allometric slopes obtained both with traditional and PIC regression methods. This emphasizes the need to take into account phylogenetic relatedness in scaling studies to avoid the violation of the assumption of independent observations.

11 Differential scaling is frequently observed in the morphometric variables describing the carnivoran appendicular skeleton (including scapula shape). However, neither the inclusion of different-sized species nor mixing locomotor requirements are exclusively responsible for the presence of complex allometry in scaling studies. Differential scaling, thus, could reflect a common response to multiple allometric problems.

12 As observed for other muscles in mammals, the moment arm of the ankle extensors scales to body mass in Felidae with an exponent not significantly different from 0.40, remarkably faster than calcaneus total length. This explains why the effective mechanical advantage of the ankle extensors increases with body mass, despite the fact that limb posture does not change in felid species. Furthermore, this finding is consistent with the hypothesis of isometric scaling of ground reaction forces.

13 Locomotor adaptations in the scapula shape of extant carnivorans seem independent of size or shared ancestry and can be related to the particular muscular function associated with each locomotor habit.

14 The results of this dissertation suggest that the carnivoran ancestor was a medium-sized, forest-dwelling mammal with mixed adaptations for arboreal and terrestrial habits (i.e., scansorial). This finding supports the placement of “miacids” at the branch leading to extant Carnivora.

Resumen en español

INTRODUCCIÓN GENERAL

Locomoción animal

Los animales se mueven para buscar comida, pareja o territorio, y para escapar de los depredadores o de un entorno hostil (Biewener, 2003). Así pues, la **locomoción animal**, definida como el acto de autopropulsión de un animal, es esencial para su supervivencia, por lo que existirán presiones selectivas que actúen tanto sobre los sistemas y estrategias locomotoras empleados por los animales (Alexander, 2002).

Dependiendo del sustrato sobre el que se muevan, los animales presentan diferentes **hábitos locomotores**: nadar en el agua, excavar bajo el suelo, trepar soportes inclinados, volar por el aire,... Todos estos hábitos locomotores requieren estrategias locomotoras características, es decir, modificaciones particulares a la dinámica, cinética y coordinación de la locomoción. Por ejemplo, los animales acuáticos han de superar la resistencia del agua para avanzar, los terrestres evitar que su peso colapse sus extremidades, y los arborícolas mantener el equilibrio sobre los estrechos soportes sobre los que avanzan. En consecuencia, dado que la mayoría de animales se mueven sobre diferentes sustratos, estos presentan múltiples hábitos locomotores. El conjunto de hábitos locomotores de un animal y la frecuencia con la que los usa definen su **patrón locomotor**.

La locomoción en vertebrados es posible gracias a su característico **sistema musculoesquelético**, formado por huesos, músculos, tendones y otros tejidos conectivos. En particular, los huesos proveen un lugar de inserción a los músculos y, mediante articulaciones móviles, forman un sistema de palancas sobre el que actúan los músculos para producir el movimiento (Alexander, 2002; Biewener, 2003). De este modo, la morfología ósea, es decir, la forma y estructura de los huesos, está íntimamente relacionada con el tamaño y posición de los músculos que en ellos se insertan, y también con la magnitud y dirección de las fuerzas que producen (p. ej. Roberts, 1974; Argot, 2001).

Así pues, el estudio de la morfología ósea permite tanto la identificación de adaptaciones funcionales en la musculatura como el uso de dichas adaptaciones para inferir la morfología y producción de fuerza de los músculos relacionados (p. ej. Smith y Savage, 1956; Cartmill, 1985). Además, entender la morfología funcional de los huesos de las especies vivientes nos permite reconstruir la biología y ecología de especies extintas gracias a sus fósiles (p. ej. Argot, 2001; Spaulding y Flynn, 2009). Este tipo de estudios se agrupan en el campo de la **ecomorfología** (Ricklefs y Miller, 1999).

El estudio ecomorfológico de las adaptaciones a diferentes hábitos locomotores generalmente se lleva a cabo mediante uno de dos enfoques alternativos: categorías o continuos. El primero consiste en asignar una categoría locomotora a cada especie en base al hábito principal de su patrón locomotor, o bien a una combinación de éste y alguna propiedad biomecánica característica de su locomoción (p. ej. Taylor, 1974; Van Valkenburgh, 1987). Estas categorías generalmente se conocen como **tipos de locomoción**. El segundo enfoque considera que los diferentes tipos de locomoción forman parte de un continuo, por lo que el grado de adaptación a un hábito locomotor concreto se cuantifica mediante variables locomotoras (p. ej. Iwaniuk et al., 1999, cuantificaron la arborealidad de 0 a 4). La relación entre dichas variables locomotoras y la morfología ósea se determina mediante técnicas de regresión. Ambos enfoques tienen sus ventajas e inconvenientes, por lo que en esta tesis se optó por un enfoque intermedio: como en el primer enfoque, el patrón locomotor se categorizó en tipos de locomoción que, de manera similar al segundo enfoque, formaban continuos al describir el grado de adaptación a cada hábito locomotor (p. ej. de menor a mayor arborealidad: terrestre < trepador < semiarborícola < arborícola).

Tamaño, alometría e hipótesis de similitud

A medida que los animales crecen, o cambian de tamaño durante su evolución, las propiedades de su sistema musculoesquelético y los parámetros que definen su locomoción cambian con diferentes tasas (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003). Estos cambios dependientes del tamaño se conocen como **alometría** y generalmente se expresan mediante la **ecuación potencial**, en la cual se define la relación entre dos variables, x e y , mediante un coeficiente (a) y un exponente alométrico (b) (Huxley, 1932):

$$y = a \cdot x^b . \quad (1)$$

Varias hipótesis han sido formuladas para intentar entender las consecuencias de la

alometría y así poder predecir cómo las variables locomotoras y musculoesqueléticas se verán afectadas por variaciones en el tamaño corporal. Estas hipótesis se conocen de manera colectiva como **hipótesis de similitud** y proporcionan valores teóricos para el exponente alométrico basándose en diferentes limitaciones biomecánicas. Por ejemplo, la hipótesis de similitud **geométrica** se basa en la geometría euclídea y la ley cuadrático-cúbica. Según la primera, dos organismos son geométricamente similares si sus dimensiones lineales pueden igualarse multiplicándolas por una constante k ($I_1 = k \cdot I_2$). Asimismo, según la ley cuadrático-cúbica, cuando un organismo sufre un aumento proporcional de tamaño, su nueva superficie es proporcional al cuadrado del multiplicador ($A_1 = k^2 \cdot A_2$), mientras que su nuevo volumen es proporcional al cubo dicho multiplicador ($V_1 = k^3 \cdot V_2$). De este modo, si asumimos que dos organismos formados por los mismos materiales deberían tener la misma densidad, su masa corporal (M_b) será proporcional al volumen del organismo, por lo que también será proporcional a k^3 . O, dicho de otra forma, sus dimensiones lineales serán proporcionales a $M_b^{1/3}$. Otro ejemplo sería la hipótesis de similitud **elástica**, que se basa en la asunción de que todos los organismos han evolucionado para soportar de manera similar el efecto de la gravedad (es decir, para resistir cargas de pandeo y de flexión de manera similar) (McMahon, 1973). Partiendo de esa base, y asumiendo de nuevo densidad constante, las longitudes de un organismo deberían ser proporcionales a $M_b^{1/4}$ y sus diámetros a $M_b^{3/8}$.

Una propiedad de la ecuación potencial es que se linealiza al ser logaritimizada. En esta forma, el exponente alométrico representa la pendiente de la recta (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2003):

$$\log y = \log a + b \cdot \log x \quad . \quad (2)$$

No obstante, varios estudios alométricos han encontrado una curvatura significativa al representar la relación entre pares de variables logaritimizadas (p. ej. Economos, 1983; Bertram y Biewener, 1990). Esto sugiere que, en esos casos, los exponentes alométricos también varían con el tamaño, lo que se conoce como **alometría diferencial** (o compleja). Aunque las causas de este fenómeno no están claras, algunos autores han sugerido que estaría relacionado con el hecho de que los animales grandes suelen presentar huesos de las extremidades más robustos (Christiansen, 1999). A su vez, esto sería una estrategia para soportar los mayores esfuerzos asociados a su mayor tamaño y que, a partir de determinados valores de masa corporal, no pueden ser reducidos con cambios posturales (Biewener, 2003).

Carnivora

El orden Carnivora es probablemente uno de los grupos de mamíferos más carismáticos, ya que sus especies han formado parte de los mitos y leyendas de todas las culturas. Además, en la actualidad, su presencia en nuestra cotidianidad sigue siendo relevante: los carnívoros son nuestras mascotas favoritas, el símbolo de muchas marcas, o los protagonistas o antagonistas de numerosas películas.

Evolutivamente, sus especies pueden separarse en dos grupos principales: Feliformia y Caniformia. El primero incluye los gatos y panteras, las hienas y varios grupos caracterizados por de morfología “viverroide” (mangostas, civetas, ginetas,...), mientras que el segundo agrupa perros, osos, focas, mofetas, mapaches, hurones y similares (Wozencraft, 2005; Wilson y Mittermeier, 2009). Las relaciones filogenéticas entre estos grupos han recibido una atención renovada en la última década (ver Nyakatura y Bininda-Emonds, 2012, y sus referencias), lo que ha resultado en una considerable revisión de las familias previamente definidas (pasando de 11 a 16).

Con sus más de 280 especies vivientes, el orden Carnivora es uno de los grupos más especiosos de mamíferos (Wozencraft, 2005). Los carnívoros se encuentran en todos los continentes, salvo Australia y la Antártida, y en todos los océanos del mundo (Goswami y Friscia, 2010; Wilson y Mittermeier, 2009). Además, sus especies abarcan un enorme rango de tamaños corporales, dietas y hábitos locomotores. Todas estas características hacen a este grupo especialmente adecuado para los estudios ecomorfológicos, como los presentados en esta tesis.

Finalmente, cabe destacar que algunos autores sostienen que el orden Carnivora es un grupo evolutivamente conservador en lo relativo a hábitos locomotores y morfología apendicular, llegando a sugerir que la mayoría de diferencias morfológicas entre especies de carnívoros probablemente sean de naturaleza alométrica (p. ej. Oxnard, 1968; Bertram y Biewener, 1990; Day y Jayne, 2007). Sin embargo, este argumento ha sido duramente criticado por otros autores, los cuales se apoyan en las numerosas diferencias morfológicas, locomotoras y posturales descritas en Carnivora (p. ej. Jenkins y Camazine, 1977; Heinrich y Biknevičius, 1998; Iwaniuk et al., 1999). Esta diferencia de opiniones ha inspirado en gran parte la realización de esta tesis. Estudios anteriores han demostrado que tanto el tamaño como la filogenia influyen significativamente la morfología apendicular en Carnivora (p. ej. Bertram y Biewener, 1990; Christiansen, 1999; Day y Jayne, 2007). La pregunta es, ¿limitan estos efectos la morfología ósea en Carnivora?

Métodos comparativos filogenéticos

La mayoría de análisis estadísticos asumen que las observaciones son independientes entre sí, es decir, que se han muestreado independientemente de la misma distribución (Sokal y Rohlf, 1995). No obstante, las especies no pueden considerarse independientes en este sentido, pues son parte de una filogenia estructurada jerárquicamente (Felsenstein, 1985). Esta violación de la asunción de independencia provoca un aumento en la tasa de errores de tipo I (es decir, falsos positivos) (Martins y Garland, 1991; Rohlf, 2006). Esto ha llevado al desarrollo de varios métodos que incorporan esta estructura jerárquica en los análisis interespecíficos: los **métodos comparativos filogenéticos** (MCFs).

Uno de estos métodos es la **autocorrelación filogenética**, que divide la varianza en un rasgo morfológico en un componente filogenético y otro residual o adaptativo (Cheverud et al., 1985). A continuación, la varianza atribuida al efecto filogenético se descarta y los análisis estadísticos se llevan a cabo en el componente adaptativo de la varianza. Este método ha sido duramente criticado, pues ambos componentes no son mutuamente exclusivos, es decir, parte de la varianza de cualquier rasgo probablemente estará correlacionada con factores filogenéticos y adaptativos al mismo tiempo (Westoby et al., 1995). Una segunda categoría de MCFs incluye los **mínimos cuadrados generalizados filogenéticos** (MCGF) y metodologías similares (p. ej. Martins & Hansen, 1997). Estos métodos incluyen en la matriz de covarianzas residual tanto la estructura filogenética como el modelo evolutivo asumido (Rohlf, 2006). De este modo, a diferencia de los métodos corrientes de mínimos cuadrados, que asumen que los residuos son independientes y de distribución normal, los MCGF asumen que éstos siguen una distribución normal multivariante cuya matriz de covarianzas es función del tiempo evolutivo entre las diferentes especies y sus ancestros. Finalmente, otra categoría de MCFs son los métodos de mínima evolución, como el **método de parsimonia de cambio cuadrático** propuesta por Maddison (1991). No obstante, estos métodos no se preocupan específicamente de la violación de la asunción de independencia, sino que se formularon para reconstruir los valores de los caracteres morfológicos en los nodos internos de una filogenia (es decir, los estados ancestrales de un carácter).

En esta tesis, la violación de la asunción de independencia se abordó usando **contrastos filogenéticamente independientes** (CFI; Felsenstein, 1985), un caso especial de MCGF. Este método se basa en que, dado que la evolución de un rasgo es independiente en cada linaje, las diferencias entre los valores de dicho rasgo en dos nodos adyacentes también

deben ser independientes entre sí. Así pues, brevemente, para aplicar esta metodología primero se estiman los valores de los nodos internos de la filogenia (mediante medias ponderadas por tiempo evolutivo) y después se calcula la diferencia entre los valores de cada par de nodos adyacentes. Estas diferencias (también llamadas contrastes), que como hemos explicado son independientes entre sí, pueden usarse para realizar los análisis estadísticos en lugar de los valores de cada especie, evitando pues la violación de la asunción de independencia de las observaciones.

OBJETIVOS

Objetivo principal

El objetivo principal de esta tesis ha sido explorar y cuantificar el efecto de la función, el tamaño y la filogenia en la morfología del esqueleto apendicular de las especies del orden Carnivora mediante análisis morfométricos y biomecánicos.

Objetivos específicos

Para conseguir este objetivo, esta tesis fue dividida en cuatro secciones, cada una representando un enfoque metodológico diferente en el estudio de la morfología del esqueleto apendicular.

Sección A: Locomoción

De los diferentes hábitos locomotores que presentan las especies de Carnivora, el continuo entre hábitos terrestres y arborícolas plantea las mayores dificultades en la identificación de adaptaciones locomotoras en la morfología ósea. La cinética, dinámica y coordinación tanto de especies terrestres como arborícolas están bien documentadas en la literatura. Estudios similares se han ocupado de las particularidades de la locomoción en sustratos arbóreos de especies no arborícolas de pequeño tamaño. Así pues, el objetivo de esta sección fue complementar esta información previa con una caracterización de la locomoción en sustratos arbóreos de especies no arborícolas de mayor tamaño. Secundariamente, también se investigó si una especie totalmente terrestre emplearía una estrategia de locomoción similar si se viera forzada a una situación arborícola.

Sección B: Interacción

En esta sección se evaluó, por separado, el efecto de la función, el tamaño y la filogenia sobre una serie de medidas esqueléticas. Después, la posible interacción de estos factores se exploró en cada variable mediante modelos lineales generalizados. Los resultados de esta sección han permitido una interpretación más precisa de los resultados de las secciones siguientes.

Sección C: Alometría

En esta sección se determinó el patrón de alometría del esqueleto apendicular en Carnivora. Además, también se evaluó si existía alometría diferencial en las diferentes variables estudiadas. De manera más particular, en los Capítulos III y IV se estudió si el patrón de alometría de las diferentes líneas filéticas en Carnivora difería del patrón ordinal, y si la adaptación a los diferentes hábitos locomotores resultaba en desviaciones significativas del patrón de alometría del orden. Por otro lado, en el Capítulo V se exploraron las consecuencias biomecánicas de la alometría en el caso particular del calcáneo en Felidae.

Sección D: Escápula

La escápula presenta la morfología más variable de todo el esqueleto apendicular. No obstante, su variación de forma no ha sido estudiada previamente en Carnivora, por lo que dicho estudio se llevó a cabo en esta sección. De manera adicional, se describieron varias adaptaciones en la forma de la escápula a hábitos locomotores particulares. Finalmente, dichas adaptaciones se usaron para inferir el tipo de locomoción de los carnívoros ancestrales a partir de reconstrucciones de la forma de su escápula.

La búsqueda de la estabilidad sobre soportes estrechos: Un estudio experimental en gatos y perros



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Resumen

Se estudiaron las variables cinemáticas y de coordinación de dos carnívoros, uno con habilidades arborícolas reconocidas (gato) y el otro completamente terrestre (perro). Se usaron dos sustratos horizontales: una pista plana en el suelo (locomoción sobre suelo) y una pasarela estrecha elevada (locomoción sobre soportes estrechos). A pesar de su diferente nivel de familiaridad con la situación “arbórea”, ambas especies desarrollaron una estrategia para adaptarse a los soportes estrechos. La estrategia de los gatos se basó en usar velocidades más bajas en asociación con modificaciones en la duración de la fase de balanceo, para así mantener el equilibrio sobre el soporte estrecho. La estrategia de los perros dependió de velocidades elevadas para aumentar su estabilidad dinámica, aumentando la frecuencia del ciclo y reduciendo la duración de la fase de balanceo. Además, los perros presentaron una elevada variabilidad en la coordinación de las extremidades, aunque se observó una tendencia hacia patrones de coordinación similares al galope de tres tiempos. Por último, los perros también evitaron las fases de elevación totales. Aunque de manera distinta, ambas estrategias sugieren la reducción de la magnitud de las fuerzas verticales, lo que reduciría las oscilaciones verticales del centro de masa. De manera similar, las oscilaciones horizontales del mismo se reducían usando una postura agazapada.

II

Cuantificación de adaptaciones morfológicas usando medidas directas: El esqueleto apendicular en Carnivora como caso de estudio

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Resumen

El efecto de varios factores (tamaño, filogenia, locomoción) sobre la morfología del esqueleto apendicular se estudió en un conjunto de 43 variables medidas en la escápula, húmero, radio, ulna, metacarpo III, fémur, tibia y calcáneo de 435 especímenes de 143 especies de Carnivora. El tamaño fue el principal factor determinante de la morfología del esqueleto apendicular en carnívoros. Además, este efecto alométrico falseaba las diferencias entre algunas de las categorías locomotoras, enmascarando las verdaderas diferencias entre estos grupos. De este modo, el efecto de la filogenia y la locomoción se estudió en más detalle usando los residuos de las regresiones de cada variable sobre la masa corporal, lo que debería eliminar cualquier posible distorsión de los resultados causada por diferencias de tamaño. El tipo de locomoción se usó para representar la especialización locomotora, mientras que el hábitat preferido se consideró un indicador de la capacidad de la especie para realizar diferentes modos de locomoción (correr, nadar, trepar, excavar), lo que le permitiría maximizar la explotación de recursos al ser capaz de recorrer todos los sustratos disponibles en su hábitat preferido. El tipo de locomoción produjo resultados ligeramente mejores que el hábitat preferido, sugiriendo que los carnívoros favorecen la especialización locomotora. De acuerdo con estudios previos sobre la morfología del esqueleto apendicular, se detectó una fuerte señal filogenética en las variables estudiadas. Sin embargo, contrariamente a dichos estudios, el efecto filogenético no enmascaró las diferencias entre tipos de locomoción. Finalmente, los resultados de este estudio defienden la hipótesis de que el ancestro de los carnívoros actuales era un animal de forma “viverroide” que habitaba zonas boscosas y era o bien terrestre, o bien arborícola.

Patrón de alometría de la extremidad anterior en Carnivora: Tipos de locomoción y alometría diferencial



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Resumen

Se determinó el patrón de alometría de la extremidad anterior en Carnivora a partir de una muestra de 30 variables medidas en la escápula, húmero, radio, ulna y metacarpo III de 429 especímenes de 137 especies. Para ello, se realizó la regresión de cada variable sobre la masa corporal, cálculo que se llevó a cabo mediante técnicas de regresión tradicional y usando contrastes filogenéticamente independientes (CFIs). De acuerdo con estudios previos sobre la alometría del esqueleto apendicular, la conformidad tanto con la hipótesis de similitud geométrica como con la de similitud elástica fue escasa. También se determinó el patrón de alometría de varias líneas filéticas y tipos de locomoción en Carnivora, que en varios de estos casos se desviaba significativamente del patrón establecido para el orden. Se halló alometría diferencial en varias de las variables estudiadas, tanto en la muestra completa como en algunas de las submuestras filogenéticas y de tipo de locomoción. Contrariamente a los resultados de estudios previos, se hallaron diferencias significativas entre los exponentes alométricos obtenidos mediante regresión tradicional y CFIs, lo que enfatiza la necesidad de incorporar la estructura filogenética en los estudios alométricos. A raíz de estos y previos resultados, concluimos que las hipótesis de similitud son demasiado simplistas para describir los patrones de alometría del esqueleto apendicular en Carnivora, y por ello proponemos que nuevas hipótesis de similitud deberían construirse a partir de las semejanzas entre los patrones de alometría de muestras filogenéticamente estrechas de especies con requerimientos locomotores similares. Este estudio sería un primer paso en esa dirección.

IV

Patrón de alometría de la extremidad posterior en Carnivora: Tipos de locomoción y alometría diferencial

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Resumen

Se determinó el patrón de alometría de la extremidad posterior en Carnivora a partir de una muestra de 13 variables medidas en el fémur, tibia y calcáneo de 429 especímenes de 141 especies. Para ello, se realizó la regresión de cada variable sobre la masa corporal, cálculo que se llevó a cabo mediante técnicas de regresión tradicional y usando contrastes filogenéticamente independientes (CFIs). Se hallaron diferencias significativas entre los exponentes alométricos obtenidos con ambos métodos, lo que enfatiza la necesidad de incorporar la estructura filogenética en los estudios alométricos. En conjunto, el patrón de alometría de la extremidad posterior en Carnivora se ajusta a las predicciones de la hipótesis de similitud geométrica, aunque se detectaron algunas desviaciones de dichas predicciones (incluyendo alometría diferencial), especialmente en relación con adaptaciones a la locomoción acuática. También se determinó el patrón de alometría de varias líneas filéticas y tipos de locomoción en Carnivora. El patrón de algunas familias se desviaba significativamente del patrón alométrico establecido para el orden, pero no el de las submuestras por tipo de locomoción, lo que sugiere que el patrón de alometría de la extremidad posterior está influenciado de manera más marcada por las relaciones filogenéticas que por los hábitos locomotores y también que dicho patrón es más conservador que el de la extremidad anterior. Por último, junto con nuestro estudio previo sobre la extremidad anterior en Carnivora, los resultados de este estudio sugieren que, en carnívoros grandes no acuáticos, los mayores esfuerzos que sufren los huesos durante la locomoción debido al aumento de tamaño se compensan principalmente mediante cambios posturales en las extremidades, no modificando el patrón de alometría de las mismas. No obstante, en el caso de las extremidades anteriores, que sufren mayores esfuerzos debido a la distribución asimétrica del peso del animal, también se pudo observar un aumento en la robustez de sus huesos.

Alometría y mecánica del calcáneo en Felidae: Similitud geométrica sin alometría diferencial



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Resumen

Se midieron seis variables esqueléticas en el calcáneo de 60 especímenes de 22 especies de Felidae para determinar cómo dichas variables escalaban con la masa corporal y si presentaban alometría diferencial. La ecuación potencial ($y = a \cdot x^b$) se usó para estudiar la alometría con la masa corporal de las seis variables, comparando métodos de regresión tradicionales y contrastes filogenéticamente independientes. De acuerdo con estudios similares comparando dichas metodologías, no se hallaron diferencias significativas entre los exponentes alométricos obtenidos con ambos métodos. En conjunto, el patrón de alometría del calcáneo en Felidae se ajustó a las predicciones de la hipótesis de similitud geométrica, pero no a las de la hipótesis de similitud elástica. El brazo del momento de los extensores del tobillo aumentaba con la masa corporal con un exponente no diferente significativamente de 0.40. Esto indicaba que el *tuber calcanei* aumentaba mucho más deprisa con la masa corporal que la longitud total del calcáneo, lo que explicaría porqué la ventaja mecánica efectiva de los extensores del tobillo aumenta con la masa corporal en félidos pese a que su postura apendicular no lo hace. Además, este hallazgo concuerda con la hipótesis de crecimiento isométrico de las fuerzas de reacción del sustrato. No se detectó alometría diferencial en ninguna de las variables estudiadas, lo que reflejaría el similar patrón locomotor de todas las especies de Felidae. Así pues, los resultados de este estudio sugieren que las diferencias entre los exponentes alométricos de los mamíferos “grandes” y “pequeños” se deberían a la inclusión de especies con diferente tipo de locomoción en dichas categorías.



Evolución del tamaño y forma de la escápula en Carnivora: Adaptaciones locomotoras y alometría diferencial de forma

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Resumen

Se estudió el efecto del tamaño, la filogenia y el patrón locomotor en la forma de 213 escápulas de 101 especies de Carnivora, para lo cual se digitalizaron las coordenadas tridimensionales de 34 puntos homólogos (*landmarks*) y se usaron técnicas de morfometría geométrica. Las especies muestreadas abarcaban todo el rango de tamaño y patrones locomotores del orden. Los resultados de este estudio indicaban que, en Carnivora, la forma de la escápula está determinada por la compleja interacción de efectos alométricos, filogenéticos y funcionales. Además, se detectó alometría diferencial en la forma de la escápula de este grupo, lo que probablemente se debe al diferente patrón alométrico de las diferentes familias de carnívoros. De manera similar, la mayoría de la variación de forma asociada a cambios alométricos estaba causada por cambios de tamaño a lo largo de las líneas filéticas. La variación de forma asociada al hábito locomotor se estudió mediante análisis de variables canónicas y funciones discriminantes. La mayoría de hábitos locomotores se diferenciaban significativamente del resto en base a la forma de la escápula, aunque las funciones discriminantes produjeron elevadas tasas de clasificación errónea al comparar carnívoros semiarbóricolas y semifosoriales con el resto de tipos de locomoción. Las adaptaciones locomotoras en la forma de escápula de los carnívoros vivientes parecen independientes del tamaño y el origen común, y se pueden relacionar con la función muscular. Estas adaptaciones locomotoras se utilizaron para inferir los hábitos locomotores de los nodos internos de la filogenia de Carnivora, para los cuales se había reconstruido el tamaño y forma de la escápula mediante parsimonia de cambio cuadrático ponderado. Según la forma y tamaño de su escápula, el ancestro de los carnívoros era un animal trepador de mediano tamaño (es decir, que pasaba la mayor parte de su tiempo en el suelo, pero era un bueno trepando).

DISCUSIÓN GENERAL

Locomoción arborícola

La comparación de la locomoción sobre suelo y sobre soportes estrechos ha demostrado que los animales emplean una estrategia locomotora diferente en cada caso y que, además, estas estrategias son diferentes en animales con un diferente grado de arborealidad (Capítulo I). Los mamíferos arborícolas, como la mayoría de primates y algunas zarigüeyas, presentan adaptaciones tan marcadas para moverse en el dosel forestal que modifican también los parámetros que definen su locomoción sobre el suelo (p. ej. extremidades prensiles, pasos de secuencia diagonal,...; Larson et al., 2000; Schmitt y Lemelin, 2002). Por otro lado, los mamíferos terrestres carecen de las adaptaciones morfológicas necesarias para evitar balancearse y caer al moverse sobre soportes estrechos (p. ej. Cartmill, 1985). Es por ello que estas especies se desplazan por este tipo de sustratos a elevadas velocidades, lo que aumenta su estabilidad dinámica. De manera adicional, el uso de patrones asimétricos de coordinación y la reducción de las fases de elevación total permiten a estas especies tanto un mayor control sobre sus movimientos como disminuir activamente las oscilaciones del soporte. Por último, las especies con un grado intermedio de arborealidad (es decir, las especies trepadoras) emplean una estrategia locomotora común para aumentar su estabilidad al desplazarse sobre sustratos arbóreos. Esta estrategia consiste principalmente en un avance más lento que sobre el suelo y en cambios deliberados en la posición de sus manos/pies. El hecho de que los animales empleen estrategias locomotoras diferentes en función del grado de arborealidad respalda el uso de categorías locomotoras en estudios ecomorfológicos, ya que estas diferentes estrategias probablemente requieran diferentes adaptaciones morfológicas. Los resultados de las Secciones C y D confirman este argumento, pues en ellas se han descrito varias diferencias, tanto en los patrones de alometría como en la forma de la escápula, entre especies con un

diferente grado de arborealidad.

De las diferentes adaptaciones a la locomoción arborícola, los pasos de secuencia diagonal, característicos de la mayoría de primates y otros mamíferos arborícolas (Hildebrand, 1967; Cartmill et al., 2002; Schmitt y Lemelin, 2002), permiten un mejor equilibrio sobre soportes estrechos, pues reducen el balanceo al presentar mayores superficies de soporte (Rollinson y Martin, 1981). Aunque el origen de este tipo de pasos no está claro, su uso siempre está relacionado a la locomoción sobre soportes estrechos (Schmitt y Lemelin, 2002). De este modo, se hubiera esperado detectar pasos de secuencia diagonal en las situaciones arbóreas estudiadas en el Capítulo I. El hecho de que este tipo de pasos no se observara ni una sola vez en perros o gatos sugiere que la locomoción en soportes estrechos no es suficiente para estimular su uso. Una explicación alternativa sería que los patrones neuronales responsables de este tipo de coordinación no se hallan desarrollado evolutivamente en Carnívora. Finalmente, otra posible explicación sería que la aparición de los pasos de secuencia diagonal requiera una mayor familiaridad con los sustratos arbóreos, es decir, una habituación previa o el entrenamiento en su uso.

Como reflexión final a este apartado sobre la locomoción arborícola cabe destacar que, en futuros estudios, sería interesante documentar la estrategia locomotora de los carnívoros arborícolas (como el binturong, *Artictis binturong*, o el kinkajú, *Potos flavus*) para confirmar que es similar a la de otros mamíferos arborícolas. Del mismo modo, estudios similares a los realizados en el Capítulo I deberían llevarse a cabo en mamíferos no arborícolas grandes, como los osos o las panteras, lo cual permitiría comprobar si la estrategia descrita para especies pequeñas y medianas también se aplica a estos animales. Finalmente, dado que los resultados de la Sección D sugieren que las adaptaciones locomotoras relacionadas con la arborealidad en la forma de la escápula consisten principalmente en el desarrollo de las zonas de inserción de la musculatura asociada a trepar, sería interesante estudiar la locomoción tanto de especies arborícolas como no arborícolas sobre soportes estrechos inclinados y al trepar por superficies verticales. Todos estos estudios agradecerían el uso de técnicas de cineradiografía y electromiografía, pues estos métodos permitirían una mejor integración del estudio de las variables locomotoras y las musculoesqueléticas.

Factores determinantes de la morfología del esqueleto apendicular

Las Secciones B a D han demostrado que la morfología del esqueleto apendicular en

Carnivora está determinada por la interacción del tamaño corporal, las relaciones filogenéticas y la función de sus elementos. Además, esta interacción es compleja y varía en las diferentes variables estudiadas.

El tamaño parece ser el principal factor determinante de la morfología del esqueleto apendicular en Carnivora, tal y como demuestran los resultados del Capítulo II y los elevados coeficientes de correlación obtenidos en la Sección C. Estos resultados concuerdan con estudios previos sobre la alometría del esqueleto apendicular y sobre el efecto del tamaño en la mayoría de variables describiendo la cinética, dinámica y coordinación de la locomoción (p. ej. Alexander et al., 1979; Bertram y Biewener, 1990; Christiansen, 1999; Casinos et al., 2012). El hecho de que las diferencias de tamaño interespecíficas ocasionaran diferencias ficticias al comparar grupos taxonómicos y funcionales (Capítulo II) plantea dudas sobre la validez de estudios ecomorfológicos previos, ya que se basan en usar las medidas del esqueleto apendicular de las especies vivientes para inferir la ecomorfología de especies extintas (p. ej. Van Valkenburgh, 1987; Argot, 2001). De este modo, si esta distorsión alométrica no se corrige adecuadamente (usando residuos de regresión, por ejemplo), cualquier inferencia basada en este tipo de medidas podría ser errónea. Algunos autores han “evitado” este tipo de distorsiones usando índices, cocientes entre dos o más medidas osteológicas, pues asumen que al ser magnitudes adimensionales deben ser independientes del tamaño corporal (p. ej. Oxnard, 1968; Van Valkenburgh, 1987; Iwaniuk et al., 1999). El problema con este tipo de “corrección” es que, como expuso Aiello (1981), esto sólo se cumple si el numerador y el denominador escalan con el tamaño corporal con el mismo exponente alométrico, y esto, como se demuestra en la Sección C, rara vez se cumple. En conclusión, el uso de residuos de regresión parece ser la corrección más adecuada en estudios ecomorfológicos.

En relación a la supuesta naturaleza conservadora del orden Carnivora en términos de hábito locomotor y morfología apendicular (p. ej. Oxnard, 1968; Bertram y Biewener, 1990; Day y Jayne, 2007), los resultados de esta tesis claramente refutan tal afirmación. En primer lugar, los resultados del Capítulo II revelaron que el efecto alométrico creaba diferencias ficticias entre categorías locomotoras, en lugar de ser su principal fuente de variación, como sugerían los autores citados anteriormente. Por otro lado, el patrón de alometría del esqueleto apendicular difería entre varios tipos de locomoción y entre éstos y el patrón establecido para el orden (Capítulos III y IV). De este modo, ni el hábito locomotor ni la morfología apendicular en Carnivora podrían describirse como “conservadores” o ser considerados limitados por las relaciones filogenéticas.

No hay que olvidar, sin embargo, que se detectó una fuerte señal filogenética en las variables estudiadas (Capítulo II), en sus patrones de alometría (Capítulos III–V), y en la forma de la escápula (Capítulo VI). El hecho de que las familias más jóvenes del orden se originaran en la transición del Oligoceno al Mioceno (hace unos 18 – 24 Ma.) explicaría que la mayor parte de la variabilidad morfológica en el esqueleto apendicular en Carnivora se dé a nivel de familia (Capítulo II), pues han tenido milenios para desarrollar rasgos filogenéticos característicos. Del mismo modo, esto también aclararía cómo es posible encontrar al mismo tiempo una señal filogenética tan fuerte y una gran variabilidad morfológica en términos locomotores, pues cada familia ha tenido tiempo para desarrollar adaptaciones particulares a los diferentes hábitos locomotores. Aunque cabe destacar que en algunos casos se han adquirido adaptaciones similares en las diferentes familias (es decir, evolución convergente), como es el caso de la forma de la escápula en las especies cursoriales (Capítulo VI).

Hablando de tiempo evolutivo y variabilidad morfológica, los félidos vivientes merecen especial consideración. Este grupo se originó en una reciente radiación evolutiva hace unos 11 millones de años (Johnson et al., 2006), durante los cuales sus especies han desarrollado una postura apendicular y hábito locomotor similares (Day y Jayne, 2007; Wilson y Mittermeier, 2009). Además, los elevados coeficientes de correlación y estrechos intervalos de confianza obtenidos para esta familia en la Sección C sugieren una reducida variabilidad morfológica. No obstante, esta familia también presenta uno de los mayores rangos de tamaño corporal en el orden Carnivora, lo que indicaría que la variabilidad morfológica de este grupo no está tan limitada como su reciente radiación evolutiva podría sugerir. Estudios previos han demostrado que los animales grandes presentan extremidades más erectas que los pequeños para reducir la magnitud de los momentos producidos en las articulaciones por la fuerza de reacción del sustrato, que aumenta proporcionalmente a su masa corporal (Biewener, 2005). Dado que, como se ha comentado, la postura apendicular apenas varía en Felidae, deberían existir otros mecanismos para reducir los esfuerzos que causan dichos momentos. Los resultados del Capítulo V demuestran que, en el tobillo, esto se consigue por el rápido aumento del brazo de palanca de los extensores del tobillo relativo a la longitud total del calcáneo. Algo similar debe ocurrir en el codo, pues un patrón similar se observó en la longitud y orientación del olécranon, el brazo de palanca de los extensores del codo (Capítulo III). Otro impactante ejemplo de la variabilidad morfológica que puede originarse en tan corto tiempo evolutivo es la marcada convergencia en la forma de la escápula entre el guepardo (*Acinonyx jubatus*) y otras

especies adaptadas a la carrera, como los cánidos y hienas actuales (Capítulo VI).

Cambiando de tema, en marcado contraste con la amplia variabilidad observada en las dimensiones del esqueleto apendicular, las proporciones relativas de los segmentos de la extremidad anterior son bastante constantes en Carnivora, como se había descrito anteriormente para éste y otros grupos de mamíferos (Schmidt, 2008; Schmidt y Fischer, 2009). Esta constancia puede ser explicada por varios factores. Por un lado, el desarrollo ontogenético de los diferentes segmentos de la extremidad está regulado por dos grupos de genes: *Emx2* y *Pax1* se encargan de la escápula, mientras que el resto de segmentos son definidos por un gradiente de expresión de los complejos *HoxA* y *HoxD* (Pellegrini et al., 2001, y sus referencias). Esto sugeriría que el desarrollo del segmento proximal (escápula) es independiente del de los segmentos medio (húmero) y distal (antebrazo). Por otro lado, desde un punto de vista biomecánico, se ha demostrado que las extremidades de postura flexionada, típicas de los mamíferos pequeños, son más estables si sus segmentos tienen una similar longitud, mientras que las extremidades extendidas típicas de mamíferos grandes requieren segmentos con diferentes proporciones para autorregular su estabilidad (Seyfarth et al., 2001; Fischer y Blickhan, 2006). Esto sugeriría la existencia de un mecanismo que controle las proporciones de todos los segmentos de la extremidad. Además, también sugeriría que las proporciones de los segmentos apendiculares deberían ser menos similares al aumentar el tamaño corporal. No obstante, éste no es el caso, dado que los segmentos de los carnívoros pequeños no presentan longitudes relativas similares, lo que podría indicar que este grupo evolucionó de un ancestro con extremidades extendidas y que las especies pequeñas mantuvieron sus proporciones disimilares, dada la constancia de éstas.

Por último, cabe destacar que la principal cuestión sobre los factores que influyen la morfología apendicular en Carnivora que ha quedado sin responder hace referencia a las causas de la alometría diferencial. Originalmente, este fenómeno fue atribuido al hecho de que resistir el efecto de la gravedad sólo debería causar problemas estructurales en especies grandes, de ahí que presentaran diferente patrón alométrico que las pequeñas (Economos, 1983). Esto fue extendido posteriormente a que los mamíferos grandes y pequeños tienen diferentes requerimientos locomotores (Bertram y Biewener, 1990; Christiansen, 1999a). Además, dado que los mamíferos pequeños parecían escalar geoméricamente mientras que los grandes lo hacían elásticamente, Christiansen (1999b) sugirió que los animales mantenían la resistencia a esfuerzos de flexión desarrollando diáfisis progresivamente más gruesas. Los resultados de la Sección C sólo apoyan este

planteamiento en parte, pues no se halló alometría compleja en las familias con vastas diferencias de tamaño entre sus especies (p. ej. Felidae, Canidae). Además, aunque Ursidae parecía conformar mejor a la hipótesis de similitud elástica por los bajos exponentes alométricos obtenidos para la longitud de sus huesos, los diámetros tendían a aumentar con menores exponentes que el resto de familias, pese a que sus amplios intervalos de confianza no excluyeran los elevados valores teóricos propuestos por la similitud elástica. Otro argumento en contra de esta explicación para la alometría diferencial es el hecho de que ésta se detectó en algunas familias con escasa variación de tamaño corporal, como Viverridae. Por otro lado, Bou et al. (1987) sugirieron que la baja conformidad de algunas relaciones alométricas con las hipótesis de similitud podría deberse a la inclusión de especies con diferentes requerimientos locomotores en la misma muestra. Esto se comprobó como explicación alternativa a la alometría diferencial en la Sección C. De acuerdo con esta hipótesis, se esperaba hallar este fenómeno en las submuestras que mezclaran tipos de locomoción, pero no en las que no lo hacían. Sin embargo, esto no se cumplió, ya que se detectó alometría diferencial en varias variables tanto en carnívoros trepadores como en semiarbóricolas

CONCLUSIONES

- 1 Tanto los mamíferos no arborícolas pequeños como los medianos presentan una estrategia común para desplazarse sobre soportes estrechos. Esta estrategia consiste en el uso de bajas velocidades, probablemente para reducir la magnitud de las fuerzas verticales sobre el sustrato, lo que reduciría las oscilaciones tanto de su centro de masa como del soporte.
- 2 El perro, una especie completamente terrestre, usa velocidades elevadas para aumentar su estabilidad dinámica al desplazarse sobre soportes estrechos. Además, usa pasos asimétricos y poco regulares, lo que sugiere reajustes constantes en la coordinación de las extremidades. De manera adicional, reducen las oscilaciones verticales disminuyendo la presencia de fases de elevación totales.
- 3 Las diferentes estrategias locomotoras que presentan los mamíferos para desplazarse sobre soportes estrechos presentan varias características comunes: maximización del tiempo de contacto entre el animal y el soporte, reducción de la fase de balanceo, y uso de posturas agazapadas.
- 4 La morfología del esqueleto apendicular en Carnivora está determinada por la interacción del tamaño, las relaciones filogenéticas y la función de sus elementos. Esta interacción es compleja y varía en las diferentes variables.
- 5 El tamaño es el principal efecto que determina la morfología apendicular en Carnivora. Además, crea diferencias ficticias entre categorías locomotoras y enmascara diferencias reales entre estos grupos.

6

Aunque la señal filogenética en la morfología del esqueleto apendicular es fuerte, ni los hábitos locomotores ni la morfología apendicular están limitados por una historia filogenética común en Carnivora.

7

Ni la similitud elástica ni la geométrica predicen correctamente el patrón de alometría de la extremidad anterior en Carnivora. Por otro lado, la extremidad posterior escala geométricamente. En conjunto, estos resultados enfatizan que las hipótesis de similitud son demasiado simplistas y deberían ser replanteadas en base a similitudes en los patrones de alometría de muestras filogenéticamente estrechas de especies con requerimientos locomotores similares.

8

En Carnivora, tanto la filogenia como la adaptación causan desviaciones significativas del patrón de alometría ordinal en la extremidad anterior, pero no en la posterior. Esto está probablemente relacionado con el hecho de que la extremidad anterior tiene una función locomotora y de captura/manipulación de la presa mientras que la posterior sólo tiene función locomotora.

9

En carnívoros grandes no acuáticos, el aumento en los esfuerzos asociados con la locomoción sufridos por los huesos se compensan principalmente con cambios posturales y no con modificaciones en el patrón de alometría del esqueleto apendicular.

10

Contrariamente a estudios anteriores comparando ambas metodologías, se hallaron diferencias entre los exponentes alométricos obtenidos mediante regresión tradicional y contrastes independientes. Esto enfatiza la necesidad de tener en cuenta las relaciones filogenéticas en los estudios alométricos para evitar la violación de la asunción de independencia de las observaciones.

11

Se detectó alometría diferencial en las variables morfométricas que describen el esqueleto apendicular en Carnivora (incluyendo la forma de la escápula). No obstante, ni la inclusión de especies con diferente tamaño ni con diferentes requerimientos locomotores explican por separado la presencia de este fenómeno en estudios alométricos. Así pues, la alometría diferencial podría reflejar una respuesta común a múltiples problemas alométricos.

12

Como se observó en otros mamíferos, el brazo del momento de los extensores del tobillo aumenta con la masa corporal en Felidae con un exponente alométrico no diferente significativamente de 0.40. Este rápido crecimiento, relativo a la longitud total del calcáneo, explica cómo la ventaja mecánica efectiva de los extensores del tobillo aumenta con la masa corporal a pesar de que la postura apendicular no varía en félidos. Además, este hallazgo concuerda con la hipótesis de crecimiento isométrico de la fuerza de reacción del sustrato.

13

Las adaptaciones locomotoras en la forma de la escápula de los carnívoros actuales parecen independientes del tamaño corporal y de un origen común, y pueden ser relacionadas con la actividad muscular característica de los diferentes hábitos locomotores.

14

Los resultados de esta tesis sugieren que el ancestro de los carnívoros actuales era un mamífero de mediano tamaño que habitaba zonas boscosas y presentaba adaptaciones mixtas a hábitos terrestres y arborícolas (es decir, probablemente era trepador). Este hallazgo concuerda con la posición de los "miácidos" en la rama que dará lugar a los carnívoros actuales.

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Published Papers



The search for stability on narrow supports: an experimental study in cats and dogs

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ABSTRACT

Kinematic and coordination variables were studied in two carnivorans, one with known locomotor capabilities in arboreal substrates (cat), and the other a completely terrestrial species (dog). Two horizontal substrates were used: a flat trackway on the ground (overground locomotion) and an elevated and narrow runway (narrow-support locomotion). Despite their different degree of familiarity with the 'arboreal' situation, both species developed a strategy to adapt to narrow supports. The strategy of cats was based on using slower speeds, coupled with modifications to swing phase duration, to keep balance on narrow supports. The strategy of dogs relied on high speeds to gain in dynamic stability, and they increased cycle frequency by reducing swing phase duration. Furthermore, dogs showed a high variability in limb coordination, although a tendency to canter-like coordination was observed, and also avoided whole-body aerial phases. In different ways, both strategies suggested a reduction of peak vertical forces, and hence a reduction of the vertical oscillations of the centre of mass. Finally, lateral oscillation was reduced by the use of a crouched posture.

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1. Introduction

The gaits employed by animals when walking or running overground, and their corresponding dynamics and kinematics, have been rigorously studied since the 19th century (e.g., Marey, 1873; Muybridge, 1899; Manter, 1938; Hildebrand, 1966, 1980, 1985; Demes et al., 1994; Lee et al., 1999; Larson et al., 2000; Cartmill et al., 2002; Fischer et al., 2002; Abourachid, 2003; Hutchinson et al., 2006; Maes et al., 2008). Nevertheless, the ground is not the only support on which animals move; they also move on branches high in the forest canopy or dig their way through the ground. Each substrate requires different anatomical, morphological, and mechanical adaptations, as well as modifications to the dynamics and kinematics of locomotion (Biewener, 2003).

Locomotion on arboreal substrates has not been as thoroughly studied as overground locomotion, but its main particularities have already been covered (Cartmill, 1974, 1985; Meldrum, 1991; Schmitt, 1999, 2003a; Schmitt and Lemelin, 2002; Lemelin et al., 2003; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). The main problem affecting arboreal locomotion is the tendency of animals to roll (rotate around their sagittal axis) and topple from the support because all their support points are effectively collinear,

which greatly reduces their support polygon. Several solutions to this problem, each involving different morphological adaptations, have been described (Cartmill, 1985): (i) relatively short limbs, as in arboreal viverrids (Taylor, 1970), or the use of a crouched posture (Schmidt and Fischer, 2010), keep the body's centre of mass close to the support and minimise lateral oscillation; (ii) prehensile hands and/or feet allow gripping the branch and thus exerting a torque that resists the toppling moment, as in primates (Rollinson and Martin, 1981; Vilensky and Larson, 1989; Schmitt, 1999), some opossums (Schmitt and Lemelin, 2002; Lemelin et al., 2003), and tupaiids (Sargis, 2001); (iii) the reduced body size of small animals, like squirrels, overcomes the toppling problem by spreading the support points relatively more widely on the surface of the branch; and (iv) a foolproof solution to totally avoid toppling is hanging underneath the branch, like sloths do. Another source of locomotor instability during arboreal locomotion is the round section of branches, which increases the potential of slipping off them. Animals with prehensile hands and/or feet avoid this problem by firmly grasping the support; while clawed animals, whose grasping abilities are reduced or absent, change limb placement during arboreal locomotion to reorient substrate reaction forces inwards to the branch, and thus prevent slipping off it (Schmitt, 2003a; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). Finally, another problem affecting arboreal locomotion are vertical oscillations of the support. Branches, especially the fine ones, tend to deflect under an animal's weight, which not only hinders joint stabilisation, but

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might also toss the animal from the support due to elastic recovery. Schmitt (1999) proposed that animals use compliant gaits as a solution to this problem. Compliant gaits are characterised by substantial limb yield, which reduces vertical oscillations of the body (and thus of the support) and encourages long contact times, which in turn allows the reduction of stride frequency (and thus the potential of branch sway). Furthermore, compliant gaits reduce bone and joint stresses associated with flexed-limb gaits (Schmitt, 1999). The use of compliant gaits in primates, marsupials and other arboreal mammals was later confirmed by Larney and Larson (2004). In addition to compliant gaits, the use of a crouched posture has also been proposed as a mechanism to reduce vertical oscillations of the body both in compliant (Schmitt, 1999) and stiff gaits (i.e., when limb yield is low; Bishop et al., 2008). For the latter case, the authors proposed that, if limb protraction and angular excursion remained unaltered, the use of a crouched posture would reduce vertical displacement of the centre of mass by creating a smaller pendulum (and thus reducing potential energy fluctuations; Bishop et al., 2008). Finally, at higher speeds, ambling gaits have also been proposed as a solution to reduce vertical oscillations of the support, since they allow animals to maintain at least one foot in contact with the substrate during a stride, thus reducing peak vertical forces on the support (Schmitt et al., 2006).

Most studies on arboreal locomotion, though, focus on primates and, to a lesser extent, on some didelphids, since they consider these groups arboreal specialists, which present a set of adaptations to moving and foraging in an arboreal setting so marked that it makes their terrestrial locomotion distinct from that of other animals. These adaptations involve prehensile extremities, showing more protracted arm postures at touch-down, producing lower peak vertical substrate reaction forces with the forelimbs than with the hindlimbs, and using diagonal-sequence gaits almost exclusively when walking on narrow supports (Hildebrand, 1967; Vilensky and Larson, 1989; Demes et al., 1994; Larson et al., 2000; Schmitt and Lemelin, 2002). Nevertheless, arboreal specialists are not the only animals known to use arboreal substrates. As stated by Lammers and Biknevicius (2004), many small mammals use fallen logs and branches on the forest floor as arboreal runways. Furthermore, many terrestrial species often climb trees to escape predators or while hunting (MacDonald, 1984; Wilson and Mittermeier, 2009). Since stability in locomotion is directly linked to performance in escaping or hunting behaviours, and thus directly linked to fitness, it would be vital for these terrestrial mammals navigating arboreal substrates (non-arboreal specialists) to adapt their locomotion and increase their stability.

To date, locomotion on arboreal supports in non-arboreal specialists has only been studied in small species: the common marmoset (*Callithrix jacchus*) (Schmitt, 2003b), the grey short-tailed opossum (*Monodelphis domestica*) (Lammers and Biknevicius, 2004), and the rat (*Rattus norvegicus*) (Schmidt and Fischer, 2010). To increase their stability on arboreal supports, these animals reduced peak vertical forces to reduce the vertical oscillation of the centre of mass. Both the common marmoset and the rat used similar speeds and had similar contact times (i.e., duty factor, and thus stance phase duration) in overground and arboreal locomotion, while the grey short-tailed opossum used lower speeds and had longer contact times during arboreal locomotion. Schmidt and Fischer (2010) proposed that the reduction of speed could only be accomplished if some grasping ability is retained.

In the light of these results, we wonder how a larger non-arboreal specialist (for instance, a ground-dwelling carnivoran pursuing its prey up into the forest canopy) will adapt its kinematics and coordination to the arboreal substrate. Will larger mammals use the same strategy as the smaller ones? The first aim of this study was thus to determine how a medium-sized non-arboreal specialist adjusts its kinematics and coordination to adapt to an arboreal

substrate. For our experiments, we chose the domestic cat (*Felis silvestris catus*), which is accustomed to moving comfortably along branches, rails, and similar narrow, elevated supports. Taking into account the possible solutions for increasing stability presented above, cats were expected to increase stance phase duration, and thus decrease stride frequency. Slower speeds on narrow supports than on flat ground, as was found for the grey short-tailed opossum (Lammers and Biknevicius, 2004), were also expected, since cats can use their claws to grip the support. We also expected that they would display a more crouched posture in the 'arboreal' situation to bring the centre of mass closer to the support.

Secondly, we wondered whether the strategy employed by non-arboreal specialists to adapt to the arboreal situation, if there was any, would be a universal solution for all terrestrial species. That is, if we encouraged a completely terrestrial species into an arboreal-like situation, would it arrive at the same solution to keep balance and advance on the narrow support? To answer this question, we used a protocol similar to the one used for cats to study the kinematics and coordination of the domestic dog (*Canis lupus familiaris*) when moving along a narrow, elevated support, before comparing both strategies. We chose the dog because it is a completely terrestrial species whose kinematics and coordination overground have already been thoroughly studied (Hildebrand, 1968; Lee et al., 1999; Maes et al., 2008).

2. Materials and methods

All animals were healthy specimens, with no known pathologies that might affect their vision, balance, or locomotion. Due to the different degree of familiarity of the studied species with the arboreal situation, different experimental settings were used for each species. This way, animals were able to move along the support, but were at the same time forced to search for stability.

2.1. Cats

Seven cats (age = 5.9 ± 3.5 years; shoulder height = 0.27 ± 0.02 m; body mass = 4.4 ± 0.7 kg) were filmed on the ground and in an 'arboreal' situation (narrow-support locomotion). In overground locomotion, the cats moved along an 8 m flat carpet (Fig. 1A), while the arboreal situation was simulated by a wooden bar ($0.03 \text{ m} \times 0.03 \text{ m} \times 2.50 \text{ m}$) raised to a height of 0.75 m (Fig. 1B). The trestles raising the wooden bar also prevented it from deflecting under the cats' weight, thus avoiding external

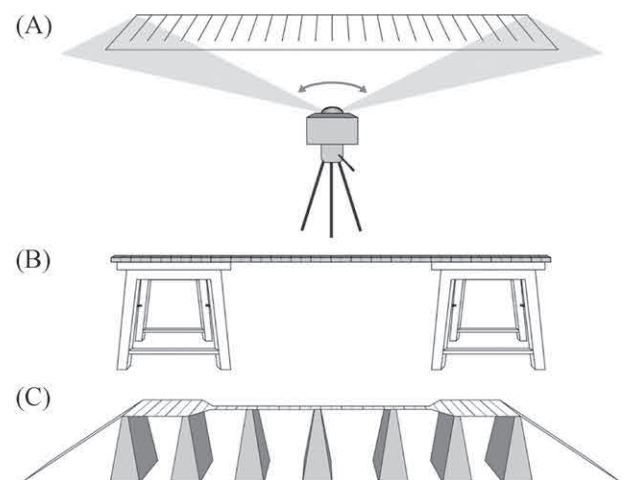


Fig. 1. Experimental situations for the comparison between (A) overground and (B and C) narrow-support locomotion for cats (B) and dogs (C). See text for details.

perturbations to their stability (e.g., induced vertical oscillations of the centre of mass). Black lines, perpendicular to the axis of locomotion, were painted at 0.05 m intervals both on the carpet and on the wooden bar and used to assess the location of each foot at touch-down (accuracy: 0.02 m). In both cases, the cats were placed at one end of the structure (bar or carpet) and were encouraged to go to the other end of it. A high-speed video camera (Basler A504K; Basler Electric Co., Highland, IL, USA), placed perpendicular to the trackway, 3.0 m from its centre (field: 1.0 m; resolution: 1280 pixels/m), was used to film the cats at a frequency of 125 Hz.

We are aware that the experimental situation that we used to represent arboreal locomotion is just an approximation, given that we used a narrow, square surface to simulate a support that tends to be round in section. Nevertheless, support width was approximately the same as feet width, which would probably affect stability to a similar degree as a round support of approximately half the body width of the animal. Although this last methodology is useful for studies dealing with changes in the orientation of ground reaction forces on arboreal settings (e.g., Lammers and Biknevicius, 2004), the former provides better insight on the effect of collinear limb placement.

2.2. Dogs

Five Belgian Shepherd dogs (age = 7.3 ± 1.7 years; shoulder height = 0.61 ± 0.04 m; body mass = 28.0 ± 5.0 kg) were filmed in an 'arboreal' situation. A 9 m long runway raised to a height of 1.5 m was used in this experimental situation. The elevated runway included a central narrow part ($0.15 \text{ m} \times 5.0 \text{ m}$) simulating the arboreal situation, and two wide parts ($0.5 \text{ m} \times 2.0 \text{ m}$) allowing the dog to stabilise prior to and after the narrow part (Fig. 1C). The whole structure was reinforced with small beams between the supports to avoid its deflection under the weight of the dogs, which would introduce external perturbations to their stability. Furthermore, since we were interested in the effect of support width, not support slipperiness, the whole surface of the runway was covered with a mix of paint and sand as an anti-slip coat. Black lines, perpendicular to the axis of locomotion, were painted on the runway at 0.10 m intervals and used to assess the location of each foot at touch-down (accuracy: 0.05 m). Since the dogs were trained for agility contests, they moved along the runway when asked by their owners. A high-speed video camera (Basler A504K), placed perpendicular to the runway, 10.0 m from its centre and at a height of 2.5 m (field: 2.0 m; resolution: 640 pixels/m), was used to film the dogs at a frequency of 125 Hz.

In the case of dogs, support width was about one and a half times the width of their feet, since dogs refused to perform the exercise on supports narrower than 15 cm. Nevertheless, this situation is comparable to the potential 'arboreal' situations that terrestrial mammals may face (e.g., a fallen log traversing a gap). Finally, given that the aim of this study was to search for possible modifications to kinematic and coordination variables of locomotion when comparing the 'arboreal' and the usual (overground) situation, we needed a minimum degree of regularity, which would not have been achievable if the animals had advanced on a truly arboreal substrate.

For overground locomotion, we revisited the data from a previous study that comprised all gaits of Belgian Shepherd dogs analysed in the anteroposterior sequence (APS) framework (Maes et al., 2008). Comparison between our data in the 'arboreal' situation and overground locomotion data from Maes et al. (2008) was possible because we used the same dog breed (Belgian Shepherds), and because the experimental procedure was based on the same processes.

2.3. Video analysis and data processing

All locomotor analyses in this study were carried out in the framework of the APS approach, since it allows the study of all kinds of interlimb coordination – symmetrical or asymmetrical gaits and unsteady locomotion – with the same set of variables (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). The APS method has already been described elsewhere (Maes et al., 2008, p. 140), and will only be briefly summarized here. The records were analysed using Virtual Dub (version 1.6.12; <http://www.virtualdub.org/>). The timings of touch-down (when the foot makes contact with the ground) and lift-off (when the last toe leaves the ground) of each limb were noted using frame number. A maximal error of one frame (i.e., 8.0 ms) was estimated for touch-down and lift-off timings. The positions of the feet on each touch-down were determined using the black lines marked on all experimental supports. The data were visualised using classical gait diagrams (Marey, 1873) and track diagrams (Abourachid et al., 2007), which allowed us to spot APSs and to manually identify gaits.

After video analysis, in each APS the following kinematic variables were calculated for the first forelimb to contact the ground (referred to hereafter as reference limb): cycle duration (D ; in seconds), corresponding to the time between consecutive footfalls of the same foot; cycle frequency ($F = 1/D$; Hz); stance (St ; s) and swing (Sw ; s) phase duration, corresponding to the time that the foot is in contact with the ground, and the time that it is lifted, respectively, during each cycle; and stride length (L ; m), corresponding to the distance between consecutive footprints of the same foot. Speed (u ; m/s) was calculated using stride length and cycle duration ($u = L/D$).

We also calculated the following temporal coordination variables: fore lag (FL; %) and hind lag (HL; %), corresponding to the time between the footfalls of both limbs of a pair, fore and hind limb, respectively, in relation to the cycle duration of the reference limb; and pair lag (PL; %), corresponding to the time between footfalls of the first limb of each pair to contact the ground in relation to the cycle duration of the reference limb. Complementarily, we calculated the following spatial coordination variables: fore gap (FG; %) and hind gap (HG; %), corresponding to the distance between the footfalls of both limbs of a pair, fore and hind limb, respectively, relative to the stride length of the reference limb; and pair gap (PG; %), corresponding to the distance between the footfalls of the first limb of each pair to contact the ground as a percentage of the stride length of the reference limb (Abourachid, 2003; Abourachid et al., 2007; Maes et al., 2008). Positive PG values indicate that the hindfoot is placed on the support in front of the forefoot, while negative PG values correspond to the hindfoot being placed behind the forefoot. Finally, to assess regularity in limb coordination during locomotion, we compared PL values between successive sequences, thus defining the irregularity index (IrI) as the absolute value of the difference between PL of sequence n and PL of sequence $n - 1$ ($IrI_n = |PL_n - PL_{n-1}|$).

To test for differences in the mean values of both kinematic and coordination variables between overground and narrow-support locomotion, Mann–Whitney non-parametric tests were performed using SPSS for Windows (release 15.0.1 2006; SPSS Inc., Chicago, IL, USA), since not all the data were normally distributed and homoscedasticity was not always observed. Values of $p < 0.05$ were considered statistically significant.

Regarding the relationship between each variable and speed, we used either the power equation or a linear model of regression, whichever was had a better r^2 . All equations were calculated using least-squares regression (Sokal and Rohlf, 1995). Possible differences between the regression slopes of overground and narrow-support locomotion were accounted for using an F -test with a significance level of 0.05.

Table 1

Regressions on speed for overground and arboreal locomotion in cats and dogs. A power equation ($y = ax^b$) was used for all regressions except for L , in which a linear model of regression ($y = a + bx$) was used.

	Overground					Narrow support					
	<i>a</i>	<i>b</i>	CI _a	CI _b	R ²	<i>a</i>	<i>b</i>	CI _a	CI _b	R ²	<i>p</i> value
<i>Cats</i>											
<i>F</i>	1.898	0.628	1.859 to 1.937	0.598 to 0.658	0.799	1.930	0.646	1.853 to 2.009	0.602 to 0.689	0.677	>0.05
<i>St</i>	0.347	−0.720	0.340 to 0.356	−0.754 to −0.687	0.810	0.332	−0.813	0.326 to 0.355	−0.859 to −0.767	0.749	<0.01
<i>Sw</i>	0.183	−0.391	0.176 to 0.189	−0.445 to −0.337	0.325	0.201	−0.071	0.190 to 0.213	−0.133 to −0.009	0.012	–
<i>L</i>	0.258	0.296	0.244 to 0.272	0.270 to 0.322	0.548	0.246	0.322	0.229 to 0.262	0.284 to 0.360	0.409	>0.05
<i>Dogs</i>											
<i>F</i>	1.433	0.395	1.390 to 1.477	0.363 to 0.426	0.722	1.365	0.592	1.187 to 1.569	0.471 to 0.711	0.413	<0.01
<i>St</i>	0.509	−0.928	0.488 to 0.530	−0.970 to −0.884	0.887	0.608	−1.082	0.518 to 0.715	−1.221 to −0.943	0.639	<0.05
<i>Sw</i>	0.250	0.061	0.237 to 0.262	0.009 to 0.112	0.023	0.216	−0.094	0.183 to 0.255	−0.236 to 0.048	0.013	–
<i>L</i>	0.480	0.292	0.440 to 0.520	0.277 to 0.306	0.866	0.639	0.171	0.474 to 0.805	0.119 to 0.221	0.245	<0.01

Values in italics denote non-significant regressions.

CI_a, 95% confidence interval for *a*; CI_b, 95% confidence interval for *b*; *F*, cycle frequency (Hz); *L*, stride length (m); *p* value, significance of the comparison of slopes between overground and narrow-support locomotion (“–” denotes that no comparison could be made due to non-significant regressions); R², determination coefficient; *St*, stance phase duration (s); *Sw*, swing phase duration (s).

3. Results

A total of 425 APs were obtained for cats in overground locomotion, while 403 sequences were filmed in the narrow-support situation. Cats did not show great difficulties in performing the exercise. On the contrary, they sometimes even performed a couple of locomotor sequences along the wooden bar, then turned around with no effort, and returned to the starting point. Speed values for cats ranged from 0.21 to 0.72 m/s. For dogs, only 134 APs could be obtained for narrow-support locomotion, since they showed greater difficulties in performing the exercise. Even though they were used to agility training, they sometimes fell or jumped off the runway. Their speed ranged from 1.54 to 4.19 m/s. Since data from Maes et al. (2008) for overground locomotion comprised a much wider range of speeds (from 0.4 to 10.0 m/s), their dataset was reduced to 232 APs that matched our speed range.

3.1. Cats

As expected, cats used significantly slower speeds in narrow-support than in overground locomotion (mean ± standard deviation: 0.42 ± 0.10 vs. 0.53 ± 0.11 m/s, respectively; $p < 0.001$). Regarding the slopes of either frequency or stride length, there were no significant differences between both situations (Table 1 and Fig. 2A,B). Nevertheless, the relative contribution of stance and swing phases differed in both situations. In narrow-support locomotion, stance phase duration decreased with increasing speed significantly faster than in overground locomotion (Table 1). Thus, although mean stance phase duration was longer in narrow-

support locomotion at low speeds, these differences disappeared at higher speeds (Fig. 2C). Swing phase duration, while decreasing with speed in overground locomotion, was independent of speed in narrow-support locomotion (Table 1 and Fig. 2D) and also showed lower mean values (0.24 ± 0.04 vs. 0.22 ± 0.04 s, respectively; $p < 0.001$).

In both situations, cats used the lateral walk exclusively as their preferred gait. The values of temporal coordination variables (lags) were always close to the theoretical values defined by Abourachid (2003), although their variability slightly exceeded the classically accepted 5% (Hildebrand, 1966; Maes et al., 2008), especially for the hindlimbs (HL = 51.1 ± 6.4% and 49.3 ± 6.9% for overground and narrow-support locomotion, respectively; Table 2 and Fig. 3A,B). Temporal coordination between sequences was highly regular in both situations, since PL variation between consecutive APs was on average <5% (Irl < 5%, Table 2). Pair lag values decreased from a mean of 83% to 75% as speed increased in both overground and narrow-support locomotion. Regarding significant differences in coordination variables between overground and narrow-support locomotion, FL values were significantly higher and HL and PL were significantly lower when cats moved along the wooden bar compared to overground locomotion. Finally, regarding spatial coordination, PG values were significantly lower in narrow-support locomotion (Table 2). In fact, when walking overground, cats usually placed each hindfoot in front of its corresponding forefoot (PG > 0%), while they placed the hindfeet behind the forefeet when moving along the wooden bar (PG < 0%). Together with some differences found in kinematic variables, this finding suggests the use of a different locomotor strategy in each situation.

Table 2

Comparison between coordination variables in overground and narrow-support locomotion in both cats and dogs. FG, fore gap (%); FL, fore lag (%); HG, hind gap (%); HL, hind lag (%); Irl, irregularity index (%); *n*, sample size; *p* value, significance of the comparison of mean values between overground and arboreal situations in cats (since the coordination patterns were unsteady in narrow-support locomotion compared to the steady gaits of the overground locomotion, significant differences in mean values for coordination variables could not be tested for in dogs); PG, pair gap (%); PL, pair lag (%); s.d., standard deviation.

	Cats				<i>p</i> value	Dogs			
	Overground <i>n</i> = 425		Narrow support <i>n</i> = 403			Overground <i>n</i> = 232		Narrow support <i>n</i> = 134	
	Mean	s.d.	Mean	s.d.		Mean	s.d.	Mean	s.d.
FL	49.5	3.3	50.9	4.0	<0.001	50.5	2.9	45.7	6.8
HL	51.1	6.4	49.3	6.9	<0.001	49.5	3.9	40.5	12.6
PL	80.2	5.1	79.5	4.2	<0.001	60.8	18.2	60.7	9.3
FG	50.3	4.1	50.5	5.1	0.875	50.1	2.9	45.5	6.7
HG	50.7	5.1	50.3	5.9	0.265	50.3	4.0	40.6	11.7
PG	6.8	7.3	−5.7	9.0	<0.001	11.1	17.8	5.7	11.0
Irl	3.5	2.8	2.6	2.2	0.091	3.3	3.2	6.6	4.6

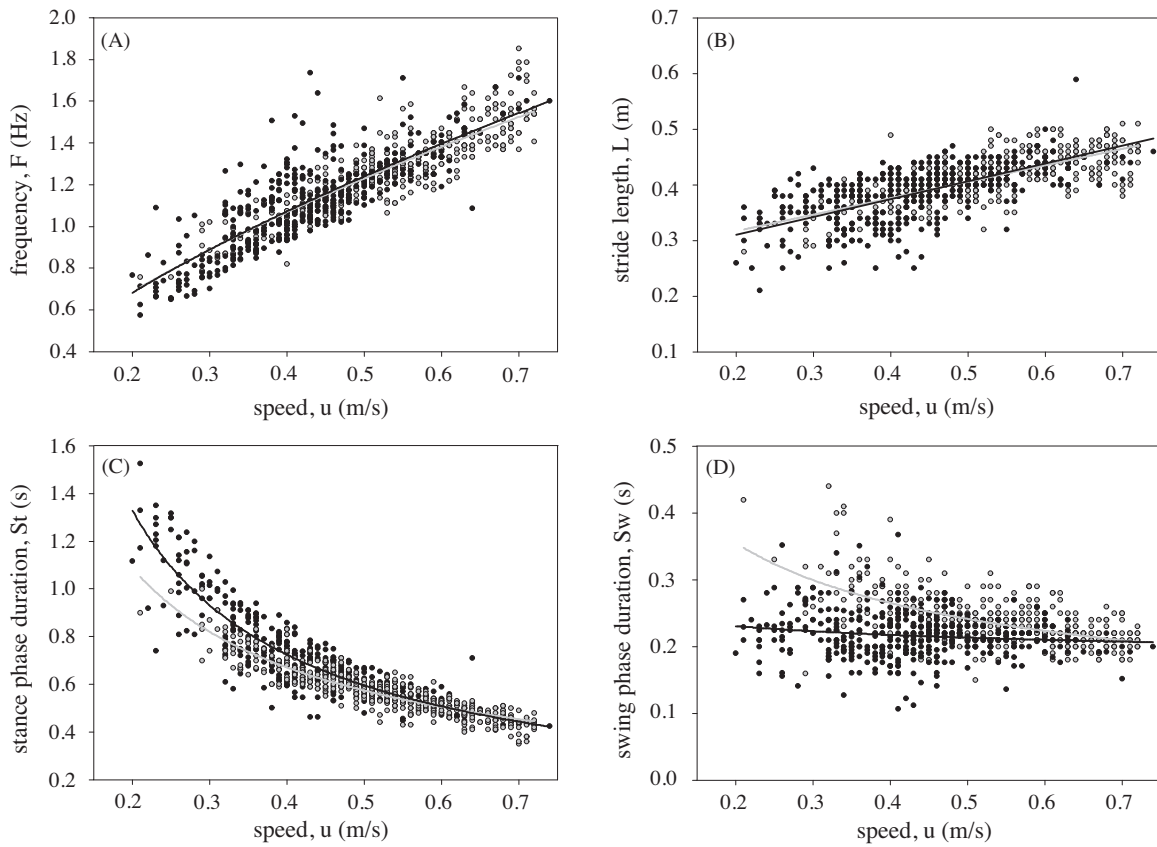


Fig. 2. Relationship between speed and (A) cycle frequency, (B) stride length, (C) stance phase duration, and (D) swing phase duration in cats. Grey dots represent overground locomotion data, black dots represent data from narrow-support locomotion.

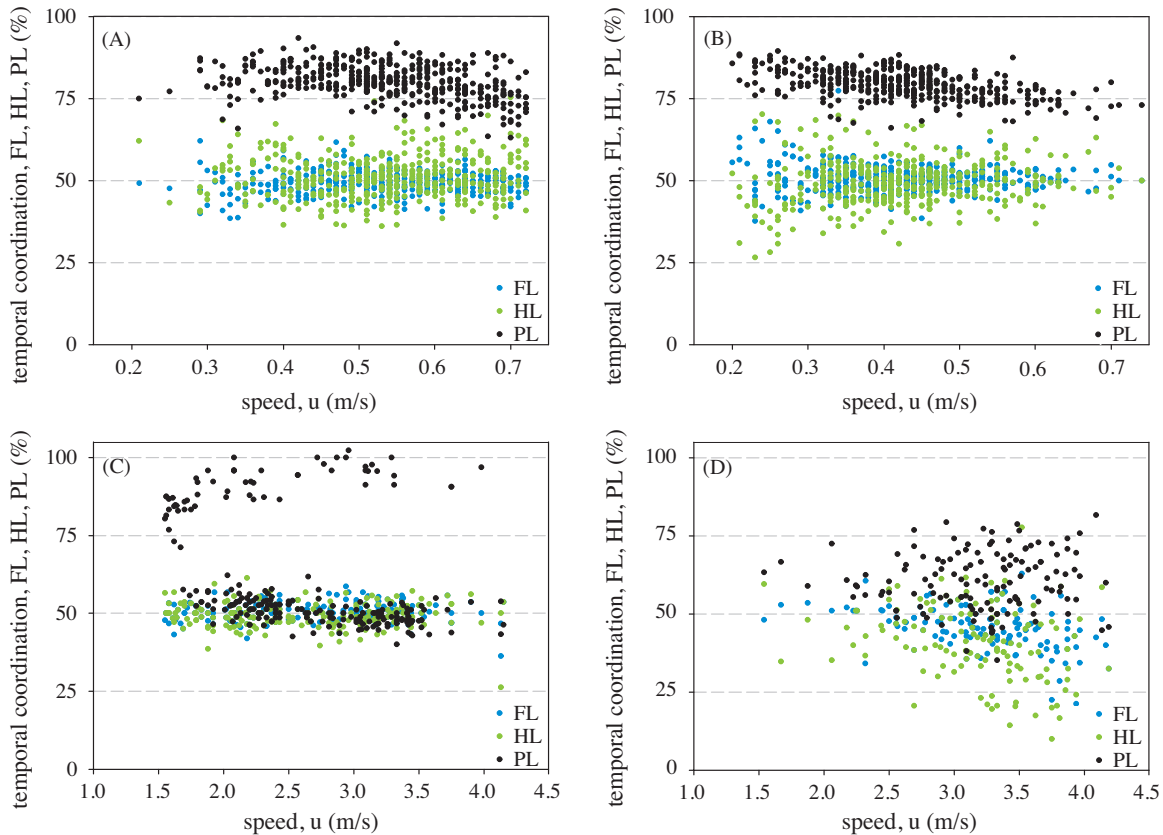


Fig. 3. Temporal coordination in (A and B) cats and (C and D) dogs. Graphs on the left correspond to overground locomotion (A and C), while those on the right represent narrow-support locomotion (B and D). Blue dots represent fore lag (FL), green dots represent hind lag (HL), and black dots represent pair lag (PL).

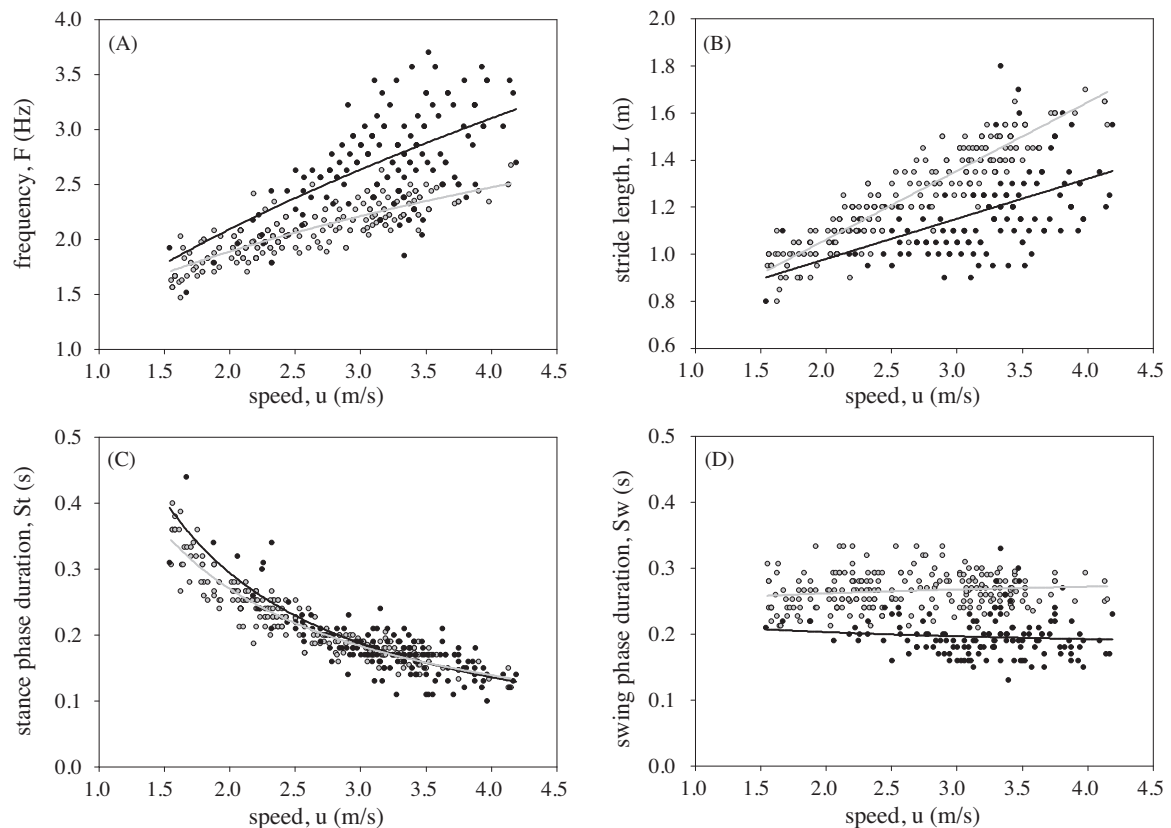


Fig. 4. Relationship between speed and (A) cycle frequency, (B) stride length, (C) stance phase duration, and (D) swing phase duration in dogs. Grey dots represent overground locomotion data, black dots represent data from narrow-support locomotion.

3.2. Dogs

Dogs tended to perform the exercise at high speeds: the mean speed for narrow-support locomotion was 3.20 ± 0.52 m/s, a value close to the top speeds found for symmetrical gaits in the study of Maes et al. (2008). Regarding the rest of the kinematic variables, cycle frequency increased significantly faster in narrow-support locomotion, with the slope obtained for the ‘arboreal’ situation almost 1.5 times the slope obtained for overground locomotion (Table 1 and Fig. 4A), which suggests the use of different locomotor strategies in each situation. On the other hand, the slope of stride length was significantly lower in narrow-support locomotion (Table 1 and Fig. 4B), probably relating to a consistent reduction or even lack of whole-body aerial phases in narrow-support locomotion. Only 24.6% of narrow-support APSs included a whole-body aerial phase, whose duration was on average only $4.7 \pm 3.1\%$ of cycle duration. Stance phase duration decreased significantly faster in narrow-support locomotion (Table 1 and Fig. 4C). Swing phase duration was independent of speed in both situations (Table 1 and Fig. 4D), and, as observed in cats, it was significantly shorter when dogs moved on the catwalk (0.27 ± 0.03 vs. 0.20 ± 0.03 s for overground and narrow-support locomotion, respectively; $p < 0.001$).

Even though we considered the same range of speeds, the coordination patterns employed in overground and narrow-support locomotion were different. When moving overground, dogs used almost exclusively symmetrical gaits (FL=HL=50±5%), with the trot as their preferred gait: of the 232 APSs analysed for overground locomotion, 30 (12.9%) corresponded to lateral walk, 30 (12.9%) to pace, 1 (0.4%) to transverse gallop, and 171 (73.7%) to trot. On the other hand, dogs preferred asymmetrical coordination patterns (FL ≠ 50±5% and/or HL ≠ 50±5%) in narrow-support locomotion, since only 28 out of 134 APSs (20.9%) were strictly sym-

metrical. Temporal coordination between sequences in overground locomotion was highly regular (Irl = $3.3 \pm 3.2\%$; Table 2), contrary to what was found in narrow-support locomotion, since Irl exceeded on average the 5% threshold (Irl = $6.6 \pm 4.6\%$; Table 2). Given that these high Irl values, together with the high standard deviation of coordination variables in narrow-support locomotion (6.8 and 12.6 for FL and HL, respectively; Table 2), make the link to gaits difficult to express, we prefer to speak of a “coordination pattern” instead of a “gait”. Only about 92 of the 134 ‘arboreal’ sequences (68.7%) appeared like gaits classically defined in locomotion studies: we found 12 (9.0%) sequences of gallop-like coordination, 45 (33.6%) corresponding to canter-like coordination, and 35 (26.1%) to trot-like coordination. Since the coordination patterns in the narrow-support situation were unsteady compared to the steady gaits of the overground situation, significant differences in mean values for coordination variables could not be tested for in dogs (Table 2 and Fig. 3C,D).

4. Discussion

4.1. A common strategy for non-arboreal specialists

The main strategy for cats to adapt to the arboreal situation was to use slower speeds (with the corresponding adjustment of all speed-related variables, e.g., longer stance phase duration), which is generally associated with lower peak vertical forces (Demes et al., 1994; Schmitt and Lemelin, 2002). Similar results were obtained by Lammers and Biknevicius (2004) when studying the dynamics of arboreal locomotion in the grey short-tailed opossum (*Monodelphis domestica*), a smaller non-arboreal specialist with limited grasping abilities that nevertheless navigates frequently on arboreal substrates. Furthermore, these authors also reported an increase in

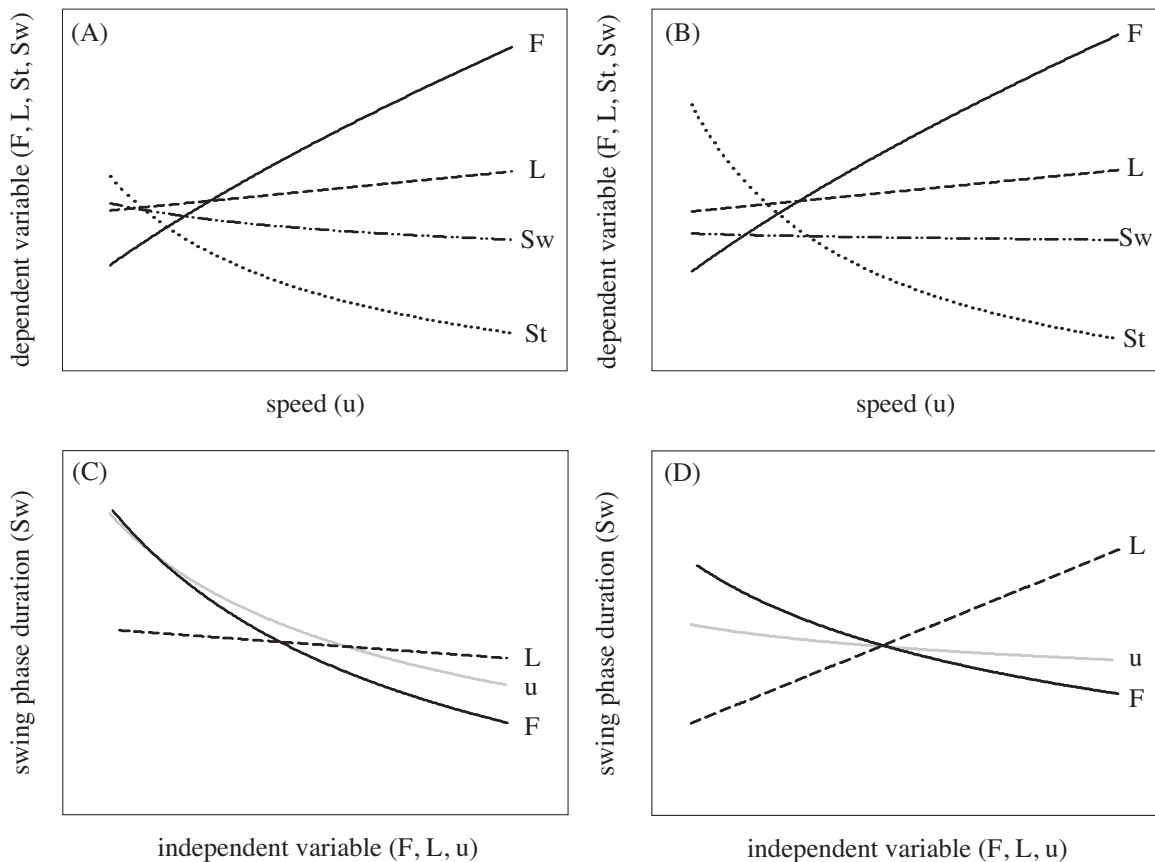


Fig. 5. Relationships (A and B) between speed and several kinematic variables, and (C and D) between swing phase duration and cycle frequency, stride length, and speed in cats. Plots on the left (A and C) represent overground locomotion data, while those on the right (B and D) correspond to narrow-support locomotion. *Abbreviations:* F, cycle frequency (Hz); L, stride length (m); St, stance phase duration (s); Sw, swing phase duration (s); u, speed (m/s).

duty factor in an arboreal situation, and significantly steeper slopes when comparing stance phase duration vs. speed in the arboreal trials with those obtained for overground trials, as observed in the present study (Table 1 and Fig. 2C). Thus, in accordance with our prediction, it seems that there is a common strategy for small and medium-sized non-arboreal specialists to increase their stability when in an arboreal situation.

Swing phase duration was the only variable that was modified during the cats' narrow-support locomotion in a way not predicted by speed: it decreased significantly with speed when cats moved overground, but its variation was independent of speed in narrow-support locomotion (Fig. 5A and B). Given that speed is directly related to changes in cycle frequency (F) and/or stride length (L), we studied the relationship between these variables and swing phase duration (Sw; Fig. 5C and D). Cycle frequency is inversely related to swing phase duration ($F = [St + Sw]^{-1}$), while in each cycle stride length is determined during the swing phase. Therefore, Sw should decrease with increasing F, and it should also be related to L in some way. As expected, as cycle frequency increased, swing phase duration decreased in both the arboreal and flat ground situations (Fig. 5C and D). Swing phase duration and stride length were not significantly related in overground locomotion in cats ($Sw = 0.280 - 0.099L$; $R^2 = 0.014$; Fig. 5C), suggesting the existence of factors other than swing phase duration to explain the increase in stride length with speed in this situation (e.g., greater angular velocities of the limb during the swing phase). On the other hand, longer strides were directly related to an increase in swing phase duration in narrow-support locomotion ($Sw = 0.114 + 0.270L$; $R^2 = 0.163$; Fig. 5D). During film analysis, it was frequently observed

that, when cats got out of balance, they quickly leaned their feet on the bar, shortening considerably swing phase duration and thus reducing stride length. It was also observed that, when there were no balance issues, cats usually made tentative steps before definitely placing their forefeet on the bar, allowing them a steadier grip, but in turn increasing swing phase duration. These observations support the relationship between swing phase duration and stride length, but they also suggest that variations in swing phase duration would be more related to balance than to speed. In summary, during undisturbed overground locomotion in the cat, the relationship between swing phase duration and speed mirrors the relationship between cycle frequency and speed (Fig. 5C). During 'arboreal' locomotion, however, a significant relationship appears between swing phase duration and stride length, probably related to the search for stability. Thus, there is a direct relationship between Sw and L, and an inverse relationship between Sw and F. This conflicting compromise between increasing speed and maintaining balance probably renders non-significant the relationship between swing phase duration and speed (since $u = LF$) (Fig. 5D).

A possible explanation for the lower pair gap values found in narrow-support locomotion could be the crouched posture adopted by most cats and several dogs when moving along the elevated support, which is characteristic of mammals moving on narrow supports (Cartmill, 1985; Schmitt and Lemelin, 2002; Lammers and Biknevicius, 2004; Schmidt and Fischer, 2010). The use of a crouched posture increases stability by bringing the centre of mass closer to the support, but it also hampers limb protraction, thus causing the hindlimbs to touch the ground not as far ahead as typically observed, and reducing pair gap values. As suggested by

Lepicard et al. (2006), for mice in potentially dangerous environmental conditions, the reduction of swing phase duration and the use of a crouched posture are a function of the animals' risk assessment of the environment.

Finally, during film analysis, it was observed that cats placed their feet obliquely to the support. That is, during locomotion on narrow supports the lower arm was kept in an adducted position during the stance phase. These observations agree with previous results on primate arboreal locomotion (Schmitt, 2003a). When comparing mediolaterally applied forces and joint angles during terrestrial and arboreal locomotion in primates, Schmitt (2003a) found that most of the studied animals showed a higher degree of adduction on the arboreal support. Lower arm adduction in the cat is probably accomplished thanks to the angle of the olecranon fossa relative to the long axis of the humerus, which has been previously related to living in densely structured habitats (Gonyea, 1978). In the case of domestic cats, this angle is about 9° , at an intermediate position between the cheetah, *Acinonyx jubatus* (3° ; highly cursorial, open terrain dweller), and the arboreal margay cat, *Leopardus wiedii* (13°). The oblique placement of the feet creates a larger support polygon, since the feet are no longer collinear, thus increasing stability. Furthermore, it probably reorients ground support forces inwards to the support, which prevents slipping off it and reduces lateral oscillations of the centre of mass (Schmitt, 2003a; Lammers and Biknevičius, 2004; Schmidt and Fischer, 2010). This finding further validates the use of a narrow, square bar to simulate arboreal supports.

4.2. Dynamic stability over balance in completely terrestrial species

As shown above, dogs tended to perform the 'arboreal' exercise at high speeds, probably relying on dynamic stability rather than on balance. To increase their speed, dogs reduced cycle duration significantly by shortening the swing phase, which recalls the strategy used by cats when out of balance. This behaviour thus seems characteristic of locomotion on narrow supports in both cats and dogs. It has been demonstrated that increased angular velocities during limb retraction in the swing phase prior to touch-down are a simple strategy to increase the stability of spring-mass running (Seyfarth et al., 2003). These increased angular velocities could account for the observed reduction of swing phase duration during 'arboreal' locomotion in dogs.

The strategy of dogs during 'arboreal' locomotion involved other striking features, namely the reduction, or even loss, of whole-body aerial phases, and important changes in coordination. Thus, it seems that completely terrestrial mammals (dogs) use a different strategy to gain stability on narrow supports from non-arboreal specialists. Considering the overlapping speed range (1.54–4.19 m/s), 72.3% of the sequences performed overground included a whole-body aerial phase (83.1% when excluding lateral walk), while only 26.3% included an aerial phase on the narrow support. The reduction of whole-body aerial phases probably was a strategy to achieve lower peak vertical forces, which reduces vertical oscillation of the centre of mass and of the support, increasing stability. This strategy has also been reported for overground locomotion in elephants (Hutchinson et al., 2006), and for arboreal ambling and cantering in primates, for which it has also been described as a strategy to maintain a secure grip on the branch, thus increasing the importance of this strategy in arboreal locomotion (Schmitt, 1999; Schmitt et al., 2006).

Regarding coordination, while dogs favoured symmetrical gaits, especially the trot, when moving overground at the specific speed range considered in this study (1.54–4.19 m/s), they used mainly asymmetrical coordination patterns when moving along the elevated narrow support. Although 48% of the APSs of narrow-support

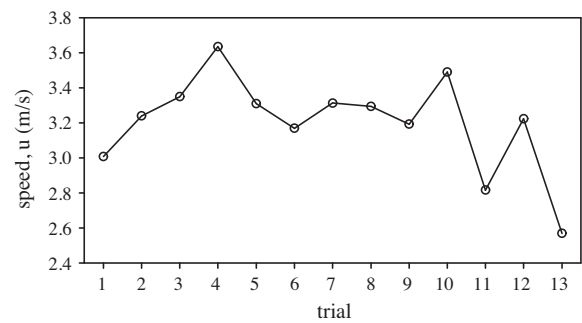


Fig. 6. Mean speed values of dogs for each successive trial of narrow-support locomotion.

locomotion could not be classified into any classically defined gait, 34% could be attributed to canter-like coordination, and 9% each to transverse gallop-like and trot-like coordination. In canter, only one of the synchronised limb couplets characterising the trot is retained, thus, by using canter-like coordination, dogs gain an additional functional step per sequence, which grants them another chance to modify their kinematics and coordination (in contrast to just two functional steps in trot; Lee et al., 1999). Furthermore, coupled with whole-body aerial phase reduction, canter-like coordination allows dogs to lean on three feet during part of the cycle, thus reducing bipedality (only two feet on the ground at the same time), which in turn enhances stability when moving forward (Hildebrand, 1980; Cartmill et al., 2002). Both canter-like and trot-like coordination are characterised by periods of diagonal bipedality, which provides mechanical stability during running, given that touch-down synchronisation of diagonal limbs opposes the forces that tend to rotate the body in both its transverse (pitch) and sagittal (roll) axis (Hildebrand, 1985; Lee et al., 1999; Cartmill et al., 2002). This may also explain why a pace-like coordination, less stable since it maximises unilateral bipedality (Cartmill et al., 2002), was never observed in narrow-support locomotion, while dogs used the pace overground (Maes et al., 2008).

These results agree with the work of Schmitt et al. (2006) in primates, whose preferred gait in asymmetrical running was the canter when moving either along a horizontal pole or overground. In the same study, Schmitt et al. (2006) stated that both ambling gaits and canter allow animals to maintain at least one foot in contact with the support during the stride, that is, to eliminate whole-body aerial phases. This loss of whole-body aerial phases cannot be accomplished at high speed trotting (e.g., in our data for dogs in narrow-support locomotion, 45.7% of the trot-like sequences included a whole-body aerial phase, whereas only 11.1% of the canter-like sequences did). They also noted that both canter and ambling gaits account for reduced periods of bipedality. According to these authors, these properties of ambling gaits and canter increase the animal's stability by lowering peak vertical forces, thus reducing vertical displacement of the centre of mass and vertical oscillation of the support. It would be interesting to study substrate reaction force patterns in cats and dogs, as has been done in primates and opossums (Schmitt, 1999; Schmitt and Lemelin, 2002; Lammers and Biknevičius, 2004; Schmidt and Fischer, 2010), to assess this decrease in peak vertical forces when these animals advance in an arboreal situation.

Finally, it could be argued that the preference of dogs for high speeds in narrow-support locomotion could be a consequence of their agility training. Although it probably influenced their first trials traversing the elevated runway, since the highest observed speed values correspond to the first trials, there might have been a learning process during the subsequent trials, in which the dogs progressively decreased their speed on the runway (Fig. 6). Never-

theless, due to the low sample size (only 3 dogs performed more than 10 trials), no significant correlation could be found between speed and trial number ($p = 0.399$).

4.3. Conclusions

Our study of the kinematics and coordination in the cat points to the existence of a global strategy for medium-sized (cats) and small (opossums) non-arboreal specialists when moving on narrow, elevated supports. This strategy consists of the use of low speeds, probably to reduce peak vertical forces, hence to reduce the oscillations of the centre of mass and those of the support. No change in gaits is needed to maintain balance.

In contrast, the completely terrestrial dogs showed greater difficulties to adapt to narrow-support locomotion. They moved at high speeds to gain in dynamic stability, using unsteady asymmetrical coordination patterns, suggesting constant readjustments in limb coordination. The reduction of whole-body aerial phases limited vertical oscillation of the centre of mass.

The only universal strategy observed was the maximisation of contact time between the animal and the support by reducing swing phase duration and also by the use of a crouched posture, which probably reduces oscillation of the centre of mass.

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Scaling and mechanics of the felid calcaneus: geometric similarity without differential allometric scaling

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Abstract

Six mechanically significant skeletal variables were measured on the calcanei from 60 Felidae specimens (22 species) to determine whether these variables were scaled to body mass, and to assess whether differential scaling exists. The power equation ($y = a \cdot x^b$) was used to analyse the scaling of the six variables to body mass; we compared traditional regression methods (standardised major axis) to phylogenetically independent contrasts. In agreement with previous studies that compared these methodologies, we found no significant differences between methods in the allometric coefficients (b) obtained. Overall, the scaling pattern of the felid calcaneus conformed to the predictions of the geometric similarity hypothesis, but not entirely to those of the elastic similarity hypothesis. We found that the moment arm of the ankle extensors scaled to body mass with an exponent not significantly different from 0.40. This indicated that the tuber calcanei scaled to body mass faster than calcaneus total length. This explained why the effective mechanical advantage of the ankle extensors increased with body mass, despite the fact that limb posture does not change in felid species. Furthermore, this finding was consistent with the hypothesis of the isometric scaling of ground reaction forces. No evidence for differential scaling was found in any of the variables studied. We propose that this reflected the similar locomotor pattern of all felid species. Thus, our results suggested that the differences in allometric coefficients for 'large' and 'small' mammals were in fact caused by different types of locomotion among the species included in each category.

Key words: biomechanics; calcaneus; differential scaling; effective mechanical advantage; Felidae; phylogenetically independent contrasts; scaling.

Introduction

The calcaneus is the largest tarsal bone in mammals; it consists of an anterior portion, where the astragalus articulates, and a posterior portion, the tuber calcanei, where the Achilles tendon inserts (Lessertisseur & Saban, 1967). The calcaneus forms a lever for the calf muscles because the Achilles tendon is shared by the gastrocnemius and soleus, the ankle extensors. The length of this lever arm determines the moment of the force produced by the limbs as they push against the ground, which causes the body to rise and advance during forward locomotion (Alexander, 1983). Furthermore, the length of the tuber calcanei is related to the muscle mechanical advantage at the ankle, which counteracts the moment exerted on the joint by the ground reaction force (Biewener, 1989, 2003).

The shape of the calcaneus is variable in mammals. It has been proposed that, given its important role in the mechanics of locomotion, this variability would probably be related to locomotor specialisation (Lessertisseur & Saban, 1967). However, size is another factor that must be taken into account (i.e. scaling). The main biomechanical consequences of scaling have been described in broadly comparative studies, and several hypotheses have been proposed to understand how increasing size affects animal design (Schmidt-Nielsen, 1984; Alexander, 2002; Biewener, 2005). These hypotheses, often referred to as similarity hypotheses, have been used to predict how anatomical structures and locomotion patterns would be affected by increasing body size. The hypothesis of geometric similarity, already supported by Hill (1950), states that two organisms are geometrically similar if their linear dimensions can be made equal by multiplying those of one of them by a constant (c). Thus, their surfaces could be made equal by multiplying by c^2 , whereas volumes should be multiplied by c^3 . Assuming a constant density (ρ), which would be logical if both organisms are made of the same materials, body mass would also be proportional to c^3 ($M_b = \rho V = \rho L^3$). Then, geometrically similar animals made of the same materials should present linear

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dimensions proportional to body mass^{1/3}. The hypothesis of elastic similarity, proposed by McMahon (1975), is based on the assumption that different-sized organisms have evolved to resist buckling and bending loads similarly (Schmidt-Nielsen, 1984). In order to maintain this similar elastic recovery, and assuming again a constant density, diameters must scale to body mass^{3/8}, and lengths to body mass^{1/4}. Nevertheless, none of those hypotheses appears to provide a universal explanation for the effects of size. For instance, mammalian linear dimensions typically conform to geometric similarity (Alexander et al. 1979) but, in Bovidae, limb bone lengths appear to follow elastic similarity (McMahon, 1975). Another important point in scaling studies is whether general allometric calculations are applicable to a large range of variations in body size. Some studies on the scaling of skeletal elements appear to indicate otherwise. Economos (1983) predicted that, because volume increases faster than surface area, the pattern for scaling cross-sectional bone areas in large mammals (over 20 kg of body mass) should be different from that used in small mammals. This hypothesis of differential scaling was somewhat confirmed on mammalian long bones, mainly in carnivores (Bertram & Biewener, 1990; Christiansen, 1999a,b), and on mammalian body length (Silva, 1998). Thus, the first aim of this study was to determine the scaling pattern of the calcaneus bone, and to assess whether differential scaling could be found in this pattern.

As pointed out by Bou et al. (1987), similarity hypotheses imply adaptive neutrality, or at least independence of the locomotor type of the species that are compared. Therefore, samples with extreme locomotor patterns should show large deviations from predicted relationships. In fact, as stated by Day & Jayne (2007), phylogenetic diversity among different-sized samples might obscure the effect of size alone. To avoid this problem, we chose Felidae as our study group, because they comprise a well-defined, phylogenetically narrow clade (Mattern & McLennan, 2000; Johnson et al. 2006) with substantial differences in body size (Wilson & Mittermeier, 2009). The sizes of different Felidae species span two orders of magnitude and bracket the suggested 20-kg body mass change point for allometric relationships (Economos, 1983). Furthermore, they have similar locomotor patterns (Day & Jayne, 2007; Wilson & Mittermeier, 2009).

We also wondered whether the scaling pattern of the felid calcaneus would be influenced by ankle mechanics. On one hand, broadly comparative studies have shown that larger animals tend to run with more erect limb postures; this reduces the magnitude of the joint moments produced by the ground reaction force (F_g) and, thus, reduces the stresses acting on the bones (for a review, see Biewener, 2005). Consequently, the effective mechanical advantage (EMA), defined as the ratio of the extensor muscle moment arm to the F_g moment arm (Fig. 1a), scales to body mass with positive allometry (e.g. $EMA_{\text{ankle}} = M_b^{0.169}$ for a large

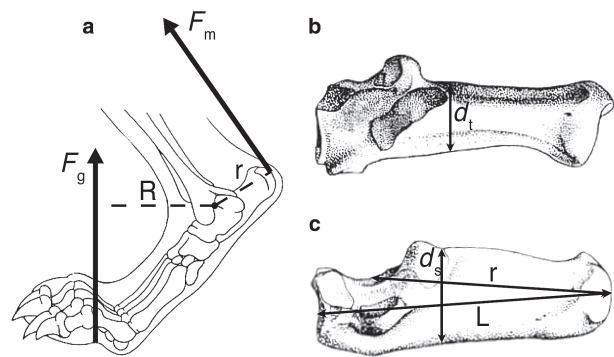


Fig. 1 Ankle anatomy and mechanics. (a) Lateral view of the distal skeletal elements of the felid hind limb and the forces acting at the ankle with their corresponding moment arms. (b) Dorsal view of the calcaneus of *Panthera* sp. (c) Medial view of the calcaneus of *Panthera* sp. Images modified from Lessertisseur & Saban (1967). Abbreviations: d_s , sagittal diameter; d_t , transverse diameter; F_g , ground reaction force; F_m , ankle extensors muscle force; L , calcaneus total length; R , moment arm of the ground reaction force; r , moment arm of the ankle extensors.

sample of mammals; Biewener, 1989). On the other hand, Day & Jayne (2007) showed that large felids do not have more upright limbs than small felids. Thus, the angle of the ankle at footfall or midstance was not significantly correlated to body mass in felids. Although they could not definitively exclude the possibility that EMA increased with size in felids, the authors suggested that it would be very unlikely, because the F_g orientation changed very little, even among phylogenetically diverse taxa (Biewener, 2005). Therefore, to support that theory, the muscle moment arms would have to increase with strong positive allometry in felids. Nevertheless, Alexander et al. (1981) have shown that muscle moment arms in mammals scaled to body mass with an exponent of 0.40 ($M_b^{0.40}$); this value was substantially higher than the exponents proposed for length scaling by similarity hypotheses (geometric similarity: $M_b^{0.33}$; elastic similarity: $M_b^{0.25}$). The muscle moment arm scaling factor ($b = 0.40$) was later supported by the work of Castiella & Casinos (1990) in insectivores and rodents. Thus, our second aim was to determine whether the moment arm of ankle extensors in felids scaled to body mass with the expected value of 0.40; this would provide evidence that EMA increased with body size in felids even though limb posture remained more or less constant. We chose the calcaneus bone, because it was assumed to have high mechanical significance.

Materials and methods

We studied 60 calcanei from 22 species of Felidae (Table 1) by measuring the total length (L), the moment arm of the ankle extensors (r), and the sagittal and transverse diameters (d_s and d_t , respectively) just distal to the calcaneus–astragalus articulation (Fig. 1b,c). The moment arm of a muscle is defined as the

Table 1 Measured specimens.

Species (abbreviation)	<i>n</i>	Average <i>M_b</i> (kg)
<i>Acinonyx jubatus</i> (Aju)	2	49.0
<i>Caracal caracal</i> (Cca)	3	11.5
<i>Felis silvestris</i> (Fsi)	4	4.5
<i>Leopardus colocolo</i> (Lco)	1	4.3
<i>Leopardus geoffroyi</i> (Lge)	2	4.5
<i>Leopardus pardalis</i> (Lpa)	2	11.2
<i>Leopardus tigrinus</i> (Lti)	1	2.5
<i>Leopardus wiedii</i> (Lwi)	1	5.4
<i>Leptailurus serval</i> (Lse)	6	11.0
<i>Lynx canadensis</i> (Lca)	1	13.6
<i>Lynx lynx</i> (Lly)	2	21.3
<i>Lynx pardinus</i> (Lpd)	4	10.2
<i>Lynx rufus</i> (Lru)	1	11.1
<i>Panthera leo</i> (Ple)	5	158.4
<i>Panthera onca</i> (Pon)	2	70.5
<i>Panthera pardus</i> (Ppa)	6	48.5
<i>Panthera tigris</i> (Pti)	6	151.2
<i>Panthera uncia</i> (Pun)	3	41.7
<i>Prionailurus viverrinus</i> (Pvv)	1	9.4
<i>Profelis aurata</i> (Pau)	1	13.2
<i>Puma concolor</i> (Pco)	4	49.1
<i>Puma yagouaroundi</i> (Pya)	2	6.2

Body mass values obtained from Frandsen (1993), Grzimek (1988) and MacDonald (1984).

M_b, average body mass for the indicated species; *n*, number of specimens measured.

perpendicular distance from the centre of rotation of the joint to the line of action of the muscle (Fig. 1a); thus, it depends upon the configuration of the limb segments. As proposed by Biewener (1989), the distance from the midpoint of the calcaneus–astragalus articulation to the posterior end of the tuber calcanei was taken as an approximation of the moment arm of the calf muscles (*r*; Fig. 1c). In the case of the generalised carnivore standing limb posture, this approximation will not diverge substantially from the actual moment arm. Furthermore, it was previously demonstrated that limb posture in Felidae was not affected by size (Day & Jayne, 2007). This study included specimens that belonged to collections housed in the Muséum National d’Histoire Naturelle of Paris (the former laboratories of Anatomie Comparée and Mammalogie), the Museu de Ciències Naturals de la Ciutadella of Barcelona, the Museo Nacional de Ciencias Naturales of Madrid, the Museo Argentino de Ciencias Naturales ‘Bernadino Rivadavia’ of Buenos Aires, and the Museo de La Plata.

The corresponding transverse second moment of area (*I*) was calculated from the diameters measured with the following formula (Alexander, 1983):

$$I = \frac{\pi \cdot \left(\frac{d_t}{2}\right)^3 \cdot d_t}{4} \quad (1)$$

This formula assumed that the sagittal plane was the major axis of flexion during quadruped locomotion (Cubo & Casinos, 1998a).

The ratio *r*/*L* was also calculated for each specimen. This non-dimensional index reflected the relative length of the calf moment arm with respect to the total length of the calcaneus. Non-dimensional indexes are typically independent of body size, which allows comparisons among specimens independent of scale. Nevertheless, we expected *r* to be proportional to *M_b*^{0.40}, which is a higher value than that expected for the scaling of *L* (*M_b*^{0.33} or *M_b*^{0.25}, according to geometric and elastic similarity, respectively). Therefore, this index should scale with positive allometry to body mass (i.e. *M_b*^{0.40–0.33} = *M_b*^{0.07} or *M_b*^{0.40–0.25} = *M_b*^{0.15}, for geometric and elastic similarity, respectively).

Because the number of specimens per species was diverse (Table 1), and we used a standard body mass for each species (based on values obtained from the literature), we used average values for variables other than body mass for every species.

We used regression methods to relate the following variables to body mass (*M_b*): *L*, *r*, *d_s*, *d_t*, *r*/*L* and *I*. All regressions were calculated with the standardised major axis method (SMA), because we were primarily interested in the regression slopes. In contrast, common least squares regression methods tend to underestimate the slope of the line-of-best-fit, because it is calculated to fit the predicted *y*-values as closely as possible to the observed *y*-values (Warton et al. 2006). We assumed the power equation:

$$y = a \cdot x^b \quad (2)$$

and 95% confidence intervals were calculated for both *a* and *b*.

Many studies (e.g. Felsenstein, 1985; Grafen, 1989; Harvey & Pagel, 1991; Christiansen, 1999a,b, 2002a,b) have discussed that, in interspecific analyses, the error terms are correlated, because species are not independent of each other, but rather can be arranged in a hierarchical sequence (phylogenetic tree). Thus, a phylogenetic signal is introduced into the analysis, and the individual points cannot be considered truly independent. Alternatively, the method of phylogenetically independent contrasts (PIC; Felsenstein, 1985) takes into account this phylogenetic signal in regressions on interspecific data; therefore, we also calculated SMA regression slopes for PIC with the PDAP: PDTREE module of Mesquite (Maddison & Maddison, 2010; Midford et al. 2010). These PIC slopes were then compared with those obtained by traditional regression analysis with an *F*-test ($\alpha < 0.01$) to assess whether this phylogenetic signal had any effect on our results. The structure of the phylogenetic tree for the included species was that described by Johnson et al. (2006), and is shown in Fig. 2.

Finally, we tested for the presence of differential scaling in the felid calcaneus with the model proposed by Jolicoeur (1989). This model would detect the presence of complex allometry in our sample (i.e. variables that are not proportional to each other, as in simple allometry):

$$\ln y = \ln A - C \cdot (\ln x_{\max} - \ln x)^D \quad (3)$$

where *A* is a constant (corresponding to *a* in Eq. 2), *C* is the allometry exponent, *x_{max}* is the maximum observed value of the independent variable (i.e. body mass, *M_b*) and *D* is the exponent of complex allometry, a time-scale factor. In our case, *D* > 1 indicated faster relative growth in small individuals, and *D* < 1 indicated that relative growth increased with size. The complex allometry hypothesis was thus accepted when *D* was significantly

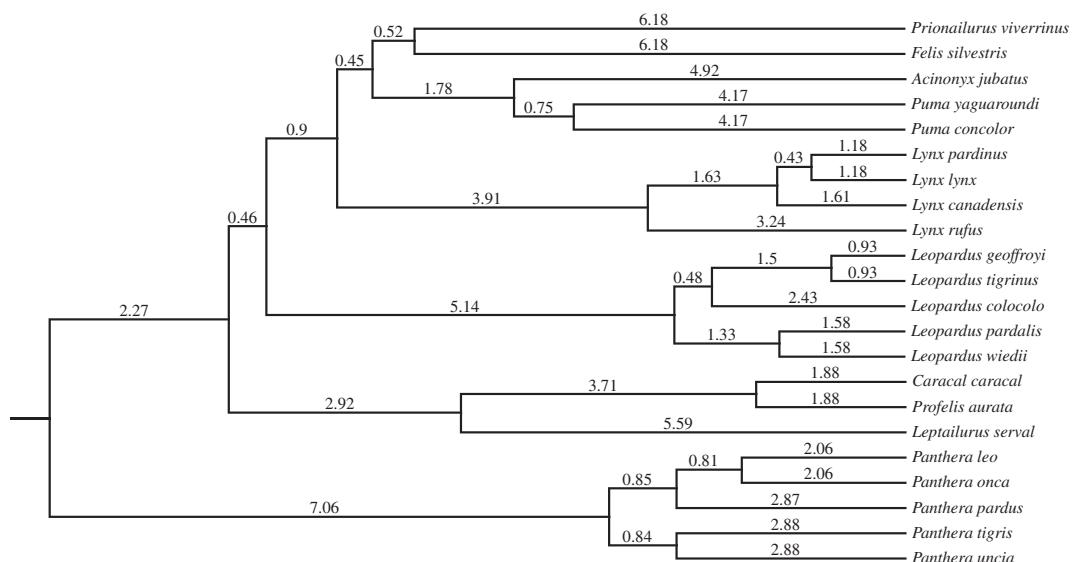


Fig. 2 Phylogenetic relationships between the 22 species of Felidae used in this study (modified from Johnson et al. 2006). The taxonomy shown is that presented by Wozencraft (2005), but with *Panthera uncia* instead of *Uncia uncia*, as proposed by Johnson et al. (2006) and Wilson & Mittermeier (2009).

different from 1 ($P < 0.05$). Equation 3 was fitted with SPSS for Windows (release 15.0.1 2006; SPSS, Chicago, IL, USA), and 95% confidence intervals were calculated for all parameters.

Results

The coefficients for the allometric equations obtained with both traditional regression analysis and PIC are shown in Table 2. No branch length transformations were necessary for PIC regressions, except in the case of the ratio r/L . For all other variables, the absolute values of the standardised contrasts were not significantly correlated to the corresponding standard deviations (Fig. 3). Consequently, we used the Rho transformation proposed by Grafen (1989) in the case of r/L .

Overall, the correlation coefficients (R) from the PIC analysis were lower than those from traditional regression (Table 2). This was consistent with previous studies that indicated a higher risk of type I errors (i.e. indicating a significant correlation between two variables when there was none) when the correlation analysis neglected the effect of phylogeny (Grafen, 1989; Christiansen, 2002a). This could explain the different findings for the ratio r/L (traditional regression: $R = 0.558$; $P = 0.011$; PIC: $R = 0.358$; $P = 0.132$; Table 2). In all cases, zero was not included in the 95% confidence interval for the slope (b) (Table 2). However, in both methodologies, the value predicted by geometric similarity ($M_b^{0.07}$) was included in the 95% confidence interval, but not the value predicted by elastic similarity ($M_b^{0.15}$).

Table 2 Regression coefficients obtained from traditional regression analysis and from PIC.

	Traditional regression					PIC		
	<i>a</i>	95% CI _a	<i>b</i>	95% CI _b	<i>R</i>	<i>b</i>	95% CI _b	<i>R</i>
<i>L</i>	17.911	15.284–20.989	0.323	0.270–0.375	0.936	0.384	0.258–0.510	0.716
<i>r</i>	11.784	9.834–14.120	0.360	0.300–0.420	0.933	0.429	0.293–0.565	0.734
<i>d_t</i>	2.833	2.299–3.492	0.349	0.280–0.419	0.904	0.392	0.252–0.532	0.647
<i>d_s</i>	5.450	4.442–6.687	0.364	0.296–0.432	0.916	0.452	0.297–0.607	0.683
<i>r/L</i>	0.617	0.575–0.662	0.060	0.037–0.084	0.558	<i>0.095</i>	<i>0.053–0.137</i>	<i>0.358</i>
<i>I</i>	23.678	10.611–52.837	1.427	1.160–1.695	0.916	1.739	1.140–2.338	0.677

All variables were plotted against body mass. The allometric coefficients (b) obtained with traditional regression analysis were not significantly different from those obtained with PIC ($P > 0.01$ for all comparisons). Values shown in italics indicate a non-significant regression.

95% CI_a, 95% confidence interval for the coefficient (a); 95% CI_b, 95% confidence interval for the allometric coefficient (b); d_s , sagittal diameter; d_t , transverse diameter; I , second moment of area; L , calcaneus total length; r , moment arm of the ankle extensors; R , correlation coefficient.

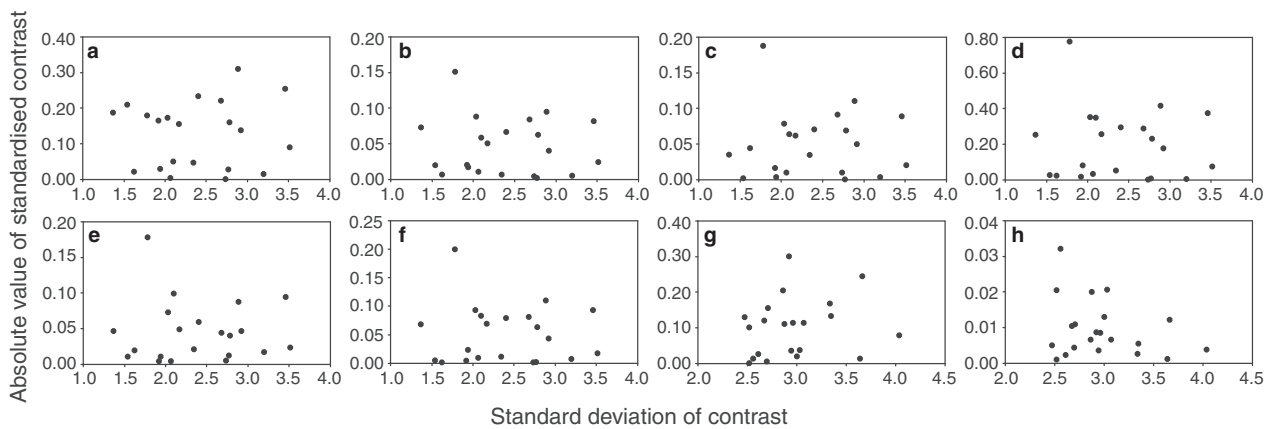


Fig. 3 Plots of standardised contrasts vs. their standard deviations. (a) body mass, M_b ($P = 0.857$); (b) calcaneus total length, L ($P = 0.782$); (c) moment arm of the ankle extensors, r ($P = 0.986$); (d) second moment of area, I ($P = 0.785$); (e) transverse diameter, d_t ($P = 0.921$); (f) sagittal diameter, d_s ($P = 0.806$); (g) body mass, M_b , after rho transformation ($P = 0.430$); (h) ratio r/L after rho transformation ($P = 0.224$). The P -values are consistent with the hypothesis that the standardised contrasts were not significantly related to their corresponding standard deviations.

Thus, although phylogeny appeared to account for most of the correlation between variables, the ratio r/L showed, as expected, a positive allometry to body mass. This indicated that the moment arm of the ankle extensors (r) provided stronger scaling than calcaneus length (L) (see below).

For variables other than the ratio r/L , the allometric coefficients (b) obtained with traditional regression analysis were not significantly different from those obtained with PIC (Table 2; Fig. 4). This was consistent with previous studies that compared these methodologies (Christiansen, 1999a,b, 2002b). This indicated that the scaling of our variables with body mass was not dependent on the phylogenetic relationships within our sample. We also found that the 95% confidence interval for the allometric coefficient (b) of the regressions for calcaneus total length (L) included 0.33, the expected value for geometrically similar animals, but not 0.25, the value proposed for elastic similarity (Schmidt-Nielsen, 1984; Table 2). On the other hand, for both diameters (d_t , d_s), the 95% confidence intervals included the values predicted by both geometric (0.33) and elastic (0.375) similarities. As expected, neither method produced a slope for the moment arm of the ankle extensors (r) that was significantly different from the predicted value for muscle moment arms (0.40; Alexander et al. 1981; Castiella & Casinos, 1990). Finally, the scaling exponent of the second moment of area (I) was not significantly different from either 1.33 or 1.50, the values expected in geometrically and elastically similar animals, respectively (Cubo & Casinos, 1998b). Overall, the scaling pattern of the felid calcaneus conformed to the predictions of geometric similarity, but not entirely to those of elastic similarity.

Results of the tests for complex allometry are shown in Table 3. In all cases, the 95% confidence interval for the exponent of complex allometry (D) included 1. Thus, no evidence for differential scaling was found in any of our variables.

Discussion

Our results showed that the scaling pattern of the felid calcaneus fit the predictions of the geometric similarity hypothesis better than the elastic similarity hypothesis. This finding was consistent with previous studies on the scaling of long bone dimensions in carnivores (Bertram & Biewener, 1990; Christiansen, 1999a). The work of Silva (1998) on the scaling of body length on a big sample of mammals also reported similar results, especially when considering terrestrial non-volant mammals, terrestrial carnivores and felids. Furthermore, our findings supported previous studies that described elastic similarity as an atypical scaling pattern found mostly in large bovids (Alexander et al. 1977, 1979; Biewener, 1983; Christiansen, 1999b; Rocha-Barbosa & Casinos, 2011). Also, consistent with previous studies (Christiansen, 1999a,b, 2002b), the phylogenetic signal had no significant effect on the scaling pattern, because we obtained similar values for the allometric coefficients (b), regardless of whether phylogeny was taken into account.

Biomechanical consequences of moment arm scaling

Our results supported the notion that muscle moment arms (r) scale to body mass as $M_b^{0.40}$ (Alexander et al. 1981; Castiella & Casinos, 1990). This indicated that a larger body mass corresponded to a longer tuber calcanei (relative to the total length of the calcaneus, which scaled to body mass as $L \propto M_b^{0.33}$). In turn, this allows the EMA of the ankle extensors to increase with body mass (Biewener, 1989) without requiring a change in the limb posture of felid species (Day & Jayne, 2007), given that the segment lengths (i.e. distances between joints) and joint angles remain unaffected by the length of the muscle moment arms.

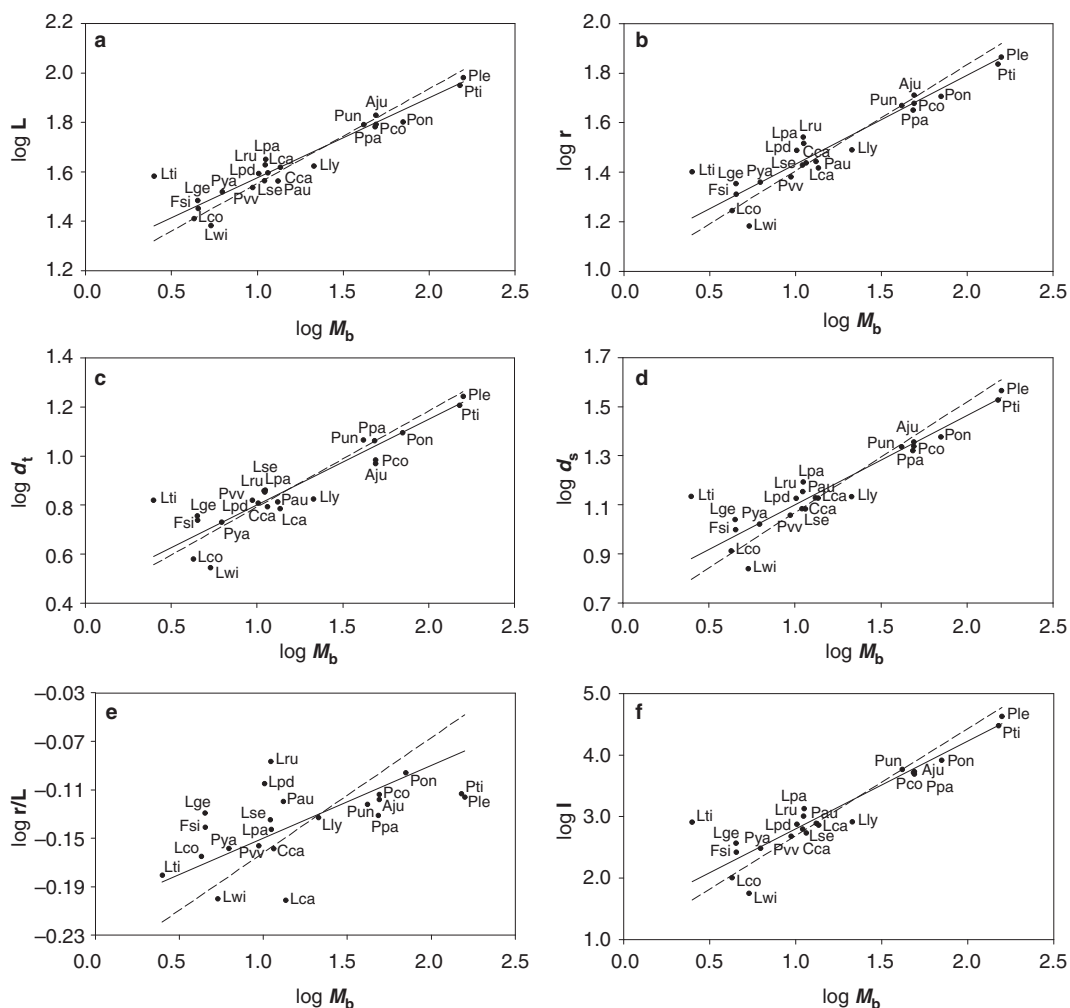


Fig. 4 Scaling by traditional regression analysis compared with scaling by PIC. Logarithmically transformed study variables were plotted against body mass (M_b). Traditional regression analysis is shown with the continuous line; PIC is shown with the broken line. (a) Calcaneus total length, L ; (b) moment arm of the ankle extensors, r ; (c) transverse diameter, d_t ; (d) sagittal diameter, d_s ; (e) ratio r/L ; (f) second moment of area, I . Species abbreviations are shown in Table 1.

Table 3 Results of the complex allometry test.

	$\ln A$	95% $CI_{\ln A}$	C	95% CI_C	D	95% CI_D	R
$\ln L$	4.569	4.348–4.791	0.425	0.187–0.663	0.782	0.447–1.118	0.943
$\ln r$	4.304	4.053–4.554	0.423	0.161–0.686	0.850	0.470–1.231	0.937
$\ln d_t$	2.881	2.575–3.188	0.503	0.166–0.839	0.712	0.323–1.101	0.915
$\ln d_s$	3.625	3.329–3.922	0.533	0.207–0.858	0.707	0.353–1.062	0.927
$\ln r/L$	-0.246	-0.326 to -0.165	0.019	-0.046 to 0.084	1.417	-0.885 to 3.719	0.578
$\ln I$	10.741	9.577–11.906	2.099	0.822–3.376	0.709	0.356–1.062	0.928

None of the exponents of complex allometry (D) deviated from 1; thus, none of our variables deviated from simple allometry. 95% CI_C , 95% confidence interval for the coefficient (C); 95% CI_D , 95% confidence interval for the exponent of complex allometry (D); 95% $CI_{\ln A}$, 95% confidence interval for $\ln A$; d_s , sagittal diameter; d_t , transverse diameter; I , second moment of area; L , calcaneus total length; r , moment arm of the ankle extensors; R , correlation coefficient.

As mentioned above, the EMA is defined as the ratio of the extensor muscle moment arm (r) to the moment arm of the ground reaction force (R). This assumes that the force

exerted by the extensor muscles (F_m) confers a mechanical advantage that counteracts the mechanical moment exerted by the ground reaction force (F_g ; Biewener, 2003).

Biewener (1989) found that, for mammalian ankle extensors, the EMA scaled to body mass with an exponent of 0.169 (± 0.046):

$$\frac{r}{R} \propto M_b^{0.169} \quad (4)$$

When r in Eq. (4) is substituted with the assumed proportionality for muscle moment arms ($r \propto M_b^{0.40}$), we can derive a hypothesis about the scaling of the moment arm of the ground reaction force (R):

$$R \propto \frac{r}{M_b^{0.169}} \propto \frac{M_b^{0.40}}{M_b^{0.169}} \propto M_b^{0.231} \quad (5)$$

Under equilibrium conditions, the moments acting on a joint must be balanced; that is, the moments of the muscle forces acting on the joint must equal the moment of the ground reaction force:

$$F_m \cdot r = F_g \cdot R \quad (6)$$

According to Alexander (1983), muscle force (F_m) is equivalent to:

$$F_m = S \cdot \sigma \quad (7)$$

where S is the cross-sectional area of the muscle and σ is the maximum isometric stress (250–300 kPa). Because σ is a constant, the following equation holds:

$$F_m \propto S \propto \frac{V}{l_f} \propto \frac{m \cdot \rho}{l_f} \quad (8)$$

where V is the volume of the muscle, l_f the mean fibre length, m the muscle mass and ρ the muscle density (1060 kg m^{-3}). In the case of pinnated muscles, a correction factor equal to the cosine of the pinnation angle should be added to l_f , but this angle can be assumed to be constant for each muscle; thus, we can disregard it with the other constants in this proportionality. Once constants have been removed, Eq. 8 can be written as:

$$F_m \propto \frac{m}{l_f} \quad (9)$$

Castiella & Casinos (1990) found that, for a large sample of mammals, muscle mass scaled to body mass as $m \propto M_b^{1.06}$, and the mean fibre length scaled to body mass as $l_f \propto M_b^{0.20}$. By substituting these values in Eq. 9, the scaling of muscle force to body mass can be hypothesised:

$$F_m \propto \frac{M_b^{1.06}}{M_b^{0.20}} \propto M_b^{0.86} \quad (10)$$

Then substituting Eq. 5 and Eq. 10 into Eq. 6:

$$M_b^{0.86} \cdot M_b^{0.40} \propto F_g \cdot M_b^{0.231} \quad (11)$$

And, finally:

$$F_g \propto \frac{M_b^{0.86} \cdot M_b^{0.40}}{M_b^{0.231}} \propto M_b^{1.029} \quad (12)$$

This supports the hypothesis proposed by Alexander et al. (1977) that the scaling of the ground reaction force is isometric, as the derived exponent of 1.029 is not significantly different from 1.

Differential scaling

To date, most studies on differential scaling have focused on comparing a sample of 'large' mammals with a sample of 'small' mammals (e.g. Economos, 1983; Christiansen, 1999b, 2002a). One problem with that approach is that it depends on a 'threshold' body mass value that is rather arbitrarily chosen for separating 'large' from 'small' mammals. Furthermore, this threshold varies depending on the group under consideration (i.e. 20 kg might be appropriate for mammals as a whole, but not for scaling among bovids). Two alternate solutions to this problem have been proposed: first, a quadratic regression can be used to test for non-linear trends in log-transformed data (Bertram & Biewener, 1990); or second, a Gompertz-derived model can be fit to bivariate data in order to quantify the deviation from simple allometry (Jolicoeur, 1989). Both methodologies can determine whether relative growth increases or decreases with size. We chose the model proposed by Jolicoeur (1989), because it was equivalent to the power equation (used to describe simple allometry) when D was not different from 1, and it was equivalent to quadratic regression (used by Bertram & Biewener, 1990) when D was not different from 2.

As mentioned above, we found no evidence of differential scaling in the felid calcaneus, despite the wide range of body masses that spanned two orders of magnitude. This result suggested that, at least in the particular case of Felidae, similarity in allometric scaling was a consequence of the similar locomotor requirements of all felid species (Day & Jayne, 2007; Wilson & Mittermeier, 2009). Another possible explanation would be a phylogenetic constraint; however, this seems unlikely, because the recent origin of this family has not prevented wide variations in felid size, for example, from the tiny *Felis nigripes* Burchell 1824 (about 1.5 kg) to well over 250 kg in the tiger (*Panthera tigris* Linnaeus, 1758) and in other species evidenced in fossils. Assuming that the similarity in allometric scaling was a consequence of the similarity in locomotor requirements, we would expect that other skeletal variables with mechanical significance would also show similar allometric scaling among felids. To investigate this, we revisited the data of previous scaling studies that included felid species and tested for complex allometry in skeletal variables. In particular, we reanalysed the data of Bertram & Biewener (1990) and that of Christiansen (1999b). As expected, we found no

evidence for complex allometry in the scaling of sagittal diameter, transverse diameter or bone circumference to bone length, or in the scaling of those four variables to body mass. This was consistent for all the long bones measured (humerus, radius, femur, tibia; Tables S1 and S2). Nevertheless, like in the original studies (Bertram & Biewener, 1990; Christiansen, 1999b) and others dealing with differential scaling (Economos, 1983; Silva, 1998), we found evidence for complex allometry when we included a large sample of carnivores in the analysis, and when we included the whole sample studied by Christiansen (1999b), which included species from several orders of mammals (Tables S1 and S2). In those cases, the samples included species with different types of locomotion (Van Valkenburgh, 1985, 1987; Wilson & Mittermeier, 2009). In light of these results, we propose that the differences found in allometric coefficients (b) between 'large' and 'small' mammals of different species (i.e. differential scaling) must be more related to differences in locomotor requirements, rather than differences in body mass. This hypothesis requires further scaling studies to investigate whether there are grade shifts (different slopes) that correspond to different types of locomotion among different species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Results of the complex allometry test using data from Bertram & Biewener (1990).

Table S2 Results of the complex allometry test using data from Christiansen (1999b).

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Limb morphometrics in Carnivora: Locomotion, phylogeny and size

Chapter I: The search for stability on narrow supports:
An experimental study in cats and dogs.

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Chapter III: Scaling pattern of the carnivoran forelimb:
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Chapter IV: Scaling pattern of the carnivoran hind limb:
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Chapter V: Scaling and mechanics of the felid calcaneus:
Geometric similarity without differential scaling.

Chapter VI: Evolution of scapula size and shape in Carnivora:
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