Behavioural flexibility:

evolutionary past and its role in a changing world

Doctoral Thesis
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To my mother and my grandmother,
Haydée Lagos and Teresa Jaramillo.

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CONTENTS

ABSTRACT

Across the history of life, most of organisms have evolved proper strategies to respond to an ever-changing world. Nowadays, human-conducted environmental changes impose an unprecedented lost of biodiversity. This thesis assesses one of the key responses to actual environmental changes, behavior flexibility. In a first approximation by a phylogenetic comparative approach I give evidences for the still tenuous link between cognition and life history by report the clearest support for the relationship between lifespan and brain size in mammals. Lifespan is core to many hypotheses regarding the advantages of enlarged brains, like the cognitive buffer hypothesis to proper respond to novel environments. In a second level, I explore for the drivers of innovation propensity, a key component of behavior flexibility. By mean of an experimental approach, I test for possible scenarios that may select for consistent individual differences in motivation, a major driver of innovation. Consistent individual differences in motivation are reported, but heritability and endocrine control features suggest that mechanism may be different of those hypothesized. Later, to approach for the role of behavioral flexibility in changing environments, I assess the behavior responses to one of the most disruptive effects of human activities on ecosystem, the urbanization. First, based on a literature review, theoretical and empirical evidences are reported for argue that behavioural flexibility is an important way to deal with urban environments. Second, using global comparative analyses in bird communities across the world, I show the importance of local process by random dispersal effects alongside habitat filtering to explain lose of biodiversity in urbanized environments. Some phylogenetic lineages appear more likely than others to thrive in urban environments, which is related to a future-returns strategy (i.e. low brood value) that allow for decrease the cost of delay reproduction and increase the opportunities to acquiring environmental information. The integrations of these results shows how the evolutionary past has shaped the traits that contribute to deal with actual environmental challenges, and highlight the expected consequences in a rapid changing, human-dominated world.

RESUMEN

A través de la historia de la vida, gran parte de los organismos han desarrollado estrategias para responder a un mundo en constante cambio. Hoy en día, las actividades humanas producen cambios ambientales a una velocidad sin precedentes, lo cual se traduce en grandes desafíos para la persistencia de biodiversidad. Esta tesis evalúa las respuesta de los animales a los cambios ambientales enfocándose en la flexibilidad del comportamiento como estrategia adaptativa. En una primera aproximación a una escala evolutiva, se otorgan evidencias del vínculo hasta ahora tenue entre la cognición e historias de vida, entregando un claro apoyo a la relación entre longevidad, vida reproductiva y el tamaño del cerebro en mamíferos. La longevidad es el centro de muchas hipótesis respecto a las ventajas de desarrollar un cerebro grande, como por ejemplo en la hipótesis del buffer cognitivo y las respuestas flexibles frente a nuevos ambientes. En un segundo nivel, se abordan factores extrínsecos e intrínsecos que podrían explicar las diferencias individuales en innovación, un componente clave en la flexibilidad del comportamiento. Por medio de una aproximación experimental, se evalúan potenciales escenarios que podrían conducir a consistentes diferencias individuales en uno de los principales factores subyacentes a la innovación (i.e. la motivación), y el potencial control endocrino sobre estos escenarios. Posteriormente, con el objetivo de evaluar el papel de la flexibilidad del comportamiento frente a los cambios ambientales actuales, se explora el rol del comportamiento frente a una de las actividades humanas mas disruptivas sobre los ecosistemas, la urbanización. Por medio de una revisión bibliográfica se entregan evidencias teóricas y empíricas que respaldan el importante rol de la flexibilidad del comportamiento para enfrentar los desafíos de una vida urbana. Finalmente, por medio de un análisis filogenético comparativo a nivel global en aves se abordan los mecanismos implicados en la perdida de biodiversidad observada en ambientes urbanos. Los resultados entregan evidencias que respaldan la importancia de procesos de dispersión local junto con el papel clave de los rasgos de historia de vida, pero de en un sentido diferente al clásicamente pensado. La integración de estos resultados muestra cómo el pasado evolutivo contribuye a hacer frente a los retos ambientales actuales, y pone de relieve posibles consecuencias ante un planeta más cambiante que nunca.

GENERAL INTRODUCTION

Through the known history of life, environmental disruptions have impacted and changed the natural environments, however in the last five decades human activities has been changing the world at unprecedented pace (Millennium Ecosystem Assessment 2005). The growing scale of human enterprises is the main responsible for the accelerated actual environmental changes, contributing to climate alterations, loss of biological diversity, eroding ecosystems around the globe (Ehrlich 1995, Vitousek 1997). Despite these fast human-conducted environmental disruptions, some organisms are doing better than ever. Uncovering the responses of species to environmental changes is challenge but a better understanding of how evolutionary history has shape behavioural responses and how these responses work in front of actual human-conducted environmental change may help us to mitigate the loss of biodiversity and manage organism that become pests with the global expansion of human population (Sih et al. 2010, 2011).

BEHAVIOUR FLEXIBILITY

In front of environmental changes the ability of an animal to adaptively modify their behaviour would provide an important adaptive potential (Lefebvre et al. 2004). Behavior flexibility facilitates the production of adaptive responses to a wide array of ecological challenges. For example, assist birds and mammals in the invasion of new environments (Sol et al. 2005, 2008) and predict bird population tendencies (Shultz et al. 2005). For one way, most of the variation among species in this traits is explained by cognitive abilities, as suggested by findings that brain size predict learning and propensity to innovate (Lefebvre et al. 1997, Reader and Laland 2002, Overington et al. 2009). On the other way, more simple cognitive process and temperament are related to innovation and learning variation within species (i.e. Cole et al. 2011, Sol et al. 2012), drivers factors that just in the last years has started to be studied. All above features and others still for unravelling contribute to the large variation that exist in behavioural flexibility among individuals, populations and species (Lefebvre et al. 2004, Lefebvre and Sol 2008).

EVOLUTIONARY PAST

Most of the responses to human-conducted environmental changes are mediated by phenotypic plasticity rather than immediate genetic changes (Hendry et al. 2008). This suggest that evolutionary history has been important in shape traits that nowadays are effective for coping with changing environments, like behaviour flexibility and associated brain size (Sih et al. 2011). One of the hypotheses for the evolution of big brains involves the cognitive buffer hypothesis. That hypothesis take into account the balance between costs in time and energy to evolve big brains and the benefits provided in the form of longer reproductive life, compensating the enormous cost of evolve big brains. Although evidence exist for the basic tenets of cognitive buffer hypothesis, as big brained birds survival longer (Sol et al. 2007), the link remain elusive in mammals and preclude us to generalize patterns. The knowledge of shared evolutionary history would provide a way to predict whom species might perform well in the actual changing environmental conditions.

INDIVIDUAL RESPONSES

Because important consequences on population dynamics and species evolution, the study of individual differences have acquired pivotal relevance in the last decade (Sih et al. 2012, Wolf and Weissing 2012). Behavioural flexibility in particular varies among individuals as consequences of underlying factors like temperament traits and other individual's features that remain to be elucidated. Species confronting human-induced environmental changes are under new selective pressures, thus understanding individual responses to actual environmental challenges may provide a way to understand evolutionary past and predict futures responses on which individuals or species would be in disadvantage and what will de potential pest (Sih et al. 2011).

RAPID HUMAN-INDUCED ENVIRONMENTAL CHANGES

Habitat loss and fragmentation are the main types of human-induced environmental changes. Because the accelerate rate of human population growth coupled with the expansion of land for urbanization, understand the mechanisms involved in the organism responses to this environmental change put enormous scientific challenges. Cities may allow an unique opportunity for comparative studies addressing the behaviour responses of animals as provide large scale examples (Anderies et al. 2007, Grimm et al. 2008). It is often assumed that urban species have adaptations to survive in such environments, yet the role of alternative processes has generally been under-appreciated. How species and individuals confront the challenges to live in these environments and the mechanisms involved, are questions that remain to be elucidate.

MAIN GOALS

This thesis has four main goals

(1) In light of the pivotal role of behavioral flexibility to generate adaptive responses to rapid environmental changes but yet poorly support for basic tenets of the cognitive buffer hypothesis, I search to provide support for and generalize the evolutionary advantages of evolve big brains.

(2) Behavior flexibility varies at individual level, but the drivers that promote individual variation in behavior flexibility are poorly knowed. I look for one of the most important promoters of innovation reported to date, motivation. I ask whether this factor promotes individual differences in innovation and if so, what are the contexts that promote their selection at individual level.

(3) In a heuristic way to assess for evidences of the role of behavior flexibility to actual environmental changes, I ask whether and how behavioral flexibility provides appropriate skills to organism that live in urbanized environments, one of the most disruptive actual environmental changes.

(4) Finally, in a more detailed study about the possible processes that allow or preclude the life in urbanized environment, I ask how the often reported patterns of biodiversity are shaped in urban environments. Taking birds as study models two hypothesized mechanism, the dispersal and environmental filter hypotheses are approached.

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Chapter 1#

Large-brained mammals live longer

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ABSTRACT

Many mammals have brains substantially larger than expected for their body size, but the reasons for this remain ambiguous. Enlarged brains are metabolically expensive and require elongated developmental periods, and so natural selection should have favoured their evolution only if they provide counterbalancing advantages. One possible advantage is facilitating the construction of behavioural responses to unusual, novel or complex socioecological challenges. This buffer effect should increase survival rates and favour a longer reproductive life, thereby compensating for the costs of delayed reproduction. Here, using a global database of 493 species, we provide evidence showing that mammals with enlarged brains (relative to their body size) live longer and have a longer reproductive lifespan. Our analysis supports and extends previous findings, accounting for the possible confounding effects of other life history traits, ecological and dietary factors, and phylogenetic autocorrelation. Thus, these findings provide support for the hypothesis that mammals counterbalance the costs of affording large brains with a longer reproductive life.

INTRODUCTION

Large brains have evolved multiple times and in multiple taxa (Jerison 1973). This is puzzling because a brain disproportionately large for a given body size is metabolically expensive (Isler & van Schaik, 2006, 2009a, b; Aiello & Wheeler, 1995) and takes a substantial time to reach structural and functional maturity (Casey et al., 2005). Long developmental periods result in significant fitness costs for large-brained species, both in terms of increased offspring mortality risk (Sacher & Staffeldt, 1974; Stearns, 2000; Deaner et al., 2003; Barrickman et al., 2008) and delayed age of first reproduction (Deaner et al., 2003; Barrickman et al., 2008). Consequently, natural selection should have favoured the evolution of large brains only if they provide advantages that counterbalance their production and maintenance costs.

Several hypotheses have been proposed to explain the adaptive advantages of larger brains (see Deaner et al., 2003; van Schaik & Deaner, 2003; Dunbar & Shultz, 2007a; Sol, 2009a), most of which assume that enlarged brains carry cognitive advantages. Among others, these include monitoring food sources that vary in space and time (Clutton-Brock & Harvey, 1980; Milton, 1988), using hard-to-eat foods (Parker & Gibson, 1977, 1979), exploiting novel foraging opportunities (Lefebvre et al., 1997), and modifying behaviour in response to conspecifics (Jolly, 1966; Humphrey, 1976; Cheney & Seyfarth, 1986; Byrne & Whiten, 1988; Whiten, 2000; Dunbar & Shultz, 2007b). The above hypotheses focus on selective advantages of enlarged brains, but do not provide an explicit explanation for how these benefits balance the developmental costs of affording large brains. However, if these benefits reflect general cognitive capacities for constructing behavioural responses to novel socio-ecological challenges, then this should reduce extrinsic mortality and partially compensate the developmental costs with a longer reproductive life (Allman et al., 1993; Allman, 2000; Deaner et al., 2003; Sol, 2007, 2009a,b). This interpretation, the so-called “cognitive buffer hypothesis”, thus integrates previous hypotheses, acknowledges that brains carry out multiple functions, and provides an explicit explanation of the benefits of brain enlargement (Allman et al., 1993; Allman, 2000; Deaner et al., 2003; Sol, 2009a).

Recently, comparative work on brain evolution has been criticised because diverse findings regarding correlates of brain enlargement have not been integrated (Healy &

Rowe, 2007). The lack of consideration of alternative hypotheses for the evolution of enlarged brains is a repeated criticism (Deaner et al., 2000; Reader & Laland, 2002; Dunbar & Shultz, 2007b). The diversity of reported correlates of brain enlargement likely reflects the fact that the brain performs multiple functions: postulating a single cognitive benefit for brain enlargement is unlikely to be successful. There is considerable evidence that species with enlarged brains for their body size show enhanced cognitive capacities, although the mechanisms behind these relationships are obscure and warrant study (reviewed in Healy & Rowe, 2007; Lefebvre & Sol, 2008). For example, multiple studies have demonstrated associations between brain size and components of behavioural flexibility, such as innovation, tool use, tactical deception, social learning, reversal-learning, and combined measures of laboratory learning performance, in both birds and primates (Lefebvre et al., 1997; 2004; Reader & Laland, 2002; 2003; Reader, 2003; van Schaik & Deaner, 2003; Byrne & Bates, 2007; Deaner et al., 2007). Evidence is also accumulating that flexibility in behaviour facilitates the production of adaptive responses to a wide array of ecological challenges (reviewed in Sol, 2009a). In birds and mammals, for example, large-brained species are more likely to be successful when introduced by humans in novel environments than are small-brained species (Sol et al. 2005, 2008). Moreover, amongst British birds, species with relatively large brains were less likely to suffer population declines (Shultz et al., 2005). Thus several lines of evidence support the idea that brain volume is associated with diverse measures of behavioural flexibility and with success in novel or changed environments, providing a route to integrate previous findings.

Surprisingly, however, evidence for a critical prediction of the cognitive-buffer hypothesis, that brain enlargement translates to increased life expectancy, remains mixed. In mammals, the animals with the largest relative brain sizes, some studies have demonstrated a significant relationship between brain size and lifespan (e.g. Deaner et al., 2003; Kaplan et al., 2003; Hakeem et al., 1996, Isler & van Schaik 2009a,b), but others did not (e.g. Ross & Jones, 1999; Barton, 1999; Judge & Carey, 2000). The disparity of results may arise from differences in the way that previous studies controlled or failed to control for confounding factors and phylogenetic effects. Moreover, previous analyses were generally based on a reduced number of species and were biased toward primates (reviewed in Barrickman et al., 2008). This focus potentially reduces the interspecific variation observed in brain size and lifespan, which could reduce the possibility of detecting patterns. Understanding the evolution of large brains is only possible if we further validate the brain-lifespan association in many taxa and with approaches that properly deal with phylogenetic and confounding factors (Lefebvre et al., 2004; Sol, 2009a). Here, we ask whether large-brained mammals live longer with a global phylogenetic-based comparative analysis covering 493 mammalian species. We extend on recent similar analyses (Isler & van Schaik 2009a,b) by taking into account previously unconsidered confounding variables, using datasets covering additional taxa (e.g. marsupials), and directly estimating and accounting for phylogenetic effects (Hansen & Orzack, 2005). We show that the association of larger brains with longer lifespan holds independently of other life history traits, of research effort, and of energetic, environmental, dietary, and habitat variables, thus providing unambiguous support for the idea that the costs of delaying reproduction in large-brained species can be partly compensated by a longer reproductive life.

MATERIAL AND METHODS

Lifespan

As an estimate of reproductive lifespan, we gathered information on maximum-recorded lifespan (in years) for 493 species of mammals from de Magalhaes et al. (2009; see references therein). The bulk of these data come from Weigl (2005). There exist alternative, more accurate estimates of reproductive lifespan (Ricklefs & Scheuerlein, 2001), but maximum-recorded lifespan provides a reasonable estimate that is available for many species (Barrickman et al. 2008, Isler and van Schaik 2009a). Barrickman et al. (2008) proposed that the age at first reproduction must be first subtracted from maximum lifespan to provide a measure of the duration of reproductive life (hereafter, ‘reproductive lifespan’), and thus to test the idea that enlarged brains are associated with longer periods of reproductive life. We thus used two lifespan measures as dependent variables: ‘lifespan’ and ‘reproductive lifespan’.

The available maximum lifespan data have some potential problems. First, they are derived from both captive and wild records. Since lifespan recorded under captive conditions may not represent that in the wild, pooling these captive and wild data could potentially obscure any true relationships (Barrickman et al., 2008). To account for this issue, we included whether lifespan was measured in captivity or the wild as a factor in the statistical model. Second, maximum lifespan estimates increase with research effort (Møller, 2006, 2007; de Magalhaes & Costa, 2009). To account for this possible bias, we estimated research effort from the number of articles listed in ISI Web of Science in July 2009 for each species. Research effort was log transformed and included as co-variate in statistical models.

Brain size

The use of whole-brain versus brain-part volumes is an important issue in testing the cognitive buffer hypothesis (Deaner et al., 2007). While a focus on one brain component may be advantageous in studying a specialized cognitive function (Healy & Rowe, 2007), the use of whole brain size is likely to be more appropriate in testing the cognitive buffer hypothesis (Barton & Harvey, 2000; Sol et al., 2008; Sol & Price, 2008). First, behavioural flexibility has multiple underlying mechanisms and arises from several processes such as perception, motor ability and cognitive processing (Deaner et al., 2003; Changizi, 2003), unlikely to be localized in a single brain area (Lewis, 2006). Second, several brain component volumes are consistently correlated with whole brain size, particularly larger parts that are involved in higher order and multimodal integration (Timmermans et al., 2001; Iwaniuk et al., 2004). Finally, as already noted, a growing number of studies have found support for an association between brain size and different measures of behavioural flexibility, such as innovation, tool use, tactical deception, and learning (reviewed in Lefebvre et al., 2004; Dunbar & Shultz, 2007a; Deaner et al., 2007; Lefebvre & Sol, 2008). Thus we used data on whole brain size, which has the additional advantage that it is available for many more species than are brain component volumes. Data on brain mass for 493 species were compiled from published information from multiple sources (see Appendix I). We subtracted 0.59 g from each rodent species datum in Mace et al. (1981), following the corrective procedure recommended by Isler & van Schaik (2006). Brain masses were either calculated from endocranial volumes or were whole brain masses. Although the use of endocranial volumes to calculate brain masses has been debated (Röhrs and Ebinger, 2001), we utilised these data because recent studies have demonstrated that it provides a reliable proxy of brain mass (Isler et al. 2008; Ashwell 2008; Finarelli and Flynn, 2009). The reliability of the brain measures utilised was previously evaluated by Sol et al. (2008) using a variance component analysis, which showed that variation across species was higher than within species. This validated the treatment of brain mass as a species character.

Larger species have larger brains, so it is necessary to estimate brain mass controlling for the allometric effect of body size. At least three methods have been proposed to do this: (1) to estimate the residuals of a log-log least-squares linear regression of brain mass against body mass; (2) to calculate the fraction of the body mass that corresponds to brain mass; and (3) to include absolute brain mass and body mass as covariates in a multivariate model (Deaner et al. 2000). We used all methods and the results are consistent. We present in the text the results obtained with the residual method, as this approach has the advantage of eliminating problems of collinearity while effectively removing body size effects (Sol et al., 2007). Body mass was obtained from the same sources as brain mass when available and complemented with published data as needed (Smith & Jungers, 1997). Following Sol et al. (2008), when more than one source per species was available, the mean values of brain mass and body mass (in grams) were utilized, and when only a range of values was available, the midpoint was used. To reduce measurement error, for each species the coefficient of variation was calculated for both brain and body mass. We removed extreme values where the coefficient of variation was extremely high (> 50%), apart from highly sexually dimorphic species (Weckerly, 1998), as these high variances were likely the consequence of a measuring error. We removed extreme data values for 11 species. Before estimating residuals of brain mass, it is necessary to control for the 'grade shift' phenomenon (Pagel & Harvey, 1988; Nunn & Barton, 2000; Sol et al., 2008). Grade shifts represent the fact that in mammals the intercept of the regression line between brain mass and body mass differs across taxonomic groups, leading to biases in residuals if left unaccounted for. To deal with this problem, Nunn and Barton (2000) proposed the estimation of the slope (*b*) of the regression with phylogenetic independent contrasts (Felsenstein, 1985). Since only a few independent contrasts will be affected by grade shifts, the effect of grade shifts on the global relationship between contrasts should be weak (Nunn & Barton, 2000; Sol et al., 2008). Following Blomberg et al. (2003), we computed the size-corrected values for brain mass in three steps. First, independent contrasts were estimated for brain mass and body mass (both log-transformed) with the PDAP module of the MESQUITE program (Garland et al., 1999; Garland & Ives, 2000). The phylogenetic tree was that proposed by Bininda-Emonds et al. (2007; corrigendum, 2008), which includes a great number of extant mammals. Second, a least squared linear regression through the origin of these contrasts (brain mass on body mass) was computed to estimate the allometric exponent (b). The relationship between contrast of brain mass and body mass was strong (R^2=0.90), therefore the use of alternative line-fitting techniques was not necessary (Barton & Harvey, 2000). Third, size-corrected values of brain mass were computed as log [brain mass/body mass^b] using raw values (not independent contrasts). Hereafter, this variable will be called "residual brain mass". The slope (b) was estimated as 0.64, close to that estimated by other studies (Harvey & Krebs, 1990; Sol et al., 2008). Because the residual brain values obtained do not completely remove the effect of body mass (correlation coefficient = 0.51), log body mass was included in all the models testing the relation between residual brain mass and lifespan.

Confounding Variables

Since the analyses are correlational, any relation between lifespan and brain mass could be obscured or inflated by the effect of other variables. We thus accounted for several factors that potentially can affect lifespan variation. First, metabolism could be an important determinant of lifespan (Harvey et al., 1991; Hofman, 1993; Allman et al., 1993; Ricklefs & Wikelski, 2002; Speakman, 2005). To control its possible effect, data for basal metabolic rate (BMR) were obtained from White et al. (2009) and included in the statistical model.

Second, life history traits are known to co-vary systematically across species (Harvey & Clutton-Brock, 1985; Promislow & Harvey, 1990; Stearns, 2000; Bielby et al., 2007). It is thus important to ensure that the apparent association between brain mass and lifespan is not spuriously created by the effect of another life history trait. Information on gestation, weaning, age at first reproduction, litter size and litters per year were taken from published literature (Ernest, 2003; de Magalhaes et al., 2009; Bielby et al., 2007). These life history traits are highly correlated with lifespan (e.g. Harvey & Clutton-Brook, 1985) as well with each other (van Schaik & Deaner, 2003; Bielby et al., 2007). Third, life history strategies vary across regions (Ricklefs, 2000; Forsyth et al., 2004; Martin et al., 2006; McNamara et al., 2008). For example, latitude has been reported to predict lifespan in birds (Møller, 2006; 2007). To account for geographic biases, maximum northern latitude (MNL) and maximum southern latitude (MSL) were gathered from breeding ranges published in the literature (Dorst & Dandelot, 1973; Strahan, 1995; Schilling et al., 1987; Mitchell-Jones et al., 1999; Kingdon, 1997; Folkens et al., 2002; Long, 2003; Patterson et al., 2003; Jackson, 2007; IUCN, 2008). We calculated three proxy variables for geographic factors from these breeding ranges: “geographic range” (the total latitude degree of breeding range), “mid-latitude point of breeding range” (calculated as (MNL+MSL)/2, following Newton, 1995), “discontinuous distribution” (coded as ‘discontinuous’ or ‘continuous’, accounting for discontinuous or continuous occupancy along the latitudinal breeding distribution). Fourth, species diet and habitat thought to be linked to lifespan (Harvey & Clutton-Brock, 1985; Bennett & Harvey, 1985; Allman et al., 1993; van Schaik & Deaner, 2003). Thus, these variables were considered in the analyses and coded as follows: primary dietary type (herbivorous, carnivorous, omnivorous and insectivorous), feeding generalism (number of these diet categories, range 1-4), primary habitat type (coastal habitat, inland waters, wetland, desert, forest, mountain, tropical rainforest, savanna, grassland, woodland, scrub-tundra, rural and urban areas) and habitat breadth (number of these habitat types used, range 1-13). Data were compiled from multiple sources (Long, 2003; Wilson & Reader, 2005; Jakson, 2007; Kingdon, 1997; Patterson et al. 2003; IUCN, 2008).

Finally, both lifespan and reproductive lifespan scale allometrically with body size (Harvey & Clutton-Brock, 1985; Blumstein & Møller, 2008; this study) so it is relevant to examine whether brain mass correlates with lifespan when the body size effect is controlled for. To account for body size effects on lifespan, we estimated the residuals of a log-log regression of lifespan (or reproductive lifespan) against body size (termed ‘residual lifespan’ or ‘residual reproductive lifespan’, respectively). Because body mass has a high phenotypic variability (Economos, 1980; Smith & Junger, 1997), the average body mass calculated can be an under- or over-estimate of the true value. This is problematic, as it causes the residuals of the response and predictor variables to be biased in the same direction, increasing the chance of type I errors (Harvey & Krebs, 1990; Barton, 1999). To avoid this problem, we separately obtained residuals of dependent and independent variables by using a different set of body masses (Harvey & Krebs, 1990; Barton, 1999; Deaner et al., 2003; Barrickman et al., 2008). This second set of body masses was obtained from Ernest (2003), complemented by other sources (Jackson, 2007; de Magalhaes et al., 2009).

Analyses

Closely-related taxa share many traits from common ancestors rather than from independent evolution, thus species' traits cannot generally be treated as statistically independent points (Felsenstein, 1985). To deal with this problem, we modelled lifespan values for species with a phylogenetic generalized least squares approach (PGLM) (Freckleton et al., 2002; Phillimore et al., 2006; Shultz & Dunbar, 2007). This method takes the phylogenetic variance/covariance matrix derived directly from the phylogenetic supertree of the species, and hence evaluates the association between variables taking into account the correlated error structure. This is done by estimating a parameter lambda (λ), which measures the degree to which the matrix follows a Brownian model (λ values near 0 implying no phylogenetic autocorrelation and values near 1 maximum phylogenetic autocorrelation). The fitted generalized least squares model (GLM) and λ were simultaneously estimated to test the effect of brain mass on maximum lifespan across species. We included interactions between predictor variables in the analyses, but none were statistically significant and thus are not reported below. PGLM analyses were conducted with R 2.7.0, (R Development Core Team, 2005), the R code kindly provided by R. P. Freckleton, and the phylogenetic hypothesis proposed by Bininda-Emonds et al. (2007, corrigendum 2008).

Following Sol et al. (2008), a minimum adequate model (MAM) was constructed by means of a backward selection approach. The initial PGLM model was composed by residual brain mass and the rest of confounding variables. Then, we sequentially dropped the variables resulting in the lowest improvement to model fit. We investigated the significance of alternative models by adding the previous variable removed from the model. Variables with $P < 0.2$ were retained in the MAM, to avoid the removal of confounding variables of weak influence. However, the standard criterion for statistical significance ($P < 0.05$) was applied throughout. Diagnostic plots were examined in order to check for outliers, heteroscedasticity, and non-normal errors.

RESULTS

We found extensive variation both in brain mass and maximum lifespan across species (Fig. 1). To test whether the lifespan of mammalian species can be explained to some degree by residual brain mass, we first used a conventional linear model (LR: linear regression) so that our results could be compared with previous studies. This model revealed a very strong relationship between residual brain mass and lifespan (coefficient ± S.E., $b = 0.49 \pm 0.04$, $t_{486}=10.98$, $P < 0.0001$, Fig 2a), even when the effect of body mass on lifespan was removed (residual brain mass versus residual lifespan: $b = 0.48 \pm 0.04$, $t_{486}= 10.86$, $P < 0.0001$, Fig. 2b).

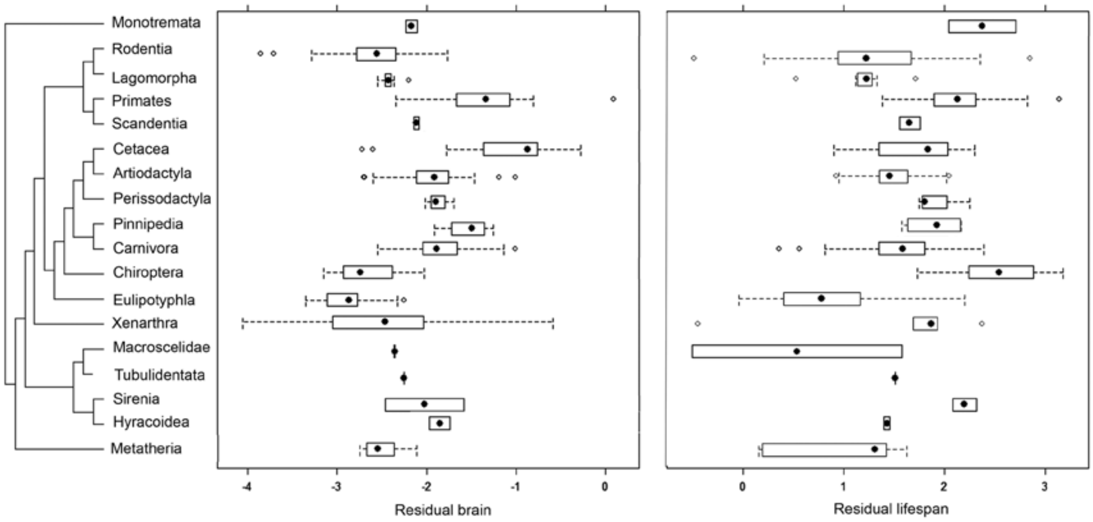


Figure 1. Box plots (median and 25 and 75% percentiles) of residual brain mass (accounting for body mass) and residual maximum lifespan (accounting for body mass) across mammalian orders, with phylogenetic relationships between taxa indicated on the left (phylogeny: Bininda-Emonds et al., 2008).

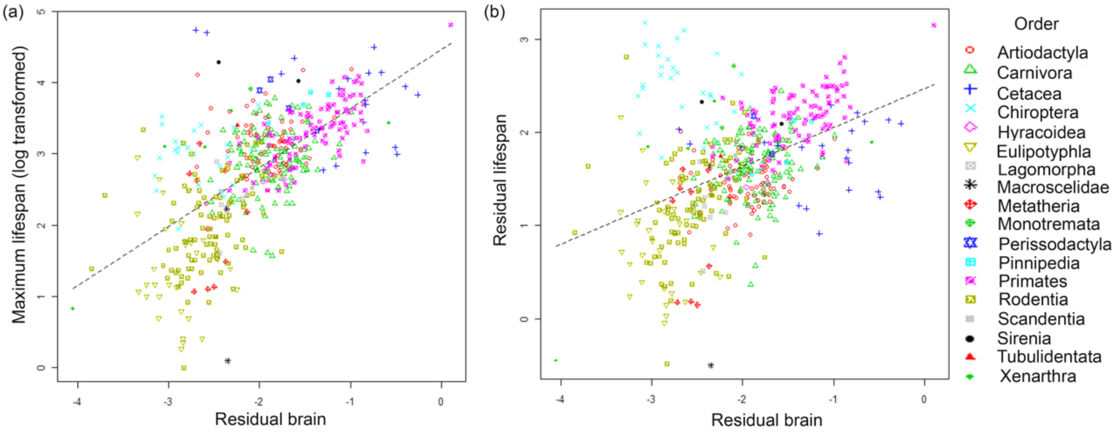
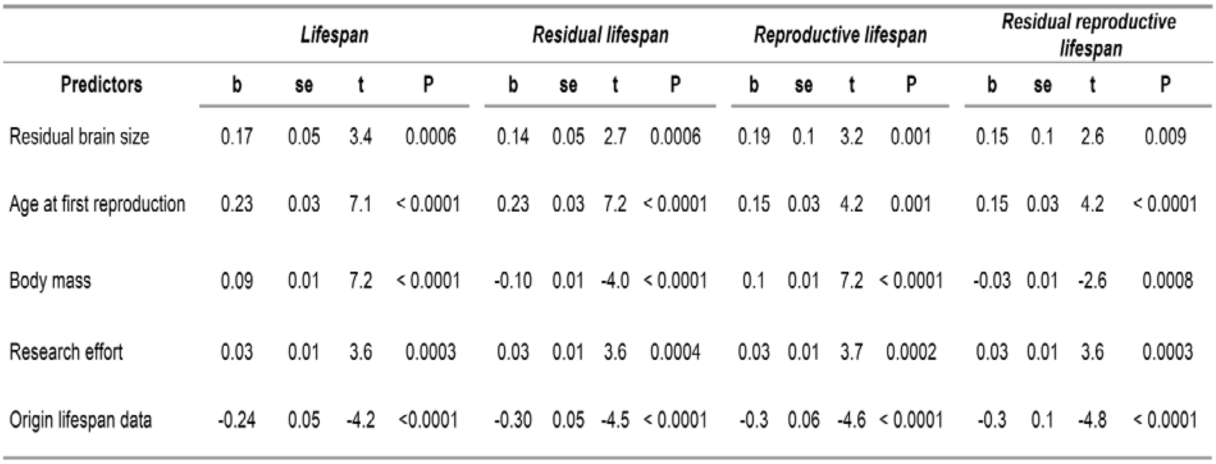


Figure 2. Relationship between residual brain size and maximum lifespan in 493 species of mammals *(a)* without (linear regression: $F_{4,486}$= 176.9, R^2= 0.59, $P < 0.0001$) and *(b)* with control for the allometric effect of body size on lifespan (linear regression: $F_{4,486}$ = 36.67, R^2= 0.22, $P < 0.0001$), Equivalent results were obtained using PGLM analysis: a: $F_{5,491}$=57.17, R^2= 0.31, $P < 0.0001$; b:$F_{5,491}$= 19.34, R^2= 0.13, $P < 0.0001$).

The LR analyses above did not include phylogenetic corrections, but it is well known that disregarding phylogenetic effects can cause misleading results when the studied traits show high phylogenetic autocorrelation. Indeed, lifespan showed significant phylogenetic autocorrelation, with a lambda estimate close to 1 (λ = 0.97; X^2 = 437.10, $P < 0.0001$ that λ is 0; X^2 = 10.89, P = 0.0009 that λ is 1). We thus used a PGLM approach. The relationship between residual brain mass and lifespan was positive and highly significant (partial regression coefficient ± S.E., b = 0.26 ± 0.04, t_{486}= 5.37, $P < 0.0001$). When the allometric effect of body mass on lifespan was incorporated in the analysis, the residuals of brain mass remained strongly associated with residuals of lifespan (PGLM: b = 0.20 ± 0.04, t_{486}=4.26, $P < 0.0001$). Due to the correlative nature of the analyses, the relationship between residual brain mass and lifespan could be spuriously caused by their common association with a third variable. None of the ecological (i.e., basal metabolic rate, primary habitat, primary diet, feeding generalism or habitat breadth) and geographic variables (i.e. geographic range, mid latitude point or discontinuous distribution) evaluated were found to be significantly associated with lifespan in the MAM (PGLM: $P > 0.05$ in all variables), and did not alter the relationship between brain mass and lifespan. From the life history traits we considered, only the age at first reproduction was significantly associated with lifespan (PGLM: $P < 0.001$, N=417; all other variables $P > 0.2$).

However, residual brain mass remained significantly associated with lifespan when age at first reproduction was taken into account (Table 1). The MAM included age at first reproduction along with residual brain mass, lifespan measure (wild or captive), research effort (log transformed) and body mass (log transformed). Recorded lifespan was longer in captive animals, in better-studied species, in heavier species, and in species with an older age at first reproduction (Table 1). The models explained 42% of variance in lifespan and 21% of variance in residuals of lifespan. Equivalent results were obtained with reproductive lifespan as the dependent variable (Table 1).

Table 1. Minimum adequate PGLS model of lifespan for 384 mammalian species (adjusted r^2 = 0.42, for lifespan, 0.21, for residual lifespan, 0.35 for reproductive lifespan and 0.16 for residual reproductive lifespan.



	Lifespan				*Residual lifespan*				*Reproductive lifespan*				*Residual reproductive lifespan*			
Predictors	**b**	**se**	**t**	**P**	**b**	**se**	**t**	**P**	**b**	**se**	**t**	**P**	**b**	**se**	**t**	**P**
Residual brain size	0.17	0.05	3.4	0.0006	0.14	0.05	2.7	0.0006	0.19	0.1	3.2	0.001	0.15	0.1	2.6	0.009
Age at first reproduction	0.23	0.03	7.1	< 0.0001	0.23	0.03	7.2	< 0.0001	0.15	0.03	4.2	0.001	0.15	0.03	4.2	< 0.0001
Body mass	0.09	0.01	7.2	< 0.0001	-0.10	0.01	-4.0	< 0.0001	0.1	0.01	7.2	< 0.0001	-0.03	0.01	-2.6	0.0008
Research effort	0.03	0.01	3.6	0.0003	0.03	0.01	3.6	0.0004	0.03	0.01	3.7	0.0002	0.03	0.01	3.6	0.0003
Origin lifespan data	-0.24	0.05	-4.2	<0.0001	-0.30	0.05	-4.5	< 0.0001	-0.3	0.06	-4.6	< 0.0001	-0.3	0.1	-4.8	< 0.0001

* The parameters (b) are the partial regression coefficients relating the predictors (residual brain size, age at first reproduction, research effort, origin of lifespan data (captive/wild) and body mass) with lifespan. Four lifespan measures are used as dependent variables: maximum lifespan, residual maximum lifespan (controlling for the allometric effects of body size), maximum reproductive lifespan (maximum lifespan-age at first reproductive) and residual reproductive lifespan. Analysis was via the phylogenetic generalized least squares method. Three confounding variables were kept in the model (criterion: $P<0.2$) but were not statistically significant ($0.12 > P > 0.07$): discontinuous distribution (b=0.04 for all four dependent variables), desert habitat (b=0.06-0.07), herbivorous diet (b=0.07-0.08).

DISCUSSION

Species of mammals with larger brains than expected for their body size tended to live longer than those with smaller brains. Although residual brain size explained only a small fraction of the variance in residual lifespan across species (about 13%, Fig. 2b), this relationship was robust and largely independent of ecological, geographic and phylogenetic effects. Thus, our results provide robust evidence that in large-brained animals the costs of delaying reproduction are in part compensated with a longer reproductive life. Lifespan is difficult to quantify, and thus estimates are subject to error, which might detract from our ability to resolve the strength of an association between brain size and lifespan. Although some of the highest values of maximum lifespan are reported in captive animals (de Magalhaes & Costa, 2009), the mixture of wild and captivity lifespan records was unlikely to affect the correlation between lifespan and brain size (Table 1; see also Allman et al., 1993; Barrickman et al., 2008). Captive conditions could be argued to not replicate the pressures faced in natural environment, but maximum lifespan may be seen as representing a physiological limit to life duration (Barrickman et al., 2008; de Magalhaes & Costa, 2009). In the same way, research effort may bias lifespan estimates (Møller, 2006; 2007; de Magalhaes & Costa, 2009), as our results show. However, the brain-lifespan association remained significant when research effort and data source was accounted for in the analyses. Many previous studies have examined the brain size-lifespan relationship (Shacher, 1959; Shacher & Staffeldt, 1974; Economos, 1980; Hofman, 1993; Allman et al., 1993; Ricklefs & Scheuerlein, 2001; Kaplan et al., 2003; Barton, 1999; Hakeem et al., 1996; Deaner et al., 2003; Barrickman et al., 2008; Isler & van Schaik 2009a, b). Our findings extend on these studies, expanding the taxonomic range studied. Moreover, several of these previous studies did not take into account the phylogenetic relationships among species and, if they did, did not estimate the level of phylogenetic autocorrelation (Hansen & Orzack, 2005). In contrast, we performed the analysis on 493 mammalian species, and the degree of shared evolutionary history was directly included into the analysis, which ensured a better estimation of the model parameters. This proved to be essential as phylogeny accounted for a substantial part of the link between lifespan and brain size (λ=0.91). Thus, the high correlations between lifespan and brain size that have been previously reported (e.g. for primates: r = 0.65, Allman et al., 1993; and for mammals: r = 0.83, Hofman, 1993) could in part be explained by shared evolutionary history among related species.

van Schaik & Deaner (2003) argued that the inclusion of some orders (e.g. *Chiroptera, Monotremes*, *Edentates*) may hide the relationship between lifespan and brain size in mammals. These taxa show lower metabolic rates, which tend to be associated with increased longevity despite their small brain size (Allman et al., 1993;

Hofman, 1993). In the present work, although these taxa were included, neither inclusion of these taxonomic groups nor metabolic rate in the analysis accounted for the lifespan-brain size correlation we document. Likewise, Harvey et al. (1991) did not find evidence for the association between basal metabolic rate and life histories. It is possible that BMR is not the most appropriate metabolic measure (Speakman, 2005). We found that although BMR and lifespan correlated, the relationship was not statistically significant when body mass was included as a covariate and phylogenetic effects were taken into account (LM: $b = -0.38$, $t_{189} = 4.70$, $P < 0.0001$; PGLM: $b = -0.08$, $t_{189} = 1.13$, $P = 0.25$).

In terms of the remaining confounding factors, our results do not indicate any significant association between lifespan and ecological variables (habitat, diet, feeding generalism, or habitat breadth), in line with findings by Harvey and Clutton-Brock (1985). Previous work in birds showed a negative association between lifespan and latitude, which can be explained by differential effects of biological and environmental interactions at different latitudes (Møller, 2007; Blumstein & Møller, 2008). Likewise, Duncan et al. (1999) found a significant correlation between lifespan and geographic range in birds. In contrast, in our study of mammals, we did not find any significant relationship between lifespan and geographic variables (mid-latitude point, range size and discontinued distribution). Mid-latitude point and range size were significantly associated with lifespan, but these association disappeared when research effort and lifespan measure (captive vs. wild) were included as co-variates in the model. Even after controlling for ecological and geographic factors, the predicted brain-lifespan association remained strong.

Age at first reproduction was the only life history trait retained in the MAM as a predictor of lifespan, along with body mass and residual brain size. This finding is consistent with previous studies in birds and mammals (Rushton 2004; Møller, 2006; Blumstein & Møller, 2008, Isler & van Schaik, 2009a). Barrickman et al. (2008) proposed that associations between brain enlargement and duration of the reproductive life must be tested by subtracting the growth period from maximum lifespan. Performing such an analysis, we found that the correlation between lifespan and relative brain size holds. Thus the observed correlation is not the result of an elongated juvenile period confounding the lifespan measure. Our results thus add to evidence for the cognitive buffer hypothesis by which a large brain assists in buffering individuals against environmental challenges by facilitating flexible behavioural responses (Allman et al. 1993; Deaner et al. 2003; Sol 2009a,b). This buffer effect should increase survival rates (Sol et al., 2007; Shultz et al. 2005) and favour a longer reproductive life, thereby partially compensating for the costs of delayed reproduction associated with the need to grow a large brain. Nevertheless, it is possible that an extended reproductive period is insufficient to fully counterbalance the costs of delayed reproduction in large-brained mammals. For example, Isler & van Schaik (2009a) demonstrated a negative correlation between the maximum rate of population increase and mammalian brain size. This raises the issue of additional counterbalancing advantages to brain enlargement (Isler & van Schaik 2009a, b).

The evidence for the brain size-lifespan association is correlational and does not necessarily reflects a causal relationship. In fact, the cognitive buffer hypothesis is just one of a set of theories that predict the brain size-lifespan correlation (Deaner et al., 2003; Sol, 2009a). For example, while the cognitive buffer hypothesis argues that large brains facilitate a longer lifespan, it is also possible that a longer lifespan selects for larger brains (Deaner et al. 2003; Sol, 2009a,b). Our results do not allow us to distinguish between these possibilities. Moreover, these different theories are not mutually exclusive and may act together to generate positive feedback favouring further increase in brain volume and longevity (Sol, 2009a,b). For instance, longevity can favour a delayed onset of reproduction, which should give parents the opportunity of prolonged investment in and contact with offspring (Covas & Griesser, 2007). This can facilitate an increase in brain size if, as the social intelligence hypothesis suggests, individuals living in stable social groups face higher cognitive demands that individuals living alone (Byrne & Corp, 2004; Dunbar & Shultz, 2007a; Shultz & Dunbar 2007). Despite its correlative nature, the finding that large-brained mammals live longer is important because it provides a solid basis from which integrate brain size evolution within a life history framework (Deaner et al. 2003; Isler & van Schaik, 2009a, b; Sol, 2009a,b). As Ricklefs (2004) notes, the evolution of large brains and cognition is rarely considered in this manner. A fruitful avenue for future research would be to elucidate the complex causal links that may help integrate brain size into the life-history strategy of the species.

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Chapter 2#

Food unpredictability, Motivation and Corticosterone levels influence the propensity to Innovate

With Oriol Lapiedra and Daniel Sol. *Unpublished*

ABSTRACT

Behavioral innovations are considered a main way animals confront environmental challenges. Although evidence is accumulating that individuals differ in innovation propensity, the underlying mechanisms remain poorly understood. In general, differences in innovativeness are thought to reflect different cognitive abilities, but besides the notable exception of a few animal taxa with extraordinary cognitive abilities, confidence in this hypothesis is undermined by a perceived lack of empirical support. In contrast, evidence is accumulating that the main factor driving innovation is motivation, in line with the “necessity drives innovation hypothesis”. However, motivation is generally assumed to be a state-dependent property and hence it should not lead to consistent individual differences in innovation. Here, we test the hypothesis that risk perception may lead to consistent differences in motivation through its effect on the endocrine system, thereby indirectly affecting the propensity to innovate. We validate this hypothesis by assessing how motivation and problem-solving performance differs in feral pigeons (*Columba livia*) with different perceptions of starvation risk. Through a battery of experiments, we first show that there exist consistent individual differences in motivation levels and that these differences account for a significant part of the individual variation in consumer innovation propensity. Interestingly, although motivation did not have a significant heritable component, it is related to glucocorticoides and hence in risk-taking behavior. These differences were not associated with the social status of the individual but with the uncertainties in food supplies in their new environment relative to that of origin. Thus, individuals used to stable food supplies were more motivated when food deprived, than those relying on less stable food supplies. Taken together, these results support the hypothesis that risk perception may lead to consistent differences in motivation and, indirectly, in the propensity to resolve ecological challenges in novel ways.

INTRODUCTION

Innovation, a key component of behavior flexibility, is an important way to deal with changes in the environment (Reader & Laland 2003; Sol et al. 2005). Recent work shows that innovation propensity consistently varies among individuals in a number of species, including house sparrows (*Passer domesticus*) (Liker & Bókony 2009), carib grackles (*Quiscalus lugubris*) (Overington et al. 2011) great tits (*Parus major*) (Cole et al. 2011; Morand-Ferron et al. 2011), blue tits (*Cyanistes caeruleus*) (Morand-Ferron et al. 2011), spotted hyenas (*Crocuta crocuta*)(Benson-Amram & Holekamp 2012) and meerkats (*Suricata suricata*) (Thornton & Samson 2012). Although such individual differences are often attributed to cognitive capacities, experimental evidence suggest that they can also result from individual variation in temperament and motivation (Laland & Reader 1999; Cole & Quinn 2012; Sol et al. 2012). Motivation in particular has been found to be the major driver of innovation, in line with the "necessity drives innovation hypothesis" (Laland & Reader 1999). For example, Laland & Reader found that in guppies (*Poecilia reticulata*), hungry individuals are more innovative than non-hungry individuals. Unlike temperament traits, however, motivation is generally supposed to be a state-dependent property and hence it should not lead to individual consistent differences in innovation. Nevertheless, there are several scenarios that may select for individual differences in motivation. For example, individuals that rely on resources that are variable and unpredictable over time may have been selected for higher motivation to search for food than those relying in more stable resource supplies (i.e. Hewitson et al. 2005). It is worth noting that the uncertainty in resources availability may result not only from living in a variable environment, but also from reduced access to food opportunities due to competition. Indeed, social conflicts that restrict access to food for some individuals, would produce stressful events that may increase basal corticosterone levels (but see Pravosudov et al. 2003). The perception of uncertainty is known to trigger the hypothalamo-pituitary-adrenal (HPA) system, which results in increased circulating corticosterone (i.e. the main glucocorticoid in birds) (Wingfield et al. 1998; Reneerkens et al. 2002). Baseline plasma concentration and acute release of corticosterone have different mechanisms of action, with different behavioural and physiological consequences (Wingfield et al. 1998; Romero 2004). For one way, glucocorticoids at baseline levels have control functions on the energetic metabolism (i.e. regulate intake, storage and mobilization of energy) (Sapolsky et al. 2000;

Landys et al. 2006). For example, in front of unpredictable long-term feeding schedules, a high-perceived risk of starvation would make individuals to maintain higher energy reserves and high basal corticosterone levels (Cuthill et al. 2000). Indeed, high basal corticosterone levels are known to promote fattening in birds, which may be considered a protection mechanism against unpredictability (Reneerkens et al. 2002). In another way, when individuals confront acute and adverse situations (i.e. predator attack), glucocorticoids secretion can increase in a few minutes. This acute increase in glucocorticoids concentration redirects behaviour and physiology to prioritizing immediate survival (sensu “emergency life-history stage”) (Wingfield et al. 1998; Sapolsky et al. 2000).

Here, we explore the intriguing possibility that motivation can be considered a temperament trait that modulates the propensity to innovative with a series of experiments in feral pigeons, *Columba livia*. Previous work has shown that motivation is a major driver of learning and innovation propensity in pigeons, the main components of behavior flexibility (Lefebvre et al. 1996; Seferta et al. 2001). Building on this finding, we ask (1) whether the motivation to innovate has an individual stable component within- and between- populations (i.e. evidence of temperament, sensu Réale et al. 2007), (2) whether individuals differ in motivation as function of the unpredictability of food sources in their environment and/or on their social status and aggressive temperament, and (3) whether motivation has an hormonal basis and an heritable component. To address these issues, we studied two pigeon populations, one that relies on food sources available on a regular basis, and another that depends on more unpredictable sources (Sol 2008). After equalizing their food necessities through a common garden experiment, we exposed pigeons from both populations to a battery of behavioural tests designed to measure motivation, consumer and motor innovation, aggressiveness and social dominance. If motivation were a response to food shortages, we would expect that motivation was higher in individuals from the population relying on unpredictable food sources and within each population, in the individuals with lower social status (i.e. less likely to obtain food under direct competition with other individuals). However, if individuals that rely on more stable resources were not used to deal with food shortages, the contrary would be true. Once experiments were finished, we took blood samples of individuals and estimate the corticosterone profile in the laboratory. To assess whether motivation had a heritable component, we conducted a breeding experiment to evaluate resemblance between offspring and parents and the potentiality of motivation to be a target of natural selection.

METHODS

Study subjects

We captured 42 individuals of free-living feral pigeons from two populations over 57 km apart (Barcelona and Moià, Catalonia, Spain) in February 2010. After capture, we took the follow biometric measures of each individual: length of the tarsus, third primary, wing and beak, with a digital caliper (error +/- 0.01 mm), and body mass, using a digital precision balance (+/- 0.01 g). Measured individuals were then marked with a unique combination of colored plastic rings, and randomly housed in four groups of 8-12 individuals in outdoor aviaries (2 x 2 x 4 m.), separated by population of origin. We provided roosting sites, *ad libitum* food (mixed commercial seeds) and water in each aviary. A habituation period of one-week preceded the battery of experiments. Although results from the lab cannot necessarily be used to draw conclusions on individual variation in innovativeness in a natural selective environment (Morand-Ferron et al. 2011), we note that our interest here is in mechanisms and these can be more easily inferred under the highly controlled conditions of the laboratory.

Our analyses were restricted to adult individuals (18 from Barcelona and 16 from Moià), which were distinguished from juveniles according to the color of the cere and the iris (Kautz & Seamans 1992). We were able to successfully sex adult individuals by observing courtship behavior (e.g. tail-dragging, bowing, driving, etc) (Johnston & Janiga 1995) and breeding activity (i.e. egg laying and incubation). A few individuals either died (n = 2) or escaped (n = 2) before completing all the tests, so sample sized may weakly vary between tests.

General experimental procedure

We quantified levels of motivation, aggressiveness, social dominance, motor and consumer innovation in a foraging context by exposing pigeons to four different tests. All tests were conducted in three periods from March 2010 to August 2011. In the first period (April-May 2010), two tests of motivation and two tests of consumer innovation were performed. In the second period (July-August 2010), pigeons were tested twice for motivation and twice for motor innovation, and were as well subjected to four tests in groups to establish social dominance and aggressiveness. In the third period (February to August 2011), two last tests of motivation were conducted to evaluate the possible long-term consistency of this trait. All these experiments were videotaped and observations were made behind a curtain to avoid disturbing the animals. Finally, a cross-fostering breeding experiment was conducted from October 2010 until March 2011 (see below). All animal care, husbandry, and experimental procedures were approved by the Generalitat de Catalunya (0152S, Dept de Medi Ambient i Habitatge).

Individual tests of motivation and innovation

At the beginning of each experimental session, we randomly selected groups of 6 pigeons from the outdoor aviaries and housed them in individual indoor cages (68 x 62 x 40 cm). Pigeons were isolated visually -but not acoustically- and provided with *ad libitum* food and water. After two days of habituation period and an overnight fasting period of 15 hours (Lefebvre et al. 1996; Bouchard et al. 2007), the next morning individuals were subjected to the corresponding test. The observers followed the entire behavior assays behind a curtain with a small hole from where sessions were recorded using digital video cameras. The same two observers (C. G-L and O. L) conducted all the behavior assays and manipulated the birds.

Motivation test - After the overnight fasting period, we approached a cage and put the habitual feeder (the same in all tests) with a seed mixture at the front of the cage. Latency to begin feeding after the disturbance was used as a measure of motivation (see Lefebvre et al. 1996; Bouchard et al. 2007; Sol et al. 2011). In case an individual did not eat in the 15-min period, a second test of 15-min was allowed once a first round of the test on the rest of individual was completed. Total latency includes the time of the second trial in seconds, when appropriate. Only individuals that solved the motivation test were included in the analyses to avoid including individuals that were not hungry or were sick without clinical signs.

Motor innovation - After the motivation test, we immediately replaced the feeder with an identical feeder covered with an opaque rigid cardboard lid and recorded the time the individual took to remove the lid and eat the food. If the individual did not solve the task after 20 min, it was considered to have failed to innovate. For individuals that did solve the task, the task was presented again two hours later to assess whether individuals had learnt how to solve the task. The latency from the first peck to the apparatus to open the lid was integrated with individual solve or not solve information, and both were the measure of motor innovation (i.e. probability of not solve across the experimental time, see analyses).

Consumer innovation test - As in the motor innovation test, the consumer innovation test started after the motivation test, when feeder with the familiar seed mixture was changed by an identical feeder containing an unfamiliar food. The novel food items were either rice or lentils, respectively colored with yellow and red natural food colorants. Both tests were conducted in consecutive days and individuals were left a maximum of 20 min to solve the task. As the motor innovation test, the individual tendency to incorporate new food resources was measured as the latency to forage from the food within the feeder integrated with individual solve or not solve information, and both were the measure of consumer innovation (i.e. probability of not eat across the experimental time, see analyses).

Group observations of social dominance and aggressiveness

After an overnight fasting period of 15 hours, we provide the habitual mix of seeds in a circular feeder (30 cm in diameter) at the center of the habitual outdoor aviary. The behavior of individuals was recorded for 20-min. We conducted four trials per each stable flocks, two in the same day (separated by two hours, approximately) and the other two the next week.

From the recorded videos, we quantified the dyadic proportions of wins and losses for each individual, the observed numbers of dyadic wins and losses in each group and total number of interactions between individuals during the 20 minutes of observation. Then, we used this information to calculate the normalized David's scores (Ds, hereafter), a dyadic dominance index that corrects for chance encounters (Devries et al. 2006). Aggressiveness of individuals was estimate as the total number of attacks initiated in each 20 min trial.

Cross-fostering experiment

In October 2010, we separated 16 breeding pairs of pigeons in outdoor breeding aviaries (2 x 2 x 4 m.). Eleven pairs were couples that had become naturally established in the outdoor aviaries, and five were chosen by picking at random individuals within each flock. Pigeons lay almost invariably clutches of two eggs (Johnston & Janiga 1995), so we interchanged one of the chicks at 4 (+/-1) days of age with another from a different breeding couple. Thus, the age difference between the cross-fostered individuals was of two days or less. All chicks were individually marked using small plastic rings that were posteriorly replaced by plastic rings as the chicks grew up.

Corticosterone profile

Blood sampling

We quantified the corticosterone profile of each individual following the "capture restrain" protocol (Wingfield & Romero 2001), which is the procedure typically used in birds (Romero 2004). Hormone profiles were measured in the early morning to avoid the circadian variation in hormones concentration (Romero 2004). To avoid delays, only six individuals were tested every experimental day. After 24 hours of habituation in the indoor aviaries, with food and water *ad libitum*, the six individuals were randomly taken from their individual cages and brought into a separate room where an initial blood sample of 0.5 ml was taken from the brachial vein. The sample was obtained with a maximum delay of five minutes to measure unstressed, baseline concentrations. Next, the individuals were kept in individual opaque cotton bags for 30 minutes later, after which a second blood sample was extracted to measure stress-induced concentrations. The blood samples were stored in heparinized tubes and kept in a fridge with dry ice to be transported to the laboratory the same day, immediately after extraction.

Sample processing and Radioimmunoassay

Within the same extraction day, the heparinized tubes were centrifuged in the laboratory at 3000 rpm for five minutes. Plasma was removed and stored at –20° C until Radioimmunoassay. To obtain corticosterone measures, hormone was extracted from plasma with ether and assayed by radioimmunoassay in duplicates based on Wingfield et al. (1992). The assays were conducted in the Institute of Animal Physiology at Autonomous University of Barcelona.

Statistical analyses

Behavioral tests

To assess for individual consistency in the behavioral responses to the tests an intraclass correlation coefficient (ICC) was used (Nakagawa & Schielzeth 2010). To model motivation and innovation latencies, we used survival analysis. Some feeding latencies were truncated because some individuals not solved the test at the 20 minutes limit time of the behavioral test. As already noted in previous works (Dingemanse et al. 2010; Sol et al. 2011, 2012; Bókony et al. 2012), regressions and ANOVAs give the same response value to all individuals that failed to complete the task and these censored variables are unlikely to meet the assumption of normality. Thus we used instead survival analyses, which deal with these types of data by analyzed the success or failure of the response to a test across the experimental time. Specifically we used mixed effects cox models, which fit a cox model containing both random and fixed effects. In all models, we initially included in addition of the variables being tested the following variables: sex, weight, population of origin, type of food (only consumer innovation test) and the morphological variables. To avoid co-linearity problems, we used the factors of Principal Component Analysis (PCA) instead actual morphological variables in the models (i.e. high correlation of morphological variables). Factors were estimated based on a correlation matrix of the tarsus, tail, wing and bill lengths, all log-transformed. The two first components of the PCA were used as accounted for 86% of variation in morphology. We used a model selection procedure based on ΔAICc to identify the best model or models. Akaike weights estimate the probability that a given model is actually the best model in the model set. Parameters of the models presented in the text are those from the best model. Interaction terms were evaluated and just showed when there exist (i.e. were significative). All analyses were performed by R software (R Development Core Team 2009). The packages irr (ICC), coxme (survival models) and MuMin (model selection) were used.

Parent-offspring resemblance (h^2)

The heritability (h^2) of a given trait is the ratio of additive genetic variance (σ^2_A) over total phenotypic variance ($\boldsymbol{\sigma^2_P}$), and can be estimated by the slope (b) of the corresponding parent–offspring regression (Falconer & Mackay 1996). Mother, father and mid-parent (i.e. average the absolute values of both parents) values of motivation, were regressed on mean chick values (Drent et al. 2003) by mean of generalized linear models (GLM) by the stats package. In a way to account for parental environment effects, we performed the same regression described above, but just for the foster group.

RESULTS AND DISCUSSION

Is motivation driving innovation propensity?

Regarding the consumer innovation task, an important proportion of individuals successfully solved the tasks (70% for the yellow rice task and 83% for the red lentils task). These high values are in line with previous studies (Sol et al. 2012), and highlight that most individuals are capable of adopting novel foods when they need so (Overington et al. 2009). Confirming also previous studies (Sherwin 2003, Overington et al. 2011, Bókony et al. 2012; but see Sol et al. 2012a), the probability of taste novel foods was primarily related to motivation (Best cox model: $z = 3.46$, $P < 0.001$) (see table 1 for general model).

Table 1. Survival models relating probability of solve the motor innovation and probability of eat in the consumer innovation tests, as a function of motivation and a set of confounding variables.

Experiments	**coefficient**	**exp (coef)**	**S.E. (coef.)**	**z**	**P**
Consumer innovation					
Site (Moià)	-0.172	0.841	0.474	-0.36	0.72
Sex (male)	-0.35	0.704	0.532	-0.66	0.51
Food type (rice)	-0.184	0.831	0.327	-0.56	0.57
Order food	-0.315	0.729	0.318	-0.99	0.32
Motivation*	39.87	0.001	11.90	3.18	**< 0.01**
Comp 1	-2.29	0.100	5.510	-0.42	0.68
Comp 2	-3.70	0.024	4.307	-0.86	0.39
Dominance	0.197	1.218	0.170	1.16	0.25
Weight	0.002	1.002	0.010	0.21	0.83
Motor innovation					
Site (Moià)	-0.008	0.991	0.654	-0.01	0.99
Sex (male)	0.347	1.415	0.876	0.40	0.69
Weight	-0.02	0.979	0.013	-1.48	0.140
Trial (2)	1.095	2.991	0.369	2.97	**< 0.01**
Comp 1	-2.031	0.131	7.881	-0.26	0.80
Comp 2	-13.552	0.130	7.616	-1.78	**0.07**
Motivation*	1.314	3.722	0.968	1.36	0.17
Dominance	0.163	1.177	0.280	0.58	0.56

* Total latency of motivation test is expressed as $\log_{10}$ (1/Total latency in seconds) to make higher values to describe higher motivation.

Regarding the motor innovation experiment, 53% of pigeons solved the task. In the same way, Overington et al. (2011) found that 55 % (N = 36) of carib grackles (*Q. mexicanus*) solving a novel motor task, and in a lesser extent 22 % of invasive common mynas (N = 33) (Sol et al. 2012). Pigeons were consistent in the performance over two consecutives trials of motor tasks (ICC = 0.39, 95% CI 0.06 - 0.76, P < 0.0001), indicating that those individuals that perform well in the first trial do well in the second one. Furthermore, when comparing the time elapsed to open the lid between the first and the second trial of the motor innovation task, latency to solve the problem decreased significantly (z = 2.99, P < 0.01), suggesting that individuals had learnt to solve the task (see figure 1) (Morand-Ferron et al. 2011).

Despite motivation was retained in the best models accounting for motor innovation propensity, and unlike previous studies (Overington et al. 2011; Sol et al. 2012), motivation did not have any clear effect on motor innovation (Best cox model: z = 1.42, P = 0.16; see table 1 for general model). Instead, successful innovators were better characterized by having a small body mass, but marginally significative (Best cox model: z = -1.87, P = 0.06, i.e. lean bird solve faster), long tail and wings with a short beak (i.e. PCA component 2) (Best cox model: z = -2.52, P < 0.05). Thus, we found mixed evidence for the influence of motivation on individuals' ability to innovate (i.e. positive influence on consumer innovation but not effect on motor innovation).

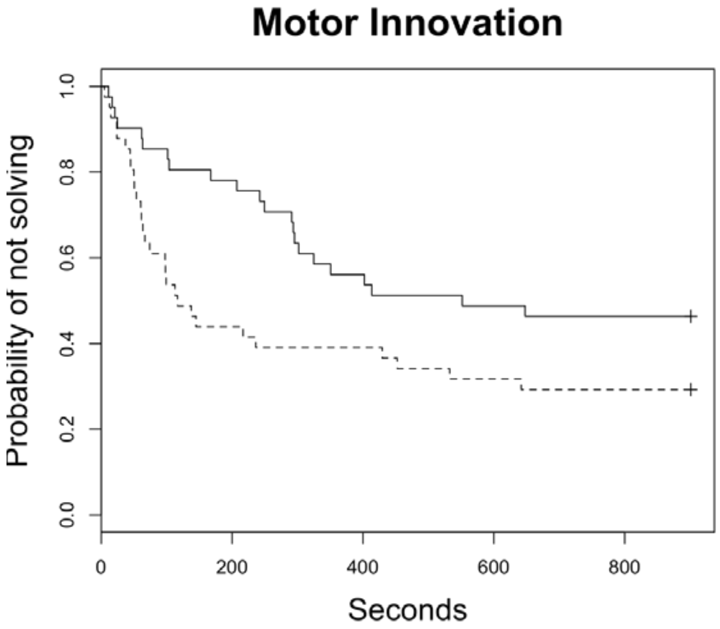

Figure 1. Differences in latency to solve the motor innovation test between the first and the second attempt. In the survival curves, solid lines represent the first attempt whereas the dashed line represents the second attempt. Only individuals solving the first test are included.

Is motivation a temperament trait?

There was individual consistency in the expression of motivation in the short-term, when we take the test performed in one elapsed day (ICC = 0.71, 95% CI, 0.49 - 0.85, P < 0.001, N = 31), but also when we analyze the tests after several fasting treatments, encompassing more than one year of captivity (ICC = 0.32, 95% CI, 0.15 - 0.53, P < 0.001, N = 23). This stable component was present in the two studied populations (Moià: ICC = 0.23, 95% CI, 0.05 - 0.53, P < 0.01, N = 14; Barcelona: ICC = 0.52, 95% CI, 0.25 - 0.82, P < 0.001, N = 9). These results are consistent with the observations of Sol et al. (2012) who found individual consistency (16%) for motivation in common mynas. Our results suggest that there may be a consistent individual basis underpinning motivation state in feral pigeons that may be relevant in the determination of several biologically important behaviors.

Are there individual differences in motivation as a function of variability of food opportunities?

The role of the environment:

There were consistent differences among populations in the expression of motivation. Using the short-term motivation tests, the best model retained population of origin as fixed effect, showing that pigeons from the population with more stable food resources (Moià) have higher levels of motivation than those from the more variable and unpredictable population (Barcelona) (Cox model: $z = 2.38$; $P < 0.05$). Although factor 2 of the PCA as well as was retained, this was not significative ($z = -1.55$, $P = 0.12$) (See Figure 2).

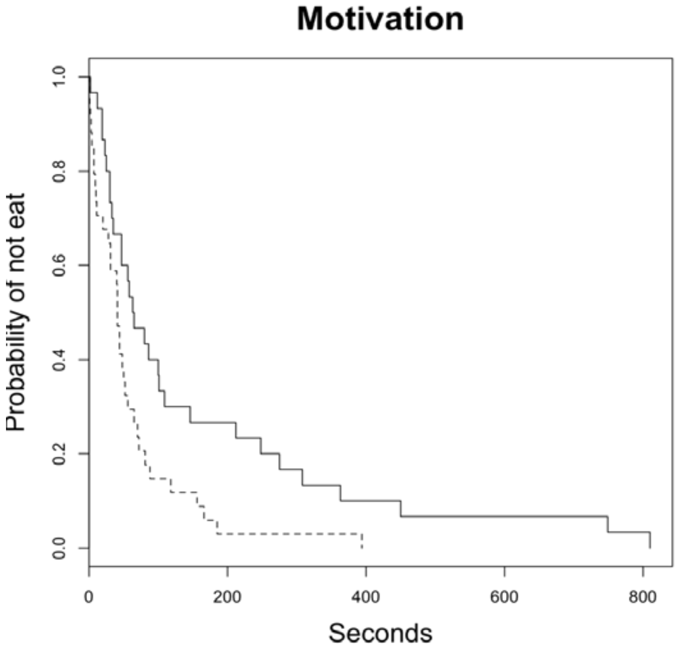

Figure 2. Latencies to eat in the motivation short-term test as function of uncertainties of food supplies in the population of origin. In the survival curves, solid lines represent pigeons from the more unstable food supplies (Barcelona), whereas the dashed line represents individuals from the more stable food supplies (Moià).

Using the long-term motivation tests, a similar pattern emerges: the best model retained population of origin and factor 2 of the PCA, but an interaction term shows that shorth-beaked individuals with long wings and long tail from the more unstable food source population showed lower levels of motivation than those from the more stable and predictable population (Best cox model: z = -2.01; P < 0.05).

The role of social relationships

Feral pigeons showed consistent individual differences in the level of aggressiveness (ICC = 0.29, 95% CI, 0.12 - 0.49, P < 0.001, N = 33), indicating that this is a temperament trait (Réale et al. 2007). We modeled motivation as a function of dominance, aggressive temperament, sex, body mass and morphology within each population, with individual identity coded as random factor. For individuals from Barcelona, the best model for short-term motivation retained aggressiveness and factor 2 of the PCA, but factors are not significative (P > 0.2, for both). Likewise, taking motivation tests from all year of captivity, the best model retained again aggressiveness and morphology (i.e. factor 2 of the PCA). Although morphology was not accounting for motivation (P > 0.1), more aggressive pigeons tend to be more motivated, but not significative (Best cox model: z = 1.66, P = 0.09). In contrast to Barcelona, for the group of Moià, males (Best cox model: z = 2.24, P < 0.05) and smaller individuals (factor 1 of the PCA) (Best cox model: z = 2.22, P < 0.05) showed higher levels of motivation in the short-term period. The same pattern emerges in the long-term period of motivation (males z = 2.89, P < 0.01; smaller individuals, z = 2.55, P < 0.05).

There is a genetic component of motivation?

The parent–offspring resemblance analyses yielded no evidence for a genetic component of motivation (see table 2). Rather, offspring motivation tended to be higher for less motivated non-foster parents than for more motivated parents (b = -0.34; P = 0.03; heritability = -78%). A negative heritability may be product of small sample size (Rymer & Pillay 2011). Alternatively, heritability may have been altered because of an increase in environmental variance under stressful conditions (Bitume et al. 2011), although it is unlikely that pigeons perceive captivity as a very stressful conditions.

Table 2. Relationships and narrow sense heritability (h^2) calculated for regressions between parents (fathers, mothers, and foster fathers and mothers) and their young offspring for motivation behavior. Significant values are showing in bold.

Comparisons	**B ± SE**	**P**	**h^2 ±**
Offspring on parents			
Motivation mother	-0.09 ± 0.20	0.66	- 18 ± 40
Origen parents (Moià)	6.87 ± 2.04	**<0.01**	-
Foster group (yes)	-0.16 ± 0.28	0.57	-
Weight	-4.24 ±1.67	**<0.01**	-
Motivation mother: origin (Moià)	1.22 ± 0.39	**<0.01**	-
Motivation Father*	- 0.34 ± 0.15	**0.03**	- 78 ± 30
Origen parents (Moià)	0.60 ± 0.31	**0.06**	-
Foster group (yes)	-0.10 ± 0.30	0.74	-
Weight	-2.84 ± 1.77	0.12	-
Motivation mid-parents	-0.39 ± 0.25	0.13	- 78 ± 50
Origen parents (Moià)	20.74 ± 4.73	**<0.001**	-
Foster group	-0.14 ± 0.26	0.59	-
Weight	-3.01 ± 1.61	**0.07**	-
Motivation mid-parent: origin (Moià)	1.41 ± 0.51	**<0.001**	-
Offspring on foster parents			
Motivation foster mother	-0.11 ± 0.26	0.66	- 22 ± 52
Origen parents (Moià)	7.11 ± 2.69	**0.02**	-
Weight	-2.66 ± 2.59	0.33	-
Motivation mother: origin (Moià)	1.25 ± 0.55	**0.05**	-
Motivation foster father	0.24 ± 0.13	0.11	48 ± 26
Origen parents (Moià)	7.83 ± 1.70	**<0.01**	-
Weight	-2.74 ± 1.83	0.16	-
Motivation father: origin (Moià)	1.41 ± 0.35	**<0.01**	-
Motivation mid-parents	0.06 ± 0.29	0.82	6 ± 30
Origen parents (Moià)	7.85 ± 2.53	**0.01**	-
Weight	-2.41 ± 2.13	0.28	-
Motivation mid-parent: origin (Moià)	1.41 ± 0.51	**0.02**	-

* Interaction term was not significant

Is baseline corticosterone involved in the phenotypic variation of motivation?

If the genetic component of motivation is small and largely affected by environmental factors, then why this stable component of motivation persists, even one year after living under new environmental conditions? As a possible explanation, we assessed the potential role of corticosterone in the patterns of variation in motivation. The best models of variation in motivation in the short-term (see Table 3) consistently suggest that individuals with high baseline corticosterone showed lower motivation levels (All best cox models: $z = -2.5$, $P < 0.05$). However, although best models accounting for long-term motivation consistently retained baseline corticosterone (see table 3), just morphology (i.e. component 2 of PCA) accounted for variation in motivation (Best cox model: $z = -2.91$, $P < 0.01$; i.e. individuals of long tail and long wings with short beck were more motivated). Thus, although the effect of corticosterone on motivation is evident in the short term of 6 months, one year later this effect is less clear. This is in line with those reported by Schoech et al. 2007, who found that in Florida scurb-jay (*Aphelocoma coerulescens*), individuals from an environment with variable and unpredictable food resources, even supplemented with food for a long time maintain high corticosterone concentration (Schoech et al. 2007). For one way, long-term moderate increase in baseline corticosterone levels appear to enhance spatial memory and would be an adaptation for unpredictable environments (Pravosudov 2003). On the other way, more motivated individuals where more probably to acquire new food resources, and may be one of the mechanistic link between high rates of innovations showed by urban birds (Møller 2009; Evans et al. 2011). Individuals living in urban environments may confront food shortage habitually, and then forced to try new food. Thus, baseline corticosteroid concentrations would underpin part of the stable component on motivation and a key interface for adaptation of organism to changing environments. Finally, peak levels of corticosterone concentration showed no effect on motivation short-term (Best cox model: $z = -0.77$, $P = 0.44$) neither for motivation long-term (Best cox model: $z = -1.13$, $P < 0.26$). This is in line with their different biological and ecological function, on an “emergency life history stage” (Wingfield et al 1998; Sapolsky et al. 2000).

Table 3. Comparison of candidate models of motivation based on ΔAICc and relative Akaike weights. Both short term and long term variation in motivation were assessed. Only the best models (ΔAICc < 2) and the variables (fixed effects) appearing in at least one of these models are presented. Variables includes in the global model are sex, dominance, aggressiveness, body size, site of origin and baseline corticosterone. Individual identity was adjusted as random factor.

Motivation	**Baseline corticosterone**	**Weight**	**Origin site**	**Comp 2**	**Dominance**	**df**	**AICc**	**ΔAICc**	**Weight**
Short-term									
	+					2	281.08	0.0	0.11
	+		+			3	282.33	1.25	0.06
	+	+				3	282.61	1.54	0.05
Long-term									
	+			+		3	1114.68	0.0	0.14
	+		+	+			1116.61	1.93	0.05
	+			+	+		1116.65	1.97	0.05

CONCLUSIONS

In a recent review, Thorton & Lukas (2012) highlighted that animal cognition experiments frequently reveal striking individual variation but rarely consider its causes. Thus, evidence from a single individual is sometimes considered sufficient to demonstrate the cognitive capacity of a species, which detracts from the value of individual variation in understanding cognitive development and evolution. Our experiments identify important variation in innovation propensity among pigeons and confirm previous evidences that such variation is in part driven by the motivational state of the individual. More important, however, the experiments revealed that, contrary to common wisdom in non-human animals, motivation has a stable component that is not merely explained by age, sex or social status but that presumably arises from differences in the neuroendocrine system. Although we do not assess for the consistency in corticosterone profile, literature suggest that this have an stable component at individual level (Cockrem & Silverin 2002; Kralj-Fiser et al. 2007; Romero & Reed 2008). There was no evidence that differences in motivation exhibited a heritable component, so more probably they reflect environmental factors related to rearing conditions and/or previous experience.

The glucocorticoid response has a significant heritability in captive bird species (Odeh et al. 2003; Evans et al. 2006), and could be a potential target of natural selection (Carere et al. 2010). Thus, assess this possibility would be a valuable task. Regardless of the cause, the existence of a stable component in motivation can potentially underlie part of the differences in innovation propensity observed between individuals.

In humans, nobody question that some individuals are more motivated than others to do some tasks, whether because of inherited or learnt mechanisms. In non-human animals, however, the possibility that motivation is a temperament trait is rarely considered. Although more evidence is needed to demonstrate that motivation has a stable component that goes beyond simply differences in sex, age or social status, our results open the possibility that motivation is a temperament trait. If so, its influence in innovativeness and learning may be more superior than generally thought (see Wolf et al. 2007).

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Chapter 3#

Behavioural flexibility for a life in the city

With Daniel Sol and Oriol Lapiedra. *Submitted*

ABSTRACT

Although most human-induced environmental changes occur faster than species can adapt, it is believed that many animals are able to cope with such alterations by plastically adjusting their behaviour to the new environmental demands. Here, we ask whether and how such behavioural flexibility assists animals in dealing with the urbanization process, one of the primary causes of biodiversity loss and biotic homogenization. Based on a literature review, we present both theoretical and empirical arguments to argue that behavioural flexibility is an important way animals deal with urban environments. Although influential in all stages of the colonization of urban habitats, behavioural flexibility appears to be particularly important during establishment, allowing among other things to better exploit novel resources, avoid disturbance by humans and communicate in noisy environments. However, the paucity reporting fitness measures precludes to draw firm conclusions. Our understanding of the factors that allow the arrival to and population growth in urban habitats is even more deficient. Because the urbanization process is expected to continue threatening biodiversity in the nearby future, there is some urgency to better understand how behavioural flexibility helps animals to cope with such environmental alterations.

INTRODUCTION

From all rapid human-induced environmental changes (HIREC, sensu Sih et al. 2011), the urbanization process is probably the most important current threat to biodiversity (Shochat et al. 2006a; Chace & Walsh 2006; McKinney 2006). Urbanization involves a number of important environmental alterations (McKinney 2002, 2006; Shochat et al. 2006a): natural vegetation is replaced by built structures and fragmented by buildings and roads; food sources become artificial, and often abundant and spatially concentrated; disturbance from humans increases; the community of predators/enemies change; and pollution is more frequent with regards to night-time lights, noise and chemicals. These habitat alterations have several major consequences for biodiversity (Grimm et al. 2008). First, it generally reduces species diversity and evenness, despite increases in abundance of some taxa (Shochat et al. 2006a; McKinney 2006). Second, it alters the species composition of the communities, favouring biotic homogenization (McKinney 2006). Proposed mechanisms for changes in richness, evenness and composition include ecological factors, like increased food availability and relaxed predation on the dominant species, and species traits like increased competitive ability of some urban species (Faeth et al. 2005; Anderies et al. 2007; Shochat et al. 2010) and behavioural flexibility (Timmermans 1999; Sol 2003; Shochat et al. 2006b; Møller 2009). In this review we focus on behavioural flexibility. The construction of behavioural responses is thought to allow animals dealing with novel environmental challenges, facilitating population persistence in conditions where environmental alterations occur faster than the species can adapt (Sasvári 1985). However, the possibility that behavioural flexibility may assist individuals to become urban dwellers has only recently been appreciated and has never been integrated into a coherent framework.

In this review, we ask whether and how behavioural flexibility assists in the different stages through which a species passes to become an urban dweller, thus indirectly addressing its importance in accounting for urban biodiversity patterns. Behavioural flexibility is considered for some an ambiguous concept that may apply to many different things. It is therefore important not only to properly define it (see below), but also to describe in which particular behavioural domains and ecological contexts is useful to behave in a plastic way. To this purpose, we reviewed the literature searching for studies that test for differences in behaviour among urban and non-urban individuals and species. Because the ecology of a species describes how plastic behaviours translate to population dynamics, we also discuss how two main ecological correlates of behavioural flexibility -life history and niche breadth- may affect the varying success of species in urbanized environments.

A THEORETICAL FRAMEWORK

Stages to become an urban dweller

As shown in Fig. 1, the colonization of urban environments may be described in three main stages -arrival, establishment and increase- which then facilitate geographic spread and evolutionary adjustments (Evans et al. 2010). At each stage the ecological challenges vary, and so do the role of behavioural adjustments. Not all species need to pass all the stages to become an urban exploiter, however. In fact, there are four different origins for urban dweller species: (1) Species that thrive during the transformation of the natural habitat into an urban habitat; (2) Species that are displaced during this transformation but then re-colonize the new environment from the surroundings; (3) Species that colonize urban areas from regions unaffected by the alterations; and (4) Species introduced by humans. The first and last categories involve species that are either already present in the area or that have been deliberately or accidentally transported and introduced by humans; thus, in these cases the causes of arrival are already known, and the question of how a species has become an urban dweller turns to how this has either persisted despite disturbances or established in the novel environment, and what factors have led to their current densities and subsequent spread. The categories 2 and 3 essentially reflect a natural colonization process, and hence include all four stages; the main difference between them relates to the importance of long-distance dispersal.

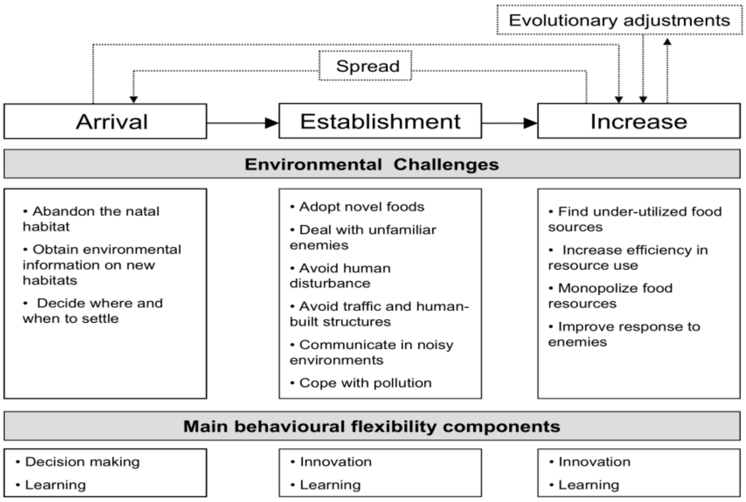

Figure 1. Schematic representation of the three main stages of the colonization of urban environments, with their environmental challenges and the main components of behavioural flexibility involved in dealing with them.

Whether a species passes through all their relevant stages, and hence becomes an urban dweller, depends on environmental factors, especially the history of urban development and the quality of urban habitats, but also on species' ecological and life-history traits (Evans et al. 2009; Møller 2009). The importance of ecological factors and species traits may vary from one stage to another, and it is even possible that certain traits positively influence progression through one stage, but delay progression through another (Evans et al. 2010).

An operational definition of behavioural flexibility

Behavioural flexibility may be defined as the general cognitive capacity of an animal to adaptively modify its behaviour (Lefebvre et al. 2004). This includes acquiring new behaviours or modifying pre-existing ones, defining behaviour in terms of both preferences and motor patterns. Unlike other plastic responses, flexible behavioural responses are generally not context specific, are reversible, and can be generalized to situations that differ partially or totally from those in which they were initially acquired (Robinson & Dukas 1999). Thus, behavioural flexibility provides a great adaptive potential to deal with a variety of novel or unfamiliar problems in a variety of ecological contexts.

Novel or modified behaviours are the result of three main cognitive processes: innovation (i.e. the acquisition of novel behaviours; Lefebvre et al. 1997; Reader & Laland 2003; Ramsey et al. 2007), learning (i.e. the acquisition of new information influencing performance in decisions and behaviours; Dukas 2004) and decision making (i.e. the determination of action based on the known states of relevant environmental features and experience; Dukas 2004)). Thus, much of the variation in the degree of behavioural plasticity, notably among species, is due to differences in cognitive abilities, as suggested by the finding that brain size (and particularly the association areas of the brain) predicts a significant fraction of variation in the propensity for innovation and learning (Lefebvre et al. 1997; Reader & Laland 2002; Overington et al. 2009). Innovation, learning and decision making are in turn influenced by more simple cognitive processes (e.g. attention, perception and memory to gather and retain information), emotional temperament traits (e.g. degree of boldness or activity levels), and motivational states (e.g. hungry, hurry). These factors may also be modified by simple learning mechanisms like habituation (i.e. the decrease of a behavioural response with the repetition of a stimulus that is neither rewarding nor detrimental), although temperament traits may sometimes be quite consistent over time (Sih et al. 2004; Réale et al. 2010). All these factors contribute to the enormous variation that exist in behavioural flexibility among individuals, populations and species (Lefebvre et al. 2004; Lefebvre & Sol 2008).

Life history and behavioural flexibility

Life history defines the way organisms allocate time and energy to reproduction, growth and survival (Stearns 1992; Roff 2002), and hence represents a nexus between behavioural decisions and population dynamics. One important axis of variation is the fast-slow continuum, which defines the trade off from “highly reproductive species” (fast-lived) at one end to “survivor species” (slow-lived) at the other end (Sæther & Bakke 2000). Fast-lived species tend to prioritize current over future reproduction, exhibiting as a result a high potential for population growth (Sol et al. 2012c). However, because they concentrate all reproductive effort in a few reproductive events, the fitness cost of losing a breeding attempt is high (i.e. they have high brood value). In contrast, slow-lived species tend to prioritize adult survival, and hence show lower mortality and longer lives. As a result, they show less variation in population fluctuations and, because their brood value is lower, the fitness costs of delaying or skipping reproduction is also lower and individuals can engage in reproductive activities only when conditions are favourable (Sol et al. 2012c). Species that exhibit higher behaviourally flexibility, as measured by brain size relative to body size, are aligned to the slow-lived extreme of this continuum (Deaner et al. 2003; Sol 2009; Barton & Capellini 2011).

Ecological generalism and behavioural flexibility

The degree of ecological generalism dictates how individuals use the habitats and resources, and hence it is expected to affect energy inputs and population growth in novel environments (Bonier et al. 2007). Behavioural flexibility is related to the degree of ecological generalism through two opposed forces. First, a behaviourally flexible animal is more capable of using novel habitats and resources that require behavioural adjustments, which should facilitate niche expansion; instead, a less flexible animal will tend to avoid novelty situations because of its more limited capacity to behaviourally adjust their behaviour (Greenberg 1990). Second, behavioural flexibility is itself limited by the degree of ecological generalism of individuals because morphological and physiological specialization limit the number of motor patterns and foods types they can use. Thus, although behavioural flexibility and ecological generalism are different concepts, it is expected that ecological generalists tend to be more behaviourally plastic than ecological specialists (Klopfer 1967; Greenberg 1990). At the generalist extreme of the generalist-specialist continuum, there are the opportunistic species that base their lives in the search for new opportunities and that rely on a high behavioural flexibility to adjust behavioural patterns to the continuous challenges they have to face; at the specialist extreme, there are the species that avoid exploring and adopting novel opportunities, for example though neophobic responses (Greenberg 1990), and that consequently do not tend to alter their behaviour.

EMPIRICAL EVIDENCE FOR THE IMPORTANCE OF BEHAVIOURAL FLEXIBILITY

The ability to adjust the behaviour to novel situations may have consequences for each of the stages that makes a species an urban dweller. However, because the type of behavioural response is expected between stages, we discuss the consequences for arrival, establishment and increase in separate sections. However, we admit that some behavioural responses may be useful in more than one stage.

Arrival stage

For species colonizing urban environments, the first step is arrival. Arrival is essentially a combination of two behaviours, search of novel opportunities (dispersal) and chose a new habitat where to settle (habitat selection), and we will discuss each process apart. Because not all species are able to reach and settle in urbanized environments, the arrival stage is an ecological filter that contributes to differences in biodiversity between urban and surrounding habitats, notably in terms of biodiversity loss and changes in species composition.

Dispersal

One of the main factors limiting diversity in urbanized environments is dispersal. According to the dispersal-assembly theory (Ostling 2005), dispersal may limit the distribution of species and hence may contribute to the makeup of communities (Chave 2009). Just by chance, a rare species may be absent from a site where it would have thrived, making the structure of the community to differ from that of surrounding areas. If dispersal is non-random (i.e. some species tend to move farther than others), dispersal may also change the composition of the community, adding species that are not present in the surrounding environments.

The probability of a species initially arriving in an urban area increases with the proportion of its geographic range that is urbanised (Evans et al. 2010). Urbanized environments are so widespread that it is tempting to conclude that dispersal is not an issue to understand urban biodiversity patterns. However this is not necessarily true. Indeed, the high success of many introduced species in urban habitats (Case 1996) suggests that urban communities could contain many more species that they currently have, provided that these species could have reached them. Direct evidence for a role of dispersal in facilitating urbanization are contradictory, however. The only evidence to date is a study by Møller (2009), who found that urban birds tend to show longer dispersal distances than rural birds. However, Evans et al. (2011), found no relationship between urban development and dispersal capacity. These contradictory results may reflect the metrics used to describe dispersal in each study. Evans et al. (2011) used natal dispersal estimated with recapture of banded individuals whereas Møller (2009) used the maximum distance from the mainland to an island with a permanent breeding population, which not only reflects dispersal but also establishment. Alternatively, the discrepancies may come from the region of study; Britain, where the study of Evans et al. (2011) was conducted, shows a high level of urban development and it is therefore probable that dispersal plays a minor role.

If dispersal were so important in building urban communities, we should expect an increase over time in the number of species settling in urbanized environments, a prediction supported by some evidence (Møller 2009; Møller et al. 2012). The importance of dispersal is also reflected in the common observation that some species are highly urbanized in some regions but not in others. Thus, it is likely that diversity in urbanized environments would be higher if there were no dispersal limitations.

The role of behavioural flexibility in facilitating dispersal is less clear. A priori there is no reason to expect that behavioral flexibility should enhance dispersal directly, except in the case of highly opportunistic species that continuously search for new ecological opportunities. On the contrary, if behavioural flexibility allows dealing with environmental changes (see the 'Establishment' section), they should be more able to deal with some of the pressures that may force individuals to abandon their original areas (e.g. a food shortage).

However, behavioural flexibility may be associated with dispersal indirectly if it is correlated with temperament traits or state-dependent features that do affect dispersal. Here it is important to distinguish individuals that abandon their natal or breeding areas voluntarily from those that are forced to do so. Being bold and aggressive may be advantageous to disperse voluntarily (Fraser et al. 2001; Dingemanse et al. 2003; Duckworth & Badyaev 2007; Cote et al. 2010). However, bold and aggressive individuals are not necessarily the most plastic ones. In a study of urban tree swallows *Tachycineta bicolor*, Betini & Norris (Betini & Norris 2012) did find that more aggressive individuals were better able to adjust their levels of nest defence to variation in temperature than less aggressive ones. Likewise, in great tits *Parus major*, bold individuals were less capable of gathering information on the environment and hence to adjust their behaviour when the environment changes (Marchetti & Drent 2000). In starlings *Sturnus vulgaris*, faster explorers were not less sensitive to a change in a familiar environment than slower explorers (Minderman et al. 2009). In many cases, however, individuals do not abandon the area voluntarily but are forced to do so by dominant individuals. In zenaida doves *Zenaida aurita* from Barbados, for example, the use of an urban area (the harbour) seems to have resulted from competition for territories, which forced some individuals to seek for alternative habitats (Sol et al. 2005a). According to the "necessity drives innovation" hypothesis, subordinates should be more plastic in their behavior than dominants (Laland & Reader 1999; Biondi et al. 2010; Overington et al. 2011; Morand-Ferron et al. 2011), mainly because they are less proficient foragers and hence tend to be more motivated to explore, innovate and learn. In great and blue tits *Cyanistes caeruleus*, for example, juveniles are more innovative than adults, consistent with the hypothesis (Morand-Ferron et al. 2011).

Selecting urbanized environments

Habitat selection by dispersers involves using environmental information to decide in which habitat is best to settle (Stamps 2001). The decision to settle in a habitat is generally done with incomplete information on the quality of the environment, and hence mistakes in habitat choice may have profound effects on the fitness of individuals, either because some species will avoid settling in habitats that are suitable or because others will settle in habitats that are not appropriate.

In general, we would expect individuals to attain higher fitness in habitats similar to the pre-dispersal habitat, whether because they are already phenotypically adapted or because they have previous experience (habitat trainning, Stamps 2001). For example, in a cross-fostering experiment in which eggs of blue tits *Cyanistes caeruleus* were transferred to nests of great tits and vice versa, early learning caused a shift in the feeding niche in the direction of the foster species and the shift lasted for life (Slagsvold & Wiebe 2007). However, not all species show the same degree of niche conservatism. In the above experiment, both species changed their feeding niches, but the change was greater in the great tit with its less specialized feeding behaviour (Slagsvold & Wiebe 2007).

However, why should any animal prefer a novel habitat over their traditional ones? According to classical habitat selection models (e.g. Fretwell & Lucas 1970), there are a number of situations that may make individuals decide to change habitat. In most cases, this is related to density-dependent effects that reduce the rewards of the current habitat, whether because an increase in density has increased competition for resources or because the old habitats has been altered. Thus, it is unsurprising that in highly urbanized areas many species end up using urban habitats. However, other causes are also possible. In man-eating lions, for example, prey scarcity and difficulties in hunting their usual preys drives some individual to such risky dietary specialization (Yeakel et al. 2009).

All animals use environmental cues to decide where is the best to settle, some being more restrictive (habitat specialists) than others (habitat generalists). But even ecological generalists may behave as specialists when establishing in novel environments (Sol et al. 1997). Some environmental cues convey general information and hence may be useful in new habitats. For example, introduced monk parakeets *Myiopistta monachus* in urbanized environments tend to select the tallest available trees for nesting, a cue to avoid nest predation that is also used in their natural environments (Sol et al. 1997). Other cues, however, are more context-specific and may lead to wrong decisions when used in an incorrect context. The use of inappropriate cues may affect population dynamics through ecological traps in which an animal settles preferentially in a habitat within which it does poorly relative to other available habitats (Dwernychuk & Boag 1972; Robertson & Hutto 2006). Kriska et al. (1998), for example, showed that some types of asphalt polarize light horizontally and as a result are much more attractive to mayflies than the surface of a pond or stream. However, mayflies end up laying their eggs on an inappropriate substrate where they are unable to hatch successfully. Likewise, (Witherington 1997), reported that that sea turtle hatchlings, which normally rely on light cues from the open horizon to orient after emerging, may migrate inland instead of toward the ocean due to light pollution from beachfront structures.

Flexibility in adopting new environmental cues and rejecting inappropriate ones during the habitat selection process may thus be useful in the decision to move to urbanized environments. Although the use of environmental cues is believed to be partially genetically determined (Seppänen et al. 2010), some animals may learn to use new cues or avoid old ones to decide where to settle. As an example, European flycatchers *Fycedula spp.* are able to acquire a preference for new nest-site cues —an arbitrary sign situated in a nest box (Seppänen et al. 2010). Growing evidence also suggests that animals that are more capable of gathering accurate environmental information often are also the ones that are more flexible in making behavioural decisions (e.g. Marchetti & Drent 2000; Overington et al. 2011; Sol et al. 2012a).

Sampling and settling in new environments may provide important fitness benefits, but it is also often associated with important costs. These costs include time and energy invested in exploration that could be used for reproduction and mortality costs associated with predation, accidents or starvation (Stamps 2001). Given these costs, dispersal individuals face the tradeoff between continuing searching for high quality habitats and settling in an habitat even when its quality is lower. This trade-off is expected to vary with the life history of the species. The costs are expected to be higher for species that concentrate the reproductive effort in a few reproductive events and for which the loss of a reproductive event has important fitness costs (Sol et al. 2012c). Instead, in species with low brood value the costs of delaying or skipping a reproductive event are lower, and hence may have more opportunities to explore new environments.

Due to the high relative cost and time consuming nature of actively sampling habitats, individuals of one species may use information inadvertently produced by the presence or breeding performance of individuals of other species to assess habitat quality whenever the species share needs (Parejo et al. 2008). Thus, through such learning mechanisms, increasing resident densities will result in increased immigrants arrival until the costs of interspecific competition override the benefits of heterospecific attraction (Mönkkönen & Forsman 2002).

Because urban environments are so different from natural environments, it is likely that many species avoid settling in such habitats simply because they perceive that the habitat does not offer them all niche requirements. Anthropogenic noise, for example, may preclude the settlement of males that rely on acoustic communication to attract females (see Establishment section). In some cases, the settlement in urban habitats may be the "best of a bad job". However, the quality of an habitat may be perceived in very different ways by species and even by individuals within species, and it is possible that some species actually prefer urban environments than their ancestral ones. For a few urban specialists, like feral pigeons *Columba livia* or house sparrows *Passer domesticus*, such preference for urbanized environment poses little doubts. For other species, concluding this is more problematic. There are several possible ways to assess whether an organism actually prefers one habitat over another, including observing the settlement process, determining where the dominant individuals have settled, recording site fidelity, assessing population fluctuations over time, and conducting choice experiments (Robertson & Hutto 2006). However, very few studies have directly tested whether some species have learnt to prefer urban habitats over their natural ones.

Establishment stage

The choice to settle in an urbanized environment does not guarantee the establishment of a self-sustaining population, even when individuals are able to survive and reproduce there. The probability of establishment is driven by population dynamics in the context of small populations and novel environments (Leung et al., in press; Sol et al. 2012c).

Concerning the small population dynamics, some species may fail to establish in urbanized environments because they arrive in low numbers and hence the population is highly vulnerable to extinction by demographic stochasticity and Allee effects (see references in Sol et al. 2012c). The importance of these processes is supported by the existence of a correlation between the density of species in urban and surrounding environments (Clergeau et al. 2001; Møller 2009), indicating that urbanized communities are mainly built from immigration of the subset of species that attain higher abundances in the nearby environments. Likewise, in introduced species the probability of establishment increases with the number of released individuals (Lockwood et al. 2005).

Whether and how behavioural flexibility influences small population dynamics remain controversial. Small-brained species tend to have fast-lived strategies (van Schaik & Deaner 2003; Sol 2009; Barton & Capellini 2011), and such a life history strategy has been suggested to confer advantages during invasions by allowing the population to grow faster and hence to reduce the period that it will be threatened by demographic stochasticity (Lewontin & Cohen 1969). Moreover, populations with a rapid population growth may reach higher densities, and hence produce larger propagules. However, these advantage may be in part countered by an increased risk of extinction through population fluctuations resulting from demographic stochasticity (Sol et al. 2012c). Moreover, the fitness cost of losing a breeding attempt tend to high because their short-lives give them little opportunities to reproduce in the future. It follows that under uncertain environments, like when individuals face novel environmental challenges, the probability of reproductive failure (and hence of extinction) may be higher for these species. In species that prioritize future over present reproduction, however, individuals not only are less affected by these costs but they also benefit from the possibility to skip or delay reproduction if conditions are unfavourable. This may increase the opportunities of acquiring environmental information and, through behavioural adjustments, improve performance in exploiting the resources and avoiding the enemies.

Concerning population dynamics in novel environments, the main difficulty for individuals is in dealing with situations to which the species has had no opportunity to adapt. This should generally decrease the mean fitness of the population and hence increase the risk of extinction. There is ample evidence that many species exhibit suboptimal performance in urban habitats, as reflected by their lower productivity and higher mortality compared to natural habitats (Chamberlain et al. 2009). In some cases, it is even possible that the population is not self-sustainable but depends on source-sink dynamics. However, a few species seem to perform equally well or even better in urbanized environments than in their ancestral ones, even when urbanization is extreme. Behaviourally flexibility has been suggested as one of the explanations for the success of these species (Sasvári 1979, 1985).

A animal that is exposed to a novel environment will generally face many novel environmental challenges, and success will depend on whether it can rapidly adjust their behaviour to the new scenario. Animals may devise solutions to many of the problems they face in novel environments by developing new behaviours or adjusting old behaviours to improve performance. Behavioural flexibility can be advantageous in a broad array of contexts, facilitating for instance that animals can track environmental variation, find new food opportunities, use hard-to-extract foods, avoid unfamiliar enemies or change the way they communicate with conspecifics (see TableSI, Supplementary Material).

General evidence that foraging flexibility is important to survive in novel environments is suggested in comparative analyses of human-driven introductions of birds and mammals, which shows that successful invaders are often characterized by large brains (Sol et al. 2005b, 2008). These results are relevant for urbanization because most successful invaders only occur in urbanized environments (Case 1996). However, direct tests of the prediction that urban exploiters should have larger brains are contradictory. Three studies support the prediction (Timmermans 1999; Carrete & Tella 2011; Maklakov et al. 2011). However, nor Kark et al. (2007) nor Evans et al (2011) found evidence that relative brain size influenced species responses to urban environments, although generalist species (measured by niche position rather than breadth) were favored by urban development.

In the next sections, we will briefly describe current evidence suggesting a role of behavioural flexibility in the most important challenges individuals face in urban environments (See Table SI, Supplementary material for a summary of evidences), from the need to adopt novel foods to the difficulties in dealing with habitat fragmentation.

Obtaining food sources

One of the major challenges for animals in urbanized environments is the need to acquire food supplies. Newcomers are likely to be confronted more often with novel foods than familiar ones, so they run the risk of starvation if they are unable to adjust their behaviour to adopt new foraging opportunities (Sol et al. 2011a). Many species inhabiting urban environments have shifted to use foods associated with human activities, including human refuse, artificial feeders and ornamental fruiting shrubs and trees (Tanner et al. 2010). Many birds, for example, are benefited by artificial feeders and food human refuse in hard climatic condition (see Table SI, Supplementary material).

Comparative evidence that foraging flexibility is important in urban environments is suggested in the finding that successful invaders are often characterized by a high propensity for feeding innovations (Sol & Lefebvre 2000; Sol et al. 2002, 2005b). However, only one study in birds has yielded direct evidence that urban dwellers are more innovative than non-urban dwellers (Møller 2009).

Although some of the most elaborate foraging innovations has been observed in urbanized environment (Louis Lefebvre, in prep.), most changes in foraging behavior needed to persist in urbanized environments are unlikely to require high cognitive abilities and large brains (Sol et al. 2011a, 2011b). In many cases, the innovation simply consists in adopting a novel food, which do not require a large brain (Overington et al. 2009). But even for technical innovations, like the development of a new foraging technique, the cognitive demands do not seem to be too high. In common mynas *Sturnus tristis*, for example, the probability of solving a technical innovation task consisting in lifting a lid increased with the number of pecks to the test apparatus, suggesting that the problem was solved by trial and error (Sol et al. 2011a).

The adoption of novel foraging opportunities increases with the explorative tendency of the animal. Exploration may serve to find new patches of either familiar or unfamiliar resources. There are striking differences in exploratory behaviour within and among species (Mettke-hofmann et al. 2005), both in terms of efficiency and time devoted, reflecting that the costs and benefits of exploration vary with the animal's life style. For example, a generalist behaviour or a dependency on hidden or patchily distributed food is expected to increase the value of exploration because it respectively facilitates discovering new resources and obtaining the food and often requires sustained exploration activity (Mettke-Hofmann et al. 2001; Tebbich et al. 2008). Indeed, a number of studies show that individuals from highly urbanized environments tend to be more exploratory than those from less urbanized environments (Table SI, Supplementary Material).

However, the need to explore new resources may entail costs such as exposing the animal to risks (e.g. poisons), which result in an exploration-avoidance conflict, which can be expected to interfere with the acquisition of new resources. Indeed, innovation propensity tend to be correlated with higher exploration scores and lower object neophobia (Bouchard et al. 2007; Sol et al. 2011a; Overington et al. 2011), although there are exceptions (Boogert et al. 2008).

The costs of foraging innovations may be reduced with social behaviours. First, groups may cope more effectively with unfamiliar situations through faster innovations of new solutions by some group members or reduced neophobic responses (Kijne & Kotrschal 2002; Liker & Bókony 2009). Second, groups may enhance foraging innovation by facilitating the transmission of innovations through social learning (Bouchard et al. 2007). Many urban species are social foragers, yet there is little evidence that living in urban environments increases gregariousness. One of the few cases is that of zenaida doves from Barbados, in which individuals that settled in the port area has shifted from aggressive territoriality to feed in large unaggressive groups with conspecifics (Carlier & Lefebvre 1997).

Avoiding new predators

Species that settle in urban habitats are often released from many of their main enemies, including predators and parasites (Shochat et al. 2006a). This may be one of the reasons why some herbivorous inhabiting natural reserves with large predators often approach to camp sites (pers. observ.). Optimal foraging theory predicts that when perceived predation risk is reduced, individuals should spend less time engaged in anti-predator behavior and more time engaged in other fitness-dependent activities, such as foraging (Lima & Dill 1990). This is supported by several studies (Supplementary Material), with only a few exceptions (Watson 2009). For example, lower levels of vigilance behavior has been reported in more urbanized populations of prairie dogs (Angeloni & Magle 2011) and fox squirrels (Mccleery 2009). Changes in the alarm behavior have also been reported in urban populations both regarding signaling performance (Lowry et al. 2012) and signaling reception (Partan et al. 2010).

Although the diversity of predators generally decrease in urban habitats, these habitats may support high densities and/or activity levels of many generalist and opportunistic predators, which may affect juvenile and adult mortality (Rodewald et al. 2011). This may elicit a number of additional behavioural changes. Møller & Ibáñez-Álamo (2012), for example, found that when captured by a human, urban birds wriggled less, showed higher tonic immobility, were less aggressive by biting less often, and emitted fear screams and alarm calls more often than rural birds.

Learning is usually highly efficient to deal with new or unfamiliar predators (Griffin 2003)**.** Seress et al. (2011), for example, found that house sparrows responded more strongly (i.e. had longer post-startle feeding latencies) to sparrowhawk attacks than to the control object, but they responded similarly to a cat and the control object.

Dealing with human-disturbance

Humans themselves are an important source of disturbance for animals. These disturbances may be ecologically important. Burger (1993) found that in areas of limited human activity, shorebirds devoted nearly 70% of their time foraging and

30% of their time avoiding people or predators; however, when the population of people increased, shorebirds foraged less than 40% of their time. Thus, there is a tradeoff in which the frequency of human visitation decreases the frequency of resource use by animals (Fernandez-Juricic & Sallent 2003).

Some animals can behaviourally respond to direct human disturbances by changing spatial activity. Vines (1992) reported that oystercatchers *Haematopus palliatus* shifted their foraging and nesting activities to offshore islands in response to an increase in people on the beaches in Florida. Even a species like house sparrows, which are highly dependent on human-derived food resources, tend to avoid very high human densities (Fernandez-Juricic & Sallent 2003). As alternative, some species may shift their activity diel patterns to avoid humans. Burger and Gochfeld (1991), for example, found that sanderlings not only concentrated their foraging activities in areas with fewer people but also increased time spent foraging nocturnally. Some carnivores, like bobcats and coyotes (Tigas et al. 2002) and black bears (Beckmann & Berger 2003), are also able to change the timing of their activity in response to human presence. Monkeys even adjust their behaviours to the day of the week in accordance to human activities (Duarte et al. 2011).

Perhaps the most common reported response to human disturbances is to exhibit shorter flight initiation distances (FID, hereafter) to approaching humans in more urbanized environments. Within species, this has been reported in a variety of animals, mostly birds and mammals (see Supplementary Material). In Blackbirds *Turdus merula*, for example, individuals from parks with higher pedestrian rates show lower flight distances than individuals from parks with lower pedestrian rates (Rodriguez-Prieto et al. 2009). Although the tameness of animals is thought to have an hormonal basis (Bonier 2012), there is evidence that FID show certain degree of plasticity. Blackbirds, for example, adjusted their antipredator behaviour to the specific level of pedestrian rate encountered every morning and evening in each park, with higher FID in the period with lower pedestrian rate (Rodriguez-Prieto et al. 2009). Habituation seems to be one of the mechanisms that increase tolerance to be close to humans. Young fox squirrels, for example, showed longer FID than adults from the same location, suggesting that they habituate with age (although the possibility that individuals with longer FID suffer higher mortality cannot be completely ruled out). Other species, like magpies, reduce their aggressive response toward individual humans that do not pose a threat to their nests. This is facilitated by the ability of magpies to recognize human individual features (Belguermi et al. 2011), an ability also known in some other urban species like mockingbirds (Levey et al. 2009) and pigeons (Belguermi et al. 2011). In a similar vein, in Blackbirds the rate at which individuals reduced their flight distance from low-visited parks to high-visited parks was greater for pedestrian attacks than for novel potential predator attacks, suggesting a role for habituation (Rodriguez-Prieto et al. 2009).

While some species have learned to recognize, ignore and/or tolerate humans, others do not seem to habituate to increased human disturbance, which leads to dramatic decreases in fitness, as in tigers, shorebirds and marine turtles. However, habituation is a simple learning mechanism that most animals may use. Thus, if some animals are not capable to habituate to certain conditions, this could also be due to other factors besides limited behavioural plasticity.

Avoiding traffic and human-built structures

Sources of mortality such as cars, electric lines, buildings, and windows might make urban areas unsuitable for some species. The most obvious effect is on mortality rates. In Toronto, over 30,000 lethal collisions has been recorded in only 20 buildings, according to the Fatal Light Awareness Program (http://www.flap.org). Reproductive activity can also be altered. For example, grassland birds breeding in airports have high rates of nest failure caused by mowing (Kershner & Bollinger 1996).

Experience (i.e. learning) is critical to reduce these risks. As example, young vultures perching on power lines are often electrocuted, presumably because they are clumsier fliers (Mundy 1983). Through learning, individuals can become familiar with the environment, enabling them to move in a more efficient and safer way (Stamps 1995). In urban habitats, most evidence of such behavioural adjustments relate to shifts in hours of daily activity. For example, red foxes *Vulpes vulpes* cross less streets in the early hours of the night presumably because of the increased traffic (Baker et al. 2007). These changes in behavior may be rapid, probably reflecting plasticity rather than responses to selection. However, it is also possible that the response to traffic reflects the origin of urban individuals because those that behave in a very inappropriate way are more likely to end up dead. In a recently built South American city, Carrete and Tella (2011) found that FIDs to an approaching car were shorter in urban than in rural conspecifics birds. However, the degree of urbanization was not significantly related to species' average rural FIDs but to inter-individual variability in FID. This opens the possibility that urban invaders are not individuals from apparently tame species, but rather tame individuals from behavioural flexibility species with a variable response regarding fear of people (Carrete & Tella 2011).

Communicating in noisy environments

Anthropogenic noise may have negative effects on acoustic communication because it interferences with their acoustic signals, limiting the distance at which individuals may efficiently communicate with each other (Miller et al. 2000; Slabbekoorn & den Boer-Visser 2006; Halfwerk et al. 2011). Some animals, notably birds, whales and insects, use acoustic signals to attract mates, defense territories, recognize species and advertise dangers (Catchpole & Slater 2008). Thus, anthropogenic noise may have important fitness effects for these species (Catchpole & Slater 2008).

As a way to avoid the masking of songs in noisy conditions, birds can change their acoustic signals (see Supplementary Material), for example by using signals with higher frequencies (Slabbekoorn & den Boer-Visser 2006; Halfwerk et al. 2011) and/or longer duration (Miller et al. 2000). Some of these adjustments have been shown to be plastic responses. Using playback experiments, Diaz et al.(2011) showed that serins *Serinus serinus* change song activity as a function of different noise levels between areas and days with more or less noise. Likewise, male reed buntings *Emberiza schoeniclus* adjusted their songs immediately, singing at a higher minimum frequency and at a lower rate when noise levels were high (Gross et al. 2010). These short-term adjustments in singing behavior are indicative of behavioral flexibility rather than long-term adaptation. Although these adjustments are likely to be beneficial, the response seem to be insufficient. In the case of reed-bunting, more males remained unpaired at a noisy location than at a quiet location throughout the breeding season (Gross et al. 2010). Recent studies also show that there are specific-differences in behavioral flexibility in response to increased noise. While some species can maintain their distribution and abundances thanks to modifying their communication, some are not flexible enough (Francis et al. 2011).

Dealing with light pollution

Increased artificial lighting is another anthropogenic factor that may alter activity patterns of animals. One of the most common alteration is dawn singing in birds, which occurs earlier in birds close to artificial lightning (Miller 2006; Kempenaers et al. 2010). Although in many cases light pollution may be detrimental for animals, like in the previous commented cases of mayflies and sea turtles (see Arrival section), sometimes the effects for the specie are positive. In blue tits, singing earlier has been shown to increase reproductive rates and opportunities of extra-pair copulations of males because singing earlier is a sign of male quality (Kempenaers et al. 2010).

Avoiding habitat fragmentation

Habitat fragmentation is a usual outcome of the urbanization process, affecting both the temporal and spatial patterns of habitat use in animals (Tigas et al. 2002). As a response to fragmentation, individuals may expand their home ranges to include several fragments that together provide adequate resources (Redpath 1995). However, the opposite pattern has also been described in several mammals, including racoons, coyotes, Florida key deers, and Eurasian badgers (Supplementary Material). This unexpected pattern may occur because some urban habitats may have increased resource abundances such that individuals may meet their energetic requirements in smaller areas. In Eurasian badgers *Meles meles*, smaller home ranges have been associated to the high productivity of gardens and backyards (Davison et al. 2009).

Increase stage

Once a species has established itself in an urban area, its long term persistence and impact on other species will depend on whether or not the population may increase in numbers. Like establishment, the abundance of a population also result from population dynamics. Unlike establishment, however, which is driven by population dynamics in small populations and novel environments, for abundance the above factors play no essential role and the carrying capacity and ecological interactions become more important (Leung et al., in press).

In urban habitats, some animals may reach extremely high densities. Analyzing multiple populations of the same species across Europe, Møller et al. (Møller et al. 2012) found that population density was on average 30 % higher in urban than in rural habitats, although density reached as much as 100-fold higher in urban habitats in some species. There are at least four demographic processes that can lead to higher densities of animals in cities (Stracey & Robinson 2012): increase offspring production, 2) higher adult survival, 3) higher site faithful, and 4) higher immigration from dispersing individuals. Although urban animals tend to have lower productivity per nesting attempt than their non-urban counterparts (Chamberlain et al. 2009), individuals may compensate for such reduced productivity by beginning breeding earlier than non-urban birds and hence extending their breeding season. The breeding season of urban coastal juncos *Junco hyemalis*, for example, is more than twice as long as that of the ancestral population, and they fledge approximately twice as many young (Yeh & Price 2004).

Individuals may produce more offspring, increase in population density, because of subsidized food resources and/or reduced nest predation (Anderies et al. 2007). Below we analyse each of these issues in the light of behavioural flexibility.

Food availability

Food supplementation and reduced seasonal and yearly variation are the most well-supported mechanism for the population increase of species that may efficiently use these resources (Marzluff 2001; Marzluff et al. 2001). The abundance and stability of food resources may be important in explaining biodiversity patterns in cities. Anderies et al. (2007), using a model, showed that the low frequency resource fluctuations favours strong competitors and low predation skews equilibrium populations in favour of weak competitors.

There is evidence that the high density of some urban animal is consequence of food availability. Haag-Wackernagel (1995), for example, showed experimentally that the overpopulation of pigeons in some urban areas is consequence of the great amount of food deliberately provided by humans. Pigeons exhibit high mortality rates (Sol 2008), mostly due to car accidents and diseases (Sol et al. 2000, 2003), but when there is enough food their efficiency in exploiting food opportunities and capacity of continuous breeding allow them to reach high densities (Sol & Senar 1995; Sol et al. 2000).

Species that are more proficient in using these resources are expected to be the ones showing higher densities (Shochat et al. 2004). Because innovation and learning allows improving behavioral performance, we should expect that better learners may be among the species attaining higher densities. Such population density consequences is suggested in a few studies. In Australian birds, the species that are more likely to adopt new food opportunities are also those that higher population densities (Sol et al. 2012b).

Contest competition between species is likely to play an important role in organizing urban communities (Anderies et al. 2007). The increase of one species (partially thanks to learning to take profit from human-derived resources) can hinder other species' populations through interespecific competition, contributing to community evenness. Pintor et al. (2009), in the context of biological invasions, suggested that an "aggression syndrome" may be an important to successful confront heterospecific contest encounters and attain high densities. In fact, some of the most abundant species in urban environments are also very aggressive against other species (Sol et al. 2012b). For at least one species, there is evidence that urban individuals behave more aggressively than non-urban ones, perhaps reflecting behavioural flexibility: Rural American crows *Corvus bruchyrhynchos*, has been reported to be less aggressive at nest defence than urban individuals (Knight et al. 1987).

However, not all species that reach high densities in urban environments are aggressive and socially dominant. In NSW Australia, foraging opportunism rather than aggression seem to be the primary reason of the success of exotic birds in urban environments (Sol et al. 2012b). Contest competition is facilitated by a larger body size, but body size has not been found to be a property of the most abundant urban exploiters (Sol et al. 2012b). One reason may be that social dominance is facilitated by traits other than body mass, like social behaviour. Alternatively, it may be that other forms of competition besides contest competition are more important in urban environments, including scramble and exploitative competitions. Less often appreciated is the possibility that by allowing individuals to shift to alternative resources, behavioural flexibility helps species coexistence even in presence of contest competition (Carnicer et al. 2008).

Predation

In addition of higher resource abundance, low predator pressure may also facilitate high densities of the most competitive species, which may lead to extinction of native species and prevent the immigration of other species. This bottom-up regulation may explain the low evenness of urban communities .

Human activities can change the nature of predator–prey relationships both by directly manipulating numbers of predators and prey and by providing resource subsidies (Rodewald et al. 2011). Subsidies provided in urban landscapes may decouple predator–prey relationships when generalist predators switch from natural to anthropogenic food sources, and hence reduce their impact on prey species. Despite rising in number in many European cities, Black-billed Magpies *Pica pica* have minimally impacted songbird productivity, even for species known to be sensitive to predation by corvids (Chiron & Julliard 2007).

Behavioural flexibility may reduce the population impact of predators in a number of ways. Møller (2010), for example, showed that in species inhabiting urban environment, those with ability to breed in human made structures shows a significant decrease in nesting failure that translated into a difference in reproductive success due to reductions in nest predation, compared to species breeding outdoors.

SYNTHESIS AND FUTURE PROSPECTS

Our literature review indicates that plastic behavioral adjustments are common in animals living in cities, and hence may have contributed to their success in such environments. However, our review is not exempt of biases (see also Evans et al. 2010). First, most studies involve birds and mammals, which arguably contain some of the most behaviorally flexible species. Second, there is a dominance of research is on northern temperate regions, where the urbanization process is older and more extensive. Finally, most studies focus on the establishment stage. Bearing these limitations in mind, the importance of plasticity seems changes with stage of invasion, with high flexibility more frequently observed for behaviours related to establishment**.** Although this may in part reflect that these behaviours are easier to investigate, the accumulation of evidence also coincides with a stronger theoretical framework. During the establishment stage, behavioural adjustments allow individuals to better exploit novel resources, avoid disturbance by humans and their activities, deal with generalist predators, communicate in noise environments and deal with contamination.

Although there is a recent interest in linking behaviour to the urbanization process, as indicates the fact that most publications have fives years or less, a large fraction of studies are based on comparison of behavioral traits among urbanized and less urbanized populations or species. Interpreting these differences is not always easy because the authors do not generally test whether this is plasticity. Differences can also originate from the source of immigrants, whether because individuals tend to show appropriate behaviors or there is variation and those that have are the ones that settle in urbanized environments. Alternatively, they may result from evolutionary responses. Although most studies did not assess the causes of the differences, some of the reported changes in behavior occurred so fast that they almost certainly represent primarily behavioral plasticity rather than evolutionary change. Indeed, a meta-analysis of more than 3,000 rates of recent phenotypic change suggested that most of the phenotypic changes observed in response to HIREC involve phenotypic plasticity rather than immediate genetic evolution (Hendry et al. 2008).

Studies that investigate the causes and consequences of behavioral flexibility in urban environments are scarce. For example, the mechanisms that make a species select or avoid urban habitats have rarely been investigated. Likewise, few studies has addressed the fitness consequences of adjusting behaviors to urbanized environment. Consequently, in most cases we ignore whether the behavioral response to an environmental has had any population impact and, if so, whether the response has been enough to deal with the challenge.

The integration of evolutionary responses in our framework is also controversial. In the long term, it is expected that populations locally adapt to urban environments, which should affect biodiversity patterns through a variety of mechanisms (e.g. facilitating urban species to attain higher densities, creating distinct genetic varieties or facilitating introgression with wild populations). It seems clear that anthropogenic factors may lead to divergent selection (Partecke et al. 2004; Hendry et al. 2006, 2008; Sol 2008), but how behavioural flexibility may affect these changes are less clear. By facilitating population persistence and allowing high densities, behavioural adjustments may pace the way to evolutionary changes in other phenotypic traits. However, as suggested by Price et al. (2003), high levels of plasticity may reduce the likelihood of genetic change, because the plastic response itself places the population close to a peak. Evolution may also affect the degree of behavioural flexibility. A loss of behavioural flexibility may be a usual outcome for populations that are well adjusted to the their environment (Martin II & Fitzgerald 2005). However, because the urban environment continuously expose individuals to changes, it is possible that populations never become well adapted to urban environments and always require some degree of behavioural flexibility. This is expected particularly in those species that mostly depend on the resources provided by humans, which constantly confront individuals with novel challenges. Growing in such environments may also contribute to maintain behavioural flexibility if, as suggest recent evidence, the exposition to environmental changes early in life enhances cognitive abilities (Kotrschal & Taborsky 2010).

Finally, future work will also have to evaluate whether the response of animals to urbanization is relevant to understand their response to other HIRECs. Some evidence suggests that this should be the case. Concerning climate change, for example, it is expected that the effect of extreme weather events on winter mortality is lower if animals may rely on human-supplemental food. Supporting this hypothesis, fine-scaled studies have found that winter mortality can be reduced in areas where supplemental food is present, and that this effect will be accentuated when natural food is scarce (Zuckerberg et al. 2011). The field of biological invasions may also benefit from a better understanding of how organisms survive and reproduce in urbanized environments. Because many non-indigenous species reach their highest success in human-disturbed habitats, we would expect that tolerance to urbanization is a good predictor to forecast the success of future invasions. To date, however, there is little evidence that urban dwellers are better invaders than non-urban dwellers.

Given that the impact of urbanization on biodiversity loss and alteration is expected to continue increasing in the nearby future, and because there is a renewed interest in the role of behavioral flexibility in the response to HIRECs, we anticipate that all the above issues will represent important avenues of future research.

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Chapter 4#

Winners and losers in an increasingly urbanized planet

with Daniel Sol, Dario Moreira, Joan Maspons. *Unpublished*

ABSTRACT

The urbanization process is considered a major driver of current biodiversity loss, but the causes and hence the consequences are not yet fully understood. The most general explanation is that most species do not tolerate well the environmental alterations associated with the urbanization process. However, a loss of biodiversity is also expected if urban communities are build-up from random dispersal of individuals from the surrounding habitats. Based on an analysis of bird abundances on 22 well-defined gradients of urbanization from four continents, we show here that although urbanization leads to a decrease in species diversity, this decrease cannot simply be explained by random dispersal. Instead, some species appear to be present more often than expected by chance (urban exploiters) and others less often (urban avoiders). Because most species tend to be urban avoiders, habitat filtering appears to be an important process behind the loss of biodiversity in urbanized environments. This is to be expected if most species do not possess the appropriate adaptations to persist in such environments. In support of this, some phylogenetic lineages appear more likely than others to become either urban exploiters or urban avoiders, and we detected an adaptation that could underlie such differences, a low brood value. Thus, our results suggest that the lack of tolerance to urbanization is a major cause of species loss in urban environments; because of such phylogenetic effects, extinctions associated with urbanization are expected to lead to a disproportionally loss of evolutionary history.

INTRODUCTION

The urbanization process involves one of the most pervasive and extreme forms of environmental alteration, posing a major threat to global biodiversity (McKinney 2002, 2006; Shochat et al. 2006; McDonnell & Hahs 2008). Although the impact of urbanization vary with the speed and intensity of the environmental alterations, the most pervasive consequence is a loss of biodiversity (McKinney 2002; Clergeau et al. 2006). Surprisingly, however, the causes underlying such differences remain little understood. Given that currently more than 50% of world human population lives in cities and that this percentage is expected to increase to 70% by 2050 (United Nations 2010) understanding how animals respond to the process of urbanization has become a priority for both conservation biology and human wellbeing.

According to the dominant view, the decline in species richness observed in urban communities would reflect that only a few species have the adaptive traits that confer tolerance to urbanization. When the environmental alteration is rapid and drastic, the limits of tolerance of most species are exceeded and an evolutionary response is unfeasible (Sih et al. 2011). The consequence is that the less tolerant species are lost while the most tolerant replace them, altering the structure and composition of the community (Shochat et al. 2010). Such an habitat filtering predicts a non-random pattern of species assemblage determined by ecological tolerance ('habitat filtering' hypothesis, hereafter). Current evidence that species vary in tolerance to urbanization comes from the identification of certain ecological and life history features characterizing species inhabiting urban environments (Timmermans 1999; Bonier et al. 2007; Møller 2009; Carrete & Tella 2011; Maklakov et al. 2011; see Table S1 in the Suplemmentary Material). However, the observation that traits affect the presence⁄absence of species does not necessarily imply that among the suite of co-occurring species, traits determine which species are abundant and which are rare, which really defines the success of the species in an habitat. It is plausible that a species' presence in a community could be influenced by its traits, while its dominance or rarity could be the result of a series of solely stochastic events (Cornwell & Ackerly 2010; Evans et al. 2011). Perhaps as a consequence of using simplistic measures of tolerance, few of the traits proposed to confer tolerance to urbanization are firmly supported by empirical evidence (see Table S1 in the Suplemmentary Material).

Evidence is not only scarce, but a contrary viewpoint is also possible. According to the random dispersal-assembly theory (Ostling 2005), the main criterion for species coexistence is dispersal to the same habitable region. Through random dispersal processes, some species can be common in urban habitats simply because they are highly abundant in the surrounding habitats, and hence are more likely to generate propagules. If dispersal stage of community assembly were species neutral, interpretations of the causes of community structure in urbanized environments would have to be re-thought to account for the influence of dispersal (Kembel 2009). Because rare species dominate natural communities (Preston 1948), the loss of species diversity in urbanized environments would be still expected even when tolerance is equal for all species. Consequently, the possibility that adaptations are not needed at all to understand the biodiversity alterations associated with urbanization could not be ruled out. Although this is rarely considered in the literature (but see Clergeau et al. 2001, Evans et al. 2011), the concept of neutrality is over three decades old in ecology (Caswell 1976) and has received a renewed interest in recent years (Bell 2001, Hubbell 2001).

Combining new phylogenetic methods with a high-resolution phylogenetic supertree, we contrast the filtering and dispersal-assembly theories with a global comparative analysis of birds. To this purpose, we studied changes in bird abundances along gradients of urbanization in 21 regions of four continents. Unlike most previous studies, we focus on changes in species abundance with increasing urbanization at the local scale rather than at the landscape scale, which reduces the effect of limited dispersal ability of some species and allows to define homogenous habitats and better characterize the pool of potential colonizers. We first asked whether dispersal from surrounding environments was a major factor explaining urban communities and, if so, whether dispersal alone could explain the loss of species diversity. Because this was not the case, we shifted to ask whether the loss of diversity may be better explained by varying tolerance to alterations associated with urbanization. To this end, we ask whether closely-related species tend to show similar tolerance levels and whether variation in these tolerance levels was associated with adaptations suggested to facilitate survival and reproduction of animals in such environments.

METHODS

Data base

We collected data from published studies and our own surveys (Newcastle, Australia and Valdivia, Chile) on bird species abundance from urban to more naturalized habitats from 22 areas from all continents (See details in Fig. 1, Database 1 in Supplementary Material). Although some papers also reported abundances for exotic species, these species were not considered in the present study. Following Marzluff et al. (2001), we operationally defined urbanization as a human-driven process that replaces natural vegetation for buildings and that increases human activity. This definition explicitly excludes parks and gardens, which were consequently ignored in the present study. To define the degree of urbanization, we followed Marzluff et al. (2001) and differentiated urbanized environments in “highly urbanized” environments (urban habitat, hereafter), where buildings are densely packed and parks are small or absent, and “moderately urbanized” environments (suburban habitat, hereafter), which are residential areas with single-family detached houses with backyards. The surrounding habitats considered as potential source of immigrants were rural and wildland environments. Several habitat types were sampled within studies and following the above criteria, we grouped and assigned species data abundance in surrounding, suburban or urban habitats. The studies used in our analyses report either species densities (12 from 23 studies) or number of individuals observed in a defined areas. Because most of them differ in sampled area, to obtain a measure that enables comparison we transformed abundances to densities expressing individuals per hectare (individuals/ha). The taxonomic representation of our base data consists of 842 avian native species from 121 families and 29 orders.

Figure 1. Worldwide location of the urbanization gradients. 1. Barcelona, 2. Brisbane, 3. Bristol, 4. Cameron Highlands, 5. Cayenne, 6. Dunedin, 7. La Palma, 8. La Paz, 9. Madrid, 10. Mar del Plata, 11. Newcastle, 12. Olongapo, 13. Orebro, 14. Oxord, 15. Palo Alto, 16. Phoenix, 17. Pretoria, 18. Rennes, 19. Santiago de Chile, 20. Toronto, 21. Valdivia, and 22. Valencia.

Life history data

We collected information for a set of life history traits from published sources, including scientific journals, field guides and previously compiled datasets (see the Supplementary References S1, in Supplementary Material). The traits were: i. age at first breeding, in months; ii. clutch size, measured as the modal number of eggs per nest; iii. fecundity, computed as clutch size multiplied by the number of broods per year; iv. egg mass, in grams, v. incubation period, in days; vi. fledgling period, as the number of days the young birds stay in the nest from hatching to leaving the nest; vii. lifespan, based on the oldest record of an individual age in years; viii. developmental mode, classified in four stages (altricial, semialtricial, semiprecocial and precocial) following Stark & Ricklefs (1998); and ix. adult survival, as the mean annual survival rate (Liker & Székely 2005). These variables were used to estimate the fast-slow continuum, the intrinsic rate of population growth (R max), the brood value and generation time, as explained below.

Following Bielby et al. (2007), we used a factor analysis to define variation in life history between species along the fast-slow continuum. Sol et al. (2012) found that the fast-slow continuum could be properly described with only four variables: fecundity, age of first breeding, egg size and length of the incubation period; so the factor analysis was based on a correlation matrix of all these variables (N = 316 species).

We estimated the intrinsic rate of population increase (Rmax) by solving Cole's (Cole 1954) equation using a R script published in Sol et al. (2012). The variables included in the equation were fecundity, age at first breeding and lifespan.

We expressed the value of current reproduction relative to the lifetime reproductive output of a species (henceforth, “brood value”) as log10(clutch size/[clutch size*broods per year*maximum lifespan]), following Bókony et al. (2009). Because clutch size appears in both the numerator and the denominator, this cancels to leave brood value equal to the logarithm of 1/total number of breeding attempts. Thus, the brood value can be a low number for a species that has a short lifespan and breeds several times per year, or for a species that has a long lifespan and breeds annually.

We obtained information on the following additional traits: i. body mass, measured in grams; ii. brain mass, in grams; iii. breeding habitat generalism, quantified with Resniche package (De Cáceres et al. 2011); iv. mating system (coded as polygamous vs. monogamous), v. parental care (uniparental, biparental, cooperative); vi. coloniality (solitary, facultative, semi-colonial, colonial); vii. migratory behavior (resident vs. migratory); viii. latitude of the census location; and geographic range (degrees between the limits North and South of the species distribution).

Previous work has shown that it is not brain size per se, but the extent to which the brain is either larger or smaller than that expected for a given body size which indicates adaptation for enhanced neural processing (Reader & Laland 2002; Overington et al. 2009). Two main methods have been proposed to remove the allometric effect of body size on brain size: (i) estimate the residuals of a log–log least-square linear regression of brain mass against body mass, and (ii) include absolute brain mass and body mass (both log-transformed) as covariates in a multivariate model. The two methods yielded qualitatively similar results, and for consistency with previous studies we report in the text the results obtained using the method of residuals.

Data analysis

We obtained a quantitative measure of the tolerance of a species to urbanization as the difference between its density in the urbanized environment (either in highly or moderately urbanized) and the density observed in the source environment (urbanization tolerance index, UTI) (Evans et al. 2011). Two types of UTIs were assessed; UTI_1 is the urbanization tolerance of one species in a highly urbanized area respect the surrounding, and UTI_2 is the urbanization tolerance of one species in a moderately urbanized area respect the surrounding environment. Differences in logarithms express proportional variation, and make the index independent of the abundance of the species. We logarithmically transformed observed and expected values to base 10, previous adding 1 to all values to ensure that indices of species that did not occur in one of the compared habitats could also be transformed.

To assess whether some species were less or more abundant than expected by chance, we used community simulations. For each species, we created 999 random communities of the same size that observed in the urbanized community by randomly drawing (with replacement) individuals from a community in which each species occurred in the same proportion as in the source community. Based on the null distribution of abundances in all the random communities, we identified avoiders, adapters and exploiters. We considered a species as an "avoider" if the observed abundance was equal or lower than the 2.5 percentile of the random abundances, an "exploiter" if this abundance was equal or higher than the 97.5 percentile and a "neutral" if it was observed as expected by chance.

All response variable were modeled with generalized linear mixed models (GLMM, hereafter), using a Bayesian approximation in the R-package 'MCMCglmm' (Hadfield 2009). The phylogeny, species, study location and sampling error were included as random factors. Repeatibility and phylogenetic effects in the UTIs were estimated from their corresponding random errors (Hadfield & Nakagawa 2010). The structure of errors was modified according to the distribution of the response variables (see details in the Results).

RESULTS AND DISCUSSION

In all the regions studied, the avian diversity declines with increased urbanization (Fig. 2a). In our attempt to understand this decrease, we started by validating the dispersal-assembly hypothesis. As predicted by the hypothesis, species density in both moderately and highly urbanized environments co-varies with species density in the surroundings (Table 1), confirming and generalizing previous findings.

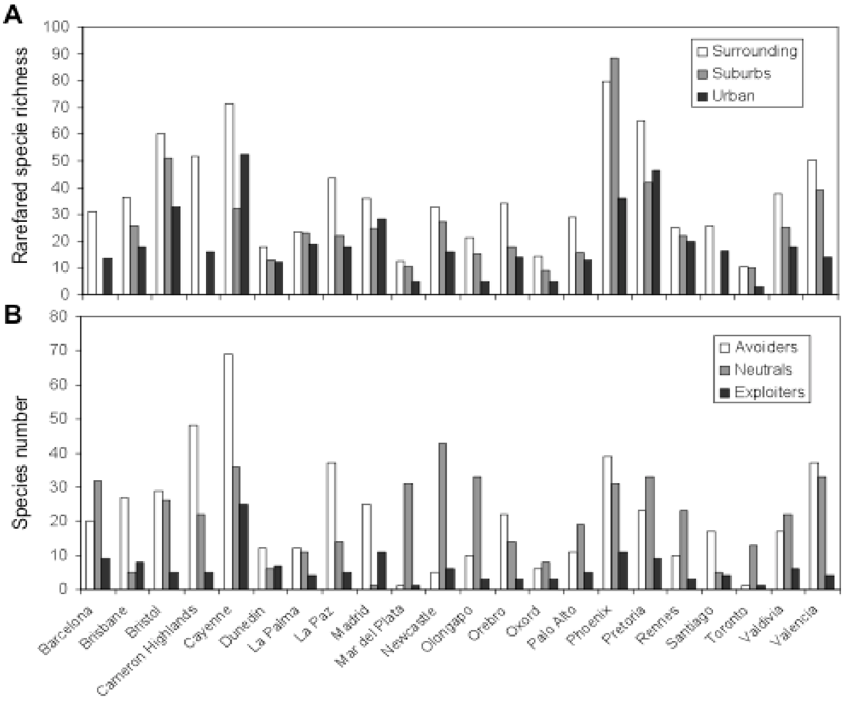

Figure 2. A. Decrease of species richness along the urbanization gradients. The values have been rarefied to take into differences in the number of individuals observed in each habitat. **B.** Number of species classified as avoiders, adapters and exploiters in each study region according to community simulations (see Methods for details).

The importance of immigration from surrounding habitats in building-up urban communities was further confirmed with our simulated communities, which indicate that the abundance of many species is close to what we would expect by random immigration (Fig. 2b). Because in the wildland rare species dominate over abundant ones and because rare species are less likely to disperse by chance, the random dispersal of individuals itself predicts a decrease in species with the increase of urbanization. For example, in Newcastle just by random dispersal there is a 50% chance that 18 species from the surrounding habitats are not present in the urban habitat, implying a 16.5% reduction in species diversity.

Table 1. Relationship between species densities in surrounding and urbanized environments over two hypothetical models, accounting for differences in sampled method between studies.

	UTI_1				UTI_2			
Fixed Terms	**Parameter Estimate (β)**	**Lower CI**	**Upper CI**	**P**	**Parameter Estimate (β)**	**Lower CI**	**Upper CI**	**P**
Log_{10} Surrounding + 0.5	0.47	0.41	0.52	<0.001	0.68	0.62	0.73	<0.001
Plot[1]	0.06	-0.18	0.33	0.620	0.08	-0.18	0.34	0.52
Transect[1]	0.14	-0.13	0.43	0.280	0.11	-0.15	0.44	0.44
Random Terms								
Location variance	0.01	0.00*	0.03	-	0.02	0.00*	0.06	-
Phylogenetic variance	0.27	0.15	0.04	-	0.13	0.02	0.26	-
Species variance	0.01	0.00*	0.04	-	0.10	0.05	0.16	-
Sampling error variance	0.02	0.00*	0.05	-	0.01	0.00*	0.05	-
Residual variation	0.41	0.36	0.45	-	0.33	0.29	0.38	-

Notes: 1000000 iterations with 500000 burn in and thinning interval of 500. $UTI_{1,}$ DIC = 2365.32; $UTI_{2,}$ DIC = 2000,84; all models for 742 species. [1] P values refer to difference to grid map sampling method. * Values < 0.01 and > 0

However, the simulations also reveal the existence of some species that are either less (i.e. urban avoiders) or more (i.e. urban exploiters) abundant than expected by chance (Fig. 2b). Further, the analyses of species occurring in several regions revealed that species are consistent in the way they respond to urbanization, with some being consistently classified as avoiders and others as exploiters (see Table 2). Avoiders tend to be more common than exploiters in all regions, implying that this non-random pattern accounts for part of the variation in biodiversity loss along the urbanization gradients. Thus, random dispersal does not seem to explain all the loss in species richness.

Table 2. Specie consistency in tolerance to different levels of urbanization, accounting for ecological and methodological differences between studies.

	Model	**R**	**Lower CI**	**Upper CI**	**DIC**	**N Species**
Without phylogeny	UTI_1	0.32	0.19	0.43	-623.62	397
	UTI_2	0.43	0.29	0.54	-1184.59	336
With Phylogeny	UTI_1	0.50	0.34	0.62	-417.73	344
	UTI_2	0.70	0.58	0.82	-1003.63	294

Notes**:** 1000000 iterations with 500000 burning and thinning interval of 500.

To further verify the habitat filtering hypothesis, we asked whether tolerance to urbanization exhibits phylogenetic effects. Because closely-related species are expected to share many adaptations due to common ancestors, they should also show similar responses to urbanization. To test this prediction, we quantified the species tolerance to urbanization as the difference in their density (log-transformed) in the urbanized habitat and in the surrounding environment (Urbanization tolerance index, UTI), tackling thus the confounding effect of propagule pressure. Assuming that individuals were free to choose among habitats and that they settle in those where their fitness was higher, a high UTI indicates that the species is an urban exploiter whereas a low UTI that it is an urban avoider. Our results show evidence of phylogenetic heritability (sensu Hadfield & Nakagawa 2010) in all the UTIs, particularly when environmental alterations are more intense (UTI_1: $H^2 = 0.38$, CI= 0.26-0.51; UTI_2: $H^2 = 0.17$, CI = 0.06-0.40). The phylogenetic heritability is even higher when controlling by confounding factors (UTI_1: $H^2 = 0.63$, CI= 0.43-0.75; UTI_2: $H^2 = 0.52$, CI = 0.23-0.73), contradicting a previous study that failed to find similar evidence (Evans et al. 2011).

The finding that shared evolutionary history between species account for an important fraction of species variation in tolerance to urbanization points to the existence of adaptations that make some species more tolerant than others to urbanization. We consequently further examined the habitat filtering hypothesis by testing whether the tolerance to urbanization is associated with adaptive traits supposed to be useful to survive and reproduce in urbanized environments. The random-assembly hypothesis does not predict any trait–abundance connection. There have been proposed a variety of adaptations that may explain variation in tolerance to urbanization (See Table S1, supplementary Material). From all the traits considered (see Methods), our results reveal that urban exploiters can be distinguished from urban avoiders on the basis of their smaller brood value (MCMCglmm, posterior mean= -10.12, 95% CI from -16.472 to -5.099, n= 319) (Figure 3). A low brood value is found in species that prioritize future over current reproduction; the reproductive effort in these species is distributed into many attempts, whether in a same season or in different ones, rather than being allocated into a few reproductive (Bókony et al. 2009). The effect of brood value holds when considering all other traits ($P < 0.001$ in all cases), including those previously shown to enhance tolerance to urbanization such as range size, residual brain size and habitat generalism (Table 3; see Table S1 in Supplementary Information for references). On the contrary, there is no trait that allows distinguishing suburban adapters from suburban avoiders (P > 0.1 in all cases), indicating that the habitat filtering is less important when urban alterations are moderate.

Table 3. MCMCglmm modelling urbanization tolerance (i.e. urban avoiders vs. urban exploiters, n = 305 binary values) as a function of brood value, sampling method, habitat generalism and range size.

		Posterior Mean	**Lower-95% CI**	**Lower-95% CI**	**Effect sampling**	**pMCMC**
Brood value		-12.76	-24.23	-4.65	8.15	<0.001
Sampling method	Grid	0.00				
	Plot	4.61	0.41	9.59	174.09	0.048
	Transect	7.20	2.26	14.26	32.68	0.032
Spring habitat breadth		5.46	-24.20	31.97	41.29	0.684
Breeding range		-0.89	-4.33	1.93	25.53	0.594

As highlighted by Sol et al. (2012), the observation that a strategy based on future reproductive returns facilitates establishment in highly urban habitats is consistent with a variety of theories, including bet-hedging, life history–buffering and cognitive-buffer theories, which conceptualize life histories as evolutionary solutions to environmental uncertainties. For an invader, unfamiliarity and insufficient adaptation to resources, enemies, and other hazards are likely to increase the risk of reproductive failure. Consequently, the inability to spread the risk over several breeding attempts and/or to delay reproduction if conditions are unfavourable may have important costs. By adopting a future-returns strategy, however, individuals not only reduce these costs but also increase the opportunities for acquiring environmental information and, through behavioural adjustments, improve performance on exploiting the resources and avoiding the enemies. Thus, our results adds to a growing literature suggesting that life history influences the way animals respond to environmental alterations.

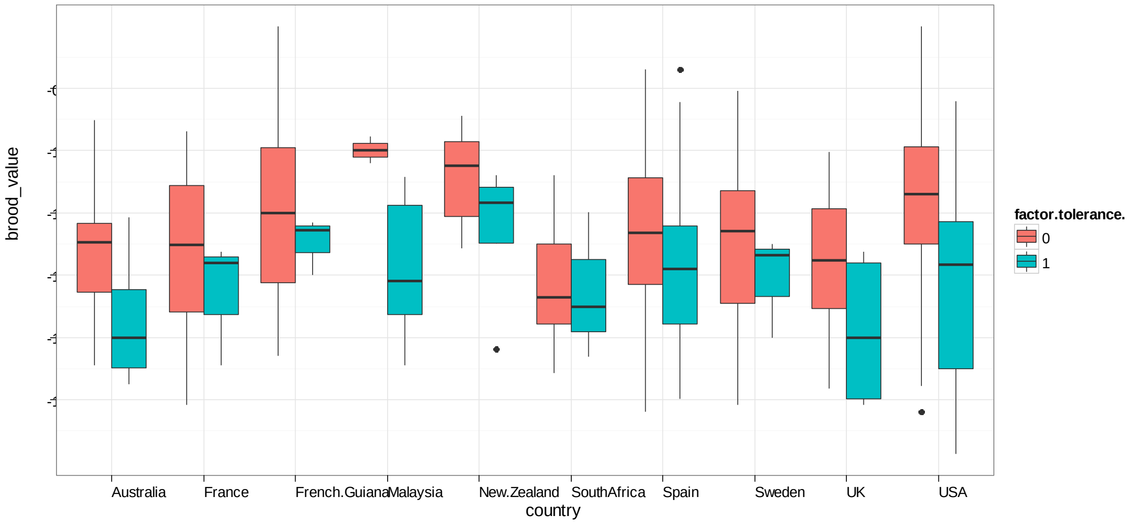

Figure 3. Differences in brood value between urban exploiters and avoiders. In legend, factor.tolerance; 0 = avoiders, 1 = exploiters.

Our results indicate that ecological filters and dispersal both play key roles in determining why some species are common and others rare or absent in highly urbanized environments. Although there is an element of chance in the species present in urban environments, our results show that urban communities are non-random assemblages of species and that this reflects differences in tolerance to the alterations caused by the urbanization process. Indeed, there is evidence that many species exhibit lower fitness in urbanized environments than in more natural environments (Chamberlain et al. 2009) and our findings suggest that these fitness effects may also explain the decline in species diversity observed in these environments. Further, tolerance to urbanization is not only consistent within species but also within higher taxonomic levels. Such a non-random distribution of urbanization tolerance across the tree of life has important implications for conservation because it implies that the urbanization process should lead to a disproportionate loss of evolutionary history (Nee & May 1997). Quantifying the magnitude of this impact will be an important avenue of future research.

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GENERAL CONCLUSIONS

Evolutionary past

I. The evolved relationship between lifespan and brain size across evolutionary time scales provide indirect evidences on how cognitive process helps to the ability of the species to cope with actual environmental challenges.

II. Evolve expensive big brains would provide ecological and evolutionary advantages that are traduced in a longer reproductive lifespan. The findings provide a solid base from which a general theory on brain evolution can be developed, helping the integration of brain evolution within a life history framework and encouraging further research.

Individual differences

III. According to our data of feral pigeons, variability in innovation propensity is promoted by consistent individual differences in motivation (rather just cognitive mechanism).However this was only clear for consumer innovation.

IV. Although there are not evidences for a genetic component on motivation, endocrine mechanism mediated by corticosterone would promote physiological and behavioral adjusts to deal with changing environments.

Urbanization process

V. theoretical and empirical evidences provide support for the pivotal role of behavioural flexibility to cope with challenges in urban environments.

VI. Although behavioural flexibility is influential in all stages of the colonization of urban habitats, it appears to be particularly important during the establishment stage, allow for better exploit novel resources, avoid disturbance by humans or communicate in noisy environments, among other urban challenges

VIII. The importance of immigration from surrounding habitats in building-up urban communities was confirmed. The abundance of many bird species in urban environments is close to what we would expect by random immigration. Because in the wild land, rare species dominate over abundant ones and because rare species are less likely to disperse by chance, the random dispersal of individuals itself predicts a decrease in species with the increase of urbanization.

IX. There is a shared evolutionary history between species that account for an important fraction of species variation in tolerance to urbanization. This point to the existence of adaptations that make some species more tolerant than others to urbanization

X. The strategy based on future reproductive returns (i.e. low brood value) is associated to establishment in highly urban habitats. This strategy can facilitate obtain information in the new environment and adjust behaviour by low costs of delay reproduction (Sol et al., 2012)

XI. A non-random distribution of urbanization tolerance across the tree of life has important consequences for conservation because the urbanization process should lead to a disproportionate loss of evolutionary history (Nee & May, 1997).

Supplementary Material

Supplementary Material
Chapter 3

Table S1. Evidence of changes in behaviour in the three main stages of the colonization of urban habitats. The literature review was based on an initial search for published in the July 2012 edition of the Thomson Reuters "Web of knowledge", using key words like "BEHAVIOR+FITNESS +URBANIZATION" or "BEHAVIORAL CHANGES+SURVIVAL+ URBANIZATION"), and subsequent searches of studies cited in those papers. From a total of 153 papers found, we removed literature reviews and papers that did not provide evidence (either negative, null or positive) for a link between behavioural flexibility and urbanization, which yielded the studies presented here (see Supplementary References S1, for bibliography)

Stage	Ecological challenges	Taxa	Approach	Type of comparison	Finding	Support for a role of BF	References
Arrival							
Reach the habitat							
		Amphibians and reptiles	Lab experiment	Among individuals	The invasive delicate skink (Lampropholis delicata) exhibited a greater tendency to hide than the congeneric non-invasive garden skink (L. guichenoti), which enabled them being unintentionally transported in ships	No	Chapple et al. (2011)
		Birds	Field experiment	Among individuals	In bluebirds (Sialia mexicana), dispersal searching for nest-boxes is biased toward highly aggressive males.	No	Duckworth & Badyaev (2007)
		Birds	Comparative	Between species	Urbanized species have broader environmental tolerance than rural congeners (elevational and latitudinal distributions) suggesting that broad environmental tolerance may predispose some birds to thrive in urban habitats.	Yes	Bonier et al. (2007)
		Birds	Field data	Within species	Previous to establishment, hunting pressure increased for northern goshawk (Accipiter gentilis) in areas surrounding the city	Yes	Rutz (2008)
		Birds	Comparative	Between species	Species with higher intra-specific variation in FID colonized urban areas more efficiently	Yes	Møller (2009)
Obtain environmental information							
		Amphibians and reptiles	Lab experiment	Among individuals	The invasive delicate skink was found to be more exploratory than the congeneric non-invasive garden skink, which enabled it to more effectively locate novel environments and basking site resources	No	Chapple et al. (2011)

	Birds	Lab experiment	Within species	Urban dark-eyed juncos (Junco hiemalis) are more exploratory (in lab conditions)	Yes	Atwell et al. (2012)
Decide whether or not to settle	Birds	Field data	Within species	Previous to establishment, northern goshawk (Accipiter gentilis) were more regularly sighted in the city	Yes	Rutz (2008)
	Birds	Field data	Within species	Previous visits to the city allowed northern goshawks (Accipiter gentilis) to perceive an increased prey availability within the city	Yes	Rutz (2008)
Establishment						
Novel foods						
	Birds	Lab experiment	Among individuals within a species	Urban house sparrows did not differ from rural sparrows in the latency to adopt novel foods	No	Bókony et al. (2012)
	Birds	Lab experiment	Among individuals within a species	Urban common mynas were less neophobic, more exploratory and more likely to innovate and learn a technical foraging task than suburban mynas, but did not differ in the latency to adopt novel foods	Yes	Sol et al. (2011)
	Birds	Observations and field experiments	Among and within species	Urban birds tend to be show lower latencies to respond to a novel food opportunity than suburban and wildland birds	Yes	Sol et al. (2012a)
	Birds	Comparative	Across species	Urban species showed higher innovation propensity than rural species	Yes	Møller, A.P. (2009)
	Birds	Comparative	Across species	Urban species did not differ significantly in relative brain size from rural species, but they tend to be more habitat generalists	No	Evans et al. (2011)
	Birds	Comparative	Across species	Urban exploiters did not differ significantly in relative brain size and propensity in feeding innovation from urban adapters, but they tended to be more social	No	Kark et al. (2007)
	Birds	Comparative	Across species	Relative brain size and feeding innovaton were positively correlated with introduction success in New Zeland, where	No	Kark et al. (2007)

			most species were restricted to urbanized environments		
Birds	Comparative	Across species	Species of passerine birds that breed in at least one city centre have relatively larger brains and are more likely to belong to large-brained families than their counterparts that avoid urban habitats	Yes	Maklakov et al. (2011)
Birds	Field experiment	Among and within species	The proportion of neophobic individuals was higher in urban habitats for both house sparrows and eared doves (Zenaida auriculata) compared to rural conspecifics but not for Shiny cowbirds (Molothrus bonairensis).	Yes	Echeverria & Vassallo (2008)
Birds	Lab experiment	Within species	Groups of urban house sparrows were more successful at solving a foraging task than rural groups	Yes	Liker & Bókony (2009)
Mammal	Observations and predictive distribution models	Within species	Foraging innovation taking profit from human resources allows opossums to live in much colder urban areas than predicted by models.	Yes	Kanda (2005)
Mammal	Observations	Within species	Urban racoons take profit from artifical food resources	Yes	Prange et al. (2004)
Mammal	Observations	Within species	Suburban Black bears (Ursus americanus) use artificial food resources and this allows them to remain less time in the hibernation dens	Yes	Beckman & Berger (2003)
Birds	Observations	Within species	Suburban Florida scrub-jays (Aphelocoma coerulescens) use human-provided food	Yes	Fleischer et al (2003)
Birds	Comparative	Between species	Urbanized species have broader environmental tolerance than rural congeners (elevational and latitudinal distributions) suggesting that broad environmental tolerance may predispose some birds to thrive in urban habitats.	Yes	Bonier et al. (2007)
Mammal	Field data	Within species	Smaller home range sizes for urban badgers are related	Yes	Davison et al.

				with the high productivity of gardens		(2009)
	Mammal	Field data	Between species	Most bat species take profit from artifical lights to hunt insects	Yes	Jung and Kalko (2010)
	Birds	Field data	Observational	Suburban Australian magpies (Gymnorhina tibicens) take profit from human-derived resources in hard climatic conditions	Yes	O'leary & Jones (2002)
	Mammal	Field data		Urban San Joaquin kit foxes (Vulpes macrotis mutica) take profit from human-derived food resources	Yes	Newsome et al. (2010)
	Birds	Field experiment	Within species	Urban starlings take profit from human-provided food	Yes	Mennechez & Clergeau (2006)
	Mammals	Field data and models	Within species	Foraging innovation taking profit from human resources allows opossums to live in much colder urban areas than predicted by models.	Yes	Kanda et al. (2009)
New enemies	Amphibian and Reptiles	Lab experiment	Within species	Snakes from introduced toad-exposed localities showed increased resistance to toad toxin and a decreased preference for toads as prey, but these changes are not attributable to learning but selection.	No	Phillips & Shine (2006)
	Birds	Lab experiment	Among individuals within a species	Urban house sparrows did not differ from rural sparrows in the latency to resume foraging after the presence of a dummy sparrowhawk	No	Bókony et al. (2012)
	Birds	Lab experiment	Among individuals within a species	In urban habitats, adult house sparrows responded more strongly and had longer post-startle feeding latencies to sparrowhawk attacks than young birds; further, older urban birds responded more strongly to the sparrowhawk than the same age groups of rural birds.	Yes	Seress et al. (2011)
	Mammal	Observation	Within species	Urban Florida Key deers (Odocoileus virginianus clavium) formed larger groups than suburban/wildland deers	Yes	Harveson et al. (2007)

	Mammal	Observation	Within species	Urban black-tailed prairie dogs (Synomys ludovicianus) exhibited reduced vigilance behavior	Yes	Magle & Angeloni (2011)
	Mammal	Field experiment	Within species	More urbanized fox squirrels (Sciurus niger) invest less time in vigilance behavior and react less to predator vocalization	Yes	Mccleery (2009)
	Birds	Field data	Within species	Escape behavior has changed in urban habitats in response todifferent predators	Yes	Møller & Ibáñez-Álamo (2012)
	Birds	Field experiment	Among species	Urban Passer domesticus shows reduced risk-sensitivity (compared to the non-urban sparrow Passer hispanoliensis	Yes	Tsurim et al. (2008)
	Birds	Field experiment	Among species	Passer hispanoliensis does not show reduced risk-sensitivity flexibility when foraging from human-derived food resources	No	Tsurim et al. (2008)
	Mammal	Field data	Within species	Urban Eurasian hedgehogs (Erinaceus europaeus) are more active after midnight presumably to avoid contact with humans/dogs.	Yes	Dowding et al. (2010)
	Mammal	Field data	Within species	Urban woodchucks (Marmota monax) did not change vigilance behavior compared to rural conspecifics	No	Lehrer et al. (2012)
	Mammals	Field data	Within species	Urban Eastern grey squirrels (Sciurus carolinensis) shift to rely more on visual antipredator signals in noisy environments	Yes	Partan et al. (2010)
	Birds	Field data	Among and within species	Urban individuals that changed to bred indoors in 11 species had lower predation rates	Yes	Møller (2010)
Human disturbances	Reptiles and Amphibian	Field data	Within species	Lizards in modified habitats spent significantly more time on bare, flat surfaces farther from refuge than lizards in natural habitats and increase sprint speed	Yes	Prosser et al. (2006)
	Birds	Field experiment	Among individuals within a species	Urban crows did not call or fly as experimenter approach to the nest, contrary to rural crows, but when they responded they behaved more agressively	Yes	Knight et al. (1987)

Birds	Observations and field experiments	Among and within species	Urban birds tend to be show lower flight distances to approaching humans than suburban and wildland birds	Yes	Sol et al. (2012b)
Birds	Comparative	Across species	Urban species showed lower flight distances to approaching humans than rural species	Yes	Møller, A.P. (2009)
Birds	Comparative	Across species	Flight initiation distances of birds increased from urban to rural sites, distances being shortest in places where human residents encouraged birds	Yes	Clucas & Marzluff (2012)
Birds	Field experiment	Across and within species	Two chough species showed reduced flight initiation distances and lower corticosterone levels in tourist than in non-tourist sites; the Alpine choughs become more gregarious in picnic areas	Yes	Jimenez et al. (2011)
Birds	Field experiment	Among individuals within a species	Urban song sparrows are bolder toward humans than rural sparrows	Yes	Evans et al. (2010); Scales et al. (2011)
Mammal	Observation	Within species	Urban Florida Key deers (Odocoileus virginianus clavium) had shorter flight initiation distances than suburban/wildland deers	Yes	Harveson et al. (2007)
Mammal	Observation	Within species	Suburban Black bears (Ursus americanus) change diel activity patterns to avoid human disturbances	Yes	Beckman & Berger (2003)
Mammal	Field experiment	Within species	More urbanized fox squirrels (Sciurus niger) react less (lower flight initiation distances) to approaching humans	Yes	Mccleery (2009)
Mammal	Field data	Within species	Suburban coyotes (Canis latrans) do not change their diel activity	No	Atwood et al. (2004)
Mammal	Field data	Within species	Urban red foxes (Vulpes vulpes) modifiy their ranging activity depending on traffic intensity	Yes	Baker et al (2007)

Mammal	Field data	Within species	Stephen's kangaroo rats (Dipodomys stephensi) under noisy conditions do not change communication behavior and perceive traffic-noise as conspecific communication	No	Shier et al (2012)
Birds	Field data	Within species	Urban house finches (Carpodacus mexicanus) increased FID and spent more time in refuges compared to less urbanized	Yes	Valcarcel & Fernández-Juricic (2009)
Birds	Field data	Within species	White-fronted plovers (Charadrius marginatus) breeding in more visited beaches return to incubate faster after human-derived disturbances	Yes	Baudains & Lloyd (2007)
Birds	Field experiments	Within species	Pigeons are able to recognize human individual faces and learn to use this information it to modify their foraging behavior in urban areas	Yes	Belguermi et al. (2011)
Birds	Field data	Within species	Urban dark-eyed juncos (Junco hiemalis) have shorter FID than wild conspecifics	Yes	Atwell et al. (2012)
Mammal	Field data	Within species	Urban Eurasian hedgehogs avoid actively foraging near roads	Yes	Dowding et al. (2010)
Mammal	Field data	Within species	Marmoset (Callithrix penicillata) movements are determined by different human activities across the week	Yes	Duarte et al. (2011)
Birds	Field data	Within species	In spite of depending on human-derived resources, house sparrows' consumption ratesdecreased in areas with very high human abundance	No	Fernandez-Juricic et al. (2003)
Birds	Field data	Between species	6 out of 28 species avoided most visited touristic areas	Yes	Heil et al. (2007)
Mammal	Field data	Within species	Urban woodchucks (Marmota monax) did not change FID compared to rural conspecifics	No	Lehrer et al. (2012)
Birds	Field experiment	Within species	Blackbirds from more visited parks show lower FID	Yes	Rodríguez-Prieto et al. (2009)

	Reptiles and Amphibian	Field data	Within species	The distance to which an observer could approach a lizard before it fled (approach distance) was generally greater in modified habitats, and lizards in modified habitats had significantly faster sprint speeds than lizards in natural habitats	Yes	Prosser et al. (2006)
	Birds	Field experiment	Within species	Wild magpies (Pica pica) can distinguish individual humans that pose a threat to their nests from humans that have not behaved in a threatening way	Yes	Lee et al. (2011)
	Mammal	Field experiment	Within species	Alpine marmots (Marmota marmota) adjust their response depending on different types of human disturbances	Yes	Mainini et al. (1993)
	Mammal	Field experiment	Within species	Olympic marmots (Marmota olympus) have shorter FID although increased wariness while foraging in sites more visited by tourists	Yes	Griffin et al. (2007)
	Mammal	Field data	Within species	Bobcats (Felis rufus) and coyotes (Canis latrans) shifted their diel activity in more urbanized areas	Yes	Tigas et al. (2002)
	Birds	Field data (quasi experiment)	Within species	Sanderlings (Calidris alba) respond to human disturbance by changing their FID only dependeing on number of people in the group	Yes	Thomas et al. (2003)
	Mammal	Field data	Within species	Bobcats and coyoteds more associated with non-natural areas had higher levels of night activity and were more likely to be in developed areas at night than during the day	Yes	Riley et al. (2003)
	Birds	Field experiment	Within species	Northern mockingbird (mimus polyglottos) can distinguish individual humans that pose a threat to their nests from humans that have not behaved in a threatening way	Yes	Leveya et al. (2009)
Pollution (noise, light, chemicals…)	Fish	Lab experiment	Within species	The cichlid fish (Pseudocrenilabrus multicolor victoriae) in turbid waters tend to behave more aggressively against conspecifics to ensure reproductive success	Yes	Gray et al. (2012)
	Reptiles and	Field experiment	Among and within species	Three of the most acoustically active pondedge species (Microhyla butleri, Rana nigrovittata and Kaloula pulchra)	Yes	Sun et al. (2005)

Amphibian			significantly decreased their calling rate as a response of anthropogenic noise. Yet under the identical stimulus regime, Rana taipehensis consistently increased its calling rate		
Birds	Observations	Within species	American robin (Turdus migratorius) start singing earlier in the morning in highly illuminated places	Yes	Miller (2006)
Birds	Observations	Within species	Great tits in urban noisy locations sing at a higher minimum frequency than those from suburban and forest habitats	Yes	Slabbekoorn & Peet (2003); Slabbekoorn & Ripmeester (2008); Slabbekoorn & Boer-Visser (2006)
Mammals	Field experiment	Within species	In male humpbacks, mating songs are longer when exposed to man-made noise (i.e. low frequency active sonar); song duration returned to normal after exposure	Yes	Miller et al. (2000)
Birds	Field data	Among and within species	Urban ash-throated flycatcher (Myiarchus cinerascens) increased singing frequeancy in noisy areas and occupancy did not change	Yes	Francis et al. (2011)
Birds	Field data	Among and within species	Urban grey flycatcher (Empidonax wrightii) did not change singing frequency in a noisy area and its occupancy declined	Not	Francis et al. (2011)
Birds	Field data	Within species	Urban serins (Serinus serinus) change their singing behavior as a funciton of noise levels		Díaz et al. (2011)
Birds	Field data	Within species	Urban European robins (Erithacus rubecula) sing more at night in more noisy areas rather than more liiuminated areas	Yes	Fuller et al. (2007)
Birds	Field experiment	Within species	Great tits (Parus major) used more their higher frequency singing types when experimentally manipulating environmental noise.	Yes	Halfwerk & Slabbekoorn (2009)

	Birds	Field data	Among and within species	Dawn singing occurs earlier in birds close to artificial lightning in 4 out of 5 common species	Yes	Kempenaers et al. (2010)
	Birds	Field data	Within species	Urban Noisy miners (Manorina melanocephala) show a noise level-dependent change in sound signal amplitude to avoid alarm-call masking	Yes	Lowry et al. (2012)
	Birds	Field experiment	Within species	Urban white crowned sparrow (Zonotrichia leucophris) have adjusted their song behavior by increasing pitch frequency	Yes	Luther & Derryberry (2012)
	Mammals	Field data	Within species	Urban Eastern grey squirrels (Sciurus carolinensis) shift to rely more on visual antipredator signals in noisy environments	Yes	Partan et al. (2010)
	Birds	Field data and field experiment	Within species	Urban blackbirds shift aspects of their song behavior in response to antropogenic noise	Yes	Mendes et al. (2011)
	Birds	Field data and field experiment	Within species	Male reed bunting (Emberiza schoeniclus) shift their song to a higher minimum frequency and lower rate in noisy environments	Yes	Gross et al. (2010)
	Birds	Field experiment	Within species	Urban great tits adjust their singing behavior in reponse to noisy environmental conditions	Yes	Halfwerk et al. (2011)
	Birds	Field data	Within species	black-capped chickadees (Poecile atricapillus) use shorter, higher-frequency songs when traffic noise is high, and longer, lower-frequency songs when noise abates	Yes	Proppe et al. (2011)
	Reptiles and Amphibian	Field data	NA	Sea turtle hatchlings rely on light cues from the open horizon to orient and migrate toward the ocean after emerging from the nest at night. However, light pollution from beachfront structures can cue hatchlings to migrate inland instead, where their survival is unlikely	No	Witherington (1997)
Habitat fragmentation	Mammal	Observation	Within species	Urban Florida Key deers (Odocoileus virginianus clavium) had smaller home ranges than suburban/wildland deers	Yes	Harveson et al. (2007)

	Mammal	Observation	Within species	Racoons (Procyon lotor)	Yes	Prange et al. (2004)
	Birds	Observations	Within species	Blackbirds (Turdus merula) in urban noisy locations sing at a higher minimum frequency than those from suburban and forest habitats	Yes	Slabbekoorn & Ripmeester (2008)
	Mammal	Field data	Within species	Suburban coyotes have smaller home ranges than wildland conspecifics	No	Atwood et al. (2004)
	Mammal	Field data	Within species	Urban badgers (Meles meles) had smaller home ranges than previous studies in rural areas	Yes	Huck et al. (2008)
	Mammal	Field data	Within species	Extreme patchiness in urban landscapes may account for the unoccupancy of areas between group ranges	Yes	Davison et al. (2009)
	Mammal	Field data	Within species	Bobcats (Felis rufus) and coyotes (Canis latrans) adjust ther ranging behavior to habitat fragmentation	Yes	Tigas et al. (2002)
Increase						
Find under-utilized food resources						
	Birds	Observations and field experiments	Among and within species	Species that were more opportunistic foragers tended to show higher densities in urban habitats	Yes	Sol et al. (2012)
	Birds	Lab experiment	Within species	Problem-solving (motor innovation) and social learning are positively related and this may facilitate fast expansion of novel behaviors	Yes	Bouchard et al (2007)
Increase efficiency in resource use						
	Reptiles and Amphibian	Lab experiment	Within species	Members from the introduced species Trachemys scripta elegans hide less from predation menace simulations than the native Mauremys leprosa, which contribute to their greater competitive ability in anthropogenically disturbed environments	Yes	Polo-Cavia et al. (2008)
	Birds	Field experiment	Among individuals within a	Urban song sparrows are more aggressive toward conspecifics than rural sparrows	Yes	Scales et al. (2011)

			species			
	Birds	Observations	Within species	Suburban Florida scrub-jays (Aphelocoma coerulescens) have higher foraging efficiency than wild land conspecifics	Yes	Fleischer et al (2003)
	Birds	Lab experiment	Within species	Urban house sparrows show constant feeding motivation irrespective from predation risks	Yes	Tsurim et al. (2010)
	Birds	Field experiments and semi-natural experiments	Within species	Urban house finches (Carpodacus mexicanus) incrased foraging efficiency per time	Yes	Valcarcel & Fernández-Juricic (2009)
Monopolize resources						
	Birds	Observations and field experiments	Among and within species	Species that were more agressive and dominant foragers did not tend to show higher densities in urban habitats	Yes	Sol et al. (2012)
	Birds	Observations	Across species	The increase of black vultures Coragyps atratus, partially thanks to learning to take profit from human-derived resources, hindered other species populations through competition	Yes	Carrete et al. (2010)
	Birds	Field experiment	Among individuals	In bluebirds (Sialia mexicana), highly aggressive males are more likely to displace aggressive mountain bluebirds from nest boxes, allowing to increase their density.	No	Duckworth & Badyaev (2007)
	Birds	Field experiment	Within species	Fast explorers and non-innovative birds had significantly more access to the feeder than slow explorers and solvers. Also, individuals that were poor competitors were good problem solvers	No	Cole & Quinn (2012)
	Birds	Field data	Between species	Common Mynas have little competitive impact on resource use (food, nesting sites) by native bird species in the urban matrix.	No	Lowe et al. (2011)
Improve response to enemies						
Spread						

Birds	Comparative	Across species	Urban exploiters tended to be more sedentary than urban adapters	Yes	Kark et al. (2007)
Birds	Observations	Within species	In great-tailed grackle (Quiscalus mexicanus), a foraging innovation (pecking death insects in cars) has presumably helped in the species spread throughout urban environments	Yes	Grabrucker & Grabrucker (2010)
Birds	Experiment	Within species	House sparrows from the 150-year-old introduced population took significantly longer to approach and consume novel foods than birds from the 28-year-old population	Yes	Martin & Fitzerald (2005)

Supplementary References

List of references used for Table S1.

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Supplementary Material
Chapter 4

Table S1. - Hypothesized characteristics of bird taxa that allow them to inhabit urban environments. Methodological assessment, geography extension, and statistical support are presented.

	Variable	Statistical procedure	Phylogenetic non independence	Urbanization Metric	Geographic extension	R^2	N individual /species or taxa	p - value	References
Wide Geographic Range	Latitudinal and altitudinal total distribution	*t*-test	Within genus analyses	Binary	World wide	-	100*	<0.0001	Bonier 2007
	European grid cell occupied	Multiple regression	PGLS	Urban density	Regional (Britain)	0.23	88	95% confidence set of models	Evans et al. 2011
	European grid cell occupied	Multiple regression	PGLS	Urban/rural density ratio	Regional (Britain)	0.0	88	95% confidence set of models	Evans et al. 2011
	Wider latitudinal range from north to south	Cluster analyses	Non	Binary	Regional (France-Switzerland)	-	110	0.005	Croci et al. 2008
	Total breeding distribution range	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.37^2	39	0.017	Moller 2009
High Population size	Population density	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.49^2	39	0.0013	Moller 2009
	Total breeding pairs in Western Palearctic region	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.66^2	39	<0.0001	Moller 2009

Biogeographic origin	Nearctic	Multivariate ordination analyses	Non	Binary	Regional (Mexico)	-	578	< 0.0001	Gonzalez-Oreja 2011
	Holarctic	Cluster analyses	Non	Binary	Regional (France-Switzerland)	-	110	<0.001	Croci et al. 2008
Omnivorous	Qualitative Category	Cluster analyses	Non	Binary	Regional (France-Switzerland)	-	110	<0.001	Croci et al 2008
	Qualitative Category	Chi Square	Non	Binary	Local (Israel)	-	46	1.0	Kark et al. 2007
	Qualitative Category	Tukey test	Non	Binary	Local (Finland)	-	26	<0.001	Jokimäki and Suhonen 1998
Granivorous	Qualitative Category	Cluster analyses	Non	Binary	Regional (France-Switzerland)	-	110	>0.1 (non value)	Croci et al 2008
	Qualitative category	Chi Square	Non	Binary	Local (Israel)	-	46	0.2	Kark et al. 2007
Diet invertebrates	Breeding use of inverts food	Multiple Regression	PGLS	Urban density	Britain	0.003	88	95% confidence set of models	Evans et al. 2011
	Breeding use of inverts food	Multiple Regression	PGLS	Urban/rural density	Britain	0.0002	88	95% confidence set of models	Evans et al. 2011
	Insects diet	Chi Square	Non	Binary	Local (Israel)	-	46	>0.1 (non value)	Kark et al. 2007

Diet plants	Use of plant material in breeding season	Multiple Regression	PGLS	Urban density	Britain	0.07	88	95% confidence set of models	Evans et al. 2011
	Use of plant material in breeding season	Multiple Regression	PGLS	Urban/rural density ratio	Britain	0.10	88	95% confidence set of models	Evans et al. 2011
Main habitat	Forest	Cluster analyses	Non	Binary	Regional	NA	110	0.002	Croci et al 2008
	Rock faces	Cluster analyses	Non	Binary	Regional	NA	110	<0.001	Croci et al 2008
Low Niche position	Use of resources which are common	Multiple Regression	PGLS	Urban density	Britain	0.18	55	95% confidence set of models	Evans et al. 2011
	Use of resources which are common	Multiple Regression	PGLS	Urban/rural density ratio	Britain	0.14	55	95% confidence set of models	Evans et al. 2011
Morphology	Very Large Wingspan	Cluster analyses	Non	Binary	Regional	NA	110	<0.001	Croci et al 2008
Dimorphism	Plumage	Cluster analyses	Non	Binary	Regional	NA	110	0.01	Croci et al. 2008
	Sexual	Chi Square	Non	Binary	Local (Israel)	NA	46	<1.0	Kark et al. 2007
	Seasonal	Chi Square	Non	Binary	Local (Israel)	-	46	1.0	Kark et al. 2007

Territorial	Qualitative category	Chi Square	Non	Binary	Local (Israel)	-	46	1.0	Kark et al. 2007
Social behavior	Live in groups	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al 2008
	Formed flocks	Chi Square	Non	Binary	Local (Israel)	-	46	0.05	Kark et al. 2007
	Colonial nesting	Chi Square	Non	Binary	Local (Israel)	-	46	0.03	Kark et al. 2007
Nesting location	Ground nesting location	Multiple Regression	PGLS	Urban density	Britain	0.02	88	95% confidence set of models	Evans et al. 2011
	Ground nesting location	Multiple Regression	PGLS	Urban/rural density ratio	Britain	0.07	88	95% confidence set of models	Evans et al. 2011
	High nesting location	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al 2008
	Medium nesting location	Cluster analyses	Non	Binary	Regional	-	110	0.01	Croci et al 2008
Nest protection	Enclosed nest	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al 2008
	Cavity nester	Chi Square	Non	Binary	Local (Israel)	-	46	<1.0	Kark et al. 2007

Dispersal ability	Arithmetic mean of natal dispersal distance	Multiple Regression	PGLS	Urban density	Regional (Britain)	0.04	55	95% confidence set of models	Evans et al. 2011
	Arithmetic mean natal of dispersal distance	Multiple Regression	PGLS	Urban/rural density ration	Regional (Britain)	0.01	55	95% confidence set of models	Evans et al. 2011
	Mainland distance	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.44^2	39	0.003	Moller 2009
	Number of subspecies	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.30^2	39	0.04	Moller 2009
Non Migrant	Resident	Multiple Regression	PGLS	Urban density	Britain	0.05	88	95% confidence set of models	Evans et al. 2011
	Resident	Multiple Regression	PGLS	Urban/rural density ratio	Britain	0.006	88	95% confidence set of models	Evans et al. 2011
	Sedentary Category	Cluster analyses	Non	Binary	Regional	-	110	0.006	Croci et al 2008
	Migratory	Chi Square	Non	Binary	Local (Israel)	-	46	0.2	Kark et al. 2007
	Sedentary Category	Tukey test	Non	Binary	Local (Finland)	-	26	<0.001	Jokimäki and Suhonen 1998
Molts per year	Just one molt per years for adult	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al. 2008

Clutch size	Average number of eggs per clutch	Chi Square	Non	Binary	Local (Israel)	-	46	0.11	Kark et al. 2007
Brood size	Up to 2 clutches	Cluster analyses	Non	Binary	Regional	-	110	0.01	Croci et al 2008
High parental investment	Altricial development	Chi Square	Non	Binary	Local (Israel)	-	46	<1.0	Kark et al. 2007
	Young remain in nets after hatching for longer time	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al 2008
	Both parents build nest	Cluster analyses	Non	Binary	Regional	-	110	0.004	Croci et al 2008
	Both parents build nest	Chi Square	Non	Binary	Local (Israel)	-	46	0.2	Kark et al. 2007
	Incubation period	Chi Square	Non	Binary	Local (Israel)	-	46	0.24	Kark et al. 2007
	Fledging age	Chi Square	Non	Binary	Local (Israel)	-	46	0.96	Kark et al. 2007
High phenotypic plasticity	Intraspecie CV of Flight initiation distance (exp)	GLMM	Taxonomic random factor	Categorical with three levels	Local (a city in Argentina)	-	42	0.049	Carrete and Tella 2011
	Reproductive timing (exp)	ANOVA	NA	Binary	Local	-	60	<0.001	Partecke et al. 2004

Stress coping ability	High antioxidants liver concentration (exp)	Logistic Regression	Standardized Independent linear contrasts	Binary	Western Paleartic	0.05	123	0.016	Møller et al. 2010
	Reduced stress response (exp)	ANOVAs	NA	Binary	Local (city in Germany)	-	43^1	<0.0001	Partecke et al. 2006
Infection coping ability	Bursa of Fabricious mass	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.69^2	39	0.012	Moller 2009
Tameness	Flight initiation distance (exp)	Paired *t*-test	Independent contrast	Binary	Regional (locations in France and Denmark)	0.80^2	44	<0.0001	Moller 2008
	Flight initiation distance	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.95^2	39	<0.0001	Moller 2009
Behavior flexibility	Relative Brain size	Multiple Regression	PGLS	Urban density	Britain	0.0004	55	95% confidence set of models	Evans et al. 2011
	Relative Brain size	Multiple Regression	PGLS	Urban/rural density	Britain	0.0004	55	95% confidence set of models	Evans et al. 2011
	Brain volume	Chi Square	Non	Binary	Local (Israel)	-	46	0.11	Kark et al. 2007
	Problem solving ability (exp)	Linear mixed models	NA	Binary	Local	-	52^1	<0.001	Liker and Bokony 2009

	Innovation rate	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.33[2]	39	0.03	Moller 2009
	Relative Brain size	GLMM	Phylogenetic Bayesian approach	Binary	Regional (Europe)	-	82	Significant (95% IC excluding 0)	Maklakov et al. 2011
Maximum Lifespan	10 years or more	Cluster analyses	Non	Binary	Regional	-	110	<0.001	Croci et al. 2008
Fecundity	Annual fecundity	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.32[2]	39	0.047	Moller 2009
Survival	Adult survival	MANOVA	Paired species comparative approach	Binary	Regional (Western Palearctic)	0.58[2]	39	0.017	Moller 2009

* Genus
[1] Individual
[2] Effect size by Pearson moment correlation
(exp) Experimental work
(non value) Variable is significantly associated to the avoider category

Database S1. Urbanization Tolerance Index (UTI) and categorical classification of tolerance for 842 avian native species from 22 areas from all continents. Repeated species in Brisbane and Valencia are census conducted in the breeding and winter seasons in the same year. More detailed information under request.

Species	Families	Location	Country	Year	Sampling method	Detectability	Effort	UTI1	UTI2	Tolerance
Acanthorhynchus_tenuirostris	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	0.412833962	neutral
Accipiter_cirrocephalus	Accipitridae	Brisbane	Australia	1992	transect	non	35.1	-0.191885526	-0.119937209	avoider
Accipiter_cirrocephalus	Accipitridae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	-0.087150176	neutral
Anas_superciliosa	Anatidae	Brisbane	Australia	1992	transect	non	35.1	-0.460730839	-0.273057707	avoider
Eolophus_roseicapillus	Cacatuidae	Brisbane	Australia	1992	transect	non	35.1	0.152610163	0.539186784	exploiter
Eolophus_roseicapillus	Cacatuidae	Brisbane	Australia	1992	transect	non	35.1	0	0.596745649	exploiter
Chenonetta_jubata	Anatidae	Brisbane	Australia	1992	transect	non	35.1	-0.276206412	-0.204258095	avoider
Chenonetta_jubata	Anatidae	Brisbane	Australia	1992	transect	non	35.1	-0.159700843	-0.159700843	avoider
Colluricincla_harmonica	Colluricinclidae	Brisbane	Australia	1992	transect	non	35.1	-0.159700843	-0.026046874	avoider
Colluricincla_harmonica	Colluricinclidae	Brisbane	Australia	1992	transect	non	35.1	-0.658541347	-0.58659303	avoider
Coracina_novaehollandiae	Campephagidae	Brisbane	Australia	1992	transect	non	35.1	-0.265865579	-0.146241185	avoider
Coracina_novaehollandiae	Campephagidae	Brisbane	Australia	1992	transect	non	35.1	0.34584234	0.422831632	exploiter
Corvus_orru	Corvidae	Brisbane	Australia	1992	transect	non	35.1	-0.541103565	-0.078763392	avoider
Corvus_orru	Corvidae	Brisbane	Australia	1992	transect	non	35.1	-0.636822098	-0.341700962	avoider
Cracticus_nigrogularis	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	-0.039508541	0.201368237	neutral
Cracticus_nigrogularis	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	0.134698574	0.024882861	exploiter
Cracticus_torquatus	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	0.450997677	avoider
Cracticus_torquatus	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	0.297020732	neutral
Dacelo_novaeguineae	Alcedinidae	Brisbane	Australia	1992	transect	non	35.1	-0.196294645	-0.017417652	avoider
Dacelo_novaeguineae	Alcedinidae	Brisbane	Australia	1992	transect	non	35.1	-0.367976785	-0.000671244	neutral
Dicaeum_hirundinaceum	Dicaeidae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	0.046503793	neutral
Dicaeum_hirundinaceum	Dicaeidae	Brisbane	Australia	1992	transect	non	35.1	-0.324511092	-0.324511092	avoider
Dicrurus_bracteatus	Dicruridae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	-0.034175618	avoider
Dicrurus_bracteatus	Dicruridae	Brisbane	Australia	1992	transect	non	35.1	-0.407485327	-0.273831358	avoider
Eudynamys_scolopacea	Cuculidae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	0.300496136	neutral
Eurystomus_orientalis	Coraciidae	Brisbane	Australia	1992	transect	non	35.1	-0.679225946	-0.40026647	avoider
Gerygone_olivacea	Acanthizidae	Brisbane	Australia	1992	transect	non	35.1	-0.443697499	-0.443697499	avoider
Glossopsitta_pusilla	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-0.537119184	0.413631491	avoider
Glossopsitta_pusilla	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-0.636822098	-0.249175785	avoider

Grallina_cyanoleuca	Monarchidae	Brisbane	Australia	1992	transect	non	35.1	1.103540592	0.962588851	exploiter
Grallina_cyanoleuca	Monarchidae	Brisbane	Australia	1992	transect	non	35.1	1.249668628	0.905902421	exploiter
Gymnorhina_tibicen	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	0.34584234	0.48720985	exploiter
Gymnorhina_tibicen	Cracticidae	Brisbane	Australia	1992	transect	non	35.1	0.185636577	0.107576618	exploiter
Hirundo_neoxena	Hirundinidae	Brisbane	Australia	1992	transect	non	35.1	1.591064607	0.387354839	exploiter
Lichenostomus_chrysops	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	-0.034175618	avoider
Lichenostomus_chrysops	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-1.058594715	-0.740305714	avoider
Lichmera_indistincta	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.159700843	0.551612287	neutral
Malurus_melanocephalus	Maluridae	Brisbane	Australia	1992	transect	non	35.1	-0.636822098	-0.636822098	avoider
Malurus_melanocephalus	Maluridae	Brisbane	Australia	1992	transect	non	35.1	-0.884606581	-0.884606581	avoider
Manorina_melanocephala	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.646263654	0.748715092	avoider
Manorina_melanocephala	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-1.002885688	0.488172992	avoider
Melithreptus_albogularis	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.658541347	-0.58659303	avoider
Melithreptus_albogularis	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.920818754	-0.787164785	avoider
Myzomela_sanguinolenta	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.77003336	-0.491073884	avoider
Geophaps_scripta	Columbidae	Brisbane	Australia	1992	transect	non	35.1	0.268845312	0.50630126	exploiter
Geophaps_scripta	Columbidae	Brisbane	Australia	1992	transect	non	35.1	0.255272505	0.728901926	exploiter
Oriolus_sagittatus	Oriolidae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	-0.034175618	avoider
Oriolus_sagittatus	Oriolidae	Brisbane	Australia	1992	transect	non	35.1	-0.276206412	-0.08853328	neutral
Pachycephala_pectoralis	Pachycephalidae	Brisbane	Australia	1992	transect	non	35.1	-0.537119184	-0.537119184	avoider
Pachycephala_rufiventris	Pachycephalidae	Brisbane	Australia	1992	transect	non	35.1	-0.159700843	-0.087752526	avoider
Pachycephala_rufiventris	Pachycephalidae	Brisbane	Australia	1992	transect	non	35.1	-0.858670847	-0.471024535	avoider
Pardalotus_punctatus	Pardalotidae	Brisbane	Australia	1992	transect	non	35.1	-0.22184875	-0.22184875	avoider
Pardalotus_punctatus	Pardalotidae	Brisbane	Australia	1992	transect	non	35.1	-0.324511092	-0.324511092	neutral
Pardalotus_striatus	Pardalotidae	Brisbane	Australia	1992	transect	non	35.1	-0.324511092	-0.324511092	avoider
Pardalotus_striatus	Pardalotidae	Brisbane	Australia	1992	transect	non	35.1	-0.871832293	-0.799883976	avoider
Petroica_rosea	Petroicidae	Brisbane	Australia	1992	transect	non	35.1	-0.324511092	-0.324511092	avoider
Phaps_chalcoptera	Columbidae	Brisbane	Australia	1992	transect	non	35.1	-0.276206412	-0.142552443	avoider
Phaps_chalcoptera	Columbidae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	0.231138825	neutral
Philemon_citreogularis	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.276206412	0.247844519	avoider
Philemon_corniculatus	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.315270435	0.347487397	avoider
Philemon_corniculatus	Meliphagidae	Brisbane	Australia	1992	transect	non	35.1	-0.814501272	0.470386533	avoider
Platycercus_adscitus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	0.159700843	0.304278287	exploiter
Platycercus_adscitus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	0.075720714	0.087759498	exploiter
Rhipidura_fuliginosa	Rhipiduridae	Brisbane	Australia	1992	transect	non	35.1	-0.087150176	-0.087150176	neutral
Rhipidura_fuliginosa	Rhipiduridae	Brisbane	Australia	1992	transect	non	35.1	-1.004798883	-0.65044814	avoider
Rhipidura_leucophrys	Rhipiduridae	Brisbane	Australia	1992	transect	non	35.1	0.477121255	0.132501993	exploiter

Rhipidura_leucophrys	Rhipiduridae	Brisbane	Australia	1992	transect	non	35.1	0.593626824	0.44915272	exploiter
Smicrornis_brevirostris	Acanthizidae	Brisbane	Australia	1992	transect	non	35.1	-0.276206412	-0.276206412	avoider
Smicrornis_brevirostris	Acanthizidae	Brisbane	Australia	1992	transect	non	35.1	-0.56427143	-0.56427143	avoider
Sphecotheres_viridis	Oriolidae	Brisbane	Australia	1992	transect	non	35.1	-0.054357662	0.40356513	neutral
Todirhamphus_macleayii	Alcedinidae	Brisbane	Australia	1992	transect	non	35.1	-0.407485327	-0.273831358	avoider
Todirhamphus_sanctus	Alcedinidae	Brisbane	Australia	1992	transect	non	35.1	-0.753327667	-0.365681355	avoider
Trichoglossus_chlorolepidotus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-0.654672329	0.799104156	avoider
Trichoglossus_chlorolepidotus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-1.236089189	0.389853265	avoider
Trichoglossus_haematodus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-0.469912882	0.546342264	avoider
Trichoglossus_haematodus	Psittacidae	Brisbane	Australia	1992	transect	non	35.1	-1.044307424	0.20047844	avoider
Zosterops_lateralis	Zosteropidae	Brisbane	Australia	1992	transect	non	35.1	0.317420412	0.882639308	exploiter
Zosterops_lateralis	Zosteropidae	Brisbane	Australia	1992	transect	non	35.1	-0.991226076	0.248242501	avoider
Hirundo_rustica	Hirundinidae	Bristol	UK	2005	grids	yes	5900	-0.09017663	-0.04275198	avoider
Sylvia_atricapilla	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.170890065	-0.112898118	avoider
Pica_pica	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.093904503	0.015794267	avoider
Larus_ridibundus	Laridae	Bristol	UK	2005	grids	yes	5900	0	0.008600172	NA
Parus_caeruleus	Paridae	Bristol	UK	2005	grids	yes	5900	-0.013467575	0.02885674	neutral
Corvus_corone	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.095268066	-0.067495488	avoider
Fringilla_coelebs	Fringillidae	Bristol	UK	2005	grids	yes	5900	-0.066160736	-0.019305155	avoider
Parus_ater	Paridae	Bristol	UK	2005	grids	yes	5900	-0.008433168	0.016390416	neutral
Turdus_merula	Turdidae	Bristol	UK	2005	grids	yes	5900	0.15402074	0.164192036	exploiter
Pyrrhula_pyrrhula	Fringillidae	Bristol	UK	2005	grids	yes	5900	-0.127104798	-0.055222791	avoider
Buteo_buteo	Accipitridae	Bristol	UK	2005	grids	yes	5900	-0.025305865	-0.016705694	avoider
Phylloscopus_collybita	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.11270428	-0.059768205	avoider
Fulica_atra	Rallidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Falco_tinnunculus	Falconidae	Bristol	UK	2005	grids	yes	5900	0	0.008600172	NA
Alcedo_atthis	Alcedinidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Carduelis_cannabina	Fringillidae	Bristol	UK	2005	grids	yes	5900	-0.10720997	-0.10720997	avoider
Gallinula_chloropus	Rallidae	Bristol	UK	2005	grids	yes	5900	-0.049218023	-0.023912157	avoider
Corvus_corax	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Tadorna_tadorna	Anatidae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.017033339	neutral
Sturnus_vulgaris	Sturnidae	Bristol	UK	2005	grids	yes	5900	0.520316529	0.246672333	exploiter
Apus_apus	Apodidae	Bristol	UK	2005	grids	yes	5900	0.148939013	0.088941083	exploiter
Sylvia_communis	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.155752684	-0.122960171	avoider
Columba_palumbus	Columbidae	Bristol	UK	2005	grids	yes	5900	-0.102238847	-0.030720494	avoider
Prunella_modularis	Prunellidae	Bristol	UK	2005	grids	yes	5900	-0.026013432	-0.015420359	neutral
Streptopelia_decaocto	Columbidae	Bristol	UK	2005	grids	yes	5900	0.282226432	0.188189381	exploiter

Corvus_monedula	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.391908044	-0.102257594	avoider
Garrulus_glandarius	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.04830468	-0.023481096	avoider
Haematopus_ostralegus	Haematopodidae	Bristol	UK	2005	grids	yes	5900	0	0.008600172	NA
Accipiter_nisus	Accipitridae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.008433168	neutral
Carduelis_carduelis	Fringillidae	Bristol	UK	2005	grids	yes	5900	-0.064940807	-0.04441914	avoider
Carduelis_chloris	Fringillidae	Bristol	UK	2005	grids	yes	5900	0.004644905	0.060900829	neutral
Erithacus_rubecula	Muscicapidae	Bristol	UK	2005	grids	yes	5900	-0.117639498	-0.007424018	avoider
Anas_strepera	Anatidae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.017033339	neutral
Sylvia_borin	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.017033339	neutral
Regulus_regulus	Reguliidae	Bristol	UK	2005	grids	yes	5900	-0.052936075	-0.021901841	avoider
Phalacrocorax_carbo	Phalacrocoracidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	0.008433168	neutral
Dendrocopos_major	Picidae	Bristol	UK	2005	grids	yes	5900	-0.033423755	-0.016390416	avoider
Parus_major	Paridae	Bristol	UK	2005	grids	yes	5900	-0.129633858	-0.033984497	avoider
Picus_viridis	Picidae	Bristol	UK	2005	grids	yes	5900	-0.033423755	-0.016390416	avoider
Ardea_cinerea	Ardeidae	Bristol	UK	2005	grids	yes	5900	-0.033423755	-0.024823584	avoider
Motacilla_cinerea	Motacillidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	0.016705694	neutral
Larus_argentatus	Laridae	Bristol	UK	2005	grids	yes	5900	0.029963223	0.149439064	neutral
Delichon_urbica	Hirundinidae	Bristol	UK	2005	grids	yes	5900	-0.057038501	-0.057038501	avoider
Passer_domesticus	Passeridae	Bristol	UK	2005	grids	yes	5900	0.700985296	0.379368769	exploiter
Larus_fuscus	Laridae	Bristol	UK	2005	grids	yes	5900	0.027152246	0.126686403	neutral
Sylvia_curruca	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	0	neutral
Tachybaptus_ruficollis	Podicipedidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Aegithalos_caudatus	Aegithalidae	Bristol	UK	2005	grids	yes	5900	0	0.039508541	neutral
Anas_platyrhynchos	Anatidae	Bristol	UK	2005	grids	yes	5900	-0.309463163	-0.136219747	avoider
Anthus_pratensis	Motacillidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Turdus_viscivorus	Turdidae	Bristol	UK	2005	grids	yes	5900	-0.025305865	0	avoider
Cygnus_olor	Anatidae	Bristol	UK	2005	grids	yes	5900	0	0.025305865	NA
Vanellus_vanellus	Charadriidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	0	neutral
Motacilla_alba	Motacillidae	Bristol	UK	2005	grids	yes	5900	0.008600172	0.017033339	NA
Emberiza_schoeniclus	Emberizidae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.017033339	neutral
Acrocephalus_scirpaceus	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.041392685	-0.041392685	avoider
Corvus_frugilegus	Corvidae	Bristol	UK	2005	grids	yes	5900	-0.023912157	0.057991947	neutral
Alauda_arvensis	Alaudidae	Bristol	UK	2005	grids	yes	5900	-0.025305865	-0.025305865	avoider
Turdus_philomelos	Turdidae	Bristol	UK	2005	grids	yes	5900	-0.080519597	-0.013572807	avoider
Columba_oenas	Columbidae	Bristol	UK	2005	grids	yes	5900	-0.071882007	-0.071882007	avoider
Saxicola_torquata	Muscicapidae	Bristol	UK	2005	grids	yes	5900	0	0.008600172	NA
Aythya_fuligula	Anatidae	Bristol	UK	2005	grids	yes	5900	-0.017033339	-0.017033339	neutral

Saxicola_rubetra	Muscicapidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	-0.008600172	neutral
Phylloscopus_trochilus	Sylviidae	Bristol	UK	2005	grids	yes	5900	-0.008433168	-0.008433168	neutral
Troglodytes_troglodytes	Troglodytidae	Bristol	UK	2005	grids	yes	5900	-0.210853365	-0.085914629	avoider
Sitta_europaea	Sittidae	Bristol	UK	2005	grids	yes	5900	-0.008600172	0	neutral
Abroscopus_superciliaris	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.076399573	NA	avoider
Acridotheres_tristis	Sturnidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.774550612	NA	exploiter
Aethopyga_saturata	Nectariniidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.542641025	NA	avoider
Alcippe_peracensis	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.805193443	NA	avoider
Arachnothera_longirostra	Nectariniidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.064563591	NA	avoider
Arachnothera_magna	Nectariniidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.410429196	NA	avoider
Arachnothera_robusta	Nectariniidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Blythipicus_rubiginosus	Picidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Brachypteryx_leucophrys	Turdidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.263273074	NA	avoider
Chloropsis_hardwickii	Chloropseidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.110087043	NA	avoider
Cinclidium_leucurum	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.099145679	NA	avoider
Cissa_chinensis	Corvidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.110087043	NA	avoider
Copsychus_saularis	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.458083409	NA	exploiter
Coracina_javensis	Campephagidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.188916995	NA	avoider
Corvus_macrorhynchos	Corvidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.0453014	NA	neutral
Cuculus_saturatus	Cuculidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.05239598	NA	neutral
Cuculus_sparverioides	Cuculidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.099145679	NA	avoider
Culicicapa_ceylonensis	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.064563591	NA	avoider
Cyornis_unicolor	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Dicaeum_ignipectus	Dicaeidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.410823967	NA	avoider
Dicrurus_remifer	Dicruridae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.563562099	NA	avoider
Ducula_badia	Columbidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.306597728	NA	avoider
Enicurus_schistaceus	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.064563591	NA	neutral
Eumyias_thalassina	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Ficedula_hyperythra	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Ficedula_solitaris	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.285475429	NA	avoider
Ficedula_westermanni	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.3201293	NA	avoider
Garrulax_erythrocephalus	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.358364504	NA	avoider
Garrulax_lugubris	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Garrulax_mitratus	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.56170306	NA	avoider
Geopelia_striata	Columbidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Glaucidium_brodiei	Strigidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.110087043	NA	avoider
Harpactes_erythrocephalus	Trogonidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral

Heterophasia_picaoides	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.888283311	NA	avoider
Hemixos_flavala	Pycnonotidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Hypsipetes_mcclellandii	Pycnonotidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.355705624	NA	avoider
Leiothrix_argentauris	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.595616247	NA	avoider
Lonchura_punctulata	Estrildidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Lonchura_striata	Estrildidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.099145679	NA	avoider
Macropygia_ruficeps	Columbidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.313416213	NA	avoider
Megalaima_franklinii	Ramphastidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.263273074	NA	avoider
Megalaima_oorti	Ramphastidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.206575469	NA	avoider
Minla_cyanouroptera	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.313416213	NA	avoider
Minla_strigula	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Napothera_brevicaudata	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.270800683	NA	avoider
Niltava_grandis	Muscicapidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.285475429	NA	avoider
Oriolus_chinensis	Oriolidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.013703439	NA	neutral
Oriolus_cruentus	Oriolidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.179811	NA	avoider
Orthotomus_atrogularis	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.141348488	NA	avoider
Orthotomus_cuculatus	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.707844433	NA	avoider
Orthotomus_sutorius	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.116796956	NA	neutral
Passer_montanus	Passeridae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	1.471687523	NA	exploiter
Pericrocotus_flammeus	Campephagidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Pericrocotus_solaris	Campephagidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.131176001	NA	avoider
Phylloscopus_trivirgatus	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.263273074	NA	avoider
Picus_chlorolophus	Picidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.039877618	NA	neutral
Picus_flavinucha	Picidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.239874231	NA	avoider
Pnoepyga_pusilla	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.141348488	NA	avoider
Pomatorhinus_hypoleucos	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Psarisomus_dalhousiae	Eurylaimidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.026987683	NA	neutral
Psilopogon_pyrolophus	Ramphastidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.382103974	NA	avoider
Pteruthius_flaviscapis	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.231785823	NA	avoider
Pteruthius_melanotis	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.292630949	NA	avoider
Pycnonotus_finlaysoni	Pycnonotidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.110087043	NA	avoider
Pycnonotus_goiavier	Pycnonotidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.294607592	NA	exploiter
Rhipidura_albicollis	Rhipiduridae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.384414465	NA	avoider
Seicercus_castaniceps	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.099145679	NA	avoider
Seicercus_montis	Sylviidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.064563591	NA	avoider
Sitta_azurea	Sittidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.120759517	NA	avoider
Spilornis_cheela	Accipitridae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.039877618	NA	neutral

Stachyris_chrysaea	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.376289649	NA	avoider
Stachyris_nigriceps	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.161656213	NA	avoider
Streptopelia_chinensis	Columbidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	0.180923788	NA	exploiter
Pellorneum_tickelli	Timaliidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.352221188	NA	avoider
Zosterops_everetti	Zosteropidae	Cameron.Highlands	Malaysia	2003	plot	non	69.58	-0.051520103	NA	neutral
Acanthisitta_chloris	Acanthisittidae	Dunedin	New.Zealand	2005	transect	non	90	-0.133538908	-0.133538908	avoider
Anthornis_melanura	Meliphagidae	Dunedin	New.Zealand	2005	transect	non	90	-1.615280361	-0.94910287	avoider
Circus_approximans	Accipitridae	Dunedin	New.Zealand	2005	transect	non	90	-0.054357662	-0.133538908	neutral
Falco_novaeseelandiae	Falconidae	Dunedin	New.Zealand	2005	transect	non	90	-0.017033339	-0.017033339	neutral
Fulica_atra	Rallidae	Dunedin	New.Zealand	2005	transect	non	90	-0.214843848	-0.214843848	avoider
Gerygone_igata	Acanthizidae	Dunedin	New.Zealand	2005	transect	non	90	-1.28082661	-0.890855531	avoider
Todirhamphus_sanctus	Alcedinidae	Dunedin	New.Zealand	2005	transect	non	90	0.00796893	-0.033423755	avoider
Hemiphaga_novaeseelandiae	Columbidae	Dunedin	New.Zealand	2005	transect	non	90	-0.924279286	-0.708679486	avoider
Hirundo_neoxena	Hirundinidae	Dunedin	New.Zealand	2005	transect	non	90	-0.085712113	-0.085712113	exploiter
Larus_dominicanus	Laridae	Dunedin	New.Zealand	2005	transect	non	90	1.021393002	0.523413262	exploiter
Larus_novaehollandiae	Laridae	Dunedin	New.Zealand	2005	transect	non	90	1.315405121	1.038235749	exploiter
Megalurus_punctatus	Megaluridae	Dunedin	New.Zealand	2005	transect	non	90	-0.10720997	-0.10720997	avoider
Mohoua_novaeseelandiae	Acanthizidae	Dunedin	New.Zealand	2005	transect	non	90	-0.619093331	-0.619093331	avoider
Petroica_macrocephala	Petroicidae	Dunedin	New.Zealand	2005	transect	non	90	-0.079181246	-0.079181246	neutral
Phalacrocorax_carbo	Phalacrocoracidae	Dunedin	New.Zealand	2005	transect	non	90	-0.093421685	-0.093421685	neutral
Prosthemadera_novaeseelandiae	Meliphagidae	Dunedin	New.Zealand	2005	transect	non	90	-0.894316063	-0.593286067	avoider
Rhipidura_fuliginosa	Rhipiduridae	Dunedin	New.Zealand	2005	transect	non	90	-1.029383778	-0.853292519	neutral
Tadorna_variegata	Anatidae	Dunedin	New.Zealand	2005	transect	non	90	-0.093421685	0.052706351	avoider
Vanellus_miles	Charadriidae	Dunedin	New.Zealand	2005	transect	non	90	0.045757491	0.346787486	exploiter
Zosterops_lateralis	Zosteropidae	Dunedin	New.Zealand	2005	transect	non	90	-1.270445908	-0.312998259	avoider
Accipiter_bicolor	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Agelaius_icterocephalus	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	0.120282252	-0.277657757	exploiter
Amazilia_fimbriata	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.034063524	0.168194021	exploiter
Amazilia_leucogaster	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.098747651	0.229290265	exploiter
Amazona_amazonica	Psittacidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.058755035	-0.058755035	avoider
Anthracothorax_nigricollis	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.252410587	-0.252410587	avoider
Aramides_axillaris	Rallidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	avoider
Arundinicola_leucocephala	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.159371582	-0.159371582	avoider
Asturina_nitida	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	0.331298953	-0.020883566	exploiter
Bubulcus_ibis	Ardeidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.1880483	-0.1880483	avoider
Buteo_magnirostris	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.118038183	-0.214948196	avoider
Buteogallus_urubitinga	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral

Butorides_striatus	Ardeidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.227798082	-0.227798082	avoider
Cacicus_cela	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	0.337626975	-0.628514758	exploiter
Calidris_minutilla	Scolopacidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.097981023	-0.078110236	exploiter
Camptostoma_obsoletum	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.252410587	-0.252410587	avoider
Capito_niger	Ramphastidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.214948196	-0.214948196	avoider
Certhiaxis_cinnamomea	Furnariidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.260221171	-0.040808825	exploiter
Chaetura_brachyura	Apodidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.014747848	0.365465628	exploiter
Chlorestes_notatus	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.016719677	-0.159371582	neutral
Chlorophanes_spiza	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Chlorostilbon_mellisugus	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.020101523	-0.419231171	exploiter
Chondrohierax_uncinatus	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	neutral
Coereba_flaveola	Coerebidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.095624483	-0.095624483	avoider
Columba_cayennensis	Columbidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.1880483	0.09277831	avoider
Columbina_minuta	Columbidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.262062665	-0.021107567	avoider
Columbina_passerina	Columbidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.283475507	-0.140436828	exploiter
Columbina_talpacoti	Columbidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.389014529	-0.396038313	avoider
Conirostrum_bicolor	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.426682446	0.079120125	exploiter
Coragyps_atratus	Cathartidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.118038183	-0.214948196	avoider
Coryphospingus_cucullatus	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Crotophaga_ani	Cuculidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.302429402	-0.789186746	avoider
Dacnis_cayana	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.443012357	-0.443012357	avoider
Deconychura_longicauda	Dendrocolaptidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.112459711	-0.112459711	avoider
Dendroica_petechia	Parulidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.182379758	-0.437188025	avoider
Donacobius_atricapillus	Donacobiidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.076026447	-0.020883566	exploiter
Egretta_thula	Ardeidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Elaenia_cristata	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.26117494	-0.358084953	avoider
Elaenia_flavogaster	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.208922669	-0.546265824	avoider
Elaenia_parvirostris	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.14275307	-0.318844329	avoider
Emberizoides_herbicola	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.286896512	-0.286896512	avoider
Empidonomus_varius	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Euphonia_violacea	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Falco_deiroleucus	Falconidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Falco_peregrinus	Falconidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.260221171	0.240017784	exploiter
Fluvicola_pica	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.367592963	0.229290265	exploiter
Formicivora_grisea	Thamnophilidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.227798082	-0.227798082	avoider
Forpus_passerinus	Psittacidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.029934697	-0.97194275	neutral
Galbula_galbula	Galbulidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	avoider

Geothlypis_aequinoctialis	Parulidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.095624483	-0.095624483	avoider
Glaucis_hirsuta	Trochilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.081484181	-0.094607078	exploiter
Harpagus_bidentatus	Accipitridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Hirundo_rustica	Hirundinidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Hylophilus_ochraceiceps	Vireonidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Hylophilus_pectoralis	Vireonidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.014133483	-0.286896512	neutral
Icterus_cayanensis	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.376451093	-0.376451093	avoider
Icterus_nigrogularis	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	0.205405512	0.067102814	exploiter
Jacana_jacana	Jacanidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.144290398	-0.144290398	avoider
Legatus_leucophaius	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.286896512	-0.286896512	avoider
Leistes_militaris	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.214948196	-0.214948196	avoider
Leptotila_verreauxi	Columbidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.240278667	-0.240278667	avoider
Lophotriccus_galeatus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Manacus_manacus	Pipridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	avoider
Megarynchus_pitangua	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Micrastur_gilvicollis	Falconidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.078110236	-0.078110236	avoider
Mimus_gilvus	Mimidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.557450726	0.081905859	exploiter
Molothrus_bonariensis	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.031458214	-0.633518206	neutral
Myiarchus_ferox	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	avoider
Myiarchus_tyrannulus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.112459711	-0.112459711	avoider
Myiophobus_fasciatus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	avoider
Myiozetetes_cayanensis	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.095402481	-0.42209079	exploiter
Ochthornis_littoralis	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Ornithion_inerme	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.173946591	-0.173946591	avoider
Oryzoborus_angolensis	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Pachyramphus_rufus	Cotingidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.202229224	-0.040808825	exploiter
Panyptila_cayennensis	Apodidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.097981023	-0.078110236	exploiter
Phaeomyias_murina	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.057467482	-0.47149431	neutral
Phaeoprogne_tapera	Hirundinidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Piaya_minuta	Cuculidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Piculus_rubiginosus	Picidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	neutral
Picumnus_exilis	Picidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.112459711	-0.112459711	avoider
Pipra_aureola	Pipridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.240278667	-0.240278667	avoider
Pitangus_sulphuratus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.012777452	0.062717596	neutral
Pluvialis_squatarola	Charadriidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.078110236	-0.078110236	avoider
Polioptila_plumbea	Polioptilidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.112459711	-0.112459711	avoider
Progne_chalybea	Hirundinidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.217237985	0.155090078	exploiter

Quiscalus_lugubris	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	1.075775886	1.275479388	exploiter
Ramphocelus_carbo	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.366894566	-1.004037768	avoider
Riparia_riparia	Hirundinidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.078110236	-0.078110236	neutral
Sakesphorus_canadensis	Thamnophilidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.063631548	-0.112459711	exploiter
Scaphidura_oryzivora	Icteridae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.297809008	-0.297809008	avoider
Sirystes_sibilator	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Spiza_americana	Cardinalidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.159371582	-0.159371582	avoider
Sporophila_americana	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.463566235	-0.706604284	avoider
Sporophila_castaneiventris	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.141818702	-0.84439283	avoider
Sporophila_lineola	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.551642259	-0.551642259	avoider
Sporophila_minuta	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.149628588	-0.450658584	neutral
Synallaxis_albescens	Furnariidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.214948196	-0.214948196	avoider
Tachornis_squamata	Apodidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.056101188	-0.040808825	neutral
Tachycineta_albiventer	Hirundinidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.063544646	0.008216183	exploiter
Tachyphonus_luctuosus	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.173946591	-0.173946591	avoider
Tachyphonus_rufus	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.323101318	-1.101252568	avoider
Tangara_cayana	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.275702736	-0.275702736	avoider
Tangara_mexicana	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.278190241	-0.676130249	avoider
Thamnophilus_amazonicus	Thamnophilidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Thamnophilus_doliatus	Thamnophilidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.57417387	-0.594377256	avoider
Thraupis_episcopus	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.019395009	-0.235409259	neutral
Thraupis_palmarum	Thraupidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.137337037	-0.352196838	avoider
Thryothorus_leucotis	Troglodytidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Tityra_cayana	Cotingidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.095624483	-0.095624483	avoider
Todirostrum_cinereum	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.143368654	-0.240278667	avoider
Todirostrum_maculatum	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.095624483	-0.095624483	avoider
Todirostrum_pictum	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Tolmomyias_sp	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	0.193159837	-0.435229093	exploiter
Actitis_macularia	Scolopacidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.144290398	-0.144290398	avoider
Tringa_solitaria	Scolopacidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.118038183	-0.214948196	avoider
Troglodytes_aedon	Troglodytidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.004294988	-0.336179678	neutral
Turdus_leucomelas	Turdidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.264833325	-0.381946725	avoider
Turdus_nudigenis	Turdidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.565475593	-0.662385606	avoider
Tyrannulus_elatus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.173946591	-0.173946591	avoider
Tyrannus_dominicensis	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.322422998	-0.342626384	avoider
Tyrannus_melancholicus	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.115046904	-0.358084953	avoider
Tyrannus_savana	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.1880483	-0.1880483	avoider

Veniliornis_cassini	Picidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.059859883	-0.059859883	avoider
Veniliornis_passerinus	Picidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.133413044	-0.376451093	avoider
Vireo_olivaceus	Vireonidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	avoider
Volatinia_jacarina	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.343689642	-0.849969125	avoider
Xenops_milleri	Furnariidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.020883566	-0.020883566	neutral
Zimmerius_gracilipes	Tyrannidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.040808825	-0.040808825	neutral
Zonotrichia_capensis	Emberizidae	Cayenne	French.Guiana	1995	plot	non	57.6	-0.112459711	-0.112459711	avoider
Accipiter_nisus	Accipitridae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.005312537	0.006921919	neutral
Anthus_berthelotii	Motacillidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.120844755	-0.074476012	avoider
Apus_unicolor	Apodidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.124076572	0.201558033	neutral
Burhinus_oedicnemus	Burhinidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.001067719	0.00509259	neutral
Buteo_buteo	Accipitridae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.006482267	0.011491104	neutral
Carduelis_cannabina	Fringillidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.010112275	0.160356877	neutral
Columba_bollii	Columbidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.067213966	-0.067213966	avoider
Columba_junoniae	Columbidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.096428682	-0.084194225	avoider
Corvus_corax	Corvidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.018828477	-0.006594021	avoider
Coturnix_coturnix	Phasianidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.001067719	0.00509259	neutral
Erithacus_rubecula	Muscicapidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.169128435	-0.122759692	avoider
Falco_pelegrinoides	Falconidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.001067719	-0.001067719	neutral
Falco_tinnunculus	Falconidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.01196728	0.001501847	neutral
Fringilla_coelebs	Fringillidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.219235134	-0.195754038	avoider
Motacilla_cinerea	Motacillidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.143476794	0.019969012	exploiter
Parus_caeruleus	Paridae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.126696648	-0.104702354	avoider
Phylloscopus_canariensis	Sylviidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.047522519	0.024263256	avoider
Pyrrhocorax_pyrrhocorax	Corvidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.080194654	-0.099938712	avoider
Regulus_regulus	Reguliidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.281710297	-0.275636149	avoider
Scolopax_rusticola	Scolopacidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.005312537	-0.005312537	neutral
Serinus_canaria	Fringillidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.273020924	0.458657501	exploiter
Streptopelia_decaocto	Columbidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.354900707	0.064463785	exploiter
Streptopelia_turtur	Columbidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.007059226	0.056277248	neutral
Sylvia_atricapilla	Sylviidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.341596018	0.333943054	exploiter
Sylvia_conspicillata	Sylviidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.037534403	-0.037534403	avoider
Sylvia_melanocephala	Sylviidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	-0.098634853	0.004027489	avoider
Turdus_merula	Turdidae	La.Palma.Island	Spain	2007	transect	yes	1092.5	0.034641486	0.243901108	neutral
Zonotrichia_capensis	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	0.157816165	0.156704014	exploiter
Carduelis_atrata	Fringillidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.138312737	-0.287328718	exploiter
Turdus_chiguanco	Turdidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.006924369	0.284422595	exploiter

Zenaida_auriculata	Columbidae	La.Paz	Bolivia	2005	plot	non	81.12	0.247784484	0.565390907	exploiter
Sicalis_olivascens	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.668927436	0.031176497	avoider
Phrygilus_punensis	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.195736616	-0.154410741	neutral
Metriopelia_ceciliae	Columbidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.254572594	-0.154457442	neutral
Colibri_coruscans	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.402738892	0.020203386	avoider
Catamenia_analis	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.447551236	-0.136582718	avoider
Asthenes_dorbignyi	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.582754836	-0.582754836	avoider
Troglodytes_aedon	Troglodytidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.221750648	-0.128996595	neutral
Carduelis_xanthogastra	Fringillidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.002445358	-0.17293274	exploiter
Phytotoma_rutila	Cotingidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.342693635	-0.206473888	avoider
Saltator_aurantiirostris	Cardinalidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.319513401	-0.018483406	avoider
Diglossa_carbonaria	Thraupidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.244313927	-0.159246702	avoider
Ochthoeca_oenanthoides	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.362548034	-0.362548034	avoider
Phrygilus_fruticeti	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.352182518	-0.352182518	avoider
Patagioenas_maculosa	Columbidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.231869108	-0.04989187	avoider
Poospiza_hypochondria	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.245727187	-0.245727187	avoider
Sappho_sparganura	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.27174062	-0.20479383	avoider
Psilopsiagon_aymara	Psittacidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.308053779	-0.308053779	avoider
Mimus_dorsalis	Mimidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.284185439	-0.284185439	avoider
Colaptes_rupicola	Picidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.205855675	-0.120788451	avoider
Phrygilus_plebejus	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.296283561	-0.296283561	avoider
Patagona_gigas	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.203529507	-0.027438248	avoider
Pygochelidon_cyanoleuca	Hirundinidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	0.235434045	avoider
Cinclodes_fuscus	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.245727187	-0.245727187	avoider
Thraupis_bonariensis	Thraupidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.163657995	-0.203529507	avoider
Ochetorhynchus_ruficaudus	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.188500517	-0.188500517	avoider
Muscisaxicola_cinerea	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.188500517	-0.188500517	avoider
Amazilia_chionogaster	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.046183657	-0.122572003	neutral
Anairetes_parulus	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.140015894	-0.073069104	avoider
Ochthoeca_leucophrys	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.156786104	-0.156786104	avoider
Turdus_fuscater	Turdidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	0.059342786	avoider
Muscisaxicola_rufivertex	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.140015894	-0.140015894	avoider
Aeronautes_andecolus	Apodidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.104398034	-0.104398034	avoider
Conirostrum_cinereum	Thraupidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Asthenes_modesta	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Upucerthia_andaecola	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.085430195	-0.085430195	avoider
Carduelis_uropygialis	Fringillidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	0.153107352	neutral

Leptasthenura_fuliginiceps	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Leptasthenura_aegithaloides	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Muscisaxicola_alpina	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Gnorimopsar_chopi	Icteridae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Phrygilus_unicolor	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.06559595	-0.06559595	avoider
Geositta_punensis	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.044812344	-0.044812344	avoider
Poospiza_boliviana	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.044812344	-0.044812344	avoider
Oreotrochilus_estella	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Lesbia_nuna	Trochilidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Geositta_rufipennis	Furnariidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Muscisaxicola_maculirostris	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Knipolegus_aterrimus	Tyrannidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Orochelidon_murina	Hirundinidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Diglossa_brunneiventris	Thraupidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Sicalis_flaveola	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Catamenia_inornata	Emberizidae	La.Paz	Bolivia	2005	plot	non	81.12	-0.022983907	-0.022983907	neutral
Aegithalos_caudatus	Aegithalidae	Madrid	Spain	2003	plot	non	253.6	-0.113149838	-0.163006379	avoider
Anthus_trivialis	Motacillidae	Madrid	Spain	2003	plot	non	253.6	-0.042034184	-0.042034184	avoider
Apus_apus	Apodidae	Madrid	Spain	2003	plot	non	253.6	0.119722378	0.289257626	exploiter
Carduelis_cannabina	Fringillidae	Madrid	Spain	2003	plot	non	253.6	-0.073843104	-0.087631388	avoider
Carduelis_chloris	Fringillidae	Madrid	Spain	2003	plot	non	253.6	0.368094496	0.398725352	exploiter
Certhia_brachydactyla	Certhiidae	Madrid	Spain	2003	plot	non	253.6	-0.309391339	-0.177337214	avoider
Cettia_cetti	Sylviidae	Madrid	Spain	2003	plot	non	253.6	-0.03394653	-0.00696304	avoider
Ciconia_ciconia	Ciconiidae	Madrid	Spain	2003	plot	non	253.6	0.004423217	-0.015050694	neutral
Columba_palumbus	Columbidae	Madrid	Spain	2003	plot	non	253.6	-0.064979242	-0.042687799	avoider
Corvus_corone	Corvidae	Madrid	Spain	2003	plot	non	253.6	-0.072957882	-0.072957882	avoider
Corvus_monedula	Corvidae	Madrid	Spain	2003	plot	non	253.6	-0.075068862	-0.108751976	avoider
Cuculus_canorus	Cuculidae	Madrid	Spain	2003	plot	non	253.6	-0.10837122	-0.052504541	avoider
Cyanopica_cyanus	Corvidae	Madrid	Spain	2003	plot	non	253.6	-0.149194796	-0.195652198	avoider
Delichon_urbica	Hirundinidae	Madrid	Spain	2003	plot	non	253.6	0.708072218	0.53532943	exploiter
Dendrocopos_major	Picidae	Madrid	Spain	2003	plot	non	253.6	-0.050822353	-0.057771213	avoider
Emberiza_cirlus	Emberizidae	Madrid	Spain	2003	plot	non	253.6	-0.049973975	-0.049973975	avoider
Erithacus_rubecula	Muscicapidae	Madrid	Spain	2003	plot	non	253.6	-0.360900286	-0.117230201	avoider
Ficedula_hypoleuca	Muscicapidae	Madrid	Spain	2003	plot	non	253.6	-0.049973975	-0.049973975	avoider
Fringilla_coelebs	Fringillidae	Madrid	Spain	2003	plot	non	253.6	-0.564740311	-0.386276112	avoider
Garrulus_glandarius	Corvidae	Madrid	Spain	2003	plot	non	253.6	-0.172545978	-0.172545978	avoider
Hippolais_polyglotta	Sylviidae	Madrid	Spain	2003	plot	non	253.6	-0.046673491	-0.080356604	avoider

Hirundo_rustica	Hirundinidae	Madrid	Spain	2003	plot	non	253.6	0.239521475	0.162482546	exploiter
Loxia_curvirostra	Fringillidae	Madrid	Spain	2003	plot	non	253.6	0.090387929	0.502155746	exploiter
Lullula_arborea	Alaudidae	Madrid	Spain	2003	plot	non	253.6	-0.148140992	-0.121157502	avoider
Luscinia_megarhynchos	Muscicapidae	Madrid	Spain	2003	plot	non	253.6	-0.161124427	-0.115404901	avoider
Merops_apiaster	Meropidae	Madrid	Spain	2003	plot	non	253.6	0.194504891	-0.008738614	exploiter
Miliaria_calandra	Emberizidae	Madrid	Spain	2003	plot	non	253.6	-0.12845531	-0.13540417	avoider
Motacilla_alba	Motacillidae	Madrid	Spain	2003	plot	non	253.6	0.073997513	-0.0257054	exploiter
Oriolus_oriolus	Oriolidae	Madrid	Spain	2003	plot	non	253.6	-0.131981401	-0.126050733	avoider
Parus_ater	Paridae	Madrid	Spain	2003	plot	non	253.6	-0.00246118	0.008850324	avoider
Parus_caeruleus	Paridae	Madrid	Spain	2003	plot	non	253.6	-0.333253349	-0.236135518	avoider
Passer_domesticus	Passeridae	Madrid	Spain	2003	plot	non	253.6	0.781946852	0.869883593	exploiter
Pica_pica	Corvidae	Madrid	Spain	2003	plot	non	253.6	0.070819231	0.280538739	avoider
Serinus_serinus	Fringillidae	Madrid	Spain	2003	plot	non	253.6	0.294320066	0.450067684	exploiter
Streptopelia_decaocto	Columbidae	Madrid	Spain	2003	plot	non	253.6	0.207469868	0.283858214	exploiter
Sturnus_unicolor	Sturnidae	Madrid	Spain	2003	plot	non	253.6	0.295537856	0.432987381	exploiter
Turdus_merula	Turdidae	Madrid	Spain	2003	plot	non	253.6	0.102765034	0.243796215	avoider
Carduelis_magellanica	Fringillidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.330993219	-0.234083206	neutral
Chlorostilbon_aureoventris	Trochilidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.330993219	-0.190617512	neutral
Colaptes_melanochloros	Picidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.196294645	neutral
Columba_picazuro	Columbidae	Mar.del.Plata	Argentina	2002	transect	non	19	-1.150537155	-0.247447168	avoider
Elaenia_parvirostris	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	0.104735351	neutral
Furnarius_rufus	Furnariidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.788370416	-0.068211112	neutral
Gubernatrix_cristata	Emberizidae	Mar.del.Plata	Argentina	2002	transect	non	19	0	0.096910013	NA
Guira_guira	Cuculidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.196294645	neutral
Leucochloris_albicollis	Trochilidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.516629796	-0.273591747	neutral
Milvago_chimango	Falconidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.586265724	-0.586265724	neutral
Mimus_saturninus	Mimidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	0.155887873	neutral
Molothrus_badius	Icteridae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.745966567	-0.569875308	neutral
Molothrus_bonariensis	Icteridae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.433655561	0.043465694	neutral
Myiopsitta_monachus	Psittacidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.196294645	neutral
Parula_pitiayumi	Parulidae	Mar.del.Plata	Argentina	2002	transect	non	19	0	0.096910013	NA
Pitangus_sulphuratus	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.745966567	-0.201898523	neutral
Progne_chalybea	Hirundinidae	Mar.del.Plata	Argentina	2002	transect	non	19	0.185636577	0	NA
Pyrocephalus_rubinus	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	0	0.096910013	NA
Serpophaga_subcristata	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.020203386	neutral
Sicalis_flaveola	Emberizidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.196294645	neutral
Tachycineta_leucorrhoa	Hirundinidae	Mar.del.Plata	Argentina	2002	transect	non	19	0	0.352182518	NA

Thraupis_bonariensis	Thraupidae	Mar.del.Plata	Argentina	2002	transect	non	19	0	0.096910013	NA
Troglodytes_aedon	Troglodytidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.513333427	-0.124938737	neutral
Turdus_rufiventris	Turdidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.792602308	-0.383381289	neutral
Tyrannus_melancholicus	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	0.155887873	neutral
Tyrannus_savana	Tyrannidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.196294645	-0.099384632	neutral
Zenaida_auriculata	Columbidae	Mar.del.Plata	Argentina	2002	transect	non	19	0.055665779	0.509305938	exploiter
Zonotrichia_capensis	Emberizidae	Mar.del.Plata	Argentina	2002	transect	non	19	-0.698970004	-0.187086643	neutral
Acanthiza_lineata	Acanthizidae	Newcastle	Australia	2007	transect	non	144	-0.176091259	-0.176091259	neutral
Acanthiza_pusilla	Acanthizidae	Newcastle	Australia	2007	transect	non	144	-0.082186756	-0.082186756	neutral
Acanthorhynchus_tenuirostris	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.06694679	-0.06694679	neutral
Alectura_lathami	Megapodiidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Alisterus_scapularis	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.124938737	-0.124938737	neutral
Anthochaera_carunculata	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.133538908	-0.026328939	neutral
Anthochaera_chrysoptera	Meliphagidae	Newcastle	Australia	2007	transect	non	144	0	0.017033339	neutral
Cacatua_galerita	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.13683796	-0.312929219	exploiter
Cacomantis_flabelliformis	Cuculidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Callocephalon_fimbriatum	Psittacidae	Newcastle	Australia	2007	transect	non	144	0	0.017728767	NA
Calyptorhynchus_funereus	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	0	neutral
Chenonetta_jubata	Anatidae	Newcastle	Australia	2007	transect	non	144	-0.06694679	-0.129094696	neutral
Coracina_novaehollandiae	Campephagidae	Newcastle	Australia	2007	transect	non	144	0	-0.015794267	neutral
Coracina_papuensis	Campephagidae	Newcastle	Australia	2007	transect	non	144	-0.034762106	-0.034762106	neutral
Cormobates_leucophaeus	Climacteridae	Newcastle	Australia	2007	transect	non	144	-0.051152522	-0.051152522	neutral
Corvus_coronoides	Corvidae	Newcastle	Australia	2007	transect	non	144	-0.077165955	-0.031408464	exploiter
Cracticus_nigrogularis	Cracticidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Cracticus_torquatus	Cracticidae	Newcastle	Australia	2007	transect	non	144	-0.111150452	-0.076388346	neutral
Dacelo_novaeguineae	Alcedinidae	Newcastle	Australia	2007	transect	non	144	-0.317420412	-0.176091259	avoider
Daphoenositta_chrysoptera	Neosittidae	Newcastle	Australia	2007	transect	non	144	-0.034762106	-0.034762106	neutral
Dicrurus_bracteatus	Dicruridae	Newcastle	Australia	2007	transect	non	144	0.034762106	0	NA
Egretta_novaehollandiae	Ardeidae	Newcastle	Australia	2007	transect	non	144	0.017728767	0	NA
Eolophus_roseicapillus	Cacatuidae	Newcastle	Australia	2007	transect	non	144	0.045757491	0.05999793	exploiter
Eopsaltria_australis	Petroicidae	Newcastle	Australia	2007	transect	non	144	-0.096910013	-0.096910013	neutral
Falco_peregrinus	Falconidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	0	neutral
Gallinula_tenebrosa	Rallidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Geopelia_humeralis	Columbidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Geophaps_lophotes	Columbidae	Newcastle	Australia	2007	transect	non	144	0.06694679	0.301029996	NA
Glossopsitta_concinna	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.111150452	-0.111150452	neutral
Grallina_cyanoleuca	Monarchidae	Newcastle	Australia	2007	transect	non	144	0.176091259	0.163856803	NA

Gymnorhina_tibicen	Cracticidae	Newcastle	Australia	2007	transect	non	144	-0.088941083	0.052936075	exploiter
Haliaeetus_leucogaster	Accipitridae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Hirundo_neoxena	Hirundinidae	Newcastle	Australia	2007	transect	non	144	0.111150452	0	NA
Larus_novaehollandiae	Laridae	Newcastle	Australia	2007	transect	non	144	0.327358934	0	NA
Lichenostomus_chrysops	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.138302698	-0.138302698	neutral
Lichmera_indistincta	Meliphagidae	Newcastle	Australia	2007	transect	non	144	0.017728767	0	NA
Malurus_cyaneus	Maluridae	Newcastle	Australia	2007	transect	non	144	-0.096910013	-0.096910013	neutral
Malurus_lamberti	Maluridae	Newcastle	Australia	2007	transect	non	144	-0.243038049	-0.243038049	avoider
Manorina_melanocephala	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.023065304	0.363676805	exploiter
Manorina_melanophrys	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.124938737	-0.124938737	neutral
Meliphaga_lewinii	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.163856803	-0.163856803	neutral
Menura_novaehollandiae	Menuridae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Neochmia_temporalis	Estrildidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Origma_solitaria	Acanthizidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Oriolus_sagittatus	Oriolidae	Newcastle	Australia	2007	transect	non	144	-0.034762106	-0.034762106	neutral
Pachycephala_pectoralis	Pachycephalidae	Newcastle	Australia	2007	transect	non	144	-0.082186756	-0.082186756	neutral
Pardalotus_punctatus	Pardalotidae	Newcastle	Australia	2007	transect	non	144	-0.151267675	-0.151267675	neutral
Pelecanus_conspicillatus	Pelecanidae	Newcastle	Australia	2007	transect	non	144	0.017728767	0	NA
Petroica_rosea	Petroicidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Phalacrocorax_carbo	Phalacrocoracidae	Newcastle	Australia	2007	transect	non	144	0.017728767	0	NA
Phaps_chalcoptera	Columbidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Philemon_corniculatus	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.034762106	-0.034762106	neutral
Phylidonyris_novaehollandiae	Meliphagidae	Newcastle	Australia	2007	transect	non	144	-0.176091259	-0.176091259	neutral
Platycercus_elegans	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.210853365	-0.210853365	avoider
Platycercus_eximius	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.318758763	0.056904851	avoider
Porphyrio_porphyrio	Rallidae	Newcastle	Australia	2007	transect	non	144	0	0.06694679	NA
Psephotus_haematonotus	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.017728767	-0.017728767	neutral
Psophodes_olivaceus	Eupetidae	Newcastle	Australia	2007	transect	non	144	-0.176091259	-0.176091259	neutral
Ptilonorhynchus_violaceus	Ptilonorhynchidae	Newcastle	Australia	2007	transect	non	144	-0.06694679	-0.06694679	neutral
Rhipidura_fuliginosa	Rhipiduridae	Newcastle	Australia	2007	transect	non	144	-0.163856803	-0.163856803	neutral
Rhipidura_leucophrys	Rhipiduridae	Newcastle	Australia	2007	transect	non	144	0.06694679	0	NA
Sericornis_frontalis	Acanthizidae	Newcastle	Australia	2007	transect	non	144	-0.22184875	-0.22184875	avoider
Sphecotheres_viridis	Oriolidae	Newcastle	Australia	2007	transect	non	144	0.017728767	0.017728767	NA
Strepera_graculina	Cracticidae	Newcastle	Australia	2007	transect	non	144	-0.044203662	0.121422163	neutral
Threskiornis_molucca	Threskiornithidae	Newcastle	Australia	2007	transect	non	144	0.051152522	0	NA
Threskiornis_spinicollis	Threskiornithidae	Newcastle	Australia	2007	transect	non	144	0	0.096910013	NA
Trichoglossus_chlorolepidotus	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.163856803	-0.052706351	neutral

Trichoglossus_haematodus	Psittacidae	Newcastle	Australia	2007	transect	non	144	-0.053684859	0.280345397	exploiter
Vanellus_miles	Charadriidae	Newcastle	Australia	2007	transect	non	144	0.06694679	0.034762106	NA
Zosterops_lateralis	Zosteropidae	Newcastle	Australia	2007	transect	non	144	-0.082186756	-0.082186756	neutral
Amaurornis_phoenicurus	Rallidae	Olongapo	Philippine	2004	plot	non	41.7	-0.163243025	-0.163243025	neutral
Artamus_leucorynchus	Artamidae	Olongapo	Philippine	2004	plot	non	41.7	0.150926886	0.713535261	exploiter
Bolbopsittacus_lunulatus	Psittacidae	Olongapo	Philippine	2004	plot	non	41.7	-0.733249152	-0.020038708	avoider
Centropus_unirufus	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.40155778	-0.40155778	neutral
Centropus_viridis	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.957168294	-0.488164929	avoider
Chalcophaps_indica	Columbidae	Olongapo	Philippine	2004	plot	non	41.7	-0.185349298	-0.185349298	neutral
Chrysocolaptes_lucidus	Picidae	Olongapo	Philippine	2004	plot	non	41.7	-0.426999577	-0.23511405	neutral
Copsychus_luzoniensis	Muscicapidae	Olongapo	Philippine	2004	plot	non	41.7	-0.681447602	-0.574992271	avoider
Coracina_coerulescens	Campephagidae	Olongapo	Philippine	2004	plot	non	41.7	-0.667470709	-0.667470709	avoider
Coracina_striata	Campephagidae	Olongapo	Philippine	2004	plot	non	41.7	-0.554555944	0.223595306	neutral
Corvus_macrorhynchos	Corvidae	Olongapo	Philippine	2004	plot	non	41.7	0.178230354	0.82340774	exploiter
Cyornis_rufigaster	Muscicapidae	Olongapo	Philippine	2004	plot	non	41.7	-0.06148688	-0.06148688	neutral
Dendrocopos_maculatus	Picidae	Olongapo	Philippine	2004	plot	non	41.7	-0.330552646	0.177602842	neutral
Dicaeum_hypoleucum	Dicaeidae	Olongapo	Philippine	2004	plot	non	41.7	-0.226447978	-0.226447978	neutral
Dicaeum_pygmaeum	Dicaeidae	Olongapo	Philippine	2004	plot	non	41.7	-0.314844081	-0.122958555	neutral
Dicrurus_balicassius	Dicruridae	Olongapo	Philippine	2004	plot	non	41.7	-0.84083092	-0.263594513	avoider
Dryocopus_javensis	Picidae	Olongapo	Philippine	2004	plot	non	41.7	-0.281612237	-0.175156906	neutral
Ducula_aenea	Columbidae	Olongapo	Philippine	2004	plot	non	41.7	-0.451033065	-0.451033065	neutral
Eudynamys_scolopacea	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.089246774	-0.089246774	neutral
Haliastur_indus	Accipitridae	Olongapo	Philippine	2004	plot	non	41.7	-0.031830687	-0.031830687	neutral
Hemiprocne_comata	Hemiprocnidae	Olongapo	Philippine	2004	plot	non	41.7	-0.06148688	-0.06148688	neutral
Cuculus_fugax	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.031830687	-0.031830687	neutral
Hypothymis_azurea	Monarchidae	Olongapo	Philippine	2004	plot	non	41.7	-0.245625243	-0.245625243	neutral
Ixos_philippinus	Pycnonotidae	Olongapo	Philippine	2004	plot	non	41.7	-1.099728109	-0.099411798	avoider
Loriculus_philippensis	Psittacidae	Olongapo	Philippine	2004	plot	non	41.7	-0.545245953	0.143964215	avoider
Megalaima_haemacephala	Ramphastidae	Olongapo	Philippine	2004	plot	non	41.7	-0.245625243	0.490328328	neutral
Microhierax_erythrogenys	Falconidae	Olongapo	Philippine	2004	plot	non	41.7	-0.031830687	-0.031830687	neutral
Mulleripicus_funebris	Picidae	Olongapo	Philippine	2004	plot	non	41.7	-0.115338372	-0.115338372	neutral
Oriolus_chinensis	Oriolidae	Olongapo	Philippine	2004	plot	non	41.7	-0.512710911	0.255993182	exploiter
Orthotomus_derbianus	Sylviidae	Olongapo	Philippine	2004	plot	non	41.7	-0.667470709	-0.342959617	avoider
Parus_elegans	Paridae	Olongapo	Philippine	2004	plot	non	41.7	-0.185349298	-0.185349298	neutral
Penelopides_panini	Bucerotidae	Olongapo	Philippine	2004	plot	non	41.7	-0.281612237	-0.175156906	neutral
Phaenicophaeus_cumingi	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.226447978	-0.119992647	neutral
Phaenicophaeus_superciliosus	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.40155778	-0.023361829	neutral

Phapitreron_leucotis	Columbidae	Olongapo	Philippine	2004	plot	non	41.7	-0.59832856	-0.335087125	avoider
Pitta_erythrogaster	Pittidae	Olongapo	Philippine	2004	plot	non	41.7	-0.089246774	-0.089246774	neutral
Prioniturus_luconensis	Psittacidae	Olongapo	Philippine	2004	plot	non	41.7	-0.206384619	-0.099929288	neutral
Rhabdornis_mystacalis	Rhabdornithidae	Olongapo	Philippine	2004	plot	non	41.7	-0.206384619	0.219584113	neutral
Rhipidura_cyaniceps	Rhipiduridae	Olongapo	Philippine	2004	plot	non	41.7	-0.263991382	-0.263991382	neutral
Sarcops_calvus	Sturnidae	Olongapo	Philippine	2004	plot	non	41.7	-0.535732002	0.128073585	neutral
Surniculus_lugubris	Cuculidae	Olongapo	Philippine	2004	plot	non	41.7	-0.06148688	-0.06148688	neutral
Tanygnathus_lucionensis	Psittacidae	Olongapo	Philippine	2004	plot	non	41.7	-0.345712806	0.318092781	neutral
Treron_pompadora	Columbidae	Olongapo	Philippine	2004	plot	non	41.7	-0.06148688	-0.06148688	neutral
Treron_vernans	Columbidae	Olongapo	Philippine	2004	plot	non	41.7	-0.115338372	-0.008883041	neutral
Turnix_ocellata	Turnicidae	Olongapo	Philippine	2004	plot	non	41.7	-0.031830687	-0.031830687	neutral
Zosterops_meyeni	Zosteropidae	Olongapo	Philippine	2004	plot	non	41.7	-0.505871826	-0.505871826	avoider
Aegithalos_caudatus	Aegithalidae	Orebro	Sweden	1999	plot	non	2.4	-1.102662342	-1.102662342	avoider
Anthus_trivialis	Motacillidae	Orebro	Sweden	1999	plot	non	2.4	-1.041392685	-1.041392685	avoider
Bucephala_clangula	Anatidae	Orebro	Sweden	1999	plot	non	2.4	-1.041392685	-1.041392685	avoider
Carduelis_chloris	Fringillidae	Orebro	Sweden	1999	plot	non	2.4	-0.071650885	0.439182549	neutral
Carduelis_spinus	Fringillidae	Orebro	Sweden	1999	plot	non	2.4	-0.884606581	-0.884606581	neutral
Carpodacus_erythrinus	Fringillidae	Orebro	Sweden	1999	plot	non	2.4	-0.77815125	-0.77815125	neutral
Coccothraustes_coccothraustes	Fringillidae	Orebro	Sweden	1999	plot	non	2.4	-0.884606581	-0.884606581	neutral
Columba_palumbus	Columbidae	Orebro	Sweden	1999	plot	non	2.4	-1.556302501	-0.919480403	avoider
Corvus_corone	Corvidae	Orebro	Sweden	1999	plot	non	2.4	-0.19935038	0.073369705	neutral
Corvus_monedula	Corvidae	Orebro	Sweden	1999	plot	non	2.4	0.677846502	0.828164959	exploiter
Dendrocopos_major	Picidae	Orebro	Sweden	1999	plot	non	2.4	-1.693140461	-1.056318363	avoider
Dendrocopos_minor	Picidae	Orebro	Sweden	1999	plot	non	2.4	-1.355387658	-1.355387658	avoider
Emberiza_citrinella	Emberizidae	Orebro	Sweden	1999	plot	non	2.4	-1.514104821	-1.514104821	avoider
Erithacus_rubecula	Muscicapidae	Orebro	Sweden	1999	plot	non	2.4	-1.830374783	-0.945768202	avoider
Ficedula_hypoleuca	Muscicapidae	Orebro	Sweden	1999	plot	non	2.4	-1.041392685	-0.404570588	neutral
Ficedula_parva	Muscicapidae	Orebro	Sweden	1999	plot	non	2.4	-0.425968732	-0.425968732	neutral
Fringilla_coelebs	Fringillidae	Orebro	Sweden	1999	plot	non	2.4	-0.645525685	-0.557189722	avoider
Garrulus_glandarius	Corvidae	Orebro	Sweden	1999	plot	non	2.4	-1.156347201	-1.156347201	avoider
Jynx_torquilla	Picidae	Orebro	Sweden	1999	plot	non	2.4	-0.636822098	-0.636822098	neutral
Luscinia_luscinia	Muscicapidae	Orebro	Sweden	1999	plot	non	2.4	-1.84094208	-1.84094208	avoider
Parus_caeruleus	Paridae	Orebro	Sweden	1999	plot	non	2.4	-0.314325763	-0.077438839	neutral
Parus_major	Paridae	Orebro	Sweden	1999	plot	non	2.4	-0.34186625	-0.043905486	avoider
Parus_palustris	Paridae	Orebro	Sweden	1999	plot	non	2.4	-0.636822098	0	neutral
Passer_domesticus	Passeridae	Orebro	Sweden	1999	plot	non	2.4	0.399155953	0.592052172	exploiter
Phoenicurus_phoenicurus	Muscicapidae	Orebro	Sweden	1999	plot	non	2.4	0.636822098	0	NA

Phylloscopus_sibilatrix	Sylviidae	Orebro	Sweden	1999	plot	non	2.4	-1.247154615	-1.247154615	avoider
Phylloscopus_trochilus	Sylviidae	Orebro	Sweden	1999	plot	non	2.4	-1.908485019	-0.417123325	avoider
Pica_pica	Corvidae	Orebro	Sweden	1999	plot	non	2.4	0.901441809	1.328441385	exploiter
Picus_viridis	Picidae	Orebro	Sweden	1999	plot	non	2.4	-1.156347201	-1.156347201	avoider
Sitta_europaea	Sittidae	Orebro	Sweden	1999	plot	non	2.4	-0.666177491	-0.822963595	avoider
Streptopelia_decaocto	Columbidae	Orebro	Sweden	1999	plot	non	2.4	-0.77815125	-0.141329153	neutral
Sturnus_vulgaris	Sturnidae	Orebro	Sweden	1999	plot	non	2.4	-1.009908289	-0.070773197	avoider
Sylvia_atricapilla	Sylviidae	Orebro	Sweden	1999	plot	non	2.4	-1.53571597	-0.898893872	avoider
Sylvia_borin	Sylviidae	Orebro	Sweden	1999	plot	non	2.4	-1.467361417	-1.467361417	avoider
Sylvia_curruca	Sylviidae	Orebro	Sweden	1999	plot	non	2.4	0.210853365	0.730378469	neutral
Troglodytes_troglodytes	Troglodytidae	Orebro	Sweden	1999	plot	non	2.4	-0.425968732	-0.425968732	neutral
Turdus_iliacus	Turdidae	Orebro	Sweden	1999	plot	non	2.4	-1.721535832	-1.721535832	avoider
Turdus_merula	Turdidae	Orebro	Sweden	1999	plot	non	2.4	-0.893105766	-0.321714595	avoider
Turdus_philomelos	Turdidae	Orebro	Sweden	1999	plot	non	2.4	-1.286306739	-1.286306739	avoider
Turdus_pilaris	Turdidae	Orebro	Sweden	1999	plot	non	2.4	-0.256826333	0.002972595	neutral
Cardinalis_cardinalis	Cardinalidae	Oxford	USA	2000	plot	yes	96	0.047772782	0.516776146	exploiter
Carduelis_tristis	Fringillidae	Oxford	USA	2000	plot	yes	96	-0.350248018	-0.350248018	neutral
Carpodacus_mexicanus	Fringillidae	Oxford	USA	2000	plot	yes	96	1.027965595	0.590805559	exploiter
Colaptes_auratus	Picidae	Oxford	USA	2000	plot	yes	96	-0.424881637	-0.424881637	neutral
Cyanocitta_cristata	Corvidae	Oxford	USA	2000	plot	yes	96	-0.139879086	0.43990451	neutral
Dryocopus_pileatus	Picidae	Oxford	USA	2000	plot	yes	96	-0.445604203	-0.445604203	neutral
Junco_hyemalis	Emberizidae	Oxford	USA	2000	plot	yes	96	-0.784617293	-0.009371033	avoider
Melanerpes_carolinus	Picidae	Oxford	USA	2000	plot	yes	96	-0.408239965	0.444240028	neutral
Parus_bicolor	Paridae	Oxford	USA	2000	plot	yes	96	-0.550228353	0.302251641	neutral
Parus_carolinensis	Paridae	Oxford	USA	2000	plot	yes	96	-0.79940155	0.450716064	avoider
Picoides_pubescens	Picidae	Oxford	USA	2000	plot	yes	96	-0.906873535	-0.906873535	avoider
Regulus_satrapa	Reguliidae	Oxford	USA	2000	plot	yes	96	-0.255272505	-0.255272505	neutral
Sialia_sialis	Turdidae	Oxford	USA	2000	plot	yes	96	-0.608526034	-0.608526034	avoider
Sitta_carolinensis	Sittidae	Oxford	USA	2000	plot	yes	96	-1.012415375	-0.611014834	avoider
Turdus_migratorius	Turdidae	Oxford	USA	2000	plot	yes	96	0.192959184	0.723219883	neutral
Zenaida_macroura	Columbidae	Oxford	USA	2000	plot	yes	96	0.186159654	0.994220508	exploiter
Zonotrichia_albicollis	Emberizidae	Oxford	USA	2000	plot	yes	96	-0.79518459	-0.79518459	avoider
Agelaius_phoeniceus	Icteridae	Palo.Alto	USA	1993	plot	yes	67.2	-0.589949601	-0.589949601	avoider
Anas_platyrhynchos	Anatidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.045322979	-0.045322979	neutral
Aphelocoma_californica	Corvidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.154699916	-0.059003581	neutral
Callipepla_californica	Odontophoridae	Palo.Alto	USA	1993	plot	yes	67.2	-0.193124598	-0.193124598	avoider
Calypte_anna	Trochilidae	Palo.Alto	USA	1993	plot	yes	67.2	0.06694679	0.469003364	exploiter

Carduelis_psaltria	Fringillidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.06069784	0.273755911	neutral
Carpodacus_mexicanus	Fringillidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.224537888	0.503134687	neutral
Chamaea_fasciata	Timaliidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.068185862	-0.068185862	neutral
Contopus_sordidulus	Tyrannidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.037426498	-0.037426498	neutral
Cyanocitta_stelleri	Corvidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.021189299	-0.021189299	neutral
Empidonax_difficilis	Tyrannidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.037426498	-0.037426498	neutral
Euphagus_cyanocephalus	Icteridae	Palo.Alto	USA	1993	plot	yes	67.2	-0.222460002	-0.374748346	neutral
Hirundo_pyrrhonota	Hirundinidae	Palo.Alto	USA	1993	plot	yes	67.2	0.024823584	-0.075546961	exploiter
Hirundo_rustica	Hirundinidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.045322979	-0.045322979	neutral
Icterus_galbula	Icteridae	Palo.Alto	USA	1993	plot	yes	67.2	-0.068185862	0.135934121	neutral
Junco_hyemalis	Emberizidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.059672005	-0.170261715	neutral
Melanerpes_formicivorus	Picidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.161368002	-0.161368002	avoider
Mimus_polyglottos	Mimidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.037426498	0.544636865	neutral
Myiarchus_cinerascens	Tyrannidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.068185862	-0.068185862	neutral
Parus_inornatus	Paridae	Palo.Alto	USA	1993	plot	yes	67.2	-0.331789359	-0.165095875	avoider
Parus_rufescens	Paridae	Palo.Alto	USA	1993	plot	yes	67.2	0.009908289	0.079181246	exploiter
Picoides_nuttallii	Picidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.071882007	-0.071882007	neutral
Pipilo_crissalis	Emberizidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.095780508	0.157607853	neutral
Pipilo_erythrophthalmus	Emberizidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.365487985	-0.124938737	avoider
Polioptila_caerulea	Polioptilidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.136720567	-0.136720567	avoider
Psaltriparus_minimus	Aegithalidae	Palo.Alto	USA	1993	plot	yes	67.2	0	0.049654719	exploiter
Sayornis_nigricans	Tyrannidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.149219113	-0.149219113	avoider
Sialia_mexicana	Turdidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.158362492	-0.158362492	avoider
Sitta_carolinensis	Sittidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.103803721	-0.103803721	neutral
Tachycineta_thalassina	Hirundinidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.167317335	-0.167317335	avoider
Thryomanes_bewickii	Troglodytidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.201397124	0.013446724	avoider
Toxostoma_redivivum	Mimidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.136720567	0.039370692	avoider
Turdus_migratorius	Turdidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.116351646	0.267766319	neutral
Vireo_huttoni	Vireonidae	Palo.Alto	USA	1993	plot	yes	67.2	-0.096910013	-0.096910013	neutral
Zenaida_macroura	Columbidae	Palo.Alto	USA	1993	plot	yes	67.2	0.051361368	0.244914054	exploiter
Accipiter_cooperii	Accipitridae	Phoenix	USA	1996	plot	yes	46.2	-0.019198462	0.142761395	neutral
Agelaius_phoeniceus	Icteridae	Phoenix	USA	1996	plot	yes	46.2	0.130820919	0.705241514	NA
Aimophila_ruficeps	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	0	0.01040276	NA
Amphispiza_belli	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.237360916	-0.237360916	avoider
Amphispiza_bilineata	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-1.457377197	-1.367365103	avoider
Anas_platyrhynchos	Anatidae	Phoenix	USA	1996	plot	yes	46.2	0	0.085712113	NA
Archilochus_alexandri	Trochilidae	Phoenix	USA	1996	plot	yes	46.2	-0.307560863	0.542769704	avoider

Asio_otus	Strigidae	Phoenix	USA	1996	plot	yes	46.2	-0.025554104	-0.025554104	neutral
Auriparus_flaviceps	Remizidae	Phoenix	USA	1996	plot	yes	46.2	-0.552074325	-0.000538159	avoider
Bubo_virginianus	Strigidae	Phoenix	USA	1996	plot	yes	46.2	-0.413452175	-0.413452175	avoider
Buteo_jamaicensis	Accipitridae	Phoenix	USA	1996	plot	yes	46.2	-0.410904986	-0.325192873	avoider
Buteo_swainsoni	Accipitridae	Phoenix	USA	1996	plot	yes	46.2	-0.006530867	0.02883822	neutral
Calamospiza_melanocorys	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.638337961	0.013996303	avoider
Callipepla_gambelii	Odontophoridae	Phoenix	USA	1996	plot	yes	46.2	-1.333475153	0.103322101	avoider
Calypte_anna	Trochilidae	Phoenix	USA	1996	plot	yes	46.2	0.449517621	0.885150309	exploiter
Calypte_costae	Trochilidae	Phoenix	USA	1996	plot	yes	46.2	-0.648803395	-0.408405442	avoider
Campylorhynchus_brunneicapillus	Troglodytidae	Phoenix	USA	1996	plot	yes	46.2	-0.570704781	-0.465746315	avoider
Cardinalis_cardinalis	Cardinalidae	Phoenix	USA	1996	plot	yes	46.2	-0.461489432	-0.43100011	avoider
Cardinalis_sinuatus	Cardinalidae	Phoenix	USA	1996	plot	yes	46.2	0	0.068073365	NA
Carduelis_psaltria	Fringillidae	Phoenix	USA	1996	plot	yes	46.2	-0.118449691	0.73976794	neutral
Carpodacus_mexicanus	Fringillidae	Phoenix	USA	1996	plot	yes	46.2	0.025636448	0.138625982	exploiter
Cathartes_aura	Cathartidae	Phoenix	USA	1996	plot	yes	46.2	-0.012964977	-0.002562217	neutral
Catharus_guttatus	Turdidae	Phoenix	USA	1996	plot	yes	46.2	0	0.146128036	NA
Charadrius_vociferus	Charadriidae	Phoenix	USA	1996	plot	yes	46.2	0.005232527	0.153583918	NA
Chondestes_grammacus	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.049687784	0.061207875	neutral
Chordeiles_acutipennis	Caprimulgidae	Phoenix	USA	1996	plot	yes	46.2	-0.233534508	0.143374098	avoider
Circus_cyaneus	Accipitridae	Phoenix	USA	1996	plot	yes	46.2	0	0.005232527	NA
Cistothorus_palustris	Troglodytidae	Phoenix	USA	1996	plot	yes	46.2	0	0.05897786	NA
Colaptes_auratus	Picidae	Phoenix	USA	1996	plot	yes	46.2	-0.518659335	-0.152055814	avoider
Scardafella_inca	Columbidae	Phoenix	USA	1996	plot	yes	46.2	1.874778704	1.659568384	exploiter
Contopus_sordidulus	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0	0.122960171	NA
Corvus_corax	Corvidae	Phoenix	USA	1996	plot	yes	46.2	-0.468257794	-0.457855034	avoider
Dendroica_coronata	Parulidae	Phoenix	USA	1996	plot	yes	46.2	0.238547888	0.847819347	exploiter
Dendroica_nigrescens	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.049687784	0.018385581	neutral
Dendroica_occidentalis	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.043778925	-0.043778925	neutral
Dendroica_petechia	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.025554104	0.449808871	neutral
Dendroica_townsendi	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.28082661	-0.203844328	avoider
Empidonax_difficilis	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	-0.031714413	0.102984161	neutral
Empidonax_hammondii	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0	0.030489322	NA
Empidonax_oberholseri	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	-0.049687784	0.048798617	neutral
Empidonax_wrightii	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	-0.180456064	-0.135488919	neutral
Eremophila_alpestris	Alaudidae	Phoenix	USA	1996	plot	yes	46.2	0.029091869	-0.143298746	neutral
Euphagus_cyanocephalus	Icteridae	Phoenix	USA	1996	plot	yes	46.2	0.515713321	0.510869838	NA
Falco_mexicanus	Falconidae	Phoenix	USA	1996	plot	yes	46.2	-0.019305155	-0.019305155	neutral

Falco_peregrinus	Falconidae	Phoenix	USA	1996	plot	yes	46.2	0	0.035369087	NA
Falco_sparverius	Falconidae	Phoenix	USA	1996	plot	yes	46.2	-0.197320403	-0.172915417	neutral
Geococcyx_californianus	Cuculidae	Phoenix	USA	1996	plot	yes	46.2	0	0.114954516	NA
Geothlypis_trichas	Parulidae	Phoenix	USA	1996	plot	yes	46.2	0	0.461034435	NA
Hirundo_fulva	Hirundinidae	Phoenix	USA	1996	plot	yes	46.2	-0.621309931	-0.345103519	avoider
Hirundo_rustica	Hirundinidae	Phoenix	USA	1996	plot	yes	46.2	-0.025554104	0.163502132	neutral
Icterus_cucullatus	Icteridae	Phoenix	USA	1996	plot	yes	46.2	0.606507816	0.002547189	exploiter
Icterus_galbula	Icteridae	Phoenix	USA	1996	plot	yes	46.2	-0.317176632	-0.001906197	avoider
Junco_hyemalis	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	0	0.477121255	NA
Lanius_ludovicianus	Laniidae	Phoenix	USA	1996	plot	yes	46.2	-0.410456566	0.303490594	avoider
Melanerpes_uropygialis	Picidae	Phoenix	USA	1996	plot	yes	46.2	-0.007904936	-0.584229862	exploiter
Melospiza_lincolnii	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	0	0.451832936	NA
Melospiza_melodia	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	0	0	NA
Mimus_polyglottos	Mimidae	Phoenix	USA	1996	plot	yes	46.2	0.449603957	0.479538484	exploiter
Mniotilta_varia	Parulidae	Phoenix	USA	1996	plot	yes	46.2	0	0.030489322	NA
Molothrus_aeneus	Icteridae	Phoenix	USA	1996	plot	yes	46.2	0.005232527	0.322845531	NA
Molothrus_ater	Icteridae	Phoenix	USA	1996	plot	yes	46.2	-0.523625598	0.276272249	avoider
Myiarchus_cinerascens	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	-1.018675286	-0.843462277	avoider
Myiarchus_tyrannulus	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	-0.285517829	-0.125816987	avoider
Oporornis_tolmiei	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.025554104	0.23263314	neutral
Oreoscoptes_montanus	Mimidae	Phoenix	USA	1996	plot	yes	46.2	-0.287666034	-0.206296902	avoider
Parabuteo_unicinctus	Accipitridae	Phoenix	USA	1996	plot	yes	46.2	0.005232527	0.020562159	NA
Passerculus_sandwichensis	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.673216453	-0.667983927	avoider
Passerina_amoena	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.114954516	-0.09944235	neutral
Phainopepla_nitens	Bombycillidae	Phoenix	USA	1996	plot	yes	46.2	-1.120474219	-0.39199746	avoider
Pheucticus_melanocephalus	Cardinalidae	Phoenix	USA	1996	plot	yes	46.2	-0.049687784	-0.019198462	neutral
Picoides_scalaris	Picidae	Phoenix	USA	1996	plot	yes	46.2	-0.139497457	0.212392509	neutral
Pipilo_aberti	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.149861735	1.022651382	neutral
Pipilo_chlorurus	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.129846071	0.048869332	neutral
Pipilo_erythrophthalmus	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.006530867	-0.006530867	neutral
Pipilo_fuscus	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.805768515	-0.630555506	avoider
Piranga_ludoviciana	Cardinalidae	Phoenix	USA	1996	plot	yes	46.2	0	0.094269917	NA
Polioptila_caerulea	Polioptilidae	Phoenix	USA	1996	plot	yes	46.2	-0.536481922	-0.409573592	avoider
Polioptila_melanura	Polioptilidae	Phoenix	USA	1996	plot	yes	46.2	-1.087867425	-0.142488376	avoider
Pooecetes_gramineus	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.532638583	-0.517126416	avoider
Psaltriparus_minimus	Aegithalidae	Phoenix	USA	1996	plot	yes	46.2	0	0.175213009	NA
Quiscalus_mexicanus	Icteridae	Phoenix	USA	1996	plot	yes	46.2	1.523588828	1.077643141	NA

Regulus_calendula	Reguliidae	Phoenix	USA	1996	plot	yes	46.2	-0.418790148	0.043853284	avoider
Riparia_riparia	Hirundinidae	Phoenix	USA	1996	plot	yes	46.2	-0.037788561	-0.037788561	neutral
Salpinctes_obsoletus	Troglodytidae	Phoenix	USA	1996	plot	yes	46.2	-0.663329648	-0.658097121	avoider
Sayornis_nigricans	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0	0.015512166	NA
Sayornis_saya	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0.152139128	0.295701162	exploiter
Selasphorus_rufus	Trochilidae	Phoenix	USA	1996	plot	yes	46.2	-0.019305155	-0.019305155	neutral
Sphyrapicus_nuchalis	Picidae	Phoenix	USA	1996	plot	yes	46.2	0	0.030489322	NA
Spizella_breweri	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.835594499	-0.416590547	avoider
Spizella_passerina	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-0.335792102	0.231341246	avoider
Stelgidopteryx_serripennis	Hirundinidae	Phoenix	USA	1996	plot	yes	46.2	-0.17168214	0.335928437	neutral
Sturnella_neglecta	Icteridae	Phoenix	USA	1996	plot	yes	46.2	-0.955702324	-0.576589173	avoider
Tachycineta_thalassina	Hirundinidae	Phoenix	USA	1996	plot	yes	46.2	-0.019305155	0.137959247	neutral
Thryomanes_bewickii	Troglodytidae	Phoenix	USA	1996	plot	yes	46.2	-0.451107822	0.361650124	avoider
Toxostoma_bendirei	Mimidae	Phoenix	USA	1996	plot	yes	46.2	-0.373580663	-0.130166764	avoider
Toxostoma_curvirostre	Mimidae	Phoenix	USA	1996	plot	yes	46.2	-0.516331767	-0.185401563	avoider
Troglodytes_aedon	Troglodytidae	Phoenix	USA	1996	plot	yes	46.2	-0.180456064	0.116607744	neutral
Turdus_migratorius	Turdidae	Phoenix	USA	1996	plot	yes	46.2	0	0.068073365	NA
Tyrannus_melancholicus	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0	0.005232527	NA
Tyrannus_verticalis	Tyrannidae	Phoenix	USA	1996	plot	yes	46.2	0.035429738	0.027349608	neutral
Tyto_alba	Tytonidae	Phoenix	USA	1996	plot	yes	46.2	-0.019305155	-0.019305155	neutral
Vermivora_celata	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.230751144	0.23771854	neutral
Vermivora_luciae	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.468257794	-0.437768472	avoider
Vermivora_ruficapilla	Parulidae	Phoenix	USA	1996	plot	yes	46.2	0.152376985	0.057677127	exploiter
Vermivora_virginiae	Parulidae	Phoenix	USA	1996	plot	yes	46.2	0	0.005232527	NA
Vireo_gilvus	Vireonidae	Phoenix	USA	1996	plot	yes	46.2	0	0.05897786	NA
Vireo_solitarius	Vireonidae	Phoenix	USA	1996	plot	yes	46.2	0	0.114954516	NA
Wilsonia_pusilla	Parulidae	Phoenix	USA	1996	plot	yes	46.2	-0.671817758	0.138047905	avoider
Zenaida_asiatica	Columbidae	Phoenix	USA	1996	plot	yes	46.2	0.855762945	0.514219912	exploiter
Zenaida_macroura	Columbidae	Phoenix	USA	1996	plot	yes	46.2	0.144657555	0.163173261	exploiter
Zonotrichia_leucophrys	Emberizidae	Phoenix	USA	1996	plot	yes	46.2	-1.549971884	-0.061978789	avoider
Acrocephalus_gracilirostris	Sylviidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.229373444	-0.229373444	avoider
Alopochen_aegyptiacus	Anatidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.090586662	0.090586662	NA
Amadina_erythrocephala	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0	0.408024293	neutral
Amadina_fasciata	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0	0.165500605	NA
Amandava_subflava	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.082006005	-0.129656927	neutral
Amblyospiza_albifrons	Ploceidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.521048846	-0.236003281	avoider
Anthus_cinnamomeus	Motacillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.328298135	-0.418884797	avoider

Anthus_leucophrys	Motacillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.229373444	-0.229373444	avoider
Apus_affinis	Apodidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.090586662	0	NA
Ardea_melanocephala	Ardeidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Bostrychia_hagedash	Threskiornithidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.525476854	0.796235713	exploiter
Bradypterus_baboecala	Sylviidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Burhinus_capensis	Burhinidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.129656927	-0.082006005	neutral
Nectarinia_amethystina	Nectariniidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.074913944	0.194458904	neutral
Nectarinia_talatala	Nectariniidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.455675215	0.756322813	NA
Cisticola_aridulus	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Cisticola_fulvicapillus	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.198610211	-0.198610211	avoider
Cisticola_juncidis	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0	-0.090586662	neutral
Cisticola_lais	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.090586662	-0.090586662	neutral
Cisticola_textrix	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Cisticola_tinniens	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.310415668	-0.310415668	avoider
Colius_striatus	Coliidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.399250749	0.334385172	NA
Columba_guinea	Columbidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.496779497	0.29017461	exploiter
Corvus_albus	Corvidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.090586662	0.039070265	neutral
Corythaixoides_concolor	Musophagidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.577857173	0.782388303	NA
Cossypha_caffra	Muscicapidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.266514004	0.219829006	exploiter
Cypsiurus_parvus	Apodidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.090586662	0.198610211	NA
Dicrurus_adsimilis	Dicruridae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.165500605	-0.165500605	neutral
Dryoscopus_cubla	Malaconotidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.090586662	0.047650922	NA
Elanus_caeruleus	Accipitridae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.198610211	-0.198610211	avoider
Euplectes_orix	Ploceidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.377204589	-0.359198842	avoider
Euplectes_progne	Ploceidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.285045565	-0.285045565	avoider
Eupodotis_afraoides	Otididae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Francolinus_levaillantoides	Phasianidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.285045565	-0.285045565	avoider
Fulica_cristata	Rallidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.165500605	-0.165500605	neutral
Gallinula_chloropus	Rallidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.129656927	-0.129656927	neutral
Hirundo_albigularis	Hirundinidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	0.04293574	neutral
Hirundo_dimidiata	Hirundinidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Hirundo_fuligula	Hirundinidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.229373444	0	NA
Jynx_ruficollis	Picidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.090586662	-0.04293574	neutral
Lagonosticta_rhodopareia	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.129656927	0	NA
Lamprotornis_nitens	Sturnidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.074913944	-0.035843678	neutral
Laniarius_ferrugineus	Malaconotidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.047650922	0.129656927	NA
Lanius_collaris	Laniidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.220559098	-0.016013718	neutral

Lybius_torquatus	Ramphastidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.039070265	0.128444043	neutral
Macronyx_capensis	Motacillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.521048846	-0.521048846	avoider
Merops_bullockoides	Meropidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.129656927	-0.129656927	neutral
Mirafra_africana	Alaudidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.378686862	-0.378686862	avoider
Motacilla_capensis	Motacillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.269593822	0.359934017	exploiter
Myrmecocichla_formicivora	Muscicapidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.229373444	-0.229373444	avoider
Numida_meleagris	Numididae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.472964072	-0.472964072	avoider
Oenanthe_pileata	Muscicapidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.56433644	-0.56433644	avoider
Onychognathus_morio	Sturnidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.378686862	0	NA
Oriolus_larvatus	Oriolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.047650922	0.047650922	NA
Ortygospiza_atricollis	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.378686862	-0.378686862	avoider
Passer_diffusus	Passeridae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.507604075	-0.033318379	avoider
Passer_melanurus	Passeridae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.006386799	0.422334448	neutral
Phoeniculus_purpureus	Phoeniculidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0	0.129656927	NA
Ploceus_capensis	Ploceidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0	0.165500605	NA
Ploceus_velatus	Ploceidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.141550449	0.286855957	exploiter
Porphyrio_porphyrio	Rallidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.047650922	-0.047650922	neutral
Prinia_flavicans	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.030763233	-0.198610211	neutral
Prinia_subflava	Cisticolidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.090586662	-0.090586662	neutral
Francolinus_swainsonii	Phasianidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.357100665	-0.357100665	avoider
Pycnonotus_tricolor	Pycnonotidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.389422825	0.658268137	exploiter
Pytilia_melba	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.047650922	0	NA
Saxicola_torquata	Muscicapidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.399250749	-0.399250749	avoider
Serinus_atrogularis	Fringillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.035843678	-0.035843678	neutral
Serinus_gularis	Fringillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.213186257	0.168884567	exploiter
Serinus_mozambicus	Fringillidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.129656927	0	NA
Sigelus_silens	Muscicapidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.047650922	0.198610211	NA
Lonchura_cucullata	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.56433644	0.535962619	NA
Spreo_bicolor	Sturnidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.437669468	-0.437669468	avoider
Streptopelia_capicola	Columbidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.122181958	0.562761768	neutral
Streptopelia_semitorquata	Columbidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.011392514	0.347248721	neutral
Streptopelia_senegalensis	Columbidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.526063468	0.723808987	exploiter
Struthio_camelus	Struthionidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.285045565	-0.285045565	avoider
Telophorus_zeylonus	Malaconotidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.378686862	-0.2881002	avoider
Trachyphonus_vaillantii	Ramphastidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.04293574	0.390018546	neutral
Turdoides_jardineii	Timaliidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.129656927	0	NA
Turdus_smithi	Turdidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.67310468	0.639786302	NA

Upupa_africana	Upupidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.090586662	0.194458904	neutral
Uraeginthus_angolensis	Estrildidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.357100665	0	NA
Urocolius_indicus	Coliidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.25810097	0.334385172	NA
Vanellus_armatus	Charadriidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.181722522	0.081042224	neutral
Vanellus_coronatus	Charadriidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.109144469	-0.054357662	neutral
Vanellus_senegallus	Charadriidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	-0.229373444	-0.229373444	avoider
Zosterops_pallidus	Zosteropidae	Pretoria	SouthAfrica	2006	plot	yes	50.7	0.724287396	0.747150279	exploiter
Anas_platyrhynchos	Anatidae	Rennes	France	1995	grids	non	70	-0.024074987	-0.024074987	neutral
Apus_apus	Apodidae	Rennes	France	1995	grids	non	70	0.722355966	0.423135534	exploiter
Ardea_cinerea	Ardeidae	Rennes	France	1995	grids	non	70	0.005840744	0.005218694	neutral
Buteo_buteo	Accipitridae	Rennes	France	1995	grids	non	70	-0.010723865	-0.010723865	neutral
Carduelis_cannabina	Fringillidae	Rennes	France	1995	grids	non	70	-0.014100322	-0.005074579	neutral
Carduelis_carduelis	Fringillidae	Rennes	France	1995	grids	non	70	-0.208756623	-0.09478339	avoider
Carduelis_chloris	Fringillidae	Rennes	France	1995	grids	non	70	-0.17632062	0.151726034	avoider
Certhia_brachydactyla	Certhiidae	Rennes	France	1995	grids	non	70	-0.044147621	-0.031732246	neutral
Corvus_corone	Corvidae	Rennes	France	1995	grids	non	70	0.101227977	0.073053737	neutral
Delichon_urbica	Hirundinidae	Rennes	France	1995	grids	non	70	0.101059355	0	NA
Dendrocopos_major	Picidae	Rennes	France	1995	grids	non	70	-0.006893708	-0.006893708	neutral
Emberiza_citrinella	Emberizidae	Rennes	France	1995	grids	non	70	-0.003460532	-0.003460532	neutral
Erithacus_rubecula	Muscicapidae	Rennes	France	1995	grids	non	70	-0.455554662	-0.263102394	avoider
Falco_tinnunculus	Falconidae	Rennes	France	1995	grids	non	70	-0.021602716	-0.017281342	neutral
Fringilla_coelebs	Fringillidae	Rennes	France	1995	grids	non	70	-0.522574633	-0.19695636	avoider
Garrulus_glandarius	Corvidae	Rennes	France	1995	grids	non	70	-0.027349608	-0.025399667	neutral
Hippolais_polyglotta	Sylviidae	Rennes	France	1995	grids	non	70	-0.003460532	-0.003460532	neutral
Hirundo_rustica	Hirundinidae	Rennes	France	1995	grids	non	70	-0.112605002	-0.112605002	neutral
Larus_argentatus	Laridae	Rennes	France	1995	grids	non	70	0.913813852	0.158817489	exploiter
Motacilla_alba	Motacillidae	Rennes	France	1995	grids	non	70	0.032123614	0.015122032	neutral
Muscicapa_striata	Muscicapidae	Rennes	France	1995	grids	non	70	0	0.005180513	NA
Parus_caeruleus	Paridae	Rennes	France	1995	grids	non	70	-0.252151133	-0.048269781	avoider
Parus_major	Paridae	Rennes	France	1995	grids	non	70	-0.347042878	-0.031919627	avoider
Parus_palustris	Paridae	Rennes	France	1995	grids	non	70	0	0.004536318	NA
Passer_domesticus	Passeridae	Rennes	France	1995	grids	non	70	0.009165166	0.128620639	neutral
Phoenicurus_ochruros	Muscicapidae	Rennes	France	1995	grids	non	70	0.182414652	0.002166062	NA
Phylloscopus_collybita	Sylviidae	Rennes	France	1995	grids	non	70	-0.344195716	-0.243997544	avoider
Pica_pica	Corvidae	Rennes	France	1995	grids	non	70	-0.040336558	0.102165153	neutral
Picus_viridis	Picidae	Rennes	France	1995	grids	non	70	0	0.004536318	NA
Prunella_modularis	Prunellidae	Rennes	France	1995	grids	non	70	-0.228592333	0.051206921	avoider

Regulus_regulus	Reguliidae	Rennes	France	1995	grids	non	70	-0.007747778	0.005089447	neutral
Serinus_serinus	Fringillidae	Rennes	France	1995	grids	non	70	-0.043347277	0.006329307	neutral
Sitta_europaea	Sittidae	Rennes	France	1995	grids	non	70	-0.003460532	0.006839425	neutral
Streptopelia_decaocto	Columbidae	Rennes	France	1995	grids	non	70	0.130429258	0.074614231	neutral
Sturnus_vulgaris	Sturnidae	Rennes	France	1995	grids	non	70	0.165060965	0.117969633	exploiter
Sylvia_atricapilla	Sylviidae	Rennes	France	1995	grids	non	70	-0.027757205	0.022815872	neutral
Sylvia_borin	Sylviidae	Rennes	France	1995	grids	non	70	-0.003891166	-0.001725104	neutral
Troglodytes_troglodytes	Troglodytidae	Rennes	France	1995	grids	non	70	-0.399003526	-0.079272303	avoider
Turdus_merula	Turdidae	Rennes	France	1995	grids	non	70	-0.191745769	0.153375686	avoider
Turdus_philomelos	Turdidae	Rennes	France	1995	grids	non	70	-0.017867719	0.054749758	neutral
Turdus_viscivorus	Turdidae	Rennes	France	1995	grids	non	70	-0.003460532	-0.00129447	neutral
Geranoaetus_melanoleucus	Accipitridae	Santiago	Chile	2001	transect	non	8.4	-0.425968732	NA	neutral
Parabuteo_unicinctus	Accipitridae	Santiago	Chile	2001	transect	non	8.4	-1.102662342	NA	avoider
Falco_sparverius	Falconidae	Santiago	Chile	2001	transect	non	8.4	0	NA	NA
Milvago_chimango	Falconidae	Santiago	Chile	2001	transect	non	8.4	-0.328182242	NA	neutral
Agelaius_thilius	Icteridae	Santiago	Chile	2001	transect	non	8.4	0	NA	NA
Curaeus_curaeus	Icteridae	Santiago	Chile	2001	transect	non	8.4	-0.341001094	NA	neutral
Molothrus_bonariensis	Icteridae	Santiago	Chile	2001	transect	non	8.4	1.399516397	NA	NA
Sturnella_loyca	Icteridae	Santiago	Chile	2001	transect	non	8.4	-1.917330426	NA	avoider
Zonotrichia_capensis	Emberizidae	Santiago	Chile	2001	transect	non	8.4	-0.338306115	NA	neutral
Carduelis_barbata	Fringillidae	Santiago	Chile	2001	transect	non	8.4	0.136504375	NA	exploiter
Diuca_diuca	Emberizidae	Santiago	Chile	2001	transect	non	8.4	-0.292321538	NA	neutral
Phrygilus_fruticeti	Emberizidae	Santiago	Chile	2001	transect	non	8.4	-0.77815125	NA	avoider
Sicalis_luteola	Emberizidae	Santiago	Chile	2001	transect	non	8.4	-1.204119983	NA	avoider
Aphrastura_spinicauda	Furnariidae	Santiago	Chile	2001	transect	non	8.4	-0.77815125	NA	avoider
Leptasthenura_aegithaloides	Furnariidae	Santiago	Chile	2001	transect	non	8.4	-0.923293373	NA	avoider
Asthenes_humicola	Furnariidae	Santiago	Chile	2001	transect	non	8.4	-1.53571597	NA	avoider
Tachycineta_meyeni	Hirundinidae	Santiago	Chile	2001	transect	non	8.4	-0.760566076	NA	avoider
Mimus_thenca	Mimidae	Santiago	Chile	2001	transect	non	8.4	-0.866838753	NA	avoider
Turdus_falcklandii	Turdidae	Santiago	Chile	2001	transect	non	8.4	0.616521303	NA	exploiter
Phytotoma_rara	Cotingidae	Santiago	Chile	2001	transect	non	8.4	0.449969009	NA	NA
Pteroptochos_megapodius	Rhinocryptidae	Santiago	Chile	2001	transect	non	8.4	-1.386201605	NA	avoider
Scelorchilus_albicollis	Rhinocryptidae	Santiago	Chile	2001	transect	non	8.4	-1.007178585	NA	avoider
Troglodytes_musculus	Troglodytidae	Santiago	Chile	2001	transect	non	8.4	-0.677503408	NA	avoider
Anairetes_parulus	Tyrannidae	Santiago	Chile	2001	transect	non	8.4	-0.784566352	NA	avoider
Elaenia_albiceps	Tyrannidae	Santiago	Chile	2001	transect	non	8.4	-0.083675801	NA	exploiter
Xolmis_pyrope	Tyrannidae	Santiago	Chile	2001	transect	non	8.4	-0.77815125	NA	avoider

Vanellus_chilensis	Charadriidae	Santiago	Chile	2001	transect	non	8.4	0	NA	NA
Columbina_picui	Columbidae	Santiago	Chile	2001	transect	non	8.4	0.621365147	NA	NA
Zenaida_auriculata	Columbidae	Santiago	Chile	2001	transect	non	8.4	0.238004315	NA	exploiter
Colaptes_pitius	Picidae	Santiago	Chile	2001	transect	non	8.4	-1.247154615	NA	avoider
Picoides_lignarius	Picidae	Santiago	Chile	2001	transect	non	8.4	-0.884606581	NA	avoider
Nothoprocta_perdicaria	Tinamidae	Santiago	Chile	2001	transect	non	8.4	-1.53571597	NA	avoider
Patagona_gigas	Trochilidae	Santiago	Chile	2001	transect	non	8.4	0	NA	NA
Sephanoides_sephaniodes	Trochilidae	Santiago	Chile	2001	transect	non	8.4	0.28082661	NA	NA
Agelaius_phoeniceus	Icteridae	Toronto	Canada	1975	grids	non	72	-0.397940009	-0.357322158	neutral
Bombycilla_cedrorum	Bombycillidae	Toronto	Canada	1975	grids	non	72	-0.041392685	-0.000774834	neutral
Cardinalis_cardinalis	Cardinalidae	Toronto	Canada	1975	grids	non	72	-0.556302501	-0.270436446	neutral
Carduelis_tristis	Fringillidae	Toronto	Canada	1975	grids	non	72	-0.041392685	-0.000774834	neutral
Chaetura_pelagica	Apodidae	Toronto	Canada	1975	grids	non	72	0.723103684	0.173243416	NA
Colaptes_auratus	Picidae	Toronto	Canada	1975	grids	non	72	0	0.095203549	NA
Contopus_virens	Tyrannidae	Toronto	Canada	1975	grids	non	72	0	0.095203549	NA
Cyanocitta_cristata	Corvidae	Toronto	Canada	1975	grids	non	72	-0.301029996	0.163126282	neutral
Dumetella_carolinensis	Mimidae	Toronto	Canada	1975	grids	non	72	-0.041392685	-0.041392685	neutral
Hirundo_rustica	Hirundinidae	Toronto	Canada	1975	grids	non	72	-0.397940009	-0.338354319	neutral
Icterus_galbula	Icteridae	Toronto	Canada	1975	grids	non	72	-0.361727836	-0.249754077	neutral
Melospiza_melodia	Emberizidae	Toronto	Canada	1975	grids	non	72	-0.447158031	-0.259858551	neutral
Molothrus_ater	Icteridae	Toronto	Canada	1975	grids	non	72	-0.69019608	-0.415495023	avoider
Myiarchus_crinitus	Tyrannidae	Toronto	Canada	1975	grids	non	72	0	0.020783606	NA
Parus_atricapillus	Paridae	Toronto	Canada	1975	grids	non	72	0	0.020783606	NA
Quiscalus_quiscula	Icteridae	Toronto	Canada	1975	grids	non	72	-0.786171121	-0.215036855	neutral
Spizella_passerina	Emberizidae	Toronto	Canada	1975	grids	non	72	-0.447158031	0.096910013	neutral
Turdus_migratorius	Turdidae	Toronto	Canada	1975	grids	non	72	-0.653679246	-0.195101118	exploiter
Vireo_gilvus	Vireonidae	Toronto	Canada	1975	grids	non	72	0	0.020783606	NA
Vireo_olivaceus	Vireonidae	Toronto	Canada	1975	grids	non	72	-0.176091259	-0.155307653	neutral
Zenaida_macroura	Columbidae	Toronto	Canada	1975	grids	non	72	-0.447158031	-0.090270218	neutral
Molothrus_bonariensis	Icteridae	Valdivia	Chile	2010	transect	non	96	-0.578830151	-0.578830151	avoider
Turdus_falcklandii	Turdidae	Valdivia	Chile	2010	transect	non	96	-0.441405702	0.079181246	avoider
Columba_araucana	Columbidae	Valdivia	Chile	2010	transect	non	96	-0.445863561	-0.246291206	avoider
Carduelis_barbata	Fringillidae	Valdivia	Chile	2010	transect	non	96	0.241444306	0.458153416	exploiter
Scelorchilus_rubecula	Rhinocryptidae	Valdivia	Chile	2010	transect	non	96	-0.419129308	-0.419129308	avoider
Sephanoides_sephaniodes	Trochilidae	Valdivia	Chile	2010	transect	non	96	-0.433655561	-0.061269657	avoider
Aphrastura_spinicauda	Furnariidae	Valdivia	Chile	2010	transect	non	96	-0.377418342	-0.260912772	avoider
Anairetes_parulus	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.461326988	-0.063386979	avoider

Tachycineta_meyeni	Hirundinidae	Valdivia	Chile	2010	transect	non	96	0.15490196	0.26211193	exploiter
Sylviorthorhynchus_desmursii	Furnariidae	Valdivia	Chile	2010	transect	non	96	-0.458637849	-0.458637849	avoider
Pygarrhichas_albogularis	Furnariidae	Valdivia	Chile	2010	transect	non	96	-0.163856803	-0.096910013	avoider
Colaptes_pitius	Picidae	Valdivia	Chile	2010	transect	non	96	-0.082186756	-0.082186756	avoider
Phrygilus_patagonicus	Emberizidae	Valdivia	Chile	2010	transect	non	96	-0.151267675	-0.116505569	avoider
Pteroptochos_tarnii	Rhinocryptidae	Valdivia	Chile	2010	transect	non	96	-0.243038049	-0.243038049	avoider
Xolmis_pyrope	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.111150452	-0.111150452	avoider
Diuca_diuca	Emberizidae	Valdivia	Chile	2010	transect	non	96	-0.017728767	0.049218023	neutral
Enicognathus_ferrugineus	Psittacidae	Valdivia	Chile	2010	transect	non	96	-0.360151448	0.092146223	avoider
Troglodytes_musculus	Troglodytidae	Valdivia	Chile	2010	transect	non	96	0.147215131	0.308583134	exploiter
Curaeus_curaeus	Icteridae	Valdivia	Chile	2010	transect	non	96	-0.294595886	-0.144833565	avoider
Elaenia_albiceps	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.49541004	-0.254377974	avoider
Milvago_chimango	Falconidae	Valdivia	Chile	2010	transect	non	96	0.174254916	0.174254916	exploiter
Zonotrichia_capensis	Emberizidae	Valdivia	Chile	2010	transect	non	96	-0.355878664	0.356252787	avoider
Vanellus_chilensis	Charadriidae	Valdivia	Chile	2010	transect	non	96	-0.480126765	-0.3352932	avoider
Hymenops_perspicillata	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.163856803	-0.163856803	avoider
Theristicus_melanopis	Threskiornithidae	Valdivia	Chile	2010	transect	non	96	0.387216143	-0.142961841	exploiter
Gallinago_paraguaiae	Scolopacidae	Valdivia	Chile	2010	transect	non	96	-0.138302698	-0.013363962	avoider
Sicalis_luteola	Emberizidae	Valdivia	Chile	2010	transect	non	96	-0.23768733	-0.010903363	exploiter
Lessonia_rufa	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.017728767	-0.017728767	neutral
Plegadis_chihi	Threskiornithidae	Valdivia	Chile	2010	transect	non	96	-0.500602351	-0.500602351	avoider
Larus_maculipennis	Laridae	Valdivia	Chile	2010	transect	non	96	0.311753861	-0.15490196	exploiter
Coragyps_atratus	Cathartidae	Valdivia	Chile	2010	transect	non	96	-0.22184875	-0.22184875	avoider
Sturnella_loyca	Icteridae	Valdivia	Chile	2010	transect	non	96	-0.176091259	-0.079181246	avoider
Nothoprocta_perdicaria	Tinamidae	Valdivia	Chile	2010	transect	non	96	-0.082186756	-0.082186756	avoider
Phytotoma_rara	Cotingidae	Valdivia	Chile	2010	transect	non	96	-0.051152522	0.073786214	neutral
Mimus_thenca	Mimidae	Valdivia	Chile	2010	transect	non	96	0.028028724	0.028028724	exploiter
Zenaida_auriculata	Columbidae	Valdivia	Chile	2010	transect	non	96	-0.111150452	-0.111150452	avoider
Buteo_polyosoma	Accipitridae	Valdivia	Chile	2010	transect	non	96	-0.017728767	-0.017728767	neutral
Campephilus_magellanicus	Picidae	Valdivia	Chile	2010	transect	non	96	-0.034762106	-0.034762106	neutral
Glaucidium_nanum	Strigidae	Valdivia	Chile	2010	transect	non	96	-0.017728767	-0.017728767	neutral
Scytalopus_magellanicus	Rhinocryptidae	Valdivia	Chile	2010	transect	non	96	-0.367976785	-0.367976785	avoider
Eugralla_paradoxa	Rhinocryptidae	Valdivia	Chile	2010	transect	non	96	-0.082186756	-0.082186756	avoider
Polyborus_plancus	Falconidae	Valdivia	Chile	2010	transect	non	96	-0.032184683	-0.06694679	neutral
Colorhamphus_parvirostris	Tyrannidae	Valdivia	Chile	2010	transect	non	96	-0.06694679	-0.06694679	neutral
Acrocephalus_scirpaceus	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.001992422	0.002502141	avoider
Actitis_hypoleucos	Scolopacidae	Valencia	Spain	1998	grids	non	6884.5	-0.00142409	-0.00142409	avoider

Aegithalos_caudatus	Aegithalidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	-0.001139646	avoider
Alectoris_rufa	Phasianidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Anas_platyrhynchos	Anatidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Apus_apus	Apodidae	Valencia	Spain	1998	grids	non	6884.5	0.276536155	-0.214791246	exploiter
Ardea_cinerea	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.018158594	-0.015905498	avoider
Athene_noctua	Strigidae	Valencia	Spain	1998	grids	non	6884.5	-0.004822975	-0.003694966	avoider
Bubulcus_ibis	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.0170628	0.02180589	avoider
Caprimulgus_ruficollis	Caprimulgidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Carduelis_cannabina	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.001708349	-0.001708349	neutral
Carduelis_carduelis	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.21356383	0.017917933	avoider
Carduelis_chloris	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.039290684	-0.013196912	avoider
Certhia_brachydactyla	Certhiidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Cettia_cetti	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	0.003354917	neutral
Charadrius_alexandrinus	Charadriidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	0.003639548	avoider
Cisticola_juncidis	Cisticolidae	Valencia	Spain	1998	grids	non	6884.5	-0.089642372	0.049324155	avoider
Columba_palumbus	Columbidae	Valencia	Spain	1998	grids	non	6884.5	-0.006231363	-0.006231363	avoider
Cuculus_canorus	Cuculidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Delichon_urbica	Hirundinidae	Valencia	Spain	1998	grids	non	6884.5	0.094511775	-0.023589992	exploiter
Egretta_garzetta	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Emberiza_cia	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.005105018	-0.005105018	avoider
Erithacus_rubecula	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.000823526	0.00111345	neutral
Falco_tinnunculus	Falconidae	Valencia	Spain	1998	grids	non	6884.5	-0.003028075	-0.001722649	avoider
Fulica_atra	Rallidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Galerida_cristata	Alaudidae	Valencia	Spain	1998	grids	non	6884.5	-0.005668556	-0.005668556	avoider
Gallinula_chloropus	Rallidae	Valencia	Spain	1998	grids	non	6884.5	-0.005668556	0.001055965	avoider
Hippolais_polyglotta	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.037108193	-0.025174483	avoider
Hirundo_rustica	Hirundinidae	Valencia	Spain	1998	grids	non	6884.5	-0.133759735	-0.106207157	avoider
Ixobrychus_minutus	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	avoider
Jynx_torquilla	Picidae	Valencia	Spain	1998	grids	non	6884.5	-0.001708349	-0.001708349	avoider
Lanius_excubitor	Laniidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	-1.16E-05	avoider
Lanius_senator	Laniidae	Valencia	Spain	1998	grids	non	6884.5	-0.01209722	-0.007602658	avoider
Larus_ridibundus	Laridae	Valencia	Spain	1998	grids	non	6884.5	-0.007635199	-0.007635199	avoider
Lullula_arborea	Alaudidae	Valencia	Spain	1998	grids	non	6884.5	-0.00142409	-0.00142409	avoider
Luscinia_megarhynchos	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.051839359	-0.045114838	avoider
Merops_apiaster	Meropidae	Valencia	Spain	1998	grids	non	6884.5	-0.006231363	0.025347015	avoider
Miliaria_calandra	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.007074209	-0.0059462	avoider
Motacilla_alba	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.024266976	-0.00534561	avoider

Motacilla_cinerea	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.002276309	-0.002276309	avoider
Motacilla_flava	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.006231363	-0.006231363	avoider
Muscicapa_striata	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.023859424	-0.014602322	avoider
Parus_ater	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Parus_cristatus	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.001708349	-0.001708349	avoider
Parus_major	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.032796861	-0.02702001	avoider
Passer_domesticus	Passeridae	Valencia	Spain	1998	grids	non	6884.5	-0.125839114	0.090771279	exploiter
Passer_montanus	Passeridae	Valencia	Spain	1998	grids	non	6884.5	-0.042110104	-0.035385584	avoider
Phoenicurus_ochruros	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.042110104	-0.035385584	avoider
Phylloscopus_bonelli	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	neutral
Riparia_riparia	Hirundinidae	Valencia	Spain	1998	grids	non	6884.5	-0.00142409	0.00641113	neutral
Saxicola_torquata	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	0.010295363	neutral
Serinus_canaria	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	-0.001139646	neutral
Serinus_serinus	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Streptopelia_decaocto	Columbidae	Valencia	Spain	1998	grids	non	6884.5	0.05739053	0.086148474	exploiter
Streptopelia_turtur	Columbidae	Valencia	Spain	1998	grids	non	6884.5	-0.01375873	-0.01375873	avoider
Sturnus_unicolor	Sturnidae	Valencia	Spain	1998	grids	non	6884.5	-0.111061395	-0.043240261	avoider
Sylvia_atricapilla	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.008475327	-0.007347318	avoider
Sylvia_communis	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	-1.16E-05	neutral
Sylvia_melanocephala	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.01209722	-0.009844125	avoider
Sylvia_undata	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.003410004	-0.002281995	avoider
Turdus_merula	Turdidae	Valencia	Spain	1998	grids	non	6884.5	-0.141416497	-0.122179471	avoider
Upupa_epops	Upupidae	Valencia	Spain	1998	grids	non	6884.5	-0.024945368	-0.019334395	NA
Actitis_hypoleucos	Scolopacidae	Valencia	Spain	1998	grids	non	6884.5	-0.001992422	-0.000864413	avoider
Aegithalos_caudatus	Aegithalidae	Valencia	Spain	1998	grids	non	6884.5	-0.003692966	-0.003692966	avoider
Alauda_arvensis	Alaudidae	Valencia	Spain	1998	grids	non	6884.5	-0.011541968	-0.009288873	avoider
Alcedo_atthis	Alcedinidae	Valencia	Spain	1998	grids	non	6884.5	-0.00142409	-0.00142409	avoider
Anthus_pratensis	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.060611688	0.065874493	avoider
Ardea_cinerea	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.011819683	-0.011819683	avoider
Athene_noctua	Strigidae	Valencia	Spain	1998	grids	non	6884.5	-0.003410004	-0.001156909	avoider
Bubulcus_ibis	Ardeidae	Valencia	Spain	1998	grids	non	6884.5	-0.052092471	0.069299387	avoider
Carduelis_cannabina	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.008195465	0.043896016	avoider
Carduelis_carduelis	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.306658829	0.173914935	avoider
Carduelis_spinus	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.001992422	0.040987865	neutral
Carduelis_chloris	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.026854715	0.004194356	avoider
Certhia_brachydactyla	Certhiidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	avoider
Cettia_cetti	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.001708349	0.003902624	avoider

Charadrius_alexandrinus	Charadriidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	avoider
Cisticola_juncidis	Cisticolidae	Valencia	Spain	1998	grids	non	6884.5	-0.042627641	0.071008907	avoider
Emberiza_cia	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Emberiza_cirlus	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.00142409	-0.00142409	neutral
Emberiza_schoeniclus	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	0.006154324	neutral
Erithacus_rubecula	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.061439232	-0.01024037	avoider
Falco_tinnunculus	Falconidae	Valencia	Spain	1998	grids	non	6884.5	-0.007771412	-9.14E-05	avoider
Fringilla_coelebs	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.070424924	-0.002593205	avoider
Galerida_cristata	Alaudidae	Valencia	Spain	1998	grids	non	6884.5	-0.013205599	-0.004262512	avoider
Gallinula_chloropus	Rallidae	Valencia	Spain	1998	grids	non	6884.5	-0.005950051	-0.003696955	avoider
Hirundo_rupestris	Hirundinidae	Valencia	Spain	1998	grids	non	6884.5	-0.00110745	-0.004258338	exploiter
Lanius_meridionalis	Laniidae	Valencia	Spain	1998	grids	non	6884.5	-0.003410004	-3.47E-05	avoider
Larus_michahellis	Laridae	Valencia	Spain	1998	grids	non	6884.5	-0.030305268	0.304958406	avoider
Larus_melanocephala	Laridae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Larus_ridibundus	Laridae	Valencia	Spain	1998	grids	non	6884.5	-0.037735791	-0.037113732	avoider
Lullula_arborea	Alaudidae	Valencia	Spain	1998	grids	non	6884.5	-0.007354795	-0.007354795	avoider
Luscinia_svecica	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Miliaria_calandra	Emberizidae	Valencia	Spain	1998	grids	non	6884.5	-0.001139646	-0.001139646	avoider
Motacilla_alba	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.264398672	-0.01879432	avoider
Motacilla_cinerea	Motacillidae	Valencia	Spain	1998	grids	non	6884.5	-0.038991867	-0.021286142	avoider
Otus_scops	Strigidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Parus_ater	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	avoider
Parus_cristatus	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Parus_major	Paridae	Valencia	Spain	1998	grids	non	6884.5	-0.032642409	-0.015746957	avoider
Passer_domesticus	Passeridae	Valencia	Spain	1998	grids	non	6884.5	-0.249248914	0.285959098	exploiter
Passer_montanus	Passeridae	Valencia	Spain	1998	grids	non	6884.5	-0.037162502	-0.028219416	avoider
Phalacrocorax_carbo	Phalacrocoracidae	Valencia	Spain	1998	grids	non	6884.5	-0.003126858	-0.003126858	avoider
Phoenicurus_ochruros	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.137483813	0.067465254	avoider
Phylloscopus_collybita	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.319350726	0.048967986	avoider
Podiceps_cristatus	Podicipedidae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	-0.000855014	avoider
Regulus_ignicapillus	Reguliidae	Valencia	Spain	1998	grids	non	6884.5	-0.002276309	-0.002276309	avoider
Saxicola_torquata	Muscicapidae	Valencia	Spain	1998	grids	non	6884.5	-0.024406312	0.002950561	avoider
Serinus_serinus	Fringillidae	Valencia	Spain	1998	grids	non	6884.5	-0.366569971	0.225834922	avoider
Sterna_sandvicensis	Laridae	Valencia	Spain	1998	grids	non	6884.5	-0.000855014	0.000272994	avoider
Streptopelia_decaocto	Columbidae	Valencia	Spain	1998	grids	non	6884.5	0.344214899	0.053384174	exploiter
Strix_aluco	Strigidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Sturnus_unicolor	Sturnidae	Valencia	Spain	1998	grids	non	6884.5	-0.143835295	-0.06138695	exploiter

Sturnus_vulgaris	Sturnidae	Valencia	Spain	1998	grids	non	6884.5	-0.02956814	0.125814512	avoider
Sylvia_atricapilla	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.075141625	-0.065106076	avoider
Sylvia_melanocephala	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.064984513	0.01114054	avoider
Sylvia_undata	Sylviidae	Valencia	Spain	1998	grids	non	6884.5	-0.006793442	-0.002298879	avoider
Tachybaptus_ruficollis	Podicipedidae	Valencia	Spain	1998	grids	non	6884.5	-0.00256001	-0.00256001	avoider
Troglodytes_troglodytes	Troglodytidae	Valencia	Spain	1998	grids	non	6884.5	-0.000570197	-0.000570197	avoider
Turdus_merula	Turdidae	Valencia	Spain	1998	grids	non	6884.5	-0.119046067	-0.084960282	avoider
Turdus_philomelos	Turdidae	Valencia	Spain	1998	grids	non	6884.5	-0.006512494	-0.002017931	avoider
Turdus_viscivorus	Turdidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral
Upupa_epops	Upupidae	Valencia	Spain	1998	grids	non	6884.5	-0.000285192	-0.000285192	neutral

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