Universitat Autònoma de Barcelona

Ecología del jabalí (Sus scrofa)
en ambientes mediterráneos

Albert Peris Campodarbe

Tesis doctoral
2019

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Els doctors Ignasi Marco Sánchez, professor titular d'universitat de l'àrea de coneixement de Medicina i Cirurgia Animals de la Facultat de Veterinària de la Universitat Autònoma de Barcelona, i Encarna Casas Díaz, tècnic de suport a la recerca del Departament de Sanitat i d'Anatomia Animals.

Informen:

Que la memòria titulada *Ecología del jabalí (*Sus scrofa*) en ambientes mediterráneos*, presentada per Albert Peris Campodarbe per a l'obtenció del grau de doctor en Veterinària per la Universitat Autònoma de Barcelona, s'ha realitzat sota la nostra direcció i, un cop considerat que està satisfactòriament finalitzada, n'autoritzem la presentació per tal que sigui avaluada per la comissió corresponent.

I, perquè així consti als efectes que siguin oportuns, firmem el present informe a Bellaterra, 14 de setembre de 2019.

Ignasi Marco Sánchez
Director

Encarna Casas Díaz
Directora

Albert Peris Campodarbe
Doctorand

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ABSTRACT

The wild boar (*Sus scrofa*) is a highly adaptable omnivorous ungulate, generalist in terms of habitat and trophic requirements. Their populations are increasing in a generalized way in Europe, especially in recent decades, probably due to the conjunction of biological, environmental and anthropic causes. With the increase of their populations, damage to agriculture, collisions with vehicles, and the probability of transmission of diseases such as African and classical swine fever, brucellosis, tuberculosis, salmonellosis and Aujeszky's disease have also increased.

For the correct management of the species it is necessary to have reliable and accurate demographic, distribution and space ecology data. These data, still scarce, will help guide management strategies aimed at reducing populations, as well as deterring wild boars to avoid conflicts.

In this thesis, the viability of the camera trapping to estimate population abundance and the effects that bait has on these estimates in order to increase its effectiveness, has been studied. The work also focused on spatial ecology of wild boars. Specifically, a methodological approach has been proposed to home range estimate standardization. We also evaluated the space use patterns as well as the effects of age and sex on them, and the habitat factors that condition them. The habitat chosen for this thesis has been the Mediterranean environment, as there are few studies at the Iberian Peninsula level and also worldwide. This environment has a marked spatial and seasonal heterogeneity that determines the distribution and movements of the wild boar population.

The use of bait increased the precision of abundance estimates obtained through camera trapping. In addition, the assessment of the average of wild boar group size was substantially improved. The results indicate that relative abundance indices can be a good approximation to population abundance.

Regarding the study of home ranges and spatial use patterns, the result was that neither sex nor age had an effect on home range size. Two patterns of home ranges were observed, the predominant one, made up of several disjoint activity centers and the minor one, forming a compact area. Displacements between activity centers occurred mainly in winter and spring.

On a population scale, wild boar selected forest habitats, crops, streams and water points. In addition, this selection was seasonally differentiated: in spring and summer they selected the cereal crops, and in autumn and winter they selected the oak forests and vineyard crops.

This thesis provides necessary information to facilitate the comparison between work done in other areas, both for evaluating abundances from camera trapping, as well as for analysis of home ranges and, therefore, for habitat use and selection. After clarifying the methodological aspects, data are provided on the population size and spatial ecology of the species in a Mediterranean mountain environment. The data provided will facilitate the establishment of areas and periods of greatest potential conflict with human activities as well as the possibility of evaluating the effectiveness of management measures adopted to minimize conflicts.

RESUM

El senglar (*Sus scrofa*) és un ungulat omnívor summament adaptable, generalista pel que fa al tipus d'hàbitat i de recursos tròfics. Les seves poblacions estan augmentant de manera generalitzada a Europa, especialment en les darreres dècades, probablement per la conjunció de causes biològiques de l'espècie, ambientals i antròpiques. Amb l'augment de les seves poblacions també s'han incrementat els danys a l'agricultura, les col·lisions amb vehicles i la probabilitat de transmissió de malalties com la pesta porcina africana i clàssica, la brucel·losi, la tuberculosi, la salmonel·losi i la malaltia d'Aujeszky.

Per a la gestió correcta de l'espècie cal disposar de dades demogràfiques, de la seva distribució i de l'ecologia espacial fiables i precises. Aquestes dades, escasses encara, permetran orientar les estratègies de gestió encaminades a disminuir-ne les poblacions, així com a dissuadir els senglars per evitar conflictes.

En aquesta tesi s'ha estudiat la viabilitat del trampeig fotogràfic per estimar l'abundància poblacional i els efectes que sobre aquestes estimacions té aplicar esquer a fi d'incrementar-ne l'efectivitat. També s'ha aprofundit en l'ecologia espacial dels senglars. Concretament, s'ha proposat una aproximació metodològica que facilita l'estandardització en les estimacions d'espais vitals. També s'han avaluat els patrons de l'ús de l'espai, així com els efectes de l'edat i del sexe sobre aquests patrons, i els factors d'hàbitat que els condicionen. L'hàbitat escollit per a la present tesi ha estat l'ambient mediterrani, atès que hi ha pocs estudis en l'àmbit de la península Ibèrica i també a escala mundial. Aquest ambient presenta una marcada heterogeneïtat espacial i estacional que condiciona la distribució i els moviments de la població de senglars.

L'ús d'esquer va incrementar la precisió de les estimacions d'abundància obtingudes mitjançant trampeig fotogràfic. També va millorar substancialment la valoració de la mida mitjana de grup de senglars. Els resultats assenyalen que els índexs d'abundància relativa poden ser una bona aproximació a l'abundància poblacional.

Respecte a l'estudi dels espais vitals i els patrons d'ús de l'espai, el resultat va ser que ni el sexe ni l'edat van tenir efecte en la mida dels espais vitals. Es van observar dos tipus d'espai vital, el majoritari, format per diversos centres d'activitat separats, i el minoritari, que forma una àrea compacta. La majoria de desplaçaments entre centres d'activitat es van donar principalment a l'hivern i a la primavera.

A escala de població, els senglars van seleccionar hàbitats forestals, cultius, torrents i punts d'aigua. A més, aquesta selecció va ser estacionalment diferenciada: a la primavera i a l'estiu van seleccionar els camps de cereal, i a la tardor i a l'hivern van seleccionar els alzinars i les vinyes.

La present tesi aporta informació necessària per facilitar la comparació entre treballs realitzats en altres zones, tant d'avaluació d'abundàncies a partir de trampeig fotogràfic com d'anàlisi dels espais vitals i, per tant, d'ús i selecció d'hàbitat. Aclarits els aspectes metodològics, s'aporten dades sobre l'abundància poblacional i l'ecologia espacial de l'espècie en un ambient mediterrani de muntanya. Les dades aportades facilitaran l'establiment de les zones i dels períodes de major conflicte potencial amb les activitats humanes, així com la possibilitat d'avaluar l'efectivitat de les mesures de gestió adoptades per minimitzar conflictes.

RESUMEN

El jabalí (*Sus scrofa*) es un ungulado omnívoro sumamente adaptable, generalista en cuanto al tipo de hábitat y recursos tróficos. Sus poblaciones están aumentando, especialmente en las últimas décadas, de manera generalizada en Europa, probablemente por la conjunción de causas biológicas de la especie, ambientales y antrópicas. Con el aumento de sus poblaciones también se han incrementado los daños a la agricultura, las colisiones con vehículos y la probabilidad de transmisión de enfermedades como la peste porcina africana y clásica, la brucelosis, la tuberculosis, la salmonelosis y la enfermedad de Aujeszky.

Para la correcta gestión de la especie es necesario disponer de datos demográficos, de su distribución y de la ecología espacial fiables y precisos. Estos datos, escasos todavía, permitirán orientar las estrategias de gestión encaminadas a disminuir las poblaciones, así como a disuadir a los jabalíes para evitar conflictos.

En esta tesis se ha estudiado la viabilidad del trampeo fotográfico para estimar la abundancia poblacional y los efectos que sobre estas estimaciones tiene aplicar cebo con objeto de incrementar su efectividad. También se ha profundizado en la ecología espacial de los jabalíes. Concretamente, se ha propuesto una aproximación metodológica que facilita la estandarización en las estimaciones de dominios vitales. También se han evaluado los patrones en el uso del espacio, así como los efectos de la edad y el sexo sobre estos, y los factores de hábitat que los condicionan. El hábitat escogido para la presente tesis ha sido el ambiente mediterráneo, debido a que existen pocos estudios en el ámbito de la península ibérica y también a escala mundial. Este ambiente presenta una marcada heterogeneidad espacial y estacional que condiciona la distribución y los movimientos de la población de jabalíes.

El uso de cebo incrementó la precisión de las estimaciones de abundancia obtenidas mediante trampeo fotográfico. Además, mejoró sustancialmente la valoración del tamaño medio de grupo de jabalíes. Los resultados señalan que los índices de abundancia relativa pueden ser una buena aproximación a la abundancia poblacional.

Respecto al estudio de los dominios vitales y los patrones de uso del espacio, el resultado fue que ni el sexo ni la edad tuvieron efecto en el tamaño de los dominios vitales. Se observaron dos patrones de dominio vital, el mayoritario, formado por varios centros de actividad disyuntos, y el minoritario, que forma un área compacta. La mayoría de los desplazamientos entre centros de actividad se dieron principalmente en invierno y primavera.

A escala poblacional, los jabalíes seleccionaron hábitats forestales, cultivos, torrentes y puntos de agua. Además, esta selección fue estacionalmente diferenciada: en primavera y verano seleccionaron los campos de cereal, y en otoño e invierno seleccionaron los encinares y viñedos.

La presente tesis aporta información necesaria para facilitar la comparación entre trabajos realizados en otras zonas, tanto de evaluación de abundancias a partir de trampeo fotográfico como de análisis de los dominios vitales y, por tanto, de uso y selección de hábitat. Clarificados los aspectos metodológicos, se aportan datos sobre el tamaño poblacional y la ecología espacial de la especie en un ambiente mediterráneo de montaña. Los datos aportados facilitarán el establecimiento de las zonas y periodos de mayor conflicto potencial con las actividades humanas, así como la posibilidad de evaluar la efectividad de las medidas de gestión adoptadas para minimizar conflictos.

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“Mira profundamente en la naturaleza y entonces comprenderás todo mejor”.

Albert Einstein

CAPÍTULO I

1. Introducción

1.1. El jabalí como especie

1.1.1. Taxonomía y evolución

El jabalí pertenece al antiguo clado de los ungulados, nombre genérico que recibe el grupo de mamíferos de gran porte, mayoritariamente herbívoros, que en el transcurso de la evolución han sustituido las zarpas por pezuñas. Dicha adaptación parece ligada a la vida terrestre, la alimentación herbívora y una locomoción rápida.

Los ungulados actuales pertenecen principalmente a los órdenes *Perissodactyla* (caballos, tapires y rinocerontes) y *Artiodactyla* (cerdos, pecaríes, hipopótamos, cérvidos, bóvidos, caprinos, etc.). Tanto los perisodáctilos, ungulados dotados de un número impar de dedos cubiertos por una pezuña, como los artiodáctilos, ungulados con pezuñas pares, se diversificaron en el hemisferio norte al principio del Eoceno, hace unos 54 millones de años (Ma) (Macdonald, 2001).

Los jabalíes pertenecen a la superfamilia *Suioidea*, dentro del orden de los artiodáctilos, con un gran número de familias extintas en la actualidad. La divergencia entre los suidos del continente americano (*Tayassuidae*) y los del viejo mundo (*Suidae*, por ejemplo) se produjo a finales del Eoceno o principios del Oligoceno (34,5-39,6 Ma aprox.) (Fig. 1.1).

La familia *Suidae* se hizo aparente y se diversificó durante principios del Mioceno en África, Europa y Asia. El origen del género *Sus* no está exento de controversia y mayoritariamente se sitúa entre finales del Mioceno y principios del Plioceno (10 Ma) a partir de la datación del registro fósil. Lo que es un hecho indudable es que a finales del Plioceno este género colonizó la mayor parte del continente euroasiático y de las islas del sudeste asiático (Frantz et al., 2016).

El jabalí euroasiático, representante actual de la familia *Suidae*, es uno de los mamíferos con mayor distribución mundial, aspecto que ha facilitado su diversificación. Según el grupo de especialistas de la Unión Internacional para la Conservación de la Naturaleza (UICN), existen 17 subespecies. En la península ibérica se han descrito dos: *Sus scrofa scrofa*, que se encuentra en la zona norte, y que se extiende hacia el norte de Europa, y *Sus scrofa meridionalis*, que habita en el tercio sur (Étienne, 2004).

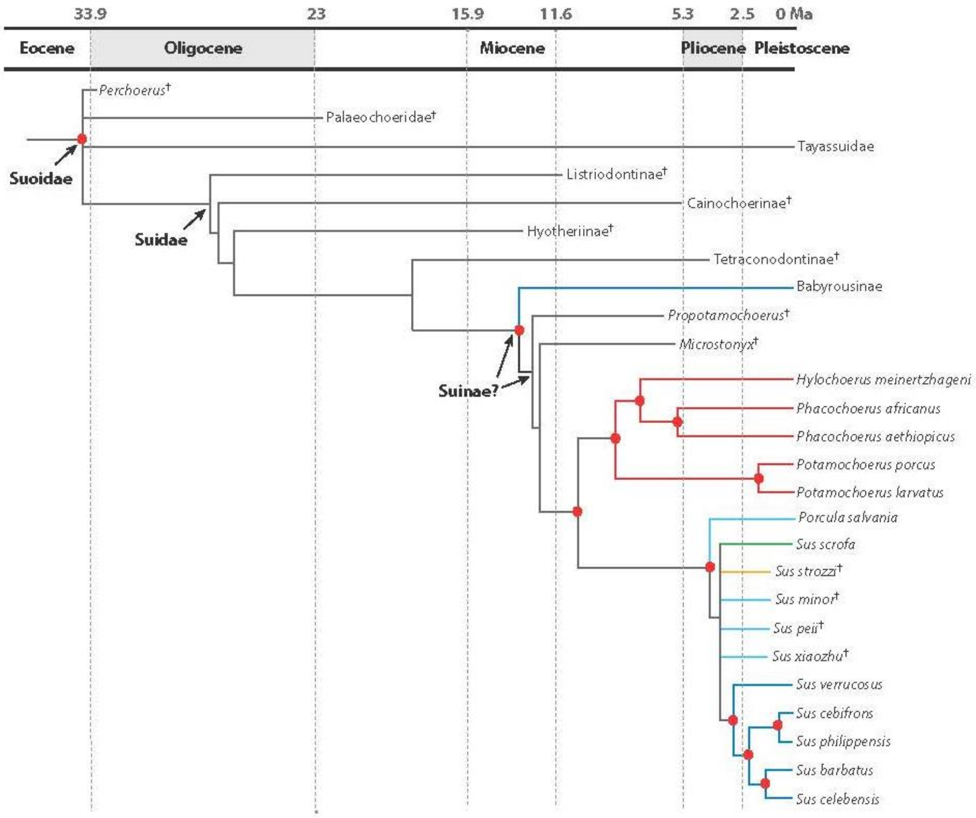


Figura 1.1. Filogenia de la superfamilia *Suioidea* (Frantz et al., 2016).

Un aspecto que dificulta el análisis taxonómico del jabalí es la gran variación genética y morfológica inducida por la domesticación. Tradicionalmente se ha pensado que la especie fue objeto de tres procesos de domesticación independientes a partir de diferentes subespecies: uno en Europa hace 8.000-9.000 años y los otros dos en Asia (Groves, 1981). Algunas formas domésticas se asilvestraron y muestran un fenotipo intermedio entre el jabalí y el cerdo doméstico, de modo que constituyeron nuevas subespecies (Rosell et al., 2001). Sin embargo, recientemente, a partir de los datos de la secuencia del genoma completo (Frantz et al., 2016), se ha evidenciado que este proceso de domesticación fue muy difuso. Durante muchos milenios se produjo la mezcla repetida y el flujo de genes de los jabalíes a las poblaciones domesticadas.

La domesticación de la especie, por tanto, no debe considerarse como una serie de eventos fijos que ocurrieron hace unos 10.000 años, sino como un proceso gradual, en el que tanto los animales como los humanos desempeñaron su papel. Inicialmente, los jabalíes podrían haberse sentido atraídos a los asentamientos humanos como una forma fácil de acceder a los alimentos, y es solo después de milenios que los humanos podrían haber comenzado a mantener a los cerdos como una especie verdaderamente domesticada. Este proceso ocurrió en Europa y China a ritmos muy diferentes, ya que los cerdos se mantuvieron en recintos dentro de asentamientos humanos en una etapa relativamente temprana en China, mientras que en Europa, hasta la Edad Media tardía, se permitió que los cerdos vagaran libremente por los bosques como rebaños domesticados (White, 2011).

1.1.2. Distribución

El jabalí es uno de los mamíferos con distribución más amplia debido a su gran expansión en el área de distribución natural de la especie y a las introducciones realizadas por los humanos fuera de su área nativa (Apollonio et al., 2010) (Fig. 1.2). Aunque es originaria de Europa, Asia y el norte de África, se pueden encontrar formas silvestres, asilvestradas e incluso formas híbridas de esta especie en todos los continentes a excepción de la Antártida (Mitchell-Jones et al., 1999; Oliver and Leus, 2008; Scandura et al., 2011).

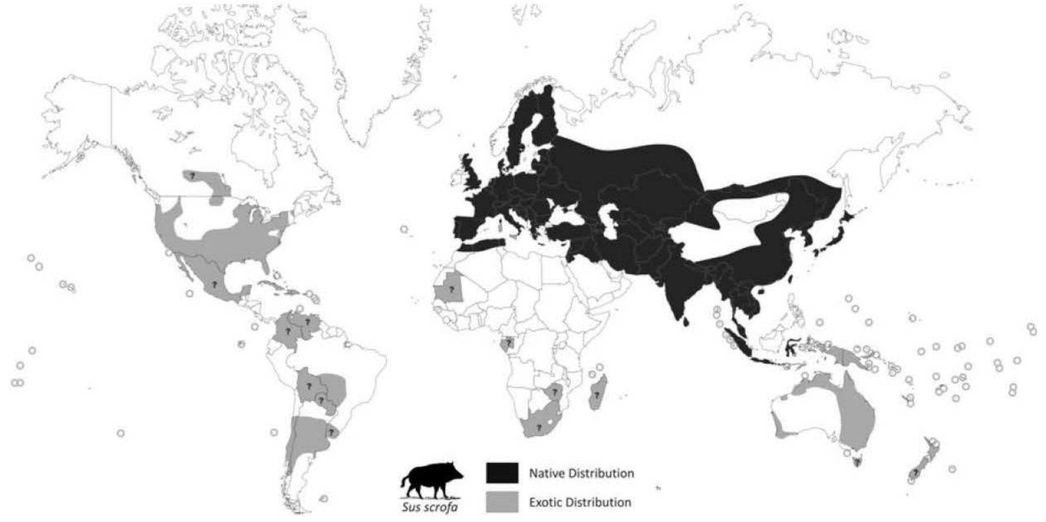


Figura 1.2. Distribución mundial de las poblaciones naturales e introducidas del jabalí (Barrios-Garcia and Ballari, 2012).

En su amplia distribución han jugado un papel importante las translocaciones. De hecho, el jabalí representa una de las introducciones intencionales de mamíferos más antiguas registradas por el ser humano. Los primeros exploradores del continente americano introdujeron ejemplares, principalmente de la variedad doméstica o cruces con jabalíes, como fuente de proteínas. Sin embargo, las introducciones más recientes están motivadas por la caza comercial (Courchamp et al., 2003; Long, 2003). El jabalí ha estado sujeto a extinciones locales (islas británicas, Escandinavia, gran parte de la antigua Unión Soviética, norte de África) en función de su incompatibilidad con las actividades agrícolas, la ganadería extensiva y la destrucción del hábitat.

Los cambios en los usos del territorio, principalmente el abandono del mundo rural, que ha propiciado la forestación de extensas zonas, han permitido tanto la recuperación natural de las poblaciones europeas como la reintroducción por parte del ser humano de nuevas variedades de jabalí en lugares donde habían desaparecido (Herrero, 2003).

1.1.3. Biología

1.1.3.1. Morfología

El jabalí es un mamífero de tamaño mediano, compacto, robusto y de complexión musculosa. Su cabeza, voluminosa y fusiforme, termina en un morro o jeta largo y se une al cuerpo mediante 7 vértebras cervicales extremadamente cortas. El cuello del jabalí, por tanto, es corto y abultado, lo cual le confiere poca movilidad. De la anatomía del jabalí destaca, además, su gran tronco, con mayor desarrollo del tercio anterior, sus extremidades cortas, cola relativamente larga con un mechón de pelo al final, orejas erectas y peludas, y pelaje abundante.

Presenta dimorfismo sexual. Los machos son mayores y pesan alrededor del 20 % más que las hembras (de media entre 70 y 90 kg los machos y 50 y 65 las hembras). Tienen el cráneo más largo y mayor desarrollo de los caninos. Los machos, además de presentar testículos, pincel de pelos en la zona del pene y una crin dorsal más desarrollada, presentan un engrosamiento más aparente alrededor del cuerpo que evita las lesiones importantes en las luchas durante la época del celo. En las hembras adultas, durante el verano, se hacen aparentes las mamas (Rosell et al., 2001).

1.1.3.2. Pelaje

El color del pelaje es variable, comúnmente de tonos que van del grisáceo al negro. Las extremidades y el hocico suelen ser más oscuros que el resto del cuerpo. Presentan una crin que se eriza en estados de alerta o en interacciones agonísticas.

En nuestras latitudes, el jabalí presenta un cambio estacional del pelaje. En verano, las cerdas (pelos largos y ásperos) son más cortas y poco densas, mientras que en invierno el pelaje lo forman las cerdas y una borra de pelos densos y suaves con una función aislante.

Las crías nacen con unas características rayas longitudinales a lo largo del cuerpo que le confieren un color críptico y les permiten pasar desapercibidas. Por su patrón de colores se les ha dado el nombre de rayones. Sobre los 5 o 6 meses de edad mudan el pelaje y adquieren una coloración rojiza uniforme, por lo que se les conoce con el nombre de bermejos (Fig. 1.3). Finalmente, entre los 10 y 12 meses de edad cambian de coloración adquiriendo las tonalidades marrones y negras de los animales adultos. Los machos de mayor edad pueden adoptar una coloración gris canosa generalizada.

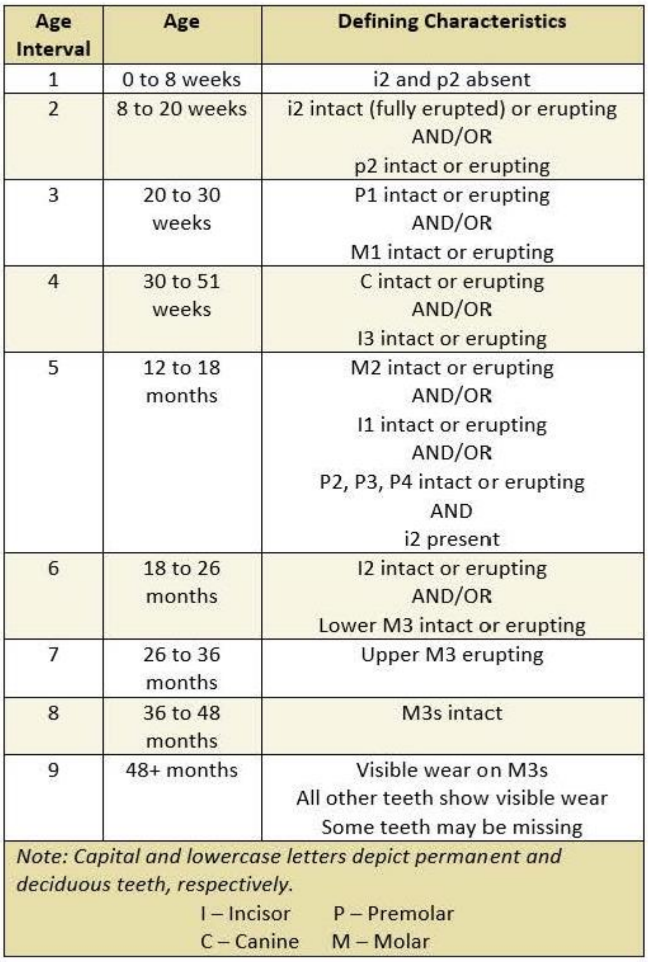
Figura 1.3. Fotografía, a la izquierda, de una hembra adulta con marca auricular y sus rayones. A la derecha grupo de bermejos.

1.1.3.3. Dentición

Los ejemplares adultos poseen un total de 44 piezas dentales, 11 en cada hemimandíbula. La fórmula de la dentición decidua es 3.1.3.0/3.1.1.0, mientras que la definitiva es 3.1.4.3/3.1.4.3 (Matschke, 1967). Los números anteriores corresponden a la fórmula dentaria de la especie, que se cifra mediante un quebrado en el que cada número representa un tipo de diente: en el numerador se consigna la cantidad de piezas de ese tipo que hay en la hemimandíbula superior; y en el denominador, la correspondiente a la hemimandíbula inferior del mismo lado. Concretamente, por orden se numeran los incisivos, caninos, premolares y molares. Los caninos, también llamados colmillos o navajas, son las piezas dentales más aparentes. En ocasiones se pueden observar exteriormente, especialmente en los machos. Los caninos superiores encajan perfectamente con los inferiores, de manera que, mediante desgaste, adquieren formas angulosas que permiten infligir heridas a otros individuos durante las luchas intraespecíficas. También los utilizan durante la defensa activa frente a depredadores y para el marcaje de la vegetación.

Tanto el tamaño como el número de piezas dentarias aumentan con la edad de los jabalíes, por lo que la dentición se usa comúnmente como sistema de datación de los individuos. Los jabalíes y cerdos salvajes se pueden clasificar en nueve intervalos de edad que vienen definidos por la erupción o reemplazo de dientes específicos desde el nacimiento hasta los tres años (Tabla 1.1). Como punto de partida se debe verificar si el canino es permanente, en tal caso consideraremos que el ejemplar se encuentra en el intervalo de edad 4 (de 30 a 51 semanas). Si el canino es deciduo, se verifica la presencia o erupción del incisivo 3 (I3). Si ni el canino es permanente ni los I3 están presentes, consideraremos que el individuo se encuentra como máximo en el intervalo de edad 3 (de 20 a 30 semanas).

Tabla 1.1. Clases de edad en función de la dentición, extraída de la adaptación de USDA-APHIS-Wildlife Services (2018) sobre Matschke (1967).



Age Interval	Age	Defining Characteristics
1	0 to 8 weeks	i2 and p2 absent
2	8 to 20 weeks	i2 intact (fully erupted) or erupting AND/OR p2 intact or erupting
3	20 to 30 weeks	P1 intact or erupting AND/OR M1 intact or erupting
4	30 to 51 weeks	C intact or erupting AND/OR I3 intact or erupting
5	12 to 18 months	M2 intact or erupting AND/OR I1 intact or erupting AND/OR P2, P3, P4 intact or erupting AND i2 present
6	18 to 26 months	I2 intact or erupting AND/OR Lower M3 intact or erupting
7	26 to 36 months	Upper M3 erupting
8	36 to 48 months	M3s intact
9	48+ months	Visible wear on M3s All other teeth show visible wear Some teeth may be missing

Note: Capital and lowercase letters depict permanent and deciduous teeth, respectively.

I – Incisor P – Premolar

C – Canine M – Molar

Existen otros sistemas de datación que requieren análisis alométricos o de laboratorio más complejos (Iff, 1983; Sáez-Royuela et al., 1989). Considerando que en el caso de los cerdos domésticos la erupción y el reemplazo dental se producen antes que en el jabalí, el grado de hibridación y la elevada variabilidad individual conducen a obtener estimaciones de la edad aproximadas.

1.1.3.4. Reproducción

El celo se da mayoritariamente en otoño, entre los meses de septiembre y enero, con importantes diferencias entre regiones. En general, tiene lugar una vez al año, aunque en épocas de abundancia de alimento se puede producir un nuevo celo a final de la primavera. Es conocido también que una hembra que pierde sus crías puede entrar en celo aproximadamente un mes más tarde, lo cual explicaría que podamos encontrar rayones en épocas diferentes de las habituales (Étienne, 2004). Durante el celo tienen lugar importantes luchas entre los machos que fecundan a las hembras de una o varias piaras.

La gestación dura 4 meses aproximadamente (3 meses, 3 semanas y 3 días). Los partos se producen principalmente entre febrero y abril, aunque también existe un pico menos importante de nacimientos en otoño. En los días previos al parto, la jabalina se aísla del grupo y construye una cama de parto que elabora mediante el acúmulo de hierbas y arbustos cortados por ella misma. Esta cama se suele ubicar en zonas con elevado recubrimiento arbustivo.

La reproducción de los jabalíes depende de la condición física de los ejemplares, y esto, a su vez, depende de las épocas de mayor disponibilidad de alimento. En ambientes mediterráneos, la primera ovulación de las jabalinas se da al alcanzar los 30 kg de peso como mínimo, lo cual se corresponde con los 10-11 meses de edad y coincide con los meses de la caída de la bellota, que se produce entre finales de octubre y principios de noviembre (Santos et al., 2006), pudiéndose alargar hasta enero. Sin embargo, en ambientes pobres en alimento las hembras pueden retrasar su primer celo hasta el año y medio de edad.

El número de crías por camada también está relacionado con la disponibilidad trófica y, por tanto, con la condición física de la progenitora. El mayor número de descendencia lo tienen las hembras de mayor peso. El tamaño medio de camada suele ser de 4 o 5 crías (Fernández-Llario, 2017).

Únicamente producen leche aquellas mamas de la hembra que son utilizadas por los rayones y estas son aparentes en el ralo pelaje estival. Además, las mamas anteriores producen más leche que las posteriores. Como cada cría utiliza siempre una misma mama, los animales que utilizan las mamas anteriores se desarrollan antes (Blanco, 1998).

1.1.3.5. Comportamiento y comunicación

Los jabalíes presentan una estructura social matrilineal, formada por hembras con individuos juveniles y crías. Los machos adultos suelen ser solitarios, pero en ocasiones van acompañados de individuos subadultos (Blanco, 1998; Bon et al., 1986; Maselli et al., 2014; Rosell et al., 2004). Los machos se agregan a las hembras en otoño durante el periodo de celo y constituyen grupos más numerosos (Bon et al., 1986; Dardaillon, 1984; Fernández-Llario et al., 1996; Rosell et al., 1998).

La composición de los grupos sociales, denominados piaras, cambia a lo largo del año como consecuencia del celo, los partos y la caza. Otro aspecto que condiciona la composición de las piaras es la disponibilidad de recursos tróficos. Los grupos dependen en gran medida de la presencia de las jabalinas dominantes (Gaillard et al., 1987), que son las responsables de la cohesión grupal (Janeau et al., 1988; Sodeikat and Pohlmeyer, 2003; Thurfjell, 2011). La mortalidad, principalmente de hembras adultas, se ha considerado una causa potencial que afecta la organización social de las poblaciones de jabalí (Janeau et al., 1988; Rosell et al., 2004). La caza, por tanto, puede desestabilizar las estructuras sociales y espaciales, induciendo cambios en la selección del hábitat de las hembras reproductivas, además de los cambios en la proporción de sexos de la descendencia (Keuling, 2009; Milner et al., 2007; Scillitani et al., 2010; Tuytten and McDonald, 2000).

La morfología facial indica la importancia que tiene el olfato en esta especie. Este sentido se encuentra muy desarrollado y le permite ser eficiente en la búsqueda de alimentos ocultos, llevar a cabo emparejamientos en la época de celo y detectar depredadores potenciales. El oído también es un sentido importante en el caso del jabalí y le permite detectar sonidos producidos por otras especies y vocalizaciones intraespecíficas. El menos desarrollado de sus sentidos es la vista.

En la comunicación entre individuos juegan un papel fundamental las secreciones glandulares. En este sentido, los jabalíes poseen diversos tipos de glándulas exocrinas (Rosell et al., 2001):

- Las carpianas, situadas en las extremidades anteriores, que producen una secreción más o menos continua que deja un olor característico de cada animal entre la vegetación por la que se desplazan.
- La glándula prepucial de los machos, que utilizan para dejar señales olorosas y marcar su territorio.
- Las glándulas lacrimales, que en el caso de las hembras aportan también información sobre su estado reproductivo.
- La glándula mentoniana facial, con función de marcaje.

El repertorio vocal de los jabalíes es rico. Marler (1975) propuso que la evolución de vocalizaciones graduales y discretas depende del hábitat y la estructura social de una especie. Considerando el comportamiento social de los jabalíes (Meynhardt, 1990), se podría esperar una variación acústica continua, pero el hecho de que a menudo ocupen hábitats densos y cerrados (Wilson and Mittermeier, 2011) facilitaría tipos de llamadas más discretas; ambos tipos de vocalizaciones han sido descritas (Garcia et al., 2016). Se ha clasificado el repertorio vocal de jabalí en cuatro tipos de voces: gruñidos, grito-gruñidos, gritos y sonidos tipo trompeta. Si bien la mayoría de las llamadas podrían clasificarse en estas categorías utilizando criterios objetivos, también se han encontrado evidencias que respaldan una interpretación gradual de algunas vocalizaciones. Concretamente, los chillidos-gruñidos representarían una vocalización de transición entre gruñidos y chillidos (Garcia et al., 2016).

1.1.3.6. Actividad

Los jabalíes son principalmente crepusculares y nocturnos. En las zonas donde apenas son perseguidos y cazados tienen una actividad diurna importante. Existen diferencias entre sexos y edades en cuanto al tiempo dedicado a cada actividad. Mientras que las hembras dedican gran parte de su actividad a la alimentación, tanto machos adultos como jóvenes dedican mucho más tiempo a la locomoción. Estas diferencias encuentran respuesta en la estructura social, puesto que de la capacidad de locomoción de los machos adultos depende el mayor éxito reproductivo y, en machos jóvenes, el establecimiento de jerarquías. En cuanto a las hembras, como se ha comentado anteriormente, su fecundidad depende en buena parte de su peso y, por lo tanto, de la alimentación (Blanco, 1998).

La actividad de esta especie se puede detectar indirectamente, a través de rastros muy evidentes, como son:

- Hozaduras: marcas en el suelo que se producen mientras buscan alimentos y que pueden alcanzar grandes superficies (Fig. 1.4).

Figura 1.4. Típicas hozaduras en campos sin cultivar.

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- Rascaderos: descortezamientos en especies arbóreas, principalmente resinosas, que utilizan los animales con fines de marcaje y desparasitación. Además, los rascaderos pueden contener colmilladas (Fig. 1.5).

Figura 1.5. Rascadero en pino carrasco y encina cerca de una bañera.

- Bañeras: excavaciones en terrenos arcillosos en los que se acumula agua. Los jabalíes las utilizan para revolcarse y bañarse en barro. En la proximidad de las bañeras suelen observarse rascaderos con barro y pelos adheridos a los troncos (Fig. 1.6).

Figura 1.6. Bañera o revolcadero de jabalí.

- “Chicles”: vegetación herbácea masticada para extraer minerales y nutrientes esenciales.

- Camas: lugares seleccionados para dormir que suelen estar cerca de algún árbol de gran porte. Los jabalíes limpian de hojarasca una superficie pequeña que será utilizada por un individuo o un grupo familiar.

- Paridera o nido: acumulación de hierbas y arbustos en lugares con importante cobertura arbustiva.

- Excrementos: muy característicos en cuanto a forma y tamaño. El color y textura dependerá de la alimentación. En ocasiones se encuentran en forma de letrinas con gran cantidad de ellos en lugares estratégicos (Fig. 1.7).

Figura 1.7. Excremento algo disgregado sobre acículas de pino.

- Huellas: características, con dos pezuñas redondeadas. Pueden marcarse también las pezuñas de los dedos 1 y 4, en una posición posterior y más discretamente que las principales (Fig. 1.8).

Figura 1.8. Huella de una pezuña con bordes redondeados, marcando más profundamente la parte anterior.

- Dentelladas o colmilladas: marcas aparentes de los incisivos en árboles y arbustos con finalidad de marcaje.

- Pasos: pasillos estrechos entre la maraña de arbustos y lianas, libres de vegetación, que se producen en los desplazamientos de la especie.

1.1.4. Ecología de la especie

1.1.4.1. Ecología poblacional

El jabalí presenta una tasa de reproducción muy elevada comparada con otros ungulados, lo cual se corresponde con tasas de crecimiento poblacional especialmente altas. Se ha descrito como un estratega de la r, que mediante la elevada descendencia hace frente a las numerosas bajas anuales (Bieber and Ruf, 2005; Holland et al., 2009; Keuling et al., 2013).

La mayor causa de mortalidad, con diferencia, es la caza, seguida de la colisión con vehículos. Entre las causas naturales, se producen muertes por inanición debido a condiciones climáticas extremas, enfermedades y depredación de lobo (Massei et al., 2015).

Sáez-Royuela y Tellería (1986) analizaron la evolución de las poblaciones de jabalí desde la década de los sesenta hasta los ochenta y describen un elevado incremento en las poblaciones simultáneamente en diferentes países europeos y una estabilización en la década de los ochenta. Estos incrementos poblacionales se atribuyeron a una combinación de factores biológicos, como el alto rendimiento reproductivo y el potencial de dispersión, así como a otros factores, como la falta de grandes depredadores, la reforestación, liberaciones deliberadas de la especie para la caza, la aplicación de alimentación suplementaria, la alteración del hábitat debido a actividades humanas e inviernos suaves que mejoraron su supervivencia.

En la actualidad, los factores indicados como posibles causas del incremento poblacional siguen actuando, y en la revisión de Massei *et al.* (2015) se pone de relieve este aumento en toda Europa. Un nuevo factor que habría que añadir es la estabilización o disminución del número de cazadores en la mayoría de los países.

El hecho es que las poblaciones de jabalí, en la península ibérica y el resto de Europa, están experimentado un incremento muy notable en los últimos años. Entre las causas que favorecen el aumento poblacional también se ha citado el cambio climático, que, al producirse mayores temperaturas y menor frecuencia de nevadas, facilita el acceso de los jabalíes a los alimentos durante el invierno, lo cual tiene efectos importantes en su condición física y, por tanto, en la tasa reproductiva (Jędrzejewska et al., 1997).

La adaptabilidad de la especie se manifiesta también en la rápida respuesta a la presencia de recursos tanto de origen natural como antrópico. En este sentido, Bieber y Ruf (2005), en un estudio realizado durante varias décadas en Alemania y el este de Europa, observaron que los jabalíes adaptaban sus estrategias vitales en función de las condiciones ambientales y de la producción de semillas, adelantando la madurez sexual e incrementando la fertilidad y, por tanto, la tasa de crecimiento poblacional en épocas de abundancia. Con baja disponibilidad de alimento, las hembras jóvenes no adelantaban la madurez y destinaban los recursos disponibles a la supervivencia. En las hembras adultas, por el contrario, no se observó una relación directa entre las condiciones ambientales y la fecundidad.

Como respuesta al incremento de las poblaciones de jabalí y la disminución de licencias de caza, se suele incrementar la presión cinegética mediante el aumento del número de batidas de caza recreativa y el periodo hábil. A pesar de todo, los datos de las estadísticas de caza en Europa parecen indicar que la tendencia poblacional no revierte con el incremento de la presión de caza, más bien al contrario (Álvarez, 2017) (Fig. 1.9.). La explicación en el caso de las hembras es que, al invertir más recursos en adelantar la reproducción, la mortalidad es mayor, por lo que la proporción de juveniles respecto a la de adultos es mayor que en el caso de los machos. En relación con esta respuesta, se ha observado que la contribución a la reproducción de las hembras juveniles es mucho mayor en poblaciones sometidas a elevada presión cinegética (Sabrina et al., 2009). Igual ocurre en otros mamíferos generalistas como el zorro, una intensa presión cinegética puede hacer que las hembras maduren antes y que, además, tanto el número de camadas como el número de crías por camada se incrementen.

Figura 1.9. Evolución de jabalíes cazados en las últimas décadas (Massei et al., 2015).

Toïgo *et al.* (2008) estudiaron una población de jabalíes en Francia sometida a elevada presión de caza. Observaron que, a pesar del incremento de animales cazados cada año, la población seguía aumentando, igual que pasa en la mayoría de zonas de Europa. Aunque pueda parecer una contradicción, las elevadas tasas de mortalidad producidas por la caza eran las responsables de que las hembras invirtieran más recursos en la reproducción, adelantando la edad de primera reproducción. Una prueba de la generalización de este proceso sería el rejuvenecimiento de la población, que se ha puesto de manifiesto en la edad media de los animales cazados en Cataluña y también España (Aran Servicios Medioambientales S. L., 2018).

Otros trabajos recientes ponen el foco en la disminución de las licencias de caza y la baja eficiencia de los cazadores para explicar la limitada o nula repercusión de la actividad cinegética en el control de las poblaciones de jabalí (Keuling et al., 2016; Massei et al., 2015; Quirós-Fernández et al., 2017).

1.1.4.2. Ecología trófica

Acorde a su dentición, el jabalí es una especie omnívora de amplio espectro que puede aprovechar los recursos tróficos que encuentra en los diferentes ecosistemas que ocupa. En la península ibérica, entre los alimentos de origen vegetal más frecuentes en la dieta del jabalí se encuentran las bellotas, hayucos, castañas, diferentes raíces, hierbas y cultivos como maíz, trigo, cebada, etc. En menor proporción, también se alimenta de lombrices, insectos, anfibios, reptiles, huevos, carroña en los montes, restos orgánicos en vertederos, etc.

La dieta presenta una marcada estacionalidad que le permite aprovechar los recursos que aparecen en cada época y zona. Los diferentes estudios sobre dieta del jabalí en la península ibérica ponen de manifiesto la composición principal de la fracción vegetal con pequeños aportes de proteína animal. Este patrón general presenta variaciones geográficas y estacionales, lo cual refleja la capacidad de la especie de adaptarse a la disponibilidad de alimentos localmente por hábitats y estaciones (Fernández-Llario et al., 1996).

La mayoría de los alimentos los encuentra hozando con su potente morro en el subsuelo (Blanco, 1998). Esta actividad deja unas marcas visibles denominadas hozaduras que, aunque pueden detectarse durante todo el año en suelos blandos, presentan un máximo en septiembre y un mínimo en los meses más cálidos (Fernández-Llario et al., 1996).

El agua se encuentra entre los elementos indispensables en la dieta del jabalí. Al consumir gran cantidad de frutos secos y producir abundante saliva, necesita una elevada hidratación. Este aspecto hace que, aunque la especie se adapte a lugares secos, dependa de hábitats con disponibilidad de agua (Étienne, 2004).

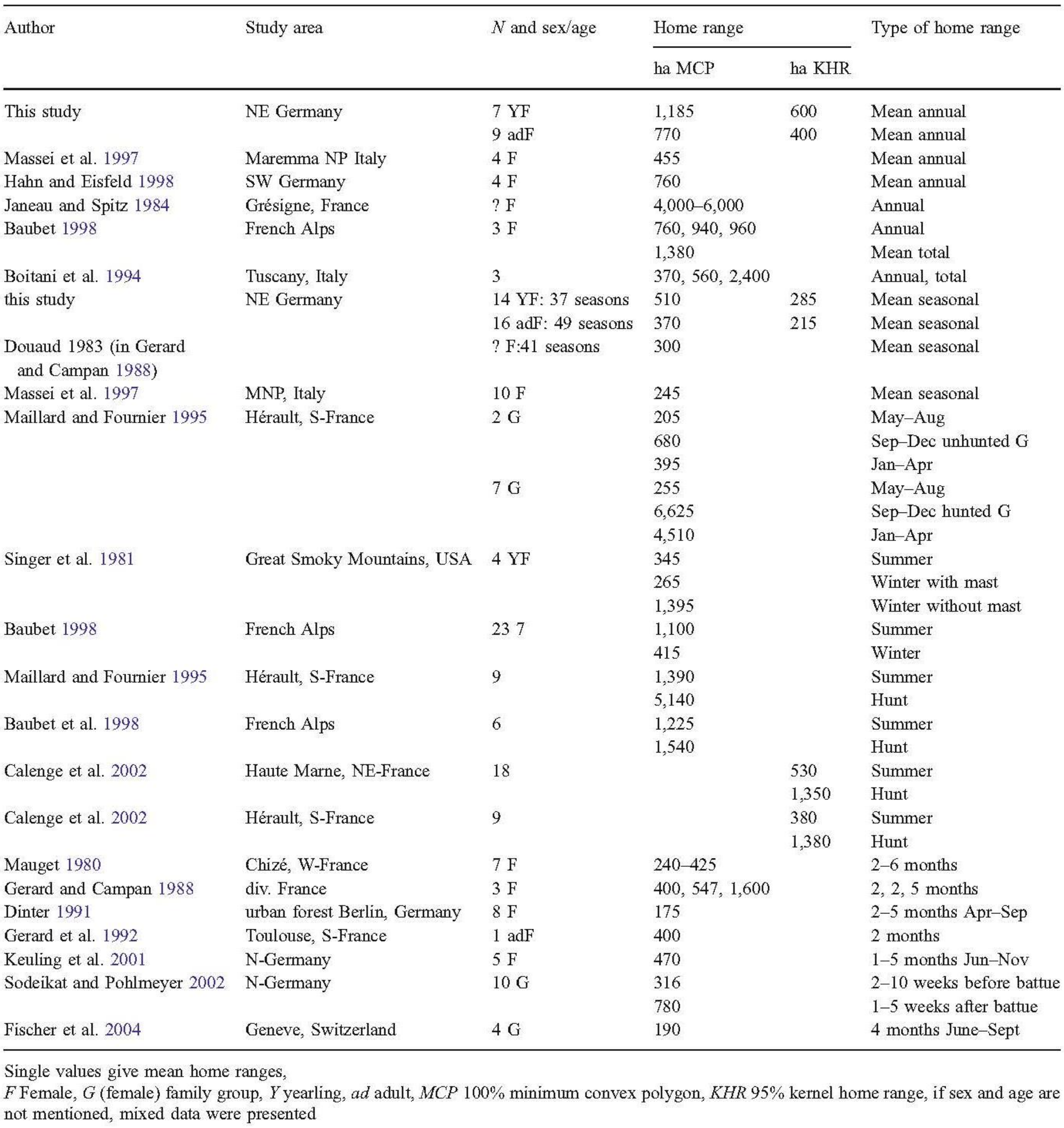
1.1.4.3. Ecología espacial (uso del espacio y selección de hábitat)

La ecología espacial de las especies, en el sentido de conocer el uso del espacio, los movimientos, el tamaño de los dominios vitales, las áreas núcleo (*core areas*) y la selección del hábitat, nos permite comprender patrones espaciales y los recursos que los condicionan.

En general, los aspectos mencionados están correlacionados, pues el uso del espacio suele ser el reflejo de la búsqueda de aquellos ambientes que proporcionan mejores refugios y zonas de alimentación.

El tamaño de los dominios vitales y la productividad de los hábitats se relacionan mediante la teoría del forrajeo óptimo (MacArthur and Pianka, 1966), dándose los dominios vitales más pequeños en determinadas temporadas y en áreas más productivas (Börger et al., 2006b; Kie et al., 2002). Las excepciones a la teoría del forrajeo óptimo están relacionadas con otras actividades para mejorar el estado físico, como aparearse y reproducirse o evitar la depredación (Lind and Cresswell, 2005). Los cambios en el tamaño de los dominios vitales también pueden depender de la estación del año, de la disponibilidad de alimento y de las molestias producidas por las actividades humanas, además de factores individuales como la edad, el estado reproductivo y el sexo. Asimismo, la disponibilidad de alimentos juega un papel decisivo en el comportamiento espacial del jabalí, ya que los cambios en la disponibilidad de recursos pueden llevar a variaciones en el uso del espacio y el hábitat (Keuling et al., 2008a) (Tabla 1.2).

Tabla 1.2. Dominios vitales obtenidos en diferentes estaciones del año y países (Keuling et al., 2008a).



Author	Study area	*N* and sex/age	Home range		Type of home range
			ha MCP	ha KHR	
This study	NE Germany	7 YF	1,185	600	Mean annual
		9 adF	770	400	Mean annual
Massei et al. 1997	Maremma NP Italy	4 F	455		Mean annual
Hahn and Eisfeld 1998	SW Germany	4 F	760		Mean annual
Janeau and Spitz 1984	Grésigne, France	? F	4,000–6,000		Annual
Baubet 1998	French Alps	3 F	760, 940, 960		Annual
			1,380		Mean total
Boitani et al. 1994	Tuscany, Italy	3	370, 560, 2,400		Annual, total
this study	NE Germany	14 YF: 37 seasons	510	285	Mean seasonal
		16 adF: 49 seasons	370	215	Mean seasonal
Douaud 1983 (in Gerard and Campan 1988)		? F:41 seasons	300		Mean seasonal
Massei et al. 1997	MNP, Italy	10 F	245		Mean seasonal
Maillard and Fournier 1995	Hérault, S-France	2 G	205		May–Aug
			680		Sep–Dec unhunted G
			395		Jan–Apr
		7 G	255		May–Aug
			6,625		Sep–Dec hunted G
			4,510		Jan–Apr
Singer et al. 1981	Great Smoky Mountains, USA	4 YF	345		Summer
			265		Winter with mast
			1,395		Winter without mast
Baubet 1998	French Alps	23 7	1,100		Summer
			415		Winter
Maillard and Fournier 1995	Hérault, S-France	9	1,390		Summer
			5,140		Hunt
Baubet et al. 1998	French Alps	6	1,225		Summer
			1,540		Hunt
Calenge et al. 2002	Haute Marne, NE-France	18		530	Summer
				1,350	Hunt
Calenge et al. 2002	Hérault, S-France	9		380	Summer
				1,380	Hunt
Mauget 1980	Chizé, W-France	7 F	240–425		2–6 months
Gerard and Campan 1988	div. France	3 F	400, 547, 1,600		2, 2, 5 months
Dinter 1991	urban forest Berlin, Germany	8 F	175		2–5 months Apr–Sep
Gerard et al. 1992	Toulouse, S-France	1 adF	400		2 months
Keuling et al. 2001	N-Germany	5 F	470		1–5 months Jun–Nov
Sodeikat and Pohlmeyer 2002	N-Germany	10 G	316		2–10 weeks before battue
			780		1–5 weeks after battue
Fischer et al. 2004	Geneve, Switzerland	4 G	190		4 months June–Sept

Single values give mean home ranges,
F Female, *G* (female) family group, *Y* yearling, *ad* adult, *MCP* 100% minimum convex polygon, *KHR* 95% kernel home range, if sex and age are not mentioned, mixed data were presented

A pesar de ser una especie generalista también en cuanto a los hábitats donde vive, se ha descrito cierta preferencia por los bosques de hoja caduca y planifolios (Fonseca, 2008, 1997; Meriggi and Sacchi, 2001), que proporcionan abundante alimento. Los bosques mixtos de coníferas son más pobres en disponibilidad de alimento, pero ofrecen lugares adecuados como refugio con abundante sotobosque. Cabe destacar que muchos de los bosques de coníferas presentes en ambientes mediterráneos son mixtos con planifolios.

En ambientes mediterráneos, la disponibilidad de agua y la distribución y productividad de bellotas de los bosques de encinas y robles son factores que condicionan la ecología espacial de la especie. La bellota constituye una pieza fundamental en la alimentación del jabalí en este tipo de ambiente (Massei et al., 1997), ya que, en ausencia de ellas, los jabalíes diversifican su alimentación.

Los campos de cultivo representan otro importante factor explicativo del uso del espacio por parte del jabalí, puesto que representan una fuente importante de recursos, principalmente en verano (Fonseca, 2008; Keuling et al., 2009; Sodeikat and Pohlmeyer, 2002).

1.1.5. Gestión de la especie

El incremento de las poblaciones de jabalí en las últimas décadas ha ido acompañado del aumento de conflicto con las personas. Entre los impactos negativos que la especie produce, destacan los daños a los cultivos, efectos sobre la abundancia de plantas y animales, especialmente en humedales, colisiones con vehículos, daños a bienes y reservorio para la transmisión de enfermedades al ganado y al ser humano (Acevedo et al., 2007; Corn et al., 2009; Engeman et al., 2011; Massei and Genov, 2004; Ruiz-Fons et al., 2008; Seward et al., 2004).

Fuera de su área de distribución natural el jabalí ha sido incluido en la lista de las 100 peores especies invasoras del mundo por el Grupo de Especialistas en Especies Invasoras de la UICN. Contrariamente, otros autores han destacado los efectos positivos incluso fuera de su área de distribución natural. En zonas donde la caza representa una fuente importante de ingresos económicos, el jabalí puede liberar la fauna silvestre de la sobreexplotación, actuando como especie objetivo de caza de reemplazo. Además, en algunas áreas esta especie proporciona presas adicionales a los carnívoros nativos (Barrios-Garcia and Ballari, 2012).

En su área de distribución natural, los jabalíes también son muy preciados como especie de caza mayor, representan un componente valioso del patrimonio natural y son una fuente de alimento para depredadores, principalmente lobos (Leaper et al., 1999; Meriggi et al., 1996).

Con el aumento de los impactos negativos, tanto propietarios y gestores, por un lado, como las administraciones, por el otro, se han visto obligados a definir y articular medidas de gestión encaminadas a disuadir a los animales para evitar daños, así como a intentar disminuir sus poblaciones. Massei, Roy y Bunting (2011) realizan una revisión de métodos utilizados para reducir el impacto de los jabalíes y cerdos salvajes. A continuación, describiremos sucintamente los más aplicados.

Métodos letales:

- Trampeo con muerte: existen varios modelos y tamaños de trampas, desde trampas de pequeño tamaño, con las que se captura uno o pocos individuos, hasta trampas de grandes dimensiones, que permiten capturar un grupo social entero. Para incrementar la probabilidad de captura se usan cebos. A pesar de no ser un método totalmente selectivo, si la especie capturada no es la deseada se puede liberar. Las trampas de gran tamaño, tipo corral, son principalmente escogidas cuando el objetivo es disminuir las poblaciones, puesto que tienen menor impacto en el comportamiento social.

- Caza: la caza en las distintas modalidades se ha usado tradicionalmente con el objetivo de reducir las poblaciones de jabalí, aunque la efectividad no está del todo contrastada. Parece que la caza se muestra efectiva en áreas con una elevada densidad de jabalíes, puesto que se pueden cazar muchos animales en periodos relativamente cortos. La caza puede producir efectos no deseados en el comportamiento espacial y reproductivo de la especie. La caza selectiva de alguna clase de edad o sexo puede mejorar la eficiencia de esta actividad como elemento de control. Concretamente, seleccionar hembras adultas, especialmente en años con poca disponibilidad de alimento, incrementaría la capacidad de control de la caza (Bieber and Ruf, 2005; Sweitzer et al., 2000), aunque las respuestas compensatorias de la especie, como la inmigración desde lugares colindantes y el incremento de la reproducción, podrían limitar el éxito de esta medida (Hanson et al., 2009), ver apartado dedicado a la ecología poblacional.

- Técnica del jabalí Judas: se utiliza un animal radiomarcado para localizar a todo el grupo social. Se ha de contar con un incremento de costes, debido a la captura y el marcaje. Además, se debe combinar con otras medidas, ya sea la caza o las trampas.

  No comentaremos el uso de lazos y el envenenamiento por ser estrategias no éticas, prohibidas en la mayoría de los países, y no selectivas.

Métodos no letales:

- Control de la fertilidad: con la aparición de inmunocontraceptivos se han salvado los obstáculos de la esterilización química por vía oral. Con una sola inyección de una vacuna se estimula la producción de anticuerpos contra la hormona liberadora de gonadotropina, responsable de la producción de las hormonas sexuales. Los animales a los que se les inyecta esta vacuna pueden permanecer infértiles de uno a cinco años. Entre los inconvenientes del método destacan los costes de captura y vacunación y la aplicabilidad a pequeña escala.

- Vallados: se utilizan principalmente para proteger campos de cultivo u otras superficies del impacto negativo de los jabalíes. Existen varios tipos de vallados, tanto electrificados como sin electrificar. Puede utilizarse una combinación de ambos. Los vallados no electrificados son principalmente redes metálicas de unos 110-120 cm de alto. Habitualmente se entierran unos 40-60 cm para evitar que los jabalíes accedan al interior escarbando. Las protecciones electrificadas consisten en dos o tres hilos metálicos conductores de electricidad, separados entre ellos de 15 a 30 cm.
  Si la instalación se hace correctamente, son sistemas eficaces para evitar daños de jabalí, aunque se debe contar con una importante inversión económica inicial para adquirir el material y realizar un mantenimiento periódico.

- Repelentes: tanto químicos como sonoros, se han mostrado ineficaces con el jabalí. Los animales se habitúan a ellos a los pocos días.

- Alimentación suplementaria: consiste en proveer alimento en lugares concretos. Se utiliza para fidelizar a los jabalíes e incrementar la probabilidad de cazarlos, así como para evitar daños en campos de cultivo. La efectividad del aporte de alimento para evitar daños a campos no está demostrada, algunos trabajos reportan éxito con dicha medida mientras que otros no. En todo caso, el aporte suplementario debe ser continuo, lo que supone elevados costes, además de que el hecho de facilitar comida hace incrementar el éxito reproductivo, la supervivencia y, por tanto, las poblaciones de jabalí.

1.2. Aspectos metodológicos

1.2.1. Censo de poblaciones

El conocimiento de las abundancias poblacionales, junto con el de la distribución de las especies, es uno de los primeros aspectos que debe abordarse en ecología y biología de la conservación. Ambas medidas —la distribución y la abundancia— facilitan la comprensión de la evolución de las poblaciones y, mediante el uso de modelos estadísticos, permiten predecir cambios en las escalas temporales y espaciales. Además, mediante estos modelos se evidencian los factores bióticos y abióticos relevantes en la descripción de las tendencias de los parámetros poblacionales.

Las medidas de gestión encaminada a disminuir efectivos de una población de jabalí y a evaluar la efectividad de estrategias de disminución de conflictos con actividades humanas necesitan como primer ingrediente las estimaciones de abundancia. Para que las estimaciones sean útiles deben ser precisas, no sesgadas y no muy costosas de conseguir. Sin embargo, los hábitos crepusculares y nocturnos del jabalí, junto con su querencia por ambientes forestales con abundancia de sotobosque, hacen complicada la tarea de censar sus poblaciones.

A continuación, describimos los métodos principalmente utilizados (ENETwild consortium et al., 2018a; Engeman et al., 2013), remarcando aquellos que destacan por su utilidad y fácil generalización:

Observación directa:

- **Detección en transectos o puntos de observación**, ya sea para la obtención de índices de abundancia relativa o para la estimación de densidades mediante el método *distance sampling method*. A parte de las limitaciones derivadas de las asunciones de dicho método, los mayores problemas de aplicación son los hábitos nocturnos y crepusculares y la baja detectabilidad de la especie en lugares con abundante vegetación arbustiva. El hecho de que el *tapetum lucidum* de los jabalíes no refleje la luz dificulta su detección nocturna aun cuando realicemos el muestreo con un faro luminoso. La utilización de nuevas tecnologías como los visores de infrarrojos y las imágenes termales ha resultado exitosa en la realización de censos (Franzetti et al., 2012).

La aplicación de estos métodos tiene un elevado coste en material y en personal. Además, los resultados dependen de la experiencia de los observadores y la calidad del material óptico empleado, lo que hace difícil la generalización de estos métodos.

- **Detección mediante fototrampeo**: en las últimas décadas, el uso de equipos fotográficos se ha generalizado con el progresivo abaratamiento de esta tecnología. Las trampas fotográficas actúan como observadores con campos de visión pequeños pero que permiten el registro continuo durante largos periodos de tiempo.

  Ubicando varios equipos en forma de redes, se pueden obtener índices de abundancia relativa. Conjugando el trampeo fotográfico con la captura y marcaje de una parte de la población mediante el método de marcaje-observación (mark-resight, MR) diversos autores han obtenido medidas útiles de densidades de jabalíes (Hebeisen et al., 2008; Sweitzer et al., 2000). Cuando no existen características individuales que permitan la identificación individual, se usan índices fotográficos de abundancia que sean una buena representación de la densidad poblacional (Engeman, 2005; Rovero and Marshall, 2009), o también se puede usar el modelo de encuentro al azar (random encounter model, REM), que permite obtener abundancias absolutas sin necesidad de marcar e identificar una parte de la población (Rowcliffe et al., 2008). Este último método ya se ha usado con éxito en jabalíes (Massei et al., 2018). También se ha empleado con éxito el *distance sampling method* aplicado al fototrampeo en otras especies (Howe et al., 2017).

  A escala mayor, se pueden utilizar los modelos de ocupación territorial (occupancy modelling) para obtener dinámicas poblacionales de ungulados a partir de datos de presencia/ausencia (Duquette et al., 2014).

  Como ya se ha dicho, el abaratamiento de los equipos fotográficos ha hecho que el uso del trampeo fotográfico se haya generalizado, lo cual permite obtener resultados interesantes y directamente aplicables a la gestión y conservación de las especies, si bien para la obtención de resultados fiables se debe realizar una atenta planificación de las campañas de muestreo. También se deben tener en cuenta tanto las asunciones de los modelos como aquellos factores que pueden sesgar los resultados. Entre ellos destaca el establecimiento de una escala espacial que se adapte a la especie objetivo, es decir, adoptar con coherencia el ámbito del área de estudio, y la distancia entre equipos fotográficos o ubicación concreta de las cámaras. Los resultados pueden variar si se localizan las cámaras al azar, si se usan caminos, pistas forestales, rastros o evidencias de actividad de las especies, o si se emplean cebos o atrayentes (naturales o no) para incrementar el éxito de encuentros con los equipos fotográficos.

Observación indirecta:

- Los **rastros** dejados por los animales han servido tradicionalmente como índice de abundancia relativa. En el caso del jabalí se ha usado principalmente el número de excrementos tanto en parcelas como a lo largo de itinerarios. La cantidad de deposiciones a lo largo de transectos se ha testado con éxito en el caso del jabalí (Acevedo et al., 2007; Vicente et al., 2004). Además, puede obtenerse un valor de agregación de la población de especial relevancia en estudios epidemiológicos. Controlar la tasa de defecación y de desaparición de los excrementos en el medio es fundamental para obtener índices no sesgados de abundancia. Aun así, el hecho de que los excrementos se encuentran habitualmente agregados dificulta el muestreo y las estimaciones.

  Aplicar técnicas genéticas a los excrementos recogidos también permite la identificación individual, de edad y sexo. Con los datos obtenidos es posible, además, aplicar distintos tipos de modelos de captura-recaptura y estimar también la abundancia poblacional. La aplicación de este método es todavía cara, requiere de gran esfuerzo y presenta limitaciones en pequeñas muestras, puesto que en parte de ellas no se encontrará suficiente material genético para llevar a cabo con éxito su identificación.

- **Estadísticas de caza**: son un método económico y que puede aplicarse a gran escala para la obtención de índices de abundancia mediante los datos de jabalíes cazados por día, lugar y modalidad de caza. Entre las limitaciones de este método está el hecho de que únicamente se obtienen datos en la temporada de caza y no se obtienen en las zonas donde la caza no está permitida. Las condiciones climáticas, la experiencia y los cambios en los esfuerzos realizados por los cazadores, así como el tipo de caza, afectan a la intensidad y efectividad de la caza y, por tanto, a los resultados. Para superar estas barreras, el esfuerzo de caza debe estandarizarse y el uso de cuotas u objetivos debe describirse completamente. En este sentido existen iniciativas para la homologación de los datos de caza. Es el caso de ENETwild consortium *et al.* (2018b), que analizó mediante cuestionarios de caza en los diferentes países de Europa la heterogeneidad en la recopilación de datos sobre las poblaciones de jabalí y ha propuesto un modelo de recopilación de datos sólido y bien informado como base de un marco de recopilación de datos común.

1.2.2. Dominios vitales

Otro aspecto relevante en ecología es el uso y selección del espacio por parte de las especies. El conocimiento del tamaño y forma de los dominios vitales, así como de los patrones que puedan existir y los factores que los condicionan, permite establecer estrategias eficaces de gestión adaptativa.

El concepto de dominio vital o área de campeo ha evolucionado también desde una visión únicamente espacial —"zona utilizada por los individuos en sus actividades normales de alimentación, reproducción y cuidado de las crías" (Burt, 1943)— a concepciones en las que entran en juego otros factores, como el tiempo, y se desarrollan modelos espaciales con probabilidades de ocurrencia de un animal durante un tiempo determinado (Kernohan et al., 2001).

Existen multitud de estudios sobre dominios vitales, pero no hay consenso sobre el mejor método para calcularlos (Laver and Kelly, 2008). Con los avances en los sistemas de posicionamiento global (GPS) para el análisis de los movimientos y dominios vitales de las especies se dispone de gran cantidad de ubicaciones y más precisas que las obtenidas mediante el método tradicional de seguimiento con sistemas de alta frecuencia (VHF). La tecnología GPS proporciona un enorme número de localizaciones disponibles, lo cual incrementa la autocorrelación en el espacio y el tiempo.

El método del mínimo polígono convexo (MPC) es conceptualmente el más sencillo. Consiste en unir mediante un polígono las localizaciones exteriores de cada individuo recogidas en un área geográfica. Este método presenta como principal inconveniente el hecho de que suele englobar extensas zonas que el animal no ha usado.

El método de densidad de áreas núcleo o kernel (KDE) es uno de los métodos más usados y con mayor aceptación para la estimación de los dominios vitales. Los dominios vitales KDE dependen únicamente del factor de amortiguación o ancho de banda (h) que, a su vez, según el algoritmo que se use en su estimación, es altamente dependiente del número de localizaciones. Para aproximar el KDE se deben emplear localizaciones no correlacionadas. Existe cierta controversia acerca de la influencia de la autocorrelación en las ubicaciones de los individuos en las estimaciones KDE. Mientras que Kie *et al.* (2010) y Fieberg (2007) aprueban su uso con la tecnología GPS, otros estudios han puesto de manifiesto los errores en la selección de anchos de banda adecuados (Hemson et al., 2005) y el incumplimiento de la asunción de independencia entre localizaciones (Swihart and Slade, 1985).

Para trabajar con localizaciones altamente correlacionadas se han desarrollado métodos alternativos de selección del ancho de banda para los KDE y de otras aproximaciones a los dominios vitales (Walter et al., 2011).

Entre los métodos no paramétricos que aparecieron primero como alternativa a los KDE, uno de los más extendidos fue el *local convex hull* (LoCoH), que generaliza el método del MPC. Se diseñó para producir dominios vitales más limitados y con mejores propiedades de convergencia que los métodos KDE paramétricos a medida que aumenta el tamaño de la muestra (Getz et al., 2007). La construcción de polígonos permite considerar barreras geográficas para los animales, aunque tiene como defecto el hecho de que las estimaciones pueden ser subjetivas según los parámetros seleccionados y precisan un gran tamaño de muestra de puntos GPS para que los dominios vitales sean precisos.

Se han empleado ampliaciones de los modelos KDE que combinan información espacial y temporal (KDE basados en movimientos, como el modelo de movimiento del puente browniano, BBMM) (Horne et al., 2007) o que tienen presente la naturaleza altamente correlacionada de los datos de movimiento (KDE autocorrelacionados o AKDE) (Fleming et al., 2015). También se han contemplado aquellos seguimientos con un intervalo de muestreo irregular (KDE con tiempo) (Katajisto and Moilanen, 2006).

Los enfoques de estimación de dominios vitales basados en la trayectoria han surgido como alternativas a los KDE tradicionales (Downs and Horner, 2012). El modelo de BBMM, presentado por Horne *et al.* (2007), mejora los métodos de kernel al modelar explícitamente la trayectoria de movimiento de un animal en lugar de los puntos individuales. Los BBMM también tienen en cuenta la incertidumbre espacial de cada ubicación y pueden manejar datos muestreados irregularmente (Gurarie et al., 2016). Puesto que los animales combinan fases de varios comportamientos diferentes a lo largo del tiempo, como reposo, alimentación, apareamiento, evasión de depredadores o termorregulación, Kranstauber *et al.* (2012) introdujeron el modelo dinámico de movimiento del puente browniano (dBBMM).

2. Objetivos

El objetivo general de la presente tesis es ampliar el conocimiento de la ecología espacial del jabalí mediante la obtención de datos demográficos en ambientes mediterráneos a escala poblacional. Los objetivos específicos derivados de dicho objetivo general son:

1. Evaluar los efectos de cebar con maíz en las estimaciones poblacionales obtenidas mediante trampeo fotográfico y el método de marcaje-observación.

2. Analizar la relación entre las estimaciones de abundancia absoluta y relativa como indicadores poblacionales del jabalí.

3. Evaluar las variaciones en tamaño y la similitud de distribuciones de utilización (*Utilization distribution*, UD) de los dominios vitales en función de: i) el tipo de seguimiento (diurno versus continuo) y ii) la intensidad de muestreo (número de localizaciones en función del tiempo transcurrido entre ellas).

4. Establecer las bases científicas que permitan la comparación de las estimaciones kernel de dominios vitales obtenidas a partir de tecnología VHF y GPS, así como entre métodos de análisis.

5. Describir los patrones de uso del espacio de los jabalíes y el papel de la estacionalidad.

6. Analizar los factores del hábitat que condicionan los desplazamientos a escala temporal y poblacional desde una perspectiva espacial.

7. Evaluar las implicaciones que los dos puntos anteriores tienen en la gestión de la especie.

CAPÍTULO II

3. Estudios realizados

Estudio I

3.1. Baiting improves wild boar population size estimates by camera trapping

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Abstract

In the last decade, camera trapping has become a widespread technique for wildlife monitoring. Although baits or attractants are commonly used to increase the likelihood of encounter, this practice has been criticised because of the potential biases in the population estimations based on these records obtained by mark-recapture or mark-resight methods, and especially in relative abundance indices (RAI). For two consecutive years, we evaluated the impact of baiting on wild boar (*Sus scrofa*) population estimates in a protected area of northeast Spain. In particular, we compared the number of boars per independent events (the group size), the estimated population size and RAI between periods with and without baiting. Baiting increased mean group size estimation and the likelihood of an encounter leading to more precise wild boar population estimates. The RAI values both at baited and unbaited campaigns correlated significantly with mark-resight abundance estimates, suggesting that these indices could be used to evaluate the boar population changes.

Keywords: Mark-resight, Population estimation, Relative Abundance Index, *Sus scrofa*, Wildlife monitoring.

Introduction

Camera trapping can be used to record wildlife when researchers are not present and has been used by wildlife ecologists since the early 1990s (Fleming et al., 2014). Thanks to remotely activated devices, also known as trail cameras, many details of the ecology of rare and elusive species have finally been revealed (Carbone et al., 2001; Nichols et al., 2011). This non-intrusive, cheap and non-invasive method has become popular, not only in conservation biology (O'Connell et al., 2011; Rowcliffe and Carbone, 2008), but also in wildlife monitoring plans (Dougherty and Bowman, 2012; Jiménez et al., 2013; Sparklin et al., 2009).

Camera trapping is also used to estimate the size of wildlife populations through mark-resight (MR) methods (O'Connell et al., 2011), which estimates abundance using the frequency of marked and unmarked individuals recorded from trail cameras (Bowden and Kufeld, 1995; McClintock et al., 2009). In populations of all unmarked and unrecognizable individuals, relative abundance indices (RAI) can also be estimated based on the number of independent events (i.e. photograph sequences) per unit of time (Massei et al., 2018; O'Brien et al., 2003; Swann and Perkins, 2014). RAI values can be influenced not only by the population abundance, but also by factors such as spatial patterns, camera trap location, etc. Therefore, they have been considered more as an activity index as opposed to the index of abundance (Sollmann, 2018). Regardless of the definition that is adopted for the RAI, the fundamental aspect which determines the applicability for managers and researchers is the relationship between the photographic rates and population abundances (Palmer et al., 2018). Few works, however, have shown the link between RAI and population size estimations (O'Connell et al., 2011; Rovero and Marshall, 2009).

Several sources of bias due to heterogeneity of capture probabilities can exist in MR studies, including camera placement, animal movement and animal behaviour. Much of the sources of heterogeneity could be accounted for using the MR models developed by McClintock (2016). The use of bait or attractants to increase the likelihood of encounter with the target species within the shooting range would be another source of heterogeneity of capture probabilities (Foster and Harmsen, 2012; Garrote et al., 2012). This practice has largely been criticised because of the potential bias in the number of records (Sollmann et al., 2013; Swann and Perkins, 2014) and the estimation of population parameters (Larrucea et al., 2007; McCoy et al., 2011). However, many researches obtain reliable abundance estimates using an MR camera trap approach (Curtis et al., 2009; Parsons et al., 2015; Rich et al., 2014).

Few efforts have been made to evaluate the effects of baiting on population estimates (Foster and Harmsen, 2012; Garrote et al., 2012; Larrucea et al., 2007), either based on MR or on RAI.

The European wild boar (*Sus scrofa*) shows one of the widest geographic ranges of all terrestrial mammals. This wild pig shows great dispersion ability (Casas-Díaz et al., 2013; Jerina et al., 2014) and is capable of inhabiting from semi-desert areas at sea level to the high European mountains (Apollonio et al., 2010). Wild boar is not only a major game species in Europe but is also a well-known source for infectious diseases in livestock and humans (Meng et al., 2009). Consequently, improvements in methods for assessing wildlife population numbers are not only welcome for wildlife researchers but also required by the current European environmental policies (Acevedo et al. 2007).

The effects of baiting on wild boar have been evaluated for different purposes, such as the improvement of hunting efficacy (Campbell et al., 2012; Geisser and Reyer, 2004) and the use of selective feeders for oral delivery of baits (Ballesteros et al., 2009), to minimise crop damage (Calenge et al., 2004), or for reproduction control (Massei et al., 2011). Baited camera traps have been used on MR studies to assess wild boar abundance (Hebeisen et al., 2008; Sweitzer et al., 2000), however no information exists about the impact of this practice on wild boar population estimates.

In this work, we took advantage of a two-year wild boar population monitoring program using camera traps and tagged wild boars in northeast Spain to evaluate the effects of baiting on wild boar group and population estimates from camera-trap data and MR methods. We also evaluated the relationship between the absolute and relative population estimates to test the feasibility of use RAI as a measure of wild boar populations.

Material and methods

Study area

The study area was located at the Wildlife Refuge Les Refardes - La Vall of 588 Ha, in the Sant Llorenc del Munt i l'Obac Natural Park (41º 39'-41º 42 'N, 1st 2nd 53'-09' E), located in northeast Spain (Fig. 3.1.1). Whereas hunting is forbidden in the wildlife refuge it is allowed in the surrounding areas. The main vegetation in the study area is pine forest including *Pinus halepensis*, *P. sylvestris* and *P. nigra* enriched with patches of holm oak (*Quercus* *ilex*) with a dense shrub layer of *Viburnum lantana*, *V. tinus*, *Crataegus monogyna*, *Arbutus unedo* and *Phyllyrea latifolia*. According to the map of land uses of Catalonia (Ibàñez i Martí and Burriel Moreno, 2010), the study area is classified as a mosaic of woods (72% forest and 20% scrubs) with patches of crops. This landscape provides shelter, food and water throughout the year, serving as an excellent habitat for wild boars.

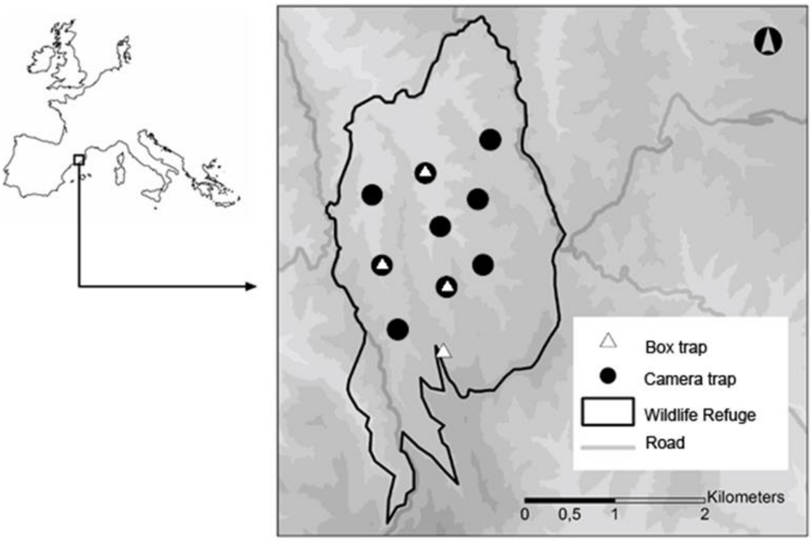

Figure 3.1.1. Study area showing camera trap distribution (solid circle) for monitoring wild boar population abundance in the Wildlife Refuge Les Refardes – La Vall, Sant Llorenç del Munt i l'Obac Natural Park, Catalonia, northeast Spain. The white triangles represent locations for wild boar trapping. Hunting activities area forbidden within the study area.

Ethics statement

No approval was needed from an ethics committee since the animals used in the present study were not sacrificed and were legally box-trapped in their own habitat. Animals were captured and manipulated by two veterinarians (FCS and ECD), authorised by the Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural - Generalitat de Catalunya, the regional authority in charge of livestock and wildlife management.

Wild boar capture and mark

Captures were conducted using four box traps, one of 2 x 1 x 1 m, two of 1.5 x 1.5 x 2.5 m and one of 2 x 1.5 x 1.5 m. Box traps were made with iron bars of 8-10 mm in diameter electro-welded into 5 x 5 cm squares. The sliding door was activated by a metallic plate (see Casas-Díaz et al., 2011 for more details). The traps were arranged to obtain a distribution as homogeneous as possible over the entire study area, with 845 m being the average distance between traps (Fig. 3.1.1). During the capture campaigns, box traps were baited daily with 300 g of maize.

Captured boars were chemically immobilised using a combination of 3 mg/kg tiletamine + 3 mg/kg zolazepam (Zoletil®, Virbac, Esplugues de Llobregat, Barcelona) plus 3 mg/kg xylazine (Xilagesic 20% ®, LaboratorisCalier, Les Franqueses del Vallès, Barcelona, Spain). The dose was calculated by approximating the weight by direct observation and was administered intramuscularly, preferably in the posterior third, with an anaesthetic dart blowgun shot.

Young individuals (< 20 kg) were handled without anaesthesia and released immediately after labelling, weighing, measuring and sampling. Adult individuals were kept under veterinary observation until they fully recovered from the effects of anaesthesia. The identification of wild boars was performed by two ear tags (Allflex, Gepork, Masies de Roda, Spain) per individual with a shape code (Fig. 3.1.2).

Figure 3.1.2. Immobilised young boar with customised ear-tags for individual identification. All individuals were marked with two ear-tags, one per pinna. To minimise stress, anaesthesia was applied in the early morning by a single person (FCS) approaching the animal.

Camera trapping

Nine camera traps (Scout Guard SG550V HCO; HCO Outdoor Products, Norcross, USA) were distributed in the study area. Four of them were placed at least 50 m from the trap cages. In order to avoid gaps in the effective trapping area and considering the behavioural movement of wild boar, the average distance between camera traps along the main streams of the study area was 712 ± 58.72 m, in line with Hebeisen et al. (2008) and Massei et al. (2018) (Fig. 3.1.1). To minimize errors associated with the assumption of a closed population, the resighting period was limited to two weeks.

Timetable for baiting

Periods with and without baiting were scheduled as shown in Fig. 3.1.3. In front of each camera, 300 g of maize was delivered twice a week during baiting periods. Maize was replaced only after the total was consumed otherwise it was not delivered. The gap between the first and second campaign in 2013 was 45 days, taking into account the last time the sampling points (locations of the camera traps) were baited, in order to minimise the bias produced by visits of wild boars that might become accustomed to locations with maize (Williams et al., 2011).

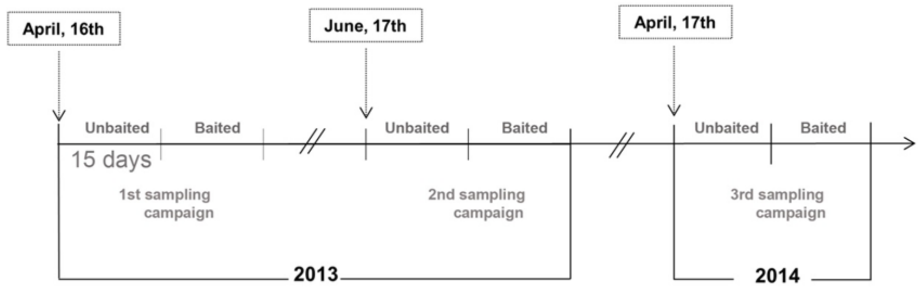

Figure 3.1.3. Timetable showing baiting periods for assessing wild boar abundance by camera trapping in the study area. The study period ran from 17th April 2013 to 17th May 2014.

Photograph classification

Williams et al. (2011) established that an interval of 9 minutes between photographs provides sufficient data for use in individual identification-based population estimations. For this reason and to avoid repeated photos on the same individuals, observations have been grouped whenever the interval of time elapsed between photographs were less than 10 minutes. These observations have been called independent events (IE) in line with Massei et al. (2018). For group size evaluation we considered the maximum number of wild boars appearing in a photo by examining consecutive photographs of each IE.

For MR population estimation, we recorded the number of IE based on recognised wild boars, tagged but unrecognised wild boars and untagged individuals by sampling campaign.

To avoid replication of photographic capture histories of animals of same social group, as well as to account for the effect of recruitment on the population estimates, we used MARK software (White and Burnham, 1999) to analyse the abundance of social groups rather than the number of individuals; groups that contained marked animals were considered as marked groups. Wild boar abundance was then obtained by multiplying the estimated number of social groups by the mean group size (Rowcliffe et al., 2008).

The delta method (Powell, 2007) in "msm" R package (Jackson, 2011) was used to incorporate the uncertainty associated with MR group abundance and the average group size on the final wild boar population estimations.

Statistical analysis

To evaluate the impact of baiting on the wild boar mean group size, we performed a generalised linear mixed model (GLMM) in which the observed variability in the group size per IE was explained by the effects of baiting (fixed categorical factor: baiting and no-baiting) and the camera trap nested within the sampling campaign was considered as a random intercept term. We established a GLMM with the same fixed and random_factors as in the previous case but with the IE number as a dependent variable to evaluate the effect of bait on encounter likelihood.

Wild boar group population abundance (number of groups), however, was estimated using the number of IE recorded from baited and unbaited cameras during each sampling campaign (Table 3.1.1) and the program MARK (McClintock, 2016).

To facilitate the interpretation and understanding, we provide in the results section the precision of abundance estimates and the proportion of IE with marked animals with respect to the total in each period. We also included the percentage of marked wild boar groups with respect to total group population estimate.

Since the number of marked individuals was unknown at the time of sampling (e.g., boars were tagged in previous year for other scientific purposes), we used the robust zero-truncated Poisson log-normal estimator [(Z)PNE] design as recommended by McClintock et al. (2016). The set of candidate models using the [(Z) PNE] included different combinations of parameters such as: the resighting rate (α), the estimate of individual heterogeneity (σ), the number of unmarked individuals in the population (U), the survival rate (ϕ) and the temporary emigration rate (γ). For our purposes α, σ and U were considered constant or allowed to vary by time while holding ϕ and γ constant. We avoid convergence difficulties of the models using the alternate optimisation method based on simulated annealing in MARK, which is more likely to find the global instead of a local maximum and used profile likelihood CI for all parameters because this procedure performs better for parameters close to the boundaries of zero and one. Considering, whenever possible, each campaign as a resight occasion, model selection for MR group wild boar population estimates were performed using the second-order corrected Akaike Information Criterion (AICc).

The abundance of wild boars was calculated by multiplying the MR group abundance estimates by average group size at baited periods. We used the group size data obtained at baited periods in order to use a realistic group size and not underestimate the abundances of wild boar (Massei et al., 2018), although the population estimates using average group size obtained in unbaited periods are also shown in table 3.3.3 to display how this parameter affects these estimates.

Two-sample z-test was used to evaluate the differences between baited and unbaited MR group estimates and their associated standard errors at each sampling campaign.

To compute the RAI, we summed the number of IE per sampling period for all camera traps and divided by number of active camera trap nights. We reported RAI as the number of IE per 100 trap-days in Table 3.1.1.

Finally, we used a weighted linear regression approach to explore whether the relationship between RAI and MR wild boar abundance estimates were affected by the effects of baiting. Along the same lines, we used the inverse of the variance of each estimate to account for different uncertainties in the RAI and MR estimations. We ran a regression model with interaction terms between RAI and bait (factor effect) to explain MR group abundance. Specifically, we used the "lm" function from "stats" R package. All statistical analyses and graphics were performed in the 3.5.0 R software (R Core Team 2018).

Results

Effects of baiting on the trapping output

Likelihood of encounters, measured as number of IE, were significantly higher at baited than unbaited periods ($\beta = 0.86$, SE= 0.09, z-value = 8.88, $p<0.0001$).

The number of marked and unmarked wild boar groups IE per sampling campaign obtained during the years 2013 and 2014 are shown in table 3.1.1. The average percentage of iEs with marked groups with respect to the total was 16.72% (range: 11.76-25.58%) in unbaited SC estimates, while 30.34% (range: 7.95-56.47%) in the baited periods. The same average percentages referred to the marked groups detected photographically with respect to the total MR wild boar groups estimated were: 27.93% (range: 21.73-35.97) and 23.3% (range: 16.2-34.56), in unbaited and baited periods respectively.

Table 3.1.1. Number of independent events (IE), wild boars marked groups and RAI values recorded during three sampling campaigns (SC) in the Wildlife Refuge Les Refardes – La Vall, Sant Llorenç del Munt i l'Obac Natural Park, Catalonia, northeast Spain. SC took place in April (1st SC), and June (2nd SC) 2013 and in April 2014 (3rd SC).

	1st SC		**2nd SC**		**3rd SC**	
	Unbaited	Baited	Unbaited	Baited	Unbaited	Baited
Number of marked groups detected	3	2	4	3	3	4
IE with tagged boars	5	7	22	48	4	46
IE with tagged boars but not identified	1	1	3	2	0	3
IE with untagged boars	34	81	64	37	30	127
RAI values	30.95	89.79	74.48	73.21	26.19	139.68

Effects of baiting on wild boar population estimates

In spite of the similar percentage of detected marked groups, at unbaited periods the number of IE with marked animals was so low that it prevented executing models with 3 occasions (three sampling campaigns). Finally, we decided for the unbaited period to estimate a model for two occasions at 2013 and one at 2014 (Table 3.1.2).

Table 3.1.2. Summary of the best models (those selected in bold) for estimating wild boar abundance by MR methods using the records from baited and unbaited cameras during three sampling campaigns (SC) in the study area. The SC took place in April (1st SC), and June (2nd SC) 2013 and in April 2014 (3rd SC). AICc = Second-order corrected Akaike Information Criterion for small sample sizes, ωi = Akaike weight. Model parameters were the resighting rate (α), individual heterogeneity (σ), the number of unmarked individuals in the population (U), and the survival and emigration rates (ϕ and γ, respectively). A dot in the suffix indicates that the parameter remained constant, whereas t refers to parameter that can vary over time.

Campaign	**Model parameters**	**AICc**	**Deviance**
Unbaited (1 and 2 SC)	$\boldsymbol{\alpha_{.}\ \sigma_t\ U_t\ \phi_{.}\ \gamma_{.}}$	**38**	**24.29**
	$\alpha_{t.}\ \sigma_{.}\ U_{.}\ \phi_{.}\ \gamma_{.}$	39.45	30.45
Unbaited (3 SC)	$\boldsymbol{\alpha_{.}\ \sigma_{.}\ U_t\ \phi_{.}\ \gamma_{.}}$	**44.4**	**35.74**
Baited	$\boldsymbol{\alpha_{.}\ \sigma_t\ U_t\ \phi_{.}\ \gamma_{.}}$	**56.94**	**42.32**
	$\alpha_t\ \sigma_{.}\ U_t\ \phi_{.}\ \gamma_{.}$	57.84	46.98
	$\alpha_t\ \sigma_t\ U_t\ \phi_{.}\ \gamma_{.}$	58.8	51.2

Mean group size during the baited periods were significantly higher ($\beta = 0.6$, SE= 0.13, z-value = 4.34, $p<0.0001$). In fact, the mean group size at baited campaigns almost doubled that when bait was not applied, providing evidence that group size is underestimated at unbaited campaigns. Therefore, we show at all figures wild boar population estimates applying the mean group sizes obtained at baiting campaigns. Mean group size and estimated population abundance, with average group size at baited and unbaited periods, for the three sampling campaigns are summarised in Table 3.1.3.

Table 3.1.3. Wild boar population estimates,_obtained from MR group abundance and average group size, using the records from baited and unbaited cameras during three sampling campaigns (SC) in the study area with associated standard error. The SC took place in April (1st SC), and June (2nd SC) 2013 and in April 2014 (3rd SC).

Population estimates	**1st SC**		**2nd SC**		**3rd SC**	
	Unbaited	**Baited**	**Unbaited**	**Baited**	**Unbaited**	**Baited**
Mean group size	2.05± 0.62	3.23± 0.4	2.27± 0.38	5.14± 0.83	1.45± 0.18	2.41± 0.21
MR Group abundance	8.49± 1.9	10.34± 0.98	7.12± 2.26	5.68± 1.53	10.8± 2.87	16.87± 1.14
Wild boar Population estimate[1]	17.43± 6.56	33.41± 5.24	16.18± 5.83	29.25±9.21	15.75± 4.65	40.79±4.51
Wild boar Population estimate[2]	27.46± 7.04	33.41± 5.24	36.66± 13.08	29.25±9.21	26.12± 7.31	40.79±4.51

[1] Direct population estimates by means of delta method, using the average group sizes and group abundances obtained in each sampling campaign.

[2] Population estimates using the delta method, the average group size after baiting and during the same sampling campaign.

Furthermore, MR wild boar population estimates were more precise (lower SE) when bait was applied than when absent. According to figure 3.1.4 and although the MR estimates in baiting periods have a higher average, the boar group estimates no significantly differs between baiting and unbaiting periods in three sampling campaigns (z-test: SC1 z= -0.67, p= 0.49; SC2 z= 0.46, p= 0.64; SC2 z= -1.7, p= 0.08).

Weighted linear regression indicated that the relationship between RAI and MR boar abundance correlated positively and significantly when bait was supplied ($\beta_{\mathrm{RAI:Baiting}} = 0.15$, t= 17.87, SE = 0.008, p<0.001) and also in plain periods of camera trapping ($\beta_{\mathrm{RAI:Unbaiting}} = 0.23$, t= 9.02, SE = 0.02, p= 0.003) (Fig. 3.1.5).

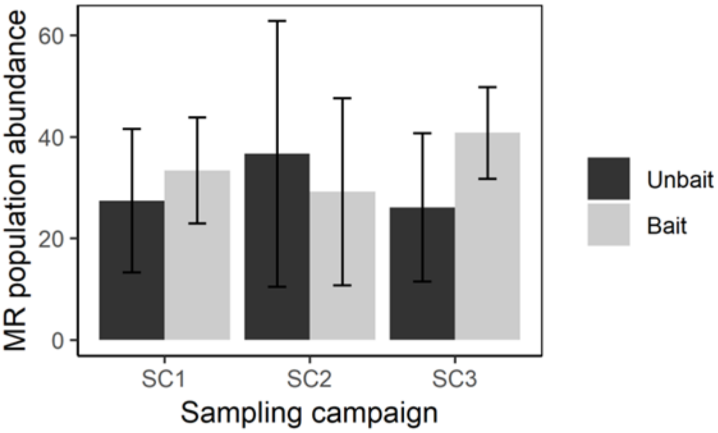

Figure 3.1.4. Bar plot representing MR wild boar population estimates and 2 SE bar at each sampling campaign, recorded by baited (grey bars) and unbaited (black bars) camera traps at study area. To not underestimate population size during the unbaited periods, population estimates were obtained using the delta method and the baited average group size assessed during the same sampling campaign.

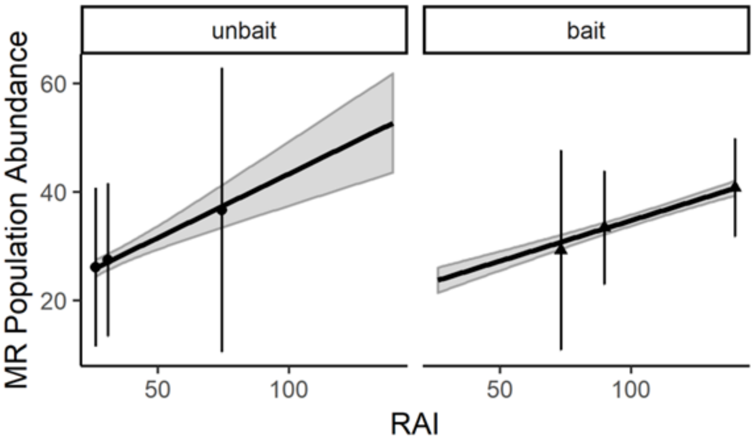

Figure 3.1.5. Scatter plot exploring the interaction between relative abundance indices (RAI defined as the number of independent encounters per SC for all camera traps and divided by number of active camera trap nights) and wild boar abundance obtained by mark resight (MR) during periods with (at right) and without (at left) baiting. Grey shadows represent the 95% Confidence Interval for the linear weighted regression predictions. Population estimates was obtained using baited mean group size a same sampling campaign, in order to not underestimate populations at unbaited periods. Vertical bars represent 2 SE of population estimates obtained by means of the delta method.

Discussion

Although baits and attractants have widely been used in wild boar research based on camera traps (Hebeisen et al., 2008; Sparklin et al., 2009; Sweitzer et al., 2000; Yasuda, 2004), no work has taken into account its potential bias on boar population estimates.

In our work the use of bait results in an increase in the number of IE and mean group size estimate. The difference between campaigns may represent different phenological stages of the population. However, the supply of bait favours an increase in the number of individuals detected per event resulting in a more realistic group size estimate. As other authors have shown, the contribution of bait makes camera trapping more efficient because it increases the number of events and facilitates the identification of both individuals and family groups (du Preez et al., 2014; Garrote et al., 2012; Gerber et al., 2012).

In a wild boar populations in Mediterranean habitat, Ballesteros et al. (2009) found no evidence of an attractant effect of bait, comparing baited detection stations with control stations. However, in the current work, the values of RAI when bait was contributed correlate better than unbaiting periods with MR abundance estimates.

The use of bait could be a potential bias specially relevant in studies using the number of IE to evaluate unmarked ungulate populations (Rovero and Marshall, 2009). In such studies applied to wild boar and based on RAI, our results show that the relationship of these indices with wild boar abundance estimates improves in baiting periods, given the better adjustment of the weighted regression for the whole range of values and a narrower associated confidence interval.

The use of abundance indices obtained by camera trap is not exempt from critical reviews (Foster and Harmsen, 2012; O'Brien, 2011; Sollmann, 2018), but they are still used and provide interesting results, especially when they can be calibrated with_reference methods of abundance estimates (Palmer et al., 2018; Rovero and Marshall, 2009). Another critical point in the application of RAIs as an estimate of abundance is the use of baits. In this sense, recent works have highlighted the improvements and feasibility of calculated RAIs with baited camera traps (Bengsen et al., 2011; Keever et al., 2017; Villette et al., 2017, 2016). Our results suggest the utility of the RAI to estimate wild boar abundance, although the small sample size (three campaigns with and three without bait) makes a clear generalization difficult. However, points used in the regression represent aggregate data (i.e. MR abundance estimates with their associated errors). The weighted regression supported the relationship between RAI and wild boar abundances and, thus, the need of incorporating a realistic average group size in wild boar population assessment programmes. Observations from direct counts (Bowler et al., 2019; Soofi et al., 2017) or baited cameras setting in the study area (Cherry et al., 2015; Massei et al., 2018; O'Connell et al., 2011) will be useful to gather such important parameter.

The wild boar population is similar within each camera trap campaign whether bait is applied or not. The third sampling campaign shows a greater difference, although not significant between abundance estimates, possibly due to discussed analysis constrains during the unbaited period. Main factors that can influence the differences between the estimates of total abundance are the values of the group size.

The group abundance estimates and mean group size could inform us of the phenological state of the species, as well as displacements of parts of the population. In this sense, it is clearly observed in the baiting period that in a short period of time, between the first and second sampling campaigns, the number of groups was reduced while the number of wild boars per group doubled. Both facts correspond to the movement of a part of the population to an area located about 7 Km to the north, while the groups that remained in the area appeared mostly with young and therefore, increased their group size. This aspect goes more unnoticed in the period without bait due to the low mean group size calculation. Displacements, both outside and within the study area, could be evaluated using a sample of individuals with radio transmitters, thereby ensuring that during the study period the population is closed, eliminating that portion of the population that was tagged and had left the study area (Ivan et al., 2013; Matthews et al., 2008). While this approach would significantly increase project costs, it would allow detailed knowledge of the movements inside and outside of the study area. As an alternative, we adopted robust MR models, which take into account data collected across both closed and open sampling periods.

As mentioned above and based on the MR population estimates obtained, bait does not appear to produce significant differences when working with marked animals. Similar to works based on other species (Gerber et al., 2012), the SE of abundance estimates decreases when bait is supplied. These factors, despite the need to generalize the results when the sample increases, indicate that the contribution of bait produces more precise and reliable estimates of the population.

Another issue that needs further research, although it transcends the objectives of this paper, are the possible effects linked to the quantity or type of attractant, whether natural or if it is a food or scent lure. In this sense, there is still controversy and little information available (Burton et al., 2015; Cusack et al., 2015; Edwards et al., 2016).

Implications for management

In recent decades, wild boar populations have increased dramatically across the geography and in some places, this increase is more evident, as in the northeast Iberian Peninsula. When this increase occurs in areas close to human activities, (crops, residential areas, rural areas, etc.) conflicts multiply in the form of damage to agricultural production, collision with vehicles, urban infrastructures, and property damage.

Some procedures for the control of wild boar populations have been implemented to end or minimise conflict, with most methods making use of baits or attractants. However, before management programs are considered, damages should be quantified and more importantly, a precise and accurate evaluation of population size and dynamics should be carried out.

Using this simple approach allowed us to perform population estimates in all campaigns at baiting periods, while only the robust MR methods could be applied in two of three sampling campaigns at unbaiting periods. These data are necessary and fundamental in wildlife management and can inform hunting management plans and, in turn, enable for the evaluation of the effectiveness of deterrents or controls. The contribution of bait has allowed us to better detect the increase of the population at the third sampling campaign. On the other hand, this population rise matched with the increment in the number of hunter-harvested boars outside the wildlife refuge (2014-15, Minuartia, 2016), most probably due to a population increase.

Apart from the requirements or assumptions derived from the statistical foundations of MR methods, the most influential factor in obtaining estimates of precise abundance is the proportion of tagged animals that are then resighted and the number of IE obtained. As a result, the most imprecise estimates occurred when the number of resightings was low.
A higher distance between cameras and a greater resighting effort by increasing number of cameras (and therefore, study area) will be an essential improvement to minimise pseudoreplication and wild boar displacements outside of the study area.

For studies that estimate population size from RAI, without having a sample of marked or identifiable animals, which take into account the methodological and sample size limitations, our results suggest the reliability of using the RAI as a measure of wild_boar abundance, both at baiting and unbaiting periods. We encourage further studies on the relationship between RAI and other indices with population reference abundances, in order to generalize the results presented.

Acknowledgements

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Estudio II

3.2. A basis for comparison of home ranges obtained with different tracking schemes: time range and fixation frequency

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Abstract

Traditional VHF radio-tracking is gradually being replaced by GPS tracking devices in spatial ecology studies, although both technologies are currently in use. Many differences exist between GPS and VHF tracking schemes, mainly related to study design and sampling intensity. These differences make it difficult to establish direct comparisons among results obtained between studies, for example, in terms of home range and habitat selection.

Our primary aim was to test the reliability of comparisons in home range estimates of wild boar (*Sus scrofa*) using different approaches and also, provide an empirical basis for linking VHS and GPS tracking data.

Using GPS tracking data from wild boar, we simulated different tracking schemes (approaches) to compare the home range estimates (size and utilization distribution) in relation to: i) time range, namely daytime vs continuous monitoring, and ii) fixation frequency, from one relocation per day for three days in a given week to daily monitoring with 24 relocations per day. Data were obtained from 15 GPS-collared individuals from three areas (five individuals per area) in Mediterranean Spain. Minimum convex polygon (MCP), 95% kernel home range (Khr95) and 50% kernel core range (Kcr50) were used to assess variability among approaches.

Similar home range sizes and high overlays were obtained between approaches by the Khr95. From Kcr50, similar estimates were also obtained across the less intensive approaches (typical of VHF tracking), but their overlap was lower than that obtained with Khr95.

Results suggested that MCP produces the greatest differences in home ranges between approaches, while Khr95 was the least biased parameter, both in size and utilization distribution.

The proposed methodological approach facilitates home range and spatial use standardisation. The species management often is carried out considering the spatial ecology data obtained through home ranges. Thus, we emphasize that scientific studies based on home range comparisons without an explicit consideration of sampling intensities and time ranges may be misleading and in need of revision.

Additional keywords: wild boar; fixed kernel; sampling intensity; GPS collars; *Sus scrofa*.

Introduction

The concept 'home range' in ecology has evolved from simple definitions such as 'area crossed by individuals in their normal activities of feeding, reproduction and care of the offspring' (Burt, 1943) to more elaborate definitions such as 'area with a defined probability of occurrence of an animal during a specified period of time' (Kernohan et al., 2001). Whatever definition is used, the size and utilization distribution of home ranges are a consequence of the ecology of animal populations and resource allocation. Thus, their study sheds light on the vital population aspects, such as spatial use and/or habitat selection and fidelity to certain locations, among others (Millspaugh and Marzluff, 2001; Spencer, 2012).

The home range has traditionally been estimated by the minimum convex polygon (MCP), which delimits the maximum territory used by an individual, encompassing external points. The main drawbacks of these estimates are that MCP usually incorporates large areas in which the animal has not been or visits infrequently. These estimates are also highly sensitive to the sample size of observed animal locations captured as GPS fixes (Millspaugh and Marzluff, 2001; White and Garrott, 1990). Today, alternative methods are used. One such method is utilization distributions (uDs), which are relative frequency distributions of animal locations over a specific period of time (Kernohan et al., 2001). uDs allow the evaluation of the occurrence probability of an animal at each point in the space (Millspaugh et al., 2000) and, therefore, can be used to delimit different 'home range' contours for the same animal. We defined UD contours (isopleths) at kernel 50% for the core range (Kcr50) and at kernel 95 as a home range estimate (Khr95). Despite a large number of available methods to delimit home ranges (Kie et al., 2010), most studies still use MCP as a generic approximation of spatial delimitation and kernel home ranges as a measure of the intensity of space use (Gula and Theuerkauf, 2013).

The emergence of telemetry with GPS technology, which allows a number of animal relocations far superior to those obtained with traditional VHF tracking devices, opens the debate on the utility and relevance of traditional methods for home range estimation (Hemson et al., 2005; Kie et al., 2010). To deal with these limitations they are developing estimators of home range that incorporates time, space, animal-specific parameters, and habitat (Walter et al., 2015). The main differences between GPS and VHF monitoring are related to study design and sampling intensity. GPS devices are quite expensive in relation to VHF devices (approx. one GPS for every 10 VHF devices). This implies that the number of individuals that can be monitored for a research project is lower than that in traditional studies using VHF devices (Fieberg and Börger, 2012). The higher fixation frequency also results in a limitation of the study period due to the lifespan of the batteries (Fieberg and Börger, 2012; Hebblewhite and Haydon, 2010). The number, time range (i.e., the ability to perform daytime, night or continuous monitoring schemes) and precision of the locations is notably increased with GPS devices (Barber-Meyer and Mech, 2014; Baubet et al., 2004; Schuler et al., 2014). Thus, today, GPS devices are gradually replacing VHF for wildlife monitoring (Barasona et al., 2014; Cagnacci et al., 2010; Thomas et al., 2011). Nonetheless, VHF tracking is still in use (Keuling et al., 2008a; Merli et al., 2017; Saïd et al., 2012a), mainly due to budget and weight limitations (Hebblewhite and Haydon, 2010). Sampling intensity in general and all of these factors in particular can notably affect home range estimates (Börger et al., 2006a; Downs et al., 2012; Girard et al., 2002; Gula and Theuerkauf, 2013; Kie et al., 2010; Seaman et al., 1999; Walter et al., 2011). However, the number of studies comparing the results from VHF and GPS tracking devices –and therefore variations in sampling intensity– is low (see Kochanny et al., 2009; Pellerin et al., 2008). This is true even though inter-group networks for sharing data on wildlife (e.g., http://euroboar.org/) promote the use of different data sources and carry out meta-analyses to advance knowledge in species ecology.

In this context, the main aim of the study was to assess variations in size and UD similarity in home range estimates in relation to: i) time range, namely daytime vs continuous monitoring, and ii) fixation frequency, from one relocation per day during three days in a week (VHF simulation) to daily monitoring of 24 relocations per day (GPS simulation). The final goal of this study is to establish a scientific basis for the direct comparison of home range estimates obtained from different tracking schemes.

Materials and methods

Study areas

Fifteen wild boars were monitored in three study areas in Mediterranean Spain, five individuals per area (Fig. 3.2.1). Sant Llorenç del Munt i l'Obac Natural Park (SNP), located in the northeast of the Iberian Peninsula (41°39' to 41°42' N, 1°53' to 2°09' W), is characterized by Mediterranean holm oak forest. Patches of mixed pinewood and a mixture of rocky cliffs with scarce vegetation are present (Pintó and Panareda, 1995). Montes de Toledo (MT), in the region of Castilla-La Mancha, south-central Spain (39°25' to 39°16' N, 4°05' to 4°23' W), is characterized by evergreen oak (*Quercus ilex*), scrublands with scattered pastures and small crops, forming dehesas (savannah-like habitats). Finally, Doñana National Park (DNP) is a protected area on the Atlantic coast of southern Spain (37°0' N, 6°30' W). DNP presents a north–south humid ecotone between the elevated Mediterranean shrublands and the low marshlands, which highly affect the distribution and abundance of wild ungulates (J. A. Barasona et al., 2014).

Figure 3.2.1. Location of the study areas in Spain: Sant Llorenç Natural Park (SNP), Montes de Toledo (MT) and Doñana National Park (DNP).

Capture and GPS-GSM monitoring

The field work was carried out between 2009 and 2015. Animals were captured with portable cage traps, approx. 3x1.5m (for further details see Barasona et al., 2013; Barasona et al., 2016; Casas-Díaz et al., 2013). Traps were baited with corn every 2-4 days both inside and outside the trap and monitored with camera traps (Model IR-3BU, Leaf River Outdoor, Taylorsville, Mississippi, USA) to determine the time of activation. Once activated, each trap was check daily, early in the morning.

When a wild boar was captured, we proceeded to sedate it following Animal Experimentation legislation and procedures approved by the Animal Experiment Committee of Castilla-La Mancha University and Departament d'Agricultura, Ramaderia, Pesca, Alimentacio i Medi Natural - Generalitat de Catalunya, for MT/DNP and SNP, respectively. The anaesthesia was injected intramuscularly in the femoral region with 5 ml anaesthetic darts (Telinject®, Römerberg, Germany) using a 14 mm diameter blowpipe (Telinject®, Römerberg, Germany) after visually estimating the weight of each animal in the trap (see protocol in Barasona et al., 2013; Casas-Díaz et al., 2011). After sedation, wild boar was removed from the traps and blindfolded.

We fitted GPS-GSM collars to adult wild boar monitored in MT and DNP (five adult wild boars from MT and five from DNP; Microsensory, Spain) and SNP (five adult wild boars; LOTEK GPS 3300S, Lotek Wireless, Ontario, Canada). Post-release monitoring was programmed to acquire 24 GPS locations per day in MT and DPN, while in SPN the collars were programmed to obtain eight locations per day at least.

Daily patterns of activity

Taking into account the seasonal and daily activity patterns of wild boar provided by Keuling et al. (2008a), Tolon et al. (2009) and Carrasco-Garcia et al. (2016), the daily periods considered were (solar hour): daytime hours between 08:00 and 18:00 and night hours between 22:00 to 04:00. These time frames defined the 'dawn', 'day', 'dusk' and 'night' periods, which were first used to determine the daily patterns of wild boar activity. The distance between each consecutive fix divided by the time elapsed between them (i.e. speed; m/h) was estimated as a measure of the daily activity pattern of the animals using data from GPS tracking (Cutrera et al., 2006). To estimate both the distance and the time elapsed between consecutive fixes we used the *adehabitatLT* R package (Calenge, 2006). Since the frequency of locations is not high enough to estimate real daily ranges (e.g. Rowcliffe et al., 2012), we used the estimations of speed as an activity index to characterize daily activity patterns.

Simulating tracking schemes: time range and fixation frequency

Individual relocations used in the analyses were obtained from GPS-GSM collars. A sub-sampling of the total relocations was randomly done to obtain five sets of data (hereafter approaches) for each animal, four of them simulating data usually obtained with VHF monitoring regimes (Boitani et al., 1994; Keuling et al., 2008a): D1) day, low intensity: one relocation in the daytime three days per week; D2) day, medium intensity: seven relocations, once a day, during daytime; C1) continuous, low intensity: one relocation in the daytime and three at night, one day per week; C2) continuous, medium intensity: three fixes per night, three nights per week and one fix in the daytime three days per week; and C3) considering all available relocations. Finally, and in order to avoid the effects of the autocorrelation in HR estimations that could be derived from replication of points during the daytime (when the wild boar is mainly resting), we generated a new data set (C4) with all fixes of at night, dawn and dusk, and only 1 every day for the daytime.

Home ranges

MCP and kernel UD were used to estimate individual home ranges (Keuling et al., 2008a; Laver and Kelly, 2008; Scillitani et al., 2010). MCP to compare home ranges sizes among approaches, while kernel UD to also compare among approaches in terms of home range size and to establish the intensity in space use and characterize the overlap among home ranges.

We estimated the Khr95 and Kcr50 using the *adehabitatHR* R package (Calenge, 2006). To calculate the bandwidth or smoothing parameter 'h', we used a fixed value for each approach and study area, since this provides a way to standardise home range estimates and allows for accurate comparisons between home ranges of different sizes and numbers of locations (Pellerin et al., 2008; Saïd et al., 2012a). These fixed 'h' values were estimated as the median of individual h-values obtained with the Likelihood Cross Validation (LCV) method, since this generally produces a better fit in the estimates and less variability (Horne and Garton, 2006). The 'h' parameter was calculated with the *spatstat* R package (Baddeley and Turner, 2005). The minimum number of relocations per individual and dataset, for home range estimation, was 14 based on previous studies (Börger et al., 2006a; Seaman et al., 1999).

Home ranges estimated from different approaches were compared in size and overlap. For testing the overlap of kernel areas among approaches, methods based on the estimation of UD overlap in three dimensions (3D) were used because they are recommended over the comparison methods in 2D (Fieberg and Kochanny, 2005). Specifically, the Bhattacharyya Affinity Index (BA; Bhattacharyya, 1943) was used since it is the most appropriate method to quantify the degree of similarity between two estimates of UD (Fieberg and Kochanny, 2005) . BA takes values between zero and one (where one suggests identical estimates) and considers the internal distribution or density of locations within the boundaries of the home range (Fieberg and Kochanny, 2005). The BA index was estimated with the *adehabitatHR* R package (Calenge, 2006) and comparisons of each approach in relation to C3 (reference approach; the most intensive tracking scheme) were performed. We therefore estimated overlap for the following dyads: D1-C3, D2-C3, C1-C3 and C2-C3. To test the similarity between uDs estimated by C3 and C4 samples we also use the BA index.

We decided to compare the Khr95 with results obtained by "dynamic Brownian bridges" (dBBMM) based on C3 set, for generalize our results and link kernel UD with newer home range estimate method. We test overlap between methods with BA index that compare similarity in the density functions. Taking into account that, for GPS data, estimators that incorporate a temporal component have been described as the most reliable regardless of whether kernel-based or Brownian bridge-based algorithms were used (Walter et al., 2015).

dBBMM quantifies the use distribution of an animal based on its movement path rather than individual points, and accounts for temporal autocorrelation, high data volumes and heterogeneous movement behaviour across all data (Kranstauber et al., 2012). For dBBMM UD estimation we used Move package (Kranstauber et al., 2018), incorporating the temporal characteristics of the movement paths. We selected same parameters for all animals; margin of 3 (12 h) to account for potential diurnal versus nocturnal movement pattern differences, location error of 11 meters and pixel size equal to kernel UD.

Data analysis

Differences among dawn, day, dusk and night in the activity index were tested using a Linear Mixed Effect (LME) Model, including activity index as a response variable, sex, period and study area as independent fixed factors, and individual as a random factor. Activity index was transformed using a log(x+1) through the log1p R function. With this transformation, variation ranges are reduced and the zeros that represent inactivity of animals remains a null value (David, 2017). Multiple comparisons were performed to test for differences among the different periods, using a Tukey post-hoc test with the glht (multcomp) function from R (Hothorn et al., 2008).

LME models were also used to assess possible differences in home range size among approaches. Thus, the response variables were MCP, Khr95 and Kcr50 (i.e. three models), with approach, sex, number of fixes and study area as fixed factors, and individual as a random factor. Response variables were log-transformed to meet assumptions of normality and homoscedasticity of residuals. For each response variable, we modelled all combinations of independent parameters. Due to a relatively small sample size, no interactions between them were included in our model set. Akaike information criterion (AIC), with a second-order correction for small sample size (AIC_C), was used to rank the models dependent on their fit (Burnham and Anderson, 2002). Models with the lowest AIC_C value were considered to be the best-fit models, and models with $\Delta AIC_c < 2$ were considered of similar quality to the most parsimonious model. Pairwise comparisons between approaches were also carried out using a Tukey post-hoc test.

Similarly, and in order to explore the effect of approach on the BA overlay index, a set of LME models was parameterized (Pinheiro et al., 2017) and ranked according to Akaike criterion: BA index as a response variable and the same fixed and random factors as in the previously described models, with the exception of the number of fixes which should not be included in the BA index model. Because the BA index was scored as a proportion, we used a logit transformation for these data (Warton and Hui, 2011) with the *logit* function (log[p/(1 - p)]) of the *car* R package (Fox and Weisberg, 2011). As in Fieberg & Kochanny (2005), we infer a high degree of overlap in home range estimates among approaches with BA index values>0.60.

Because home range sizes were generally not normally distributed, most results are reported as medians and interquartile ranges (IQRs). All statistical tests were performed with the R program (R Core Team, 2017), considering significant differences when $p<0.05$.

Results

Details of the 15 monitored individuals (six females and nine males) are shown in table 3.2.1.

Table 3.2.1. Tracked animals. Age, sex and tracking period of the monitored wild boar in the three study areas: Sant Llorenç Natural Park (SNP), Montes de Toledo (MT) and Doñana National Park (DNP).

ID	Sex	Area	date_in	date_end	days
F1	Females	SPN	21/08/2011	22/10/2011	62
F2			04/12/2013	22/02/2014	80
F3			05/12/2014	02/06/2015	179
F4		DPN	02/12/2012	30/07/2013	240
F5		MT	06/07/2009	01/01/2010	179
F6			08/11/2009	15/04/2010	158
M1	Males	SPN	03/05/2012	02/06/2012	30
M2			04/05/2015	04/08/2015	92
M3		DPN	15/12/2011	12/02/2013	425
M4			27/07/2011	03/03/2012	220
M5			07/08/2011	31/12/2012	512
M6			11/10/2012	10/08/2013	303
M7		MT	02/11/2009	14/07/2010	253
M8			28/05/2010	08/05/2011	345
M9			07/08/2010	08/04/2011	244

The median and interquartile range of the number of locations per animal and bandwidth h estimated with LCV used after sub-sampling at each tracking scheme is shown in table 3.2.2. The individual h values calculated by the LCV method show an inverse and significant relationship with the number of fixes used in the estimates (R Spearman = -0.51, p<0.001, n=75).

Table 3.2.2. Sampling characteristics of different approaches. Values of median and interquartile range of number of fixes and h value (LCV estimated) for each approach at each study area: Sant Llorenç Natural Park (SNP), Montes de Toledo (MT) and Doñana National Park (DNP). D1) day, low intensity: one relocation in the daytime three days per week; D2) day, medium intensity: seven relocations, once a day, during daytime; C1) continuous, low intensity: one relocation in the daytime and three at night, one day per week; C2) continuous, medium intensity: three fixes per night, three nights per week and one fix in the daytime three days per week; and C3) considering all available relocations.

Approach	N. fixes DNP	h-value DNP	N. fixes SNP	h-value SNP	N. fixes MT	h-value MT
D1	104 (94-156)	137.1 (119.3-242.3)	34 (31-40)	202.8 (168.1-919.7)	94 (78-96)	216.7 (169.9-355.4)
D2	231 (193-343)	114 (88.6-149)	59 (50-81)	147.7 (89.4-463.6)	182 (171-201)	216.7 (134.6-238.8)
C1	163 (127-176)	152.7 (128.1-215.1)	56 (52-76)	168.3 (136.4-770.3)	125 (103-133)	202.7 (122.2-382.1)
C2	371 (254-461)	97.4 (95.9-110.1)	125 (99-163)	120.5 (110.4-337.5)	308 (300-351)	137 (133.2-171.8)
C3	2727 (2161-3035)	66.4 (63.6-70.1)	781 (729-1160)	71.2 (48.5-106.4)	2998 (2249-4145)	115.1 (63.1-120.4)

Activity

There was a significant effect of period and study area on the individual wild boar activity index (LME model: daily period: $F_{3,34703}$=1221.5, p<0.0001; area: $F_{2,11}$=12.7, p=0.0014; sex: $F_{1,11}$=4.2, p< 0.063). Despite the differences between areas, the main activity occurred at night and dusk, while remaining at lower levels during the daytime hours (Fig. 3.2.2).

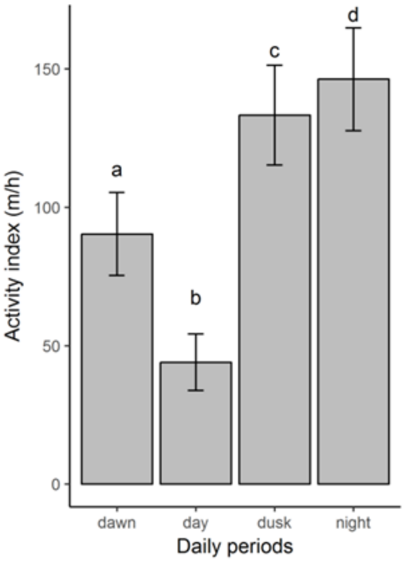


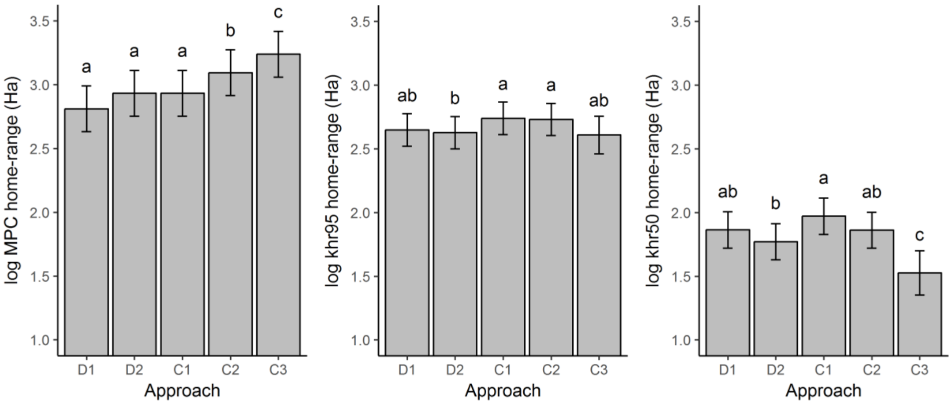
Figure 3.2.2. Activity index marginal means, measured as mean speed (in meters/hour) at each daily period. Classes sharing a lowercase letter do not differ significantly (P > 0.05) in the post-hoc statistical tests. Error bars indicate 95% confidence intervals.

Comparison of home ranges

The best-fitting models explaining the variation in home ranges included all independent factors (Table 3.2.3). The largest MCP home ranges were obtained using the C3 approach (median= 2138.9 Ha, IQR= 952 - 3775.7), followed by those obtained with C1 and C2. In addition, the effect of approach on MCP estimates was significant (see Fig. 3.2.3 and Table 3.2.4). Among all comparisons between approaches only D1, D2 and C1 produced similar MCP estimates (Fig. 3.2.3).

Table 3.2.3. Home range estimation best models selected. Set of LMEs with ΔAICc<2 for variables explaining home range estimates (MCP, Khr95 and Kcr50) in Mediterranean Spain. Number of model parameters (K), corrected Akaike information criterion (AICc) values, the best fitting model (ΔAICc) and Akaike's weights (ωi) are shown. The models were ranked dependent on the AICc value and in descending order (the most parsimonious models are on the top of each list).

Home range	Model	K	AICc	ΔAICc	ω_i
MCP	appr+zone+sex	10	88.53	0.00	0.57
	appr+sex+zone+fix	11	90.12	1.59	0.26
Khr95	appr+sex+zone+fix	11	49.1	0.00	0.71
Kcr50	appr +sex+zone+fix	11	87.3	0.00	0.92



a) b) c)

Figure 3.2.3. Marginal means of log-transformed home range estimates (a: MCP; b: Khr95 and c: Kcr50) for each approach. Classes sharing a lowercase letter do not differ significantly (P > 0.05) in the post-hoc Tukey with p-adjusted values. Error bars indicate 95% confidence intervals.

Significant effects of approach were also found in Khr95 home range estimates (Fig. 3.2.3, Table 3.2.4). In Tukey post hoc comparisons, only the C1-D2 and C2-D2 dyads showed significant differences and interestingly no differences in relation to C3 were found. Finally, we found a significant effect of approach when Kcr50 estimates were compared (Fig. 3.2.3, Table 3.2.4). The pairs of core areas C1-D2, C1-C3, C2-C3, D1-C3 and D2-C3 showed significant differences in their estimates. In Kcr50, differences between approaches were observed in comparison with C3, however, there are no differences between diurnal D1 and continuous medium sampling intensity C2 (Fig. 3.2.3).

Table 3.2.4. Variables statistics of home ranges models estimation. Results of the best-fitting LME models explaining home range estimates (MCP, Khr95 and Kcr50) in Mediterranean Spain.

	Num. df	Den. df	F-value	p-value
MCP				
(Intercept)	1	56	1702.5	<0.0001
Approach	4	56	27.4	<0.0001
Sex	1	11	15.3	0.0024
Zone	2	11	5.0	0.0277
Khr95				
(Intercept)	1	55	2759.6	<0.0001
Approach	4	55	4.1	0.0049
Sex	1	11	3.9	0.0726
Zone	2	11	8.6	0.0055
Fixes	1	55	4.6	0.0354
Kcr50				
(Intercept)	1	55	1098.14	<.0001
Approach	4	55	9.55	<.0001
Sex	1	11	0.4	0.5425
Zone	2	11	10.9	0.0025
Fixes	1	55	8.6	0.0049

We did not observe significant differences between the estimated Khr95 with samples C3 and C4, neither between them and the dBBMM with 85 isopleths (LME model: approach (Khr95$_{C3}$, Khr95$_{C4}$ and DBMM85): $F_{2,28}$= 0.37, p=0.68; area: $F_{2,11}$=12.7, p= 0.0047; sex: $F_{1,11}$= 19.15, p= 0.0011).

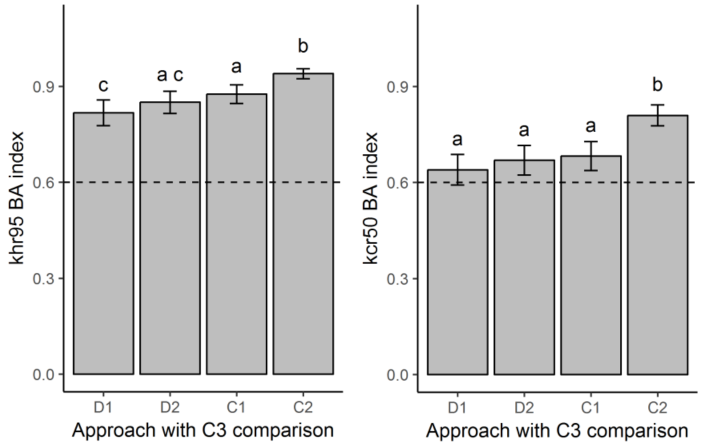
Overlap index

The best-fitting models included the approach and sex predictors to explain differences between the BA index in Khr95. The study area is also included in the second best model. For the BA index of Kcr50, the best model included all the independent variables considered (Table 3.2.5).

Table 3.2.5. Home range overlays best models. Set of LMEs with ΔAICc<2 for variables explaining the BA (Bhattacharyya Affinity) index (of Khr95 and Kcr50) with relation to the C3 approach in Mediterranean Spain. Number of model parameters (K), corrected Akaike information criterion (AIC$_c$) values, the best fitting model (ΔAICc) and Akaike's weights (ω_i) are shown. The models were ranked dependent on the AICc value and in descending order (the most parsimonious models are on the top of each list).

BA index	Model	K	logLik	AICc	ΔAICc	ω_i
Khr95	appr +sex	7	-25.56	67.3	0.00	0.57
	appr+sex+zone	9	-23.42	68.5	1.18	0.32
Kcr50	appr+sex+zone	9	-18.98	59.6	0.00	0.75

In the comparisons of the different BA similarity indexes of the Khr95 for the different approaches with C3, differences were found between approaches (Fig. 3.2.4, Table 3.2.6). BA values for the monitored individuals ranged from a median of 0.81 (IQR: 0.78- 0.83) in the D1-C3 approach comparison to 0.93 (IQR: 0.91- 0.95) in the C2-C3 comparison. In the same comparisons for the Kcr50, significant differences between approaches were found (Fig. 3.2.4, Table 3.2.6). BA values for the monitored individuals ranged from a median value of 0.65 (IQR: 0.52- 0.74) in the D1-C3 comparison to 0.81 (IQR: 0.76- 0.84) in the C2-C3 dyad.



a) b)

Figure 3.2.4. Marginal means and 95% CI of the BA (Bhattacharyya Affinity) index between each approach compared with C3. Horizontal dashed line delimits the 0.6 value, above which it can be considered a high overlap between home ranges. Classes sharing a lowercase letter do not differ significantly (P > 0.05) in the glht pairwise comparisons with fdr p-adjusted values. a) BA at Khr95 and b) BA at Kcr50.

Table 3.2.6. Variables statistics of home ranges overlay models. Results of the best fitting LME models explaining the BA (Bhattacharyya Affinity) index (Khr95 and Kcr50) in Mediterranean Spain.

BA index	Num. df	Den. df	F-value	p-value
Khr95				
(Intercept)	1	42	333.52	<.0001
Approach	3	42	48.58	<.0001
Sex	1	13	6.86	0.02
Kcr50				
(Intercept)	1	42	155.75	<.0001
Approach	3	42	26.02	<.0001
Sex	1	11	5.35	0.0411
Zone	2	11	12.12	0.0017

The median overlap BA index between kernel UDs estimated with C3 and C4 samples was high 0.96 (IQR: 0.63- 0.97). Similarly, median BA index between kernel UD and dBBMM UD home range wild boars was also high 0.9 (IQR: 0.88- 0.95).

Discussion

Methodological procedures evaluated in this paper have identified the particular cases where direct comparisons of home range estimates obtained from different tracking schemes may be addressed. Considering the importance of the correct selection of h, the use of Khr95 allows similar estimates of home range (size and UD similarity) and therefore, facilitates the comparison between studies carried out with different tracking schemes. We should be more cautious with comparisons of Kcr50 and MCP since there are differences in size and UD between tracking schemes with higher sampling intensities and those of smaller ones.

One of main problems argued in the application of kernel estimates with GPS data (large volume of fixes) is the autocorrelation, or independence in locations (Kernohan et al., 2001, but see Fieberg and Börger, 2012). The similarity, both in size and in the utilization distributions, between kernels and the dBBMM home range estimates with all the locations, allow generalizing and making our approach robust.

The activity of the wild boar is mainly nocturnal, also presenting activity at dusk and dawn, and is low during the day. This general pattern presents some seasonal variations (Keuling et al., 2008b; Massei et al., 1997; Russo et al., 1997). The activity pattern that we observed is concordant with the literature, with a minimum of activity in the daytime hours and a maximum in the night hours. These differences in activity would lead us to suspect differences in the estimation of home range areas using different approaches (Tolon et al., 2009), especially between diurnal and continuous tracking schemes (Ds and Cs approaches), and therefore support the selection of wild boar as a relevant case study. Regarding home range size, a small number of locations for each animal may imply the underestimation of the areas or, more importantly, the non-consideration of areas or locations that may be of great importance in terms of biological aspects, the selection or use of space and/or species management (Hebblewhite and Haydon, 2010). Moreover, this becomes especially relevant on a fine scale (Kcr50). We found differences between approaches in home range size estimates, but these were not consistent in relation to the parameter studied (MCP, Khr95 and Kcr50). Specifically, if we take into account the MCP calculation, maximum differences between tested approaches were observed. This result agrees Börger et al. (2006) study, which showed that the MCP method should be used with caution in the comparison of estimates of home ranges. However, in a very relevant way, no approach shows differences regarding C3 when considering Khr95. As for the Kcr50, the Ds approaches do not differ from C2 (VHF sampling approach).

In relation to home range UD, differences between approaches in relation to overlap with C3 were found. In general, the UD similarity increased as the sampling intensity increased. However, the levels of overlap are high (above 0.75) in all cases considering Khr95, confirming that this is an appropriate parameter to compare approaches in terms of UD. When we take into account the same comparisons using the Kcr50, the overlaps are somewhat smaller, only surpassing the value of 0.75 in the C2-C3 comparison. It should be noted that the values of the BA index are sensitive to the number of locations, as in the estimation of the kernel (Fieberg and Kochanny, 2005). The high degree of similarity of the home ranges with Khr95 between the diurnal and continuous approaches indicates that the diurnal monitoring allows the total Khr95 area to be estimated with some precision. These values of degree of overlap are high and similar to those obtained by Kochanny et al. (2009). Frequent variation in resting places, at small and large scales, the location of resting places near the centre of their areas of activity and some daytime activity of wild boar, are likely why diurnal resting sites produce good approximations of the total home ranges.

It is worth noting that while for most authors the sampling effort is crucial to consider when comparing estimates of home range from different studies (Börger et al., 2006a; Girard et al., 2002), other authors focus on the choice of h factor if the main focus is the study of habitat use (Huck et al., 2008). In addition, since there is no consensus regarding the best method to obtain home range estimates (Fieberg and Börger, 2012) and although this exceeds the objectives of this study, we will briefly discuss some methodological aspects. The smoothing factor h is the most relevant and critical parameter in the estimation of kernels (Silverman, 1986). Setting a fix h for all animals facilitates the standardisation of estimates of home ranges and allows accurate comparisons between different sizes and numbers of locations (Saïd et al., 2012a). The main problem is that small values of h (as obtained by the Least Squares Cross Validation LSCV method) provided small and extremely atomized home ranges, while the high values (as obtained by href) produced the opposite effect (Huck et al., 2008; Kie et al., 2010). In contrast, we obtained intermediate home ranges with greater spatial coherence fixing h per approach for all individuals of the same study area by the LCV method. The kernel methods are sensitive to sampling schemes (times and frequencies) and the number of fixes (Schuler et al., 2014). Setting h by LCV for each approach and study area, partly compensates for the differences in the size of the home ranges caused by the differences in these factors, facilitating the comparison between estimates. While some evidence was found in our study, future works are necessary to deepen the comparison of home range estimations based on different h factor selection.

Conclusions

The results obtained here suggest that not all estimates (MCP, Khr95 and Kcr50) are equally affected by tracking schemes. Khr95, paying special attention to h selection, is the most consistent between approaches, with VHF simulated approaches producing equivalent estimations of home range size and UD to C3. Accordingly, we suggest that attention be given to Khr95 home range estimations when analysing data from studies with different tracking intensity (time range and fixation frequency), even when working with species like wild boar with a marked activity pattern.

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Declarations of interest: none.

Estudio III

3.3. Home range and space use patterns of wild boar in a Mediterranean environment

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(Submitted to Zoological Research)

Abstract

The wild boar (*Sus scrofa*) is widely distributed in the Holarctic region. Its populations have increased drastically in Mediterranean environments in the last decades, generating important conflicts with human activities in the form of crop damage, natural areas, urban areas and vehicles, human and animal health. The wild boar is considered mostly sedentary, although displacements have been described between home ranges and activity centers due to hunting and seasonality of key resources. Between 2012 and 2014, we radio-tagged 26 animals in a Mediterranean environment in northeastern Spain, with the objective of describing home range sizes, patterns in space use, as well as the main drivers of species' spatial use. Neither the gender nor the age of the individuals significantly affected the home range sizes. Two types of patterns in home ranges were detected: i) a majority composed of several disjunct activity centers (two or three) and ii) a type formed by a compact area. In the former, the displacements between the different areas of activity occurred mainly in winter and spring. In either case, the marked seasonality of Mediterranean environments significantly conditioned the wild boar space use patterns. This fundamental knowledge about spatial ecology of the wild boar will allow improvements in the management strategies of the species. Since the knowledge of ecology, the seasonality of movements, the use of space and the pressure of human activities such as hunting allows to spatially and temporally guide the application of non-lethal measures such as fences, habitat management through reduced coverage or scare off wild boars by dogs. As well as allowing the management of lethal management, through hunting in different modalities and trap capture.

Keywords: kernel range, spatial ecology, radio-tracking, *Sus scrofa*

Introduction

The wild boar (*Sus scrofa*) is a terrestrial mammal with one of the largest distribution ranges in Europe, as well as being a species that occupies a great variety of habitats (Apollonio et al., 2010). In the Iberian Peninsula, it is found from the forests of the Pyrenees to the dunes of the mouth of the Guadalquivir River, passing through the different inland habitats (Fernández-Llario, 2017). In Spain, following the same trend as in greater Europe, the abundance of wild boar has increased remarkably in recent decades (Acevedo et al., 2006; Massei et al., 2015; Rosell and Herrero, 2007).

Among the proposed factors involved in population growth is a lack of predators, reforestation of rural areas, reintroductions and translocations, a global increase in temperatures and availability of food, a highly efficient reproductive strategy and ineffective management practices in the regulation of population abundance (Bieber and Ruf, 2005; Massei et al., 2011; Quirós-Fernández et al., 2017). However, population expansion and growth may be partially attributed to the ethological plasticity of the species (Podgórski et al., 2013). Its ecological plasticity is also manifested in a high degree of tolerance to human pressure, allowing it to settle in the periphery of urban areas and to feed in highly humanized cultivated environments (Cahill et al., 2012; Rosell et al., 2001). The increasing in populations of wild boar and its tolerance to human pressure have led to conflicts with humans, such as damage to fields, natural vegetation, and biodiversity as well as traffic accidents (Massei and Genov, 2004). There is a wide variety of crops affected by wild boar; corn is traditionally the most affected crop, other crops are the vineyards, fruit crops such as apple trees, peach trees or almond trees, are also highlighted others such as rapeseed, crops of dry land such as cereals and orchards. In all cases, the damages affect temporarily the fields, mainly during the maturation period. However, they are also registered damage during planting, due to the consumption of seeds. Another of the damages that are reported are those produced in irrigation systems, especially in periods of drought, when wild boars dig up and damage irrigation systems to get water. The pastures are affected due to the wild boar rooting to access food (invertebrates, bulbs, roots and rhizomes) underground. There is no data on crop damage but using crop damage hunting authorization number requested every year in Catalonia as indicator, between 2003 and 2015 these authorizations have multiplied by nine, reaching almost 7000 licenses in the last year (Rosell et al., 2019).

Another source of conflict is accidents with vehicles, in this sense, in road network owned by the Generalitat de Catalunya Catalonia (autonomous community of Spain), the increase of accidents with animals involved between 2010 and 2014 were 56% and for the particular case of wild ungulates has been 72%, considering that wild boar is involved in the 86% of accidents with animals of which the species is known (Direcció General de Forests, 2016).

The spatial ecology of the species is the result of the interaction between individuals and the environment. In this sense, the size and shape of the home ranges (in a utilization distribution (UD) sense or probability density that an animal is found at a given point in space), as well as the patterns of use within them can be conditioned by population/individual factors, environmental factors and by human activities (Kay et al., 2017; Morelle et al., 2015). Population factors such as reproduction, density and social structure, individual factors such as size, gender and age, environmental variables such as resource availability and distribution, climate, and disturbances such as recreational activities, silvicultural work, hunting and predation have all been shown to affect range behavior (Keuling et al., 2008a, 2008b; Morelle et al., 2015; Podgórski et al., 2013; Thurfjell et al., 2014). It should be noted that, in terms of the use of space, wild boar can react flexibly and individually to these factors (Morelle et al., 2015). Wild boar show marked sedentary habits (Keuling et al., 2008a; Maillard and Fournier, 1995; Mitchell et al., 2009), although human pressure, competition and territoriality can cause long-distance movements to establish new activity centers (Casas-Díaz et al., 2013; Jerina et al., 2014; Morini et al., 1995). Human pressures of hunting, despite a certain tolerance, can cause temporary or definitive movements of animals (Saïd et al., 2012a; Scillitani et al., 2010). Displacements between activity centers (i.e., each of the polygons that form a home range) have been described as a consequence of hunting activity (Scillitani et al., 2010; Sodeikat and Pohlmeyer, 2003) and seasonality of resources (Keuling et al., 2008a). In addition, urban environments provide stable and diverse sources of food, unlike the marked seasonality of trophic resources in more natural environments, which is reflected in smaller home ranges in urban environments (Podgórski et al., 2013). Weather and seasons affect the availability of food and, therefore, wild boar movement. Wild boars reduce their movement during the cold winter temperatures and increase the displacements during late summer (Thurfjell et al., 2014). In Mediterranean regions the summer period has great importance as a limiting factor of survival, as seasonal drought conditions dry and harden the ground limiting rooting activity (Massei et al., 1997). Thus, the shortage of resources in summer causes increased displacements and shifts in home ranges towards crop fields (Keuling et al., 2008a). Despite the large number of studies on wild boar ecology, there are few papers describing the home ranges of wild boar in Mediterranean environments (but see Boitani et al. 1994, Massei et al. 1997) and especially those that provide spatial patterns of the species within the home range (Keuling et al., 2008a; Maillard and Fournier, 1995).

In this context, the aim of this study was to describe the patterns of range size, drivers of spatial use and the factors that could determine these patterns in Mediterranean environments. A detailed knowledge of spatial use and information about the structure and dynamics of wild boar populations can lead to the definition of rigorous and effective management strategies that allow minimize human-boar conflict.

Material and methods

Study Area

The study was carried out in Sant Llorenç del Munt i l'Obac Natural Park, a natural area located in the pre-coastal mountain range of Catalonia in northeastern Iberian Peninsula (41° 39'- 41° 42 'N; 1° 53'-2° 09 'E; Fig. 3.3.1). Due to its geographical location, proximity to the sea and the moderate altitude (maximum of 1104 m above sea level), the Mediterranean climate corresponds to this region. Average precipitation is about 700 mm, with maximums in autumn and spring. The maximum temperatures are in summer, reaching values above 35ºC. The main substrate is limestone in the form of conglomerates. The vegetation best represented is the Mediterranean and mountain holm oak with oak (*Quercus ilex*) as a dominant. In the foothills of the mountain range, there are patches of mixed pinewoods of *Pinus nigra Salzmanii*, *Pinus sylvestris* and *Pinus halepensis*. Rocky cliffs abound with little vegetation (Pintó and Panareda, 1995).

Within the Natural Park (Fig. 3.3.1), wild boars have been captured and radio-tracked in two zones with different characteristics. The first, located to the north of the natural area, is a Wildlife Refuge of 877.41 Ha in which hunting activity is prohibited, near two small towns and with low human density and tourism. The wild boar makes partial use of the wildlife refuge, using large areas to the north with cereal fields and water availability, as well as low tourist use. The second area is located in the south. It is a controlled Hunting Zone of 610.84 Ha managed by the Generalitat de Catalunya, competent autonomous community administration, with higher touristic pressure due to the influence of urbanizations, towns and a large city.

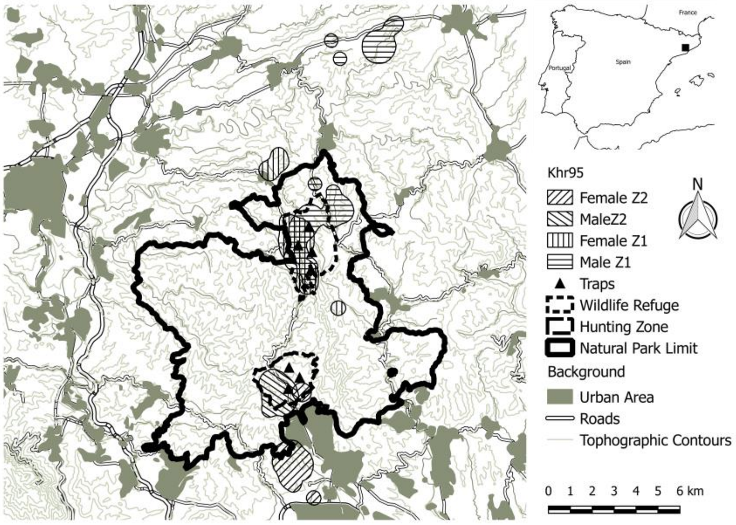


Figure 3.3.1. Sant Llorenç del Munt i l'Obac Natural Park in northeastern Iberian Peninsula. Two catch zones: Wildlife refuge in the north and hunting area in the south and examples of male and female Khr95 home range in each zone.

Trapping and radio-tracking

The field work was carried out between April 2012 and December 2014. For the capture, four trap cages were used in the northern area and three in the southern area. During the catch period, the traps were baited with maize and checked each morning while they were activated, and bait was added after boar was caught or when it had been consumed. When a boar was captured, it was anesthetized with a dart fired by a blowpipe. A combination of 3 mg/kg of tiletamine + 3 mg/kg of zolacepam (Zoletil®, Virbac, Esplugues de Llobregat, Barcelona) and 3 mg/kg of xylazine (Xilagesic 20% ®, Laboratoris Calier, Les Franqueses del Vallès, Barcelona) were applied.

The animals were classified as juveniles (<12 months of age), yearlings (12-24 months) and adults (> 24 months), following the rankings of previous studies (Calenge et al., 2002; Keuling et al., 2008a; Podgórski et al., 2013), according to dental eruption pattern (Matschke, 1967). Ear-tag emitters of approximately 40 grams with a movement sensor (TW5 twin cell ear-tag, Biotrack Ltd. Wareham, UK) were installed on adults, yearlings and juveniles over 5 months of age, both males (n=14) and females (n=12). We worked within the frequency band of 150-152 MHz.

The identification of the animals was performed by means of a plastic ear-tag (Allflex, Gepork, Masies de Roda, Spain) individualized by notches on the ear that did not carry the emitter. When more than one boar was caught at same time in the same trap, based on the assumption that these individuals belonged to the same social group and therefore, always move together, all individuals were identified but never more than two were equipped with emitter ear-tags to avoid replication in radio-tracking results. In addition, in the data analyzed only one animal per group was taken into account for the same reason.

Radio-tracking was performed at least twice a week, obtaining for each boar a fixe each day (mean±SD: 2.23±0.48 fixes per week and boar). All radiolocations were obtained during daytime from 10h to 16h, due to logistic and practical reasons, by means of approach or "homing in" to obtain a precise location and minimize the error that would be generated by triangulation (Samuel and Fuller, 1994), but avoiding movement of the animals (Gula and Theuerkauf, 2013; White and Garrott, 1990). The tracking was performed with a three-element yagui manual antenna and an Icom R90 multi-band receiver (Icom Inc, Osaka, Japan).

Home range

The resting areas of the wild boar represent a good approximation of total home ranges in Mediterranean environments, especially those estimated by the Khr95 (Peris et al., n.d.). In addition, they allow a comparison to multiple studies that used only daytime locations (e.g. Calenge et al., 2002; Maillard and Fournier, 1995; Saïd et al., 2012b; Sodeikat and Pohlmeyer, 2007).

Home ranges were estimated using the Minimum Convex Polygon (MCP) with 100% of the locations and kernel 95 (Khr95), considering different Khr95 polygons within an individual home range as activity centers. To estimate the home ranges, the approximation proposed by Peris et al. (n.d.) was used, setting the smoothing factor (h) calculated as the median of the individual estimates through Likelihood Cross Validation (Horne and Garton, 2006), using the R package "adehabitatHR" (Calenge, 2006). The minimum number of fixes used for home range estimation was 30, following the recommendations of Seaman et al. (1999) and Börger et al. (2006). Those animals with fewer locations were not taken into account in the present study. Similar to Friebel and Jodice (2009), different parameters were calculated from the data, including distance between resting sites, an index of the home range dispersion, displacements between activity centers (different polygons that compose the Khr95), the average number of points in each activity center as an estimate of the average time in each center and, finally, the percentage of overlap between home ranges (Khr95) of individuals as a proxy of the degree of population aggregation in each zone.

The value for distance between resting sites was obtained by the median of the distance between consecutive diurnal locations for each animal. The dispersion home range index was calculated as the median of the distance from all the relocations to the arithmetic center of the home range (for MCP and each Khr95 polygon), where small values indicate small and regular home ranges. Distance between activity centers were obtained as the average of the distances of the centroids of Khr95 polygons. To assess the magnitude of the displacements between activity centers, we tested if the values of distance between activity centers were > 0.5 * average values of individual dispersion home range index, indicating that the said individual had moved in search of a new center by more than half of a home range or activity center adapted from (Friebel and Jodice, 2009; Plowman et al., 2006).

The overlap between Khr95 was measured using the Utilization Distribution Overlapping Index (UDOI) developed by Fieberg and Kochanny (2005). The UDOI index takes a value of 0 when there is no overlap and 1 when the overlap is complete in uniform distributions. For non-uniform distributions of the relocations UDOI values >1 indicate high overlap, while values <1 indicate less overlap than expected relative to a uniform use of space (Fieberg and Kochanny, 2005).

Data analysis

The uDs estimation and overlaps between the Khr95 were made using the "adehabitatHR" package (Calenge, 2006). Each dyad of individuals was assigned to a category depending on the gender of its members (with three possible groups: male-male, male-female and female-female) and a second category depending on their age (with six groups: adult-adult, adult-yearling, adult-juvenile, yearling-yearling, yearling-juvenile, juvenile-juvenile). These two categorical variables were used as independent variables, together with the area of capture of the animals and UDOI values as the dependent variables, in the analysis of the variance by permutations (permutation ANOVA).

To test the effects of sex, age and area of capture (hunting area or refuge) on home range size, dispersion indexes and mean activity center area, independent linear models (LM) were developed, using the logarithmic transformation of the areas and distances, in order to achieve normality and homocedasticity of residuals in these models (Mangiafico, 2016).

To evaluate the effects of the same factors, in addition to the seasonality (spring: February 16th- May 15th; summer: May 16th- August 15th; autumn: August 16th- November 15th; winter: November 16th- February 15th), on the distances between consecutive resting places, we elaborated a linear mixed effects model (LME) in which we also transformed the dependent variable logarithmically and, as a random factor, we used the individuals.

We created a rose diagram with distribution of angles relative to north by season with "circular" (Agostinelli and Lund, 2017) and "amt" (Signer et al., 2019) packages to check the majority components in the seasonal direction of the displacements.

We used generalized linear models (GLM), with a Poisson error distribution, to evaluate the effect of gender, age or zone on the number of polygons (i.e. activity centers), in which the wild boars were present for at least a week. In the construction of all the models, given the limited sample size and the number of levels of each independent variable, only the age and gender interaction were included. Due to the high dispersion in the data, the median, rather than the mean, was used preferably as the central estimator of the home ranges. In addition, interquartile range (IQR) was added as a descriptive value of dispersion. The described models were elaborated using the "nlme" package of R (Pinheiro et al., 2017). Likewise, all other statistical tests were carried out with the program R version 3.3.3 (R Core Team, 2017) and significant differences were considered when the value of $P < 0.05$.

Results

Seventy-one wild boars were captured, of which 35 were given ear-tag emitters, although only 26 (12 females and 14 males, from different family groups) were used for the calculations, because they had a minimum of 30 locations for a minimum of two months at the end of the tracking process.

Home ranges

Locations (n=1204) were obtained for all twenty-six wild boars at an average radio-tracking time of 152 ± 85 days.

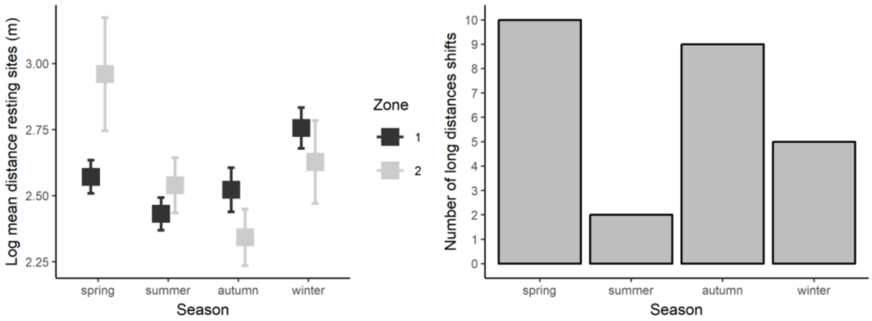
The median MCP for the 26 wild boars was 773 Ha (IQR: 360-1298 Ha), for median Khr95 it was 683 Ha (IQR: 438-762 Ha). The details by age and sex can be seen in table 3.3.1. We did not find significant differences between Khr95, for sexes, ages, their interaction or zones (LM Gender: $F_{1,25} = 1.12$, $p = 0.3$, Age: $F_{2,25} = 0.24$, $p = 0.78$, Gender*Age: $F_{2,25} = 2.41$, $p = 0.11$, Zone: $F_{1,25} = 2.77$, $p = 0.11$).

Table 3.3.1. Median and interquartile range of home ranges (MCP and Khr95) estimated by sex and age categories of wild boars in the study area.

	MCP (Ha)		**Khr95 (Ha)**	
	Female	**Male**	**Female**	**Male**
Juvenile	197.4	965.1	408.2	747.8
	(169.6-334.5)	(385.1-2642.3)	(389.8-409.3)	(654.7-795.6)
Yearling	778.9	575.6	756.3	588.2
	(645.3-965.6)	(512.2-2931.3)	(604.2-764)	(556.9-668.6)
Adult	1068.8	797.4	696.8	527.4
	(1009.9-1127.8)	(421.5-1173.2)	(681.1-712.5)	(388.8-665.9)

Patterns within the home range

The median distances between diurnal resting sites was 400 meters (IQR: 136.16- 860.52 meters). We found differences due to seasonality and for zone and season interaction, but not for the factors age, gender , zone or interactions (LME Gender: χ2 (1)= 1.05, p= 0.3, Age: χ2 (2)= 1.56, p= 0.45, Zone: χ2 (1)= 0.01, p= 0.89; Gender*Age: χ2 (2)= 1.45, p= 0.48; S Zone*Season: χ2 (3)= 9.38, p= 0.02; Season: χ2 (3)= 22.85, p<0.0001). The seasons with the greatest dispersion distances at the resting points were winter and spring (Fig. 3.3.2a). If we considered only the most important displacements between resting points (e.g., distances greater than 4500 meters as an indicator distance of movement between activity centers), the main displacements took place in the spring and autumn months (Fig. 3.3.2b). Considering that wild boar repeated resting zones when the distance between consecutive points was less than 50 meters, we determined that they repeated resting sites only 10.7% of the time. However, 8.8% of the time they moved more than 2000 meters between consecutive resting sites.



(a) (b)

Figure 3.3.2. (a) Marginal mean of distance (log transformed) between consecutive resting sites of wild boars by season and zone (1. Wildlife Refuge and 2. Hunting zone), with SE interval, (b) number of shifts or displacements greater than 4500 meters between consecutive resting sites in each season.

The median of the home range dispersion index for the MCP was 2329.86 meters (IQR: 1135.74- 3101.6 meters). If we consider the same index within activity centers, it was 517.37 meters (IQR: 344-629.1 meters). We did not find differences between genders, ages or study zones for home range dispersion in the case of MCP (LM Gender: $F_{1,25} = 0.9$, p = 0.35, Age: $F_{2,25} = 0.06$, p = 0.93, Gender*Age: $F_{1,25} = 1.76$, p = 0.19, Zone: $F_{1,21} = 0.63$, p = 0.43), or activity centers (LM Gender: $F_{1,25} = 0.27$, p = 0.6, Age: $F_{2,25} = 0.67$, p = 0.52, Gender*Age: $F_{1,25} = 0.28$, p = 0.75, Zone: $F_{1,21} = 1.16$, p = 0.29). The high value of home range dispersion in the case of the MCP (4.5 times greater than the same index for the activity centers) indicates an elongated home range composed of several more compact polygons.

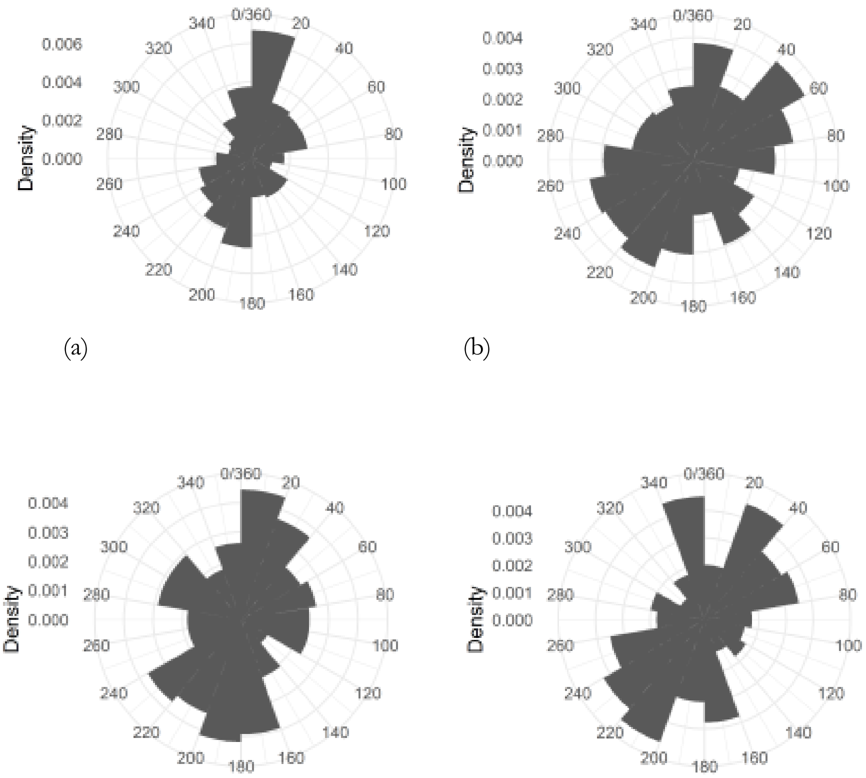
We examined the distance between activity centers to determine if there were shifts in the central tendency of the home ranges. Ten animals presented a single polygon in Khr95. For the rest, the median distance between these centers was 5203.3 meters (IQR: 4478.8-7828.5 meters).

The displacements between centers were 3.9 times greater than the limit marked as significant for the MCP home range dispersion index, showing that the wild boars separated their activity centers in search of a new area four times the size of an individual home range. If we compare the displacement with the limit value for the activity centers of Khr95, the shifts are 12 times greater than the size of activity centers.

The average number of activity centers within the Khr95 was 2.5 (IQR: 2-3 activity centers) and the average time in each of them was 2.3 months (IQR: 1.5- 2.64 months). Regarding the number of activity centers, we also found no influence of the gender, age or zone factors (GLM Gender: $\chi2$ (1)= 2.91, p= 0.08, Age: $\chi2$ (2)= 2.88, p= 0.23, Gender*Age: $\chi2$ (2)= 1.17, p= 0.55, Zone: $\chi2$ (1)= 0.38, p= 0.53).

The surface area of activity centers included in Khr95 had a median of 466.4 Ha (IQR: 337.8-523.2 ha).

Displacements between locations showed, in general, a main component with a northeastern-southwest direction (Fig. 3.3.3). While in spring the displacements were mainly in the northeast direction (Fig. 3.3.3a), in summer, there was a less predominant direction in travel (Fig. 3.3.3b). In winter, they went mainly in a southwest direction but also traveled northeast (Fig. 3.3.3d).



(a) (b)

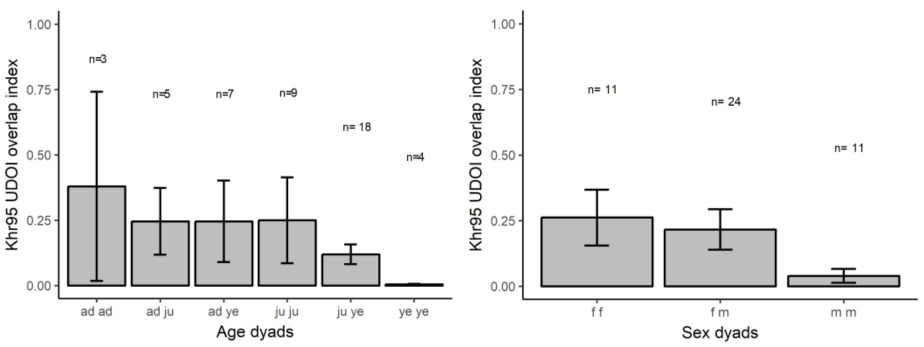
(c) (d)

Figure 3.3.3. Seasonal movement characteristics, absolute angles (for each movement) relative to North. Rose diagrams to depict the distribution of angles: Spring (a), Summer (b), Autumn (c) and Winter (d).

Home range overlays

Regarding wild boar groups tracked simultaneously in the same area (n=25), all individuals had some degree of overlap in their Khr95 home ranges. Of the 46 possible combinations, in 91.3% (n = 42) of them there was an overlap for Khr95.

The median overlap between home ranges for all boars indicates a low degree of overlap (UDOI Median = 0.0099, IQR: 0.0018-0.24). Considering the comparisons between ages, the major overlaps occured between adult individuals and the minor overlaps between yearlings (Fig. 3.3.4a). When we compared between genders, UDOI values were lower, obtaining minimums in the comparison between males (Fig. 3.3.4b). The Permutations Anova revealed that there were no effects on the overlap attributable to age and gender dyads or the capture zone considered (Perm. ANOVA, Gender: $F_{2,45} = 0.86$, $p = 0.41$, Age: $F_{5,45} = 0.95$, $p = 0.44$, Zone: $F_{1,45} = 0.2$, $p = 0.63$). No significant effect was found in the comparisons by gender, although the male-male dyad had the least overlap.



(a) (b)

Figure 3.3.4. Mean and 95% confidence interval values of UDOI overlap index at Khr95 home ranges by age (a) and sex dyads (b).

Discussion

The extent of the home ranges obtained in this study was within the range of those estimated for wild boars in similar Mediterranean environments in Italy (Boitani et al., 1994; Massei et al., 1997) and in Europe and USA (Keuling et al., 2008a; Saïd et al., 2012a), but slightly higher than Scillitani et al. (2010) and Tolon et al. (2009).

Thirty-eight percent (n=10) of the wild boar presented a compact home range area, which denotes high fidelity to the space (Keuling et al., 2008a). However, the other 62% (n=16) showed a more fragmented spatial pattern.

From the higher home range dispersion index calculated for the MCP than those of each polygon of the Khr95, we observed that home ranges of wild boars are mostly elongated. Although there is some variation, we can explain the spatial behavior of the population of wild boar through two patterns. The majority pattern was characterized by the use of compact activity centers during a variable period (mostly between 1 and 3 months) and displacements from these areas of greater use of about 5 km, to subsequently move to a new location or return to the previous one. We also observed displacements between activity centers but of much shorter duration. In particular, this pattern of movements produces longer MCP home range estimates. The minority pattern was characterized by fidelity to a compact space without movements outside this area. Displacements have been described between activity centers due to hunting (Scillitani et al., 2010) and seasonality because of the search for food resources (Keuling et al., 2008a), as well as plasticity in spatio-temporal patterns due to human pressure. Despite this, there are many studies that describe quite compact home ranges and sedentary behavior (Calenge et al., 2002; Fischer et al., 2004; Keuling et al., 2008a; Saunders and Kay, 1996).

Regarding the effect of hunting on the use of wild boar space, the work of Scillitani et al. (2010) described the displacement between home ranges of three family groups with respect to the 10 family groups and 15 solitary wild boars radio-tracked due to the high hunting pressure, while groups subjected to a small hunting pressure were more sedentary. Thurfjell et al. (2013) described the displacement of six wild boars (from a total of 15 individuals followed) between 2 and 20 km to a refuge area to return to the place of origin between 6 and 29 days due to hunting. In our case, the movement between activity centers was the majority behavior, even outside the hunting season. Despite finding seasonal differences in distances between consecutive resting places due to the type of capture zone, we must bear in mind that the refuge area is small and wild boars transcend their limits, also in the hunting season. Our results agree with these studies in the greater distances between consecutive resting places during the winter months (hunting season), although the great distances between resting places in spring are also noted, especially in the hunting zone.

Regarding the wildlife refuge zone, the animals located their resting places farther away than animals radio-tracked outside the zone, especially in the hunting season, contrary to that found by Thurfjell et al. (2013). Outside the hunting season (spring and summer), distances between consecutive resting places are shorter in the wildlife refuge than in the hunting area, reversing the process during the hunting season (Fig. 3.3.2a). Two processes could be behind this pattern; the greatest diversity of environments and food resource richness in the wildlife refuge, and especially, the lower frequency of human activities during this period in the refuge area, causing fewer disturbances and therefore, fewer displacements. In this sense, other studies have revealed the differences in different spatial and temporal parameters of the ecology of wild boar due to human activities (Ohashi et al., 2013; Podgórski et al., 2013).

When considering only the most important displacements between resting places (> 4500 m), the seasonal pattern is modified. These movements took place mainly in spring and autumn seasons. There are few studies that have revealed marked seasonal variations (Gabor et al., 1999; Keuling et al., 2008a; Lemel et al., 2003; Singer et al., 1981), and associated with zones with another habitat type, in which the changes in the climate drastically affect the availability of food. In our case, as revealed by the main seasonal displacements and seasonal directional graphs (Fig. 3.3.2b and 3.3.3), it seems likely that the displacements in spring were caused by the movement to the north, where there is greater availability of cereal crops and water. While in the fall months, they could respond to the availability of acorns in the Natural Park forests.

The spatial behavior of the wild boars has been described as an alternation between phases with important changes in the resting places, with phases in which they use the same place consecutively (Kowalski, 1985; Mauget, 1980). Our results indicate that the change from resting places to nearby areas was the most common behavior. Specifically, the typical space use by the wild boar in our Mediterranean environment consists of a frequent change of the consecutives resting places, separated from each other by 400 meters, alternating this behavior with phases of high fidelity to resting places (11% of the total) and specific phases of greater displacements (more than 2000 meters, 9% of the total). On a larger scale, we do observe some spatial fidelity since the number of activity centers used for more than a week by the animals was small (from 1 to 3), while its average surface area was relatively high (450 ha).

Although there is a lot of interindividual variation, the overlap of home ranges between ages is on average higher in the adult-adult dyad. In terms of gender, the lower overlaps are between males and the higher overlaps between females. The results show a certain spatial tolerance between adult females with juvenile individuals and yearlings of different groups, while males maintain a certain territoriality (Maillard and Fournier, 1995; Prikhod'ko, 2015; Sodeikat and Pohlmeyer, 2002; Sparklin et al., 2009). In most cases, overlaps are low since we selected individuals from different groups, an aspect that becomes relevant when observing the particularly low values of the UDOI overlap index for the core areas.

In general, despite not finding statistically significant differences, the distance between activity centers in the specimens captured in the wildlife refuge tended to be greater and followed the north-south axis, while individuals from the hunting area tended to use more compact areas and the displacements did not show such clear directionality. There have been notable exceptions that make generalizations difficult, such as a young male captured in the hunting zone who spent part of the summer in an area about 5 kilometers north, connecting both study zones. In addition, a few individuals from the hunting zone coincided with locations used by individuals from the wildlife refuge. There were also three cases of wild boars captured in the wildlife refuge that moved southward and were temporarily close to the hunting area.

Tolon et al. (2009) described that 2.1 km is the limit distance from which wild boars would not be attracted by a reserve zone where they are not hunted. In our study area, the animals have made movements inside and outside the refuge area, both during the hunting season and outside it.

The values of overlap between individuals are slightly higher than those obtained by Keuling et al. (2008b) and similar to those of Tolon et al. (2009) in the wildlife reserve area. In the literature, higher overlaps and displacements due to the hunting season have been described (Maillard and Fournier, 1995; Sodeikat and Pohlmeyer, 2003) and also due to the reserve effect (Tolon et al., 2009), although Keuling et al. (2008b) did not find changes in the overlaps after hunting. In our case, there were no differences in the home range overlaps between zones.

In Mediterranean environments, due to the marked seasonality there is spatial and temporal heterogeneity in the availability of trophic resources. This heterogeneity would cause important movements (dislocations) between activity centers and extremely elongated MCP. These aspects of the space ecology of wild boar in Mediterranean environments, not yet described as far as we know, provide essential knowledge for the management of the species, both to implement measures to prevent crop damages, and to improve the efficiency of hunting management.

Wild boar spatial patterns presented have the great value of being a key element to plan the census of the species, because without the knowledge of the spatial ecology estimates of reliable population abundance cannot be addressed (Kay et al., 2017).

The results provided on the displacements of wild boars, the space use and their seasonality, together with the knowledge of the land would allow the increase in the efficiency of hunting actions to decrease the population, focusing these actions on the forests of the Natural Park In autumn and winter. In addition, when management objective is to minimize crop damage, it has been described for feral hog that rather than reducing the number of hogs should focus on deterrence measures, since the reduction of wild pigs does not always lead to acceptable levels of reduction in damage caused by hogs (Muir and McEwen, 2007). The results presented offer a temporal and spatial perspective of the potential crop damage. The prioritization of exclusion measures to wild boars, through fences, electrified cables or guard dogs should be intensified during spring-summer in the northern part of the Natural Area, as it is the time and area of greatest potential conflict with the species.

Declarations

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Estudio IV

3.4. Habitat selection of a wild boar population in a Mediterranean environment: the role of seasonality

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Abstract

Wild boar populations have generally increased in the last few decades as have related human-wildlife conflicts. Knowledge about spatial and temporal patterns in this species is crucial to establish effective management systems. From 2012 to 2014, 26 wild boars from different social groups were radio-tracked. At the population level, a compositional analysis was carried out that highlighted the selection of forested areas, crops, streams and water points. Seasonal habitat selection was tested with generalized linear mixed effects models, which showed spring and summer selection for herbaceous crops, and selection of holm oaks forests and shrub crops in winter and autumn. These results provide key information to establish zones and periods of greatest potential conflict with human activities and to evaluate the effectiveness of adopted management measures.

Key words: resource selection, spatial ecology, *Sus scrofa*, telemetry

Introduction

Wild boar is one of the most widely distributed terrestrial mammals in Europe. It has been described as mainly a forest species, although it has great plasticity to take advantage of resources in other environments (Apollonio et al., 2010). Among other habitats, it uses planifolia forests that produce acorns as a food source (Fernández-Llario, 2017), cultivated fields (Herrero et al., 2006; Thurfjell et al., 2009), wetlands (Rosell et al., 2001) and urban and peri-urban areas (Amendolia et al., 2019; Cahill et al., 2012; Castillo-Contreras et al., 2018).

Increases in wild boar populations in recent decades, and the use of agricultural and urban areas, have resulted in numerous conflicts with humans and their activities. Impacts occur in the form of traffic accidents, damage to agriculture and infrastructure, and other interactions (Massei et al., 2015; Massei and Genov, 2004). Detailed knowledge about the boar's spatial ecology can facilitate effective management decisions aimed at limiting conflicts between wild boars and humans.

Home ranges estimated by telemetry have frequently served to highlight boars' spatial ecology related to hunting activities (Calenge et al., 2002; Scillitani et al., 2010; Sodeikat and Pohlmeyer, 2002), although seasonal effects on spatial patterns have been less frequently considered (Keuling et al., 2008a; Thurfjell et al., 2014). At a population scale, the home range size and shape as well as the intensity of use within the home range are influenced by the availability of resources, climatic factors, human activities, forest harvesting, hunting and predation (Keuling et al., 2008a, 2008b; Massei et al., 1997; Morelle et al., 2015; Podgórski et al., 2013; Thurfjell et al., 2014).

The effects of hunting on population-scale movements have been studied in depth. Although there are discrepancies in the magnitude of these effects, it seems that they depend on the intensity of the hunting activity (Keuling et al., 2008b; Scillitani et al., 2010; Sodeikat and Pohlmeyer, 2003; Tolon et al., 2009). Much less known are the effects of displacements due to other causes. Spatial heterogeneity of resource availability has scarcely been described as the main cause of seasonal displacements in home ranges (Keuling et al., 2008a; Morelle and Lejeune, 2015; Thurfjell et al., 2009).

In a previous work on the spatial use patterns of the wild boar in the same study area as the present work, it was revealed that disjunct home ranges (i.e., home ranges made up of two or three polygons separated by about 4 km) were the most common spatial pattern. In Mediterranean ecosystems, which are subject to a marked seasonality, resources are distributed heterogeneously both temporally and spatially, and thus we would expect that seasonality conditions the selection of differentiated habitats and in turn, the displacements made to take advantage of the new resources.

Spatial ecology studies of the species, through the assessment of seasonal habitat selection, make it possible to improve the efficiency of management strategies and, therefore, reduce conflicts. The establishment of a relationship between environmental variables and the distribution of species through mathematical models can be a useful planning tool, since it allows the identification of the zones and times with the greatest probability of species appearance and, therefore, highlights priorities of intervention or evaluations of management models (Amendolia et al., 2019; Franklin and Miller, 2010; Gormley et al., 2011).

The objective of our work is to determine the role of seasonality in wild boar movements. Specifically, we intend to study the factors that condition these displacements on a temporal and population spatial scale.

Material and methods

Study Area

Data were collected in Sant Llorenç del Munt i l'Obac Natural Park, a natural area located in the pre-coastal mountain range of Catalonia in the northeast of the Iberian Peninsula (41° 39'- 41° 42 'N; 1 53'-2 ° 09 'E) (Fig. 3.4.1). Due to its geographical location, proximity to the sea and moderate altitude (maximum of 1104 m above sea level), a Mediterranean climate dominates in this region. Average precipitation is about 700 mm, with maximums in autumn and spring. The maximum temperatures are in summer, reaching values above 35ºC. The main substrate is limestone in the form of conglomerates. The vegetation best represented is the Mediterranean and the mountain holm oak with oak (*Quercus ilex*) as a protagonist. In the foothills of the mountain range, there are patches of mixed pinewoods of *Pinus nigra ssp. Salzmanii*, *Pinus sylvestris* and *Pinus halepensis*. Rocky cliffs with little vegetation abound (Pintó and Panareda, 1995).

Within the Park, several activities are managed including high frequencies of visitors with a marked seasonality, a few cultivated fields, mainly for cereals and vineyards, and forestry and hunting activities mostly for big game hunting of wild boar and roe deer.

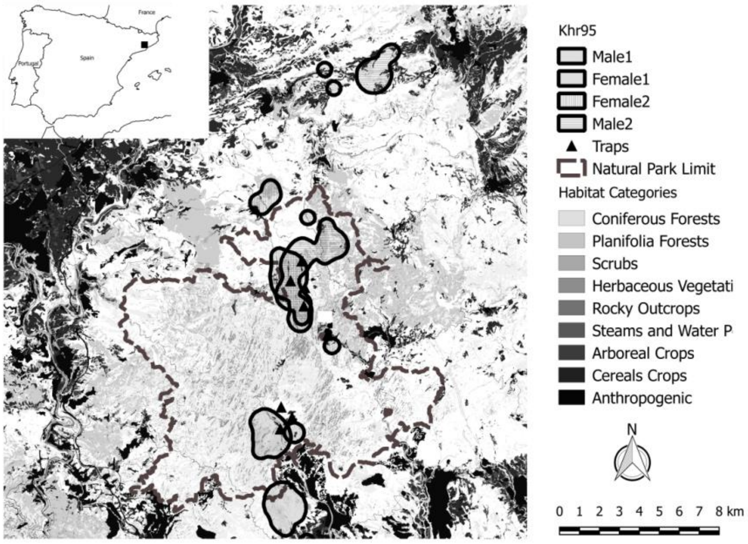

Figure 3.4.1. Study area showing the extent of Sant Llorenç del Munt i l'Obac Natural Park, the habitat categories used, cage trap locations and examples of two male and two female home ranges.

Trapping and radio-tracking

The field work was carried out from April 2012 to December 2014. For the captures, seven cage traps were used. During the catch period, the traps were baited with maize and a check was performed each morning while they were activated, with bait added when catches were produced or when it had been consumed. When a boar was captured, they were anesthetized with an anesthetic dart fired by a blowpipe. A combination of 3 mg/kg tiletamine + 3 mg/kg zolazepam (Zoletil®, Virbac, Esplugues de Llobregat, Barcelona) and 3 mg/kg xylazine (Xilagesic 20% ®, Laboratoris Calier, Les Franqueses del Vallès, Barcelona) was used. A total of 71 wild boars were captured. Ear tag emitters with movement sensors weighing approximately 40 grams (TW5 twin cell ear tag, Biotrack Ltd. Wareham, UK) were installed on 35 wild boars, although only 26 (12 females and 14 males from different groups) were used for the calculations, because they had a minimum of 30 locations for a minimum of two months at the end of the tracking process and to minimise replication. The frequency band used was 150-152 MHz.

When more than one boar was caught in the same trap, all individuals were identified but never more than two were equipped with emitter ear tags to avoid replication in radio-tracking results. In addition, in the data analyzed only one animal per group was taken into account for the same reason.

Radio-tracking was performed at least two times per week (mean±SD: 2.23±0.48). All locations were recorded with a portable GPS. Radiolocations were obtained during daytime for logistical and practical reasons by "homing in" to obtain precise data, but avoid moving the animals (Gula and Theuerkauf, 2013; White and Garrott, 1990). The radiotracking was performed with a three-element yagui manual antenna and an Icom R90 multi-band receiver (Icom Inc, Osaka, Japan).

The capture, marking and radio-tracking as well as the range of frequencies used were authorized by the *Departament de Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural de la Generalitat de Catalunya* of the Generalitat de Catalunya, competent autonomic organism.

Home ranges and habitat selection

The resting areas of the wild boar represent a good approximation of total home ranges in Mediterranean environments of the Iberian Peninsula, especially those estimated by the Khr95. In addition, they allow a comparison to multiple studies that used only daytime locations (Calenge et al., 2002; Maillard and Fournier, 1995; Saïd et al., 2012a; Wolf, 2009).

Wild boar home ranges were estimated using the Minimum Convex Polygon (MCP) with 100% of the locations, kernel 95% (Khr95), and kernel 50% (Kcr50), setting the smoothing factor (h) at 235 m, calculated as the median of the individual estimates through Likelihood Cross Validation (Horne and Garton, 2006). We used the R package "adehabitatHR" (Calenge, 2006) for these analyses.

The minimum number of fixes used for home range estimation was 30, following the recommendations of Seaman et al. (1999) and Börger et al. (2006). The nine animals with fewer locations were not taken into account in the present study.

The Land Cover Map of Catalonia (MCSC) in its fourth edition (Generalitat de Catalunya and CREAF, 2001) was used to apply environmental variables, collapsing this raster layer to nine final categories with a 20 meter per pixel resolution. Specifically, the landscape was categorized into coniferous forests, planifolia forests, scrubs, herbaceous vegetation, rocky outcrops, streams and water availability points, arboreal crops (for example vineyards and olive trees), cereal fields and anthropogenic zones.

To perform habitat selection analysis, two approaches were used. At the study area and home range levels, habitat selection was assessed using compositional analysis (Aebischer et al., 1993), 3rd and 2nd order selection respectively (Johnson, 1980), in line with III and II approaches suggested by Manly et al. (2002). This analysis uses a MANOVA to compare the proportion of habitat available and shows a rank of habitat types in order of use. At a study area level, cover types available in an MCP of all fixes of all individuals were compared to a Khr95 for each individual as used habitat. At the home range level, the proportion categories of habitats at each individual MPC, as available, were compared to Khr95 of each individual as used. At resting site level, the proportion categories of habitats at each individual Khr95 as available, were compared to core range Kcr50 of each individual as used.

Additionally, to include the seasonal variation in habitat selection, generalized linear mixed models (GLMM) with the individual identifier as a random factor were generated. Seasons were defined ecologically, in line with Keuling et al. (2008a). At a population level (2nd order selection), GLMMs were developed comparing resource covariates at each wild boar location to an equal number of random available locations within a 99% fixed kernel of all wild boar locations. For these analyses, to eliminate location errors and the need to base inference on subjectively chosen habitat categories, distance-based variables were used (Conner et al., 2003). For each habitat category, a distance raster layer with the same resolution was elaborated. "Selection" was inferred when wild boar locations were closer to habitat features than were random locations and "avoidance" inversely. Since the predictor variables presented different scales, these variables were rescaled for model performance.

The described models were elaborated using the "nlme" package of R (Pinheiro et al., 2017) and compositional analysis was carried out with the "adehabitatHS" R package (Calenge, 2006). Likewise, all other statistical tests were carried out with the program R version 3.3.3 (R Core Team, 2017) and significant differences were considered when the value of $P<0.05$.

Results

Compositional analysis

We verified by means of the compositional analysis without considering the seasonality, that the wild boars do not use the habitat at random at the study area scale. According to the ranking matrix, the most selected habitats were forested and streams or available water points, while the agricultural and anthropic environments were the least selected (Table 3.4.1).

Significant values at the home range level also were found (Table 3.4.1). At this scale, the agricultural and forest habitats producing acorns were the selected environments, while the habitats with low-lying vegetation coverage were the least selected.

At the resting place scale, significant habitat selection was also found according to the randomization tests. For these scale, wild boars selected bush crops and forest environments, while the least selected habitats were anthropic and herbaceous crops (Table 3.4.1).

Table 3.4.1. Ranked matrix of habitat type selection at different scales of all individuals (n=26). Lambda Wilk's and associated p-values at each study scale. Habitat types considered are: coniferous forests (V1), planifolia forests, mainly holm oak forests (V2), scrubs (V3), herbaceous vegetation (V4), rocky outcrops (V5), streams and water availability points (V6), shrub crops (V7), cereal fields (V8) and anthropogenic (V9). Considered scales were: Study Area (SA), Home Range (HR), Resting Sites (RS). > indicates that the variable before the symbol is preferred over the next.

Scale	Wilk's λ	P	Ranked habitat types
SA	0.19	0.002	V1>V6>V2>V4>V3>V5>V8>V7>V9
HR	0.4	0.036	V8>V7>V2>V9>V6>V1>V4>V5>V3
RS	0.15	0.001	V7>V1>V2>V3>V4>V6>V5>V9>V8

Seasonal habitat selection

At the second-order scale (study area or population), wild boar showed seasonal differences in selection for resource and landcover variables. In spring variables that best explained the distribution of wild boars were proximity to cereal crops, herbaceous habitats and, although not significantly, to streams and water points. In addition, at that time of year, boars avoided shrublands and anthropic environments (Table 3.4.2). During summer, wild boar continued to avoid anthropogenic zones, while positively selecting holm oak forests, cereal crops and stream environments (Table 3.4.2).

The best predictors of wild boar distribution during the autumn were the proximity to the oak forests, vineyards, streams and rocky outcrops. Similarly, during the winter, wild boars selected forests, both oaks and conifers, streams and water points, and vineyards. At this time of the year, anthropic environments, such as human settlements and roads were rejected (Table 3.4.2).

Table 3.4.2. Summary results from seasonal generalized linear mixed models (2^{nd} order resource selection models) for wild boars at the study area. Shown are β coefficients, standard error (SE), z-scores and *P*-values. Explanatory variables are (distance to): coniferous forests (dV1), planifolia forests, mainly holm oak forests (dV2), scrubs (dV3), herbaceous vegetation (dV4), rocky outcrops (dV5), streams and water availability points (dV6), shrub crops (dV7), cereal crops (dV8) and anthropogenic (dV9). * indicates significant p-values and therefore, the most important variables to explain each model.

Season	Model variables	β	SE	Z	*P*
Spring	Intercept	-0.164	0.087	-1.881	0.060
	dV1	0.092	0.091	1.016	0.310
	dV2	-0.075	0.076	-0.988	0.323
	dV3	0.244	0.095	2.567	0.010*
	dV4	-0.369	0.116	-3.168	0.002*
	dV5	-0.187	0.120	-1.550	0.121
	dV6	-0.160	0.094	-1.703	0.089
	dV7	-0.120	0.119	-1.010	0.312
	dV8	-0.872	0.139	-6.288	<0.001*
	dV9	0.924	0.129	7.156	<0.001*
Summer	Intercept	-0.023	0.079	-0.294	0.769
	dV1	-0.156	0.087	-1.795	0.073
	dV2	-0.558	0.102	-5.463	<0.001*
	dV3	0.012	0.083	0.148	0.882
	dV4	0.016	0.101	0.155	0.877
	dV5	0.002	0.097	0.019	0.985
	dV6	-0.314	0.087	-3.598	<0.001*
	dV7	0.138	0.096	1.433	0.152
	dV8	-0.730	0.109	-6.723	<0.001*
	dV9	0.517	0.099	5.211	<0.001*

Continuation of **table 3.4.2**.

Season	Model variables	β	SE	Z	*P*
Autumn	Intercept	-0.228	0.126	-1.808	0.071
	dV1	-0.142	0.130	-1.093	0.274
	dV2	-0.902	0.191	-4.719	<0.001*
	dV3	-0.200	0.145	-1.379	0.168
	dV4	0.143	0.140	1.015	0.310
	dV5	-0.449	0.156	-2.884	0.004*
	dV6	-0.302	0.128	-2.351	0.019*
	dV7	-0.458	0.164	-2.792	0.005*
	dV8	-0.042	0.165	-0.258	0.797
	dV9	0.102	0.154	0.662	0.508
Winter	Intercept	-0.261	0.124	-2.106	0.035
	dV1	-0.236	0.119	-1.973	0.048*
	dV2	-1.192	0.212	-5.623	<0.001*
	dV3	0.062	0.137	0.449	0.653
	dV4	0.006	0.150	0.041	0.968
	dV5	0.199	0.145	1.370	0.171
	dv6	-0.405	0.149	-2.723	0.006*
	dV7	-0.840	0.169	-4.980	<0.001*
	dV8	-0.308	0.178	-1.730	0.084
	dV9	0.480	0.158	3.046	0.002*

Discussion

Despite being a generalist species in terms of trophic requirements, the wild boar used certain categories of habitat more frequently than would be expected by random chance in all scales of analysis.

At a population scale or in a study area, the wild boar showed a preference for forest stands, both of oaks and pine trees, and for streams and water points. The selection of forested habitats by the wild boar has been widely described in different countries in Europe, especially deciduous forests, as a source of refuge and food (Amendolia et al., 2019; Boitani et al., 1994; Fonseca, 2008; Meriggi and Sacchi, 2001; Thurfjell et al., 2009; Tolon et al., 2009). Streams are used by the wild boars as corridors in their displacements as well as a water source (Castillo-Contreras et al., 2018). In addition, these places are favoured because there is more moisture at water points facilitating the rooting activity of wild boars (Meriggi and Sacchi, 2001; Truvé and Lemel, 2003; Welander, 2000).

At a home range scale, the compositional analysis showed the importance of crops, both herbaceous and shrubby, and oak forests. The importance of crops as a determinant of the distribution of wild boar has also been described previously (Herrero et al., 2006; Keuling et al., 2009; Schley and Roper, 2003; Thurfjell et al., 2009), since crops represent an important source of trophic resources at certain times of year.

When considering the most frequently used resting places (Kcr50), forests and shrub cover were again the most used environments, probably serving as places of refuge (Keuling et al., 2008a; Saïd et al., 2012a; Tolon et al., 2009). On this scale, bush crops were the most selected habitats (including vineyards and olive trees). One explanation could be that these habitats represent productive environments over a small surface area, with certain vegetal cover and forested surroundings.

Compositional analysis (Aebischer et al., 1993) allows us to address the simple question regarding differences in habitat preference at different scales. It also avoids the problems encountered with correlations by combining all observations of one animal into proportions. The use of GLMM allowed us to include possible individual variability and the effects of seasonality. In Mediterranean environments, spatial heterogeneity in the availability of resources is conditioned by a marked seasonality. Therefore, wild boars would be expected to modify their spatial patterns, as well as their habitat selection, throughout the year in order to exploit the resources that appear in each season (Keuling et al., 2008a; Morelle et al., 2015).

In a work carried out on the spatial use of wild boars in the same study area, there were no significant differences between home range sizes or displacements between the seasonal activity centres due to the age or gender of the animals. Similar results were found in other studies (Boitani et al., 1994; Cousse et al., 1994; Keuling et al., 2008a; Singer et al., 1981). Therefore, gender and age were not incorporated as covariates in habitat selection models.

In this work, seasonal habitat selection by the wild boar at a study area scale (2nd order selection) is highly differentiated. In general, the fructification period of plants in different environments corresponds to selection of the same. Thus, cereal fields, mainly wheat and barley, were selected in spring and summer when the cereal matures. Both oak forests and shrub crops, mainly vineyards and olive trees, were chosen in autumn and winter, coinciding with the mast, and grape and olive production (Ballari and Barrios-García, 2014; Massei et al., 1996).

Streams were selected in a generalized way in all seasons of the year except spring due to their ample vegetation, their ideal structure for displacements, as well as water availability. Regarding anthropic environments, wild boars avoided proximity to human settlements and infrastructure at all times of year except autumn.

Our results generally describe displacements towards cultivated areas in the growing season, since they represent feeding areas and are quieter zones than forest environments, in which the majority of human activities take place during this time (Morelle and Lejeune, 2015; Rosell et al., 2012). During autumn and winter, the fields have already been harvested, hunting season begins and the wild boars return to forest environments. Thus, the movements of the animals must adapt to these processes (Keuling et al., 2008b; Tolon et al., 2009).

These seasonal movements derived from different human activities (types of crop, harvest times, hunting, tourist activities, etc.) and spatial heterogeneity are important in decisions regarding management of the species in a protected natural area. This is especially true given African Swine Fever, an infectious disease that is at risk of entering the south of the European continent and decimating populations of both wild boar and pigs.

The present work suggests habitat variables that condition wild boar population distribution as well as seasonal variations. Through these results, management measures aimed at the prevention of conflicts between wild boar and humans can be established. Specifically, the statistical models of seasonal distribution aid in the identification of those areas with the highest probability of conflict, both spatially and temporally, and thus in the orientation and/or evaluation of management actions for the species.

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CAPÍTULO III

4. Discusión general

4.1. El jabalí, especie de éxito: consideraciones sobre su gestión

Las poblaciones de jabalí se han incrementado notablemente desde la última mitad del siglo XX, tanto en su área de distribución natural (el paleártico) como en los lugares donde ha sido introducido (Acevedo et al., 2006; Apollonio et al., 2010). Algunas causas de este aumento son la reforestación natural producida tras el abandono de la agricultura tradicional o el incremento de las zonas de refugio y de los recursos alimenticios disponibles. A dichos factores debemos sumar los intrínsecos de la especie, como son la adaptabilidad a diferentes hábitats, su elevada tasa reproductiva, su gran capacidad de explotar diferentes recursos tróficos, el incremento de zonas de cultivo de ciertos cereales (especialmente el maíz) en Europa y el aumento progresivo de las temperaturas invernales como consecuencia del cambio climático (Acevedo et al., 2006; Massei et al., 2011; Melis et al., 2006; Saïd et al., 2012a; Thurfjell, 2011).

El incremento en la distribución y abundancia de sus poblaciones puede generar impactos negativos en las actividades humanas como la agricultura y la ganadería, en los ecosistemas naturales y en los medios urbanos, así como colisiones con vehículos (Cahill et al., 2003; Marques et al., 2010). Desde el punto de vista sanitario, además, la especie actúa como hospedador de una serie de enfermedades económicamente importantes que afectan al cerdo doméstico, como la peste porcina africana, la peste porcina clásica y la enfermedad de Aujeszky, siendo especialmente relevante que la peste porcina africana haya llegado recientemente a la Unión Europea (Keuling et al., 2016). Los jabalíes también actúan como hospedadores de enfermedades como la tuberculosis, la salmonelosis y la brucelosis, que afectan a otros mamíferos, incluidos los seres humanos. El incremento de las poblaciones de jabalí y su amplia distribución favorecen el contacto entre individuos y, por tanto, la transmisión y el mantenimiento de las enfermedades en las poblaciones de fauna silvestre (Gortázar et al., 2007; Vicente et al., 2010).

Por otro lado, cabe señalar que el jabalí tiene importancia para el ser humano como especie cinegética y, asimismo, importancia ecológica como elemento clave en multitud de ecosistemas, puesto que contribuye a la mezcla del suelo, al reciclaje de nutrientes y a la diseminación de esporas y semillas (Onipchenko and Golikov, 1996; Schmidt et al., 2004).

La medida de gestión más comúnmente utilizada para reducir el tamaño poblacional, la distribución y, por tanto, los impactos negativos producidos por la especie, es la caza recreativa (Keuling et al., 2013; Massei et al., 2015). Sin embargo, no siempre se logran los objetivos deseados, ya que una elevada presión de caza conduce a un rejuvenecimiento de la población. Si, además, existe una elevada disponibilidad de alimento, esta población tendrá una tasa de reproducción mayor, lo cual limitará la eficacia de la caza como medida de regulación poblacional (Cellina, 2008; Gethöffer et al., 2007; Servanty et al., 2011). Por consiguiente, la caza recreativa no se ha mostrado suficientemente eficiente como medida para regular o disminuir la población de jabalíes, en especial cuando los intereses de los cazadores (seleccionar y abatir animales adultos) no coinciden con los de la administración competente en la gestión cinegética, que serían la eliminación de los individuos con mayor potencial reproductivo (Keuling et al., 2016).

Es por ello que diversos autores han destacado que es necesaria una buena planificación y estrategia de manejo de la actividad cinegética para conseguir dicha regulación y reducción de las poblaciones (Keuling et al., 2013; Massei and Cowan, 2014). Es más, recientemente se ha asumido que para llevar a cabo una gestión eficiente y eficaz en la consecución de los objetivos de regulación o reducción poblacional del jabalí es necesario combinar diferentes medidas de gestión, además de la caza (Keuling et al., 2016; Massei et al., 2015, 2011).

Otros aspectos que determinan el éxito de las medidas de gestión son la percepción social (tanto de cazadores como de no cazadores), los cambios de comportamiento y adaptabilidad de esta especie, la aplicación de los conocimientos científicos y, finalmente, la evaluación del impacto y éxito de las medidas llevadas a cabo (Blumstein and Berger-Tal, 2015; Keuling et al., 2016). En este sentido, a pesar del gran conocimiento adquirido sobre la biología del jabalí, existen pocos estudios acerca de la abundancia poblacional, el uso y la selección del hábitat y el comportamiento espacial (Frauendorf et al., 2016; Keuling et al., 2009; Morelle et al., 2015).

4.2. Estudios poblacionales de jabalí

Para conocer la dinámica demográfica de una especie, el primer paso a seguir es la obtención de datos precisos, fiables y sencillos de conseguir sobre las poblaciones de manera regular en el tiempo. En el caso concreto del jabalí, la información disponible sobre la dinámica de las poblaciones es escasa, principalmente debido a la dificultad de establecer censos directos en el campo (Massei et al., 2018).

La evaluación indirecta de la abundancia de las poblaciones de jabalí se realiza mayoritariamente mediante las estadísticas de caza, por ser una fuente de datos que permite trabajar a una escala muy amplia (Acevedo et al., 2014; ENETwild consortium et al., 2018a). A escala espacial menor, se han utilizado aproximaciones alternativas, entre las que destacan los trabajos que utilizan el trampeo fotográfico para obtener datos de actividad, comportamiento, abundancia y otros parámetros poblacionales (Hebeisen et al., 2008; Massei et al., 2018).

El concepto de población lleva implícito un eje espacial y, al añadir la dimensión temporal, se adquiere un conocimiento más profundo de la ecología y demografía de las especies. A través del estudio de los dominios vitales, los movimientos, las zonas de mayor frecuentación, así como la estacionalidad, se puede predecir el uso del espacio por parte de la fauna silvestre. Estos datos permiten orientar las medidas de gestión en las diferentes escalas espaciales y temporales. También ayudan a predecir daños y pueden servir para evaluar la efectividad de las medidas de gestión. No obstante, todavía existen pocos estudios enfocados a conocer la ecología espacial (comportamiento espacial) del jabalí (Morelle et al., 2015).

Entre las variables que ayudan a entender los patrones espaciales de las especies, además de los factores climáticos y las molestias causadas por la caza u otras actividades humanas, destacan las cubiertas del suelo o hábitats. Existen hábitats con gran productividad de recursos tróficos y lugares de refugio para los jabalíes, mientras que otros son más pobres. No es de extrañar, por tanto, que los jabalíes hagan un uso diferenciado de cada uno de ellos.

A través de algoritmos estadísticos se pueden elaborar modelos de distribución potencial y abundancia que facilitan la comprensión de las dinámicas a escala de país, continente o incluso de alcance mundial (Acevedo et al., 2019).

4.2.1. Evaluación del trampeo fotográfico

Actualmente, entre las tecnologías utilizadas para el estudio de la fauna salvaje, destaca el trampeo fotográfico por su generalización y potencialidad para evaluar abundancias poblacionales. El abaratamiento de los equipos fotográficos, la sencillez de uso y el hecho de ser una tecnología no invasiva han generalizado enormemente su uso (Rowcliffe and Carbone, 2008). En la aplicación del trampeo fotográfico para estimar abundancias poblacionales destacan dos métodos: captura-marcaje-recaptura (CMR) y marcaje-reobservación (MR) (O'Connell et al., 2011).

El primero (CMR) se aplica principalmente en animales con marcas en el pelaje que permiten la diferenciación individual, mientras que el segundo método (MR) se aplica en poblaciones animales en las que se necesita marcar artificialmente una parte de la población y las recapturas se substituyen por campañas de observación repetida de los animales.

Con el método MR, utilizado en nuestro estudio, se obtienen estimaciones de abundancia de la población mediante la proporción de animales marcados y no marcados en los diferentes eventos de observación fotográfica (McClintock et al., 2009). Sin embargo, recientemente se está extendiendo y tiene una mayor aceptación el uso de índices y la obtención de abundancias mediante métodos que no requieren el reconocimiento individual de los ejemplares de la población (Engeman, 2005; Rovero and Marshall, 2009; Rowcliffe et al., 2008). En todo caso, el uso de métodos menos invasivos, como los índices, precisan una calibración con métodos de abundancia de referencia para ser aplicados con garantías (Palmer et al., 2018; Rovero and Marshall, 2009).

Para aumentar la probabilidad de encuentro con la especie objetivo y, por tanto, la efectividad del trampeo fotográfico, se utilizan habitualmente cebos o atrayentes que se colocan delante de los equipos fotográficos (Foster and Harmsen, 2012; Garrote et al., 2012). Esta práctica, sin embargo, ha sido criticada por el sesgo potencial que puede provocar en la estimación de los parámetros de la población (Larrucea et al., 2007; McCoy et al., 2011). Cuando se considera al jabalí como modelo de estudio, algunos autores evitan su uso (Massei et al., 2018; Ohashi et al., 2013), mientras que otros, tanto en estudios de MR como en la obtención de índices de abundancia, sí que utilizan cebo (Hebeisen et al., 2008; Matthews et al., 2008; Sweitzer et al., 2000; Yasuda, 2004).

En el caso del jabalí se hace especialmente necesario poder disponer de métodos de estimación de abundancia sencillos y sólidos para evaluar las tendencias poblacionales y, por tanto, la efectividad de las medidas de gestión. También es muy importante conocer los efectos que tienen factores como el uso de cebo, que potencialmente pueden sesgar los resultados de las estimaciones. Es por ello por lo que el primer estudio realizado se diseñó para evaluar la abundancia de jabalí mediante trampeo fotográfico y los efectos del uso de cebo. El tamaño medio de grupo, factor decisivo en la estimación poblacional de animales sociales, fue infravalorado claramente en las sesiones en que no se aplicó cebo. Además, aunque las abundancias estimadas no difirieron significativamente entre los periodos con y sin cebo, éstas fueron más precisas (menores errores estándar) al aplicar cebo.

Además, los valores de los índices de abundancia, obtenidos con y sin cebo, se correlacionaron significativamente con las estimaciones de abundancia MR, lo cual sugiere que estos índices podrían usarse para evaluar los cambios en la población de jabalíes.

Los resultados de nuestro trabajo ponen de manifiesto la utilidad de los métodos de MR en la obtención de abundancias poblacionales, aunque los recursos necesarios para la captura y marcaje de los jabalíes hacen difícil su generalización a gran escala. En nuestro caso, han servido también como método de referencia para evaluar la utilidad de los índices de abundancia relativa.

4.3. Ecología espacial del jabalí

Los animales salvajes residentes en un espacio suelen restringir sus movimientos a zonas en las que desarrollan sus funciones vitales. El conjunto de estos lugares se conoce como dominio vital o área de campeo. Asimismo, los movimientos y desplazamientos de los animales son el resultado de interacciones entre factores intrínsecos y extrínsecos que pueden tener profundas consecuencias en la condición física de los individuos, la distribución de las especies y las dinámicas poblacionales (Van Beest et al., 2011).

Mediante técnicas como la telemetría se pueden obtener datos sobre los desplazamientos y el comportamiento espacial de los animales, que aportan información sobre patrones espaciales a diferentes escalas y permiten una mejor comprensión de los contextos fisiológicos, demográficos y ecológicos en el comportamiento espacial (Morelle et al., 2015). Por tanto, el conocimiento de cada uno de los componentes que determinan los movimientos de las especies nos permite mejorar la comprensión de su comportamiento espacial y de las relaciones con el ambiente, y con ello mejorar sustancialmente las estrategias de gestión y conservación de estas especies.

4.3.1. Comparativa metodológica

Para el cálculo del dominio vital existe, como se ha comentado anteriormente, gran variedad de aproximaciones. A pesar de su importancia, pues es un elemento clave en la interpretación del comportamiento espacial, se han realizado pocos esfuerzos destinados a estandarizar las estimaciones de dominios vitales. En la presente tesis, mediante el seguimiento por GPS de 15 jabalíes en distintos ambientes mediterráneos, se ha buscado establecer una base que permita la estandarización de las estimaciones de los dominios vitales obtenidas mediante diferentes métodos, tipos e intensidades de muestreo. Al considerar el mínimo polígono convexo (MPC), se encontraron las máximas diferencias de tamaño de dominio vital entre intensidades de muestreo, aspecto que refuerza la consideración de que el método MPC para la comparación de dominios vitales se debe emplear con precaución. La comparación de todas las intensidades y tipos de muestreo con la obtenida a partir de todas las ubicaciones GPS, aplicando el método de densidad de áreas núcleo o kernel (KDE) con la isopleta del 95 % (Khr95), no mostró diferencias significativas, lo cual evidencia que es el método de estimación más sólido. Cuando se evaluaron los KDE con isopleta del 50 % (Kcr50) las estimaciones no difirieron entre tipos de muestreo (seguimiento de día o continuo) ni para una baja intensidad de muestreo (típica de los seguimientos mediante VHF).

Por otro lado, al comparar la similitud entre las distribuciones de utilización (UD) estimadas a partir de las diferentes aproximaciones con la de referencia, se obtuvieron valores altos (superiores a 0.75) de solapamiento en todos los casos de los Khr95 y algo menores usando los Kcr50, de lo que se deduce que el uso de los primeros permite estimar dominios vitales similares tanto en tamaño como en similitud de UD y, por tanto, facilita las comparaciones entre estudios realizados con diferentes intensidades de muestreo. No obstante, debemos ser más precavidos cuando se aplica el Kcr50 y, especialmente, con los MPC, dadas las diferencias en los tamaños y las UD entre los esquemas de seguimiento que emplean elevadas intensidades de muestreo y aquellos que emplean bajas intensidades. Además, las similitudes entre áreas de campeo obtenidas a partir de los KDE y las estimaciones dBBMM permiten generalizar nuestros resultados y hacerlos más sólidos.

La aproximación metodológica propuesta en el estudio permite la comparación entre trabajos que usan los KDE con diferente intensidad de muestreo, de manera que posibilita la comparación entre dominios vitales KDE obtenidos a partir de seguimientos VHF y GPS. También se facilita un nexo entre metodologías de análisis de dominios vitales, pudiendo comparar UD obtenidas a partir de ubicaciones y movimientos (métodos tradicionales versus métodos de última generación).

4.3.2. Ecología espacial en ambientes mediterráneos

El tamaño de los dominios vitales obtenidos en los ambientes mediterráneos de montaña del nordeste de la península ibérica es similar al obtenido en ambientes parecidos de Italia (Boitani et al., 1994; Massei et al., 1997) y otros lugares de Europa (Keuling et al., 2008a).

En nuestro estudio, la forma de los dominios vitales de los jabalíes radioseguidos fue, mayoritariamente, alargada. Además, el 62 % de los animales mostraron un patrón de uso del espacio fragmentado. Basándonos en estos resultados, podemos explicar el comportamiento espacial de la población de jabalíes a partir de dos patrones. El primero, mayoritario, se caracterizó por un uso temporal de centros de actividad con desplazamientos de unos 5 km a nuevas zonas para posteriormente moverse a nuevos lugares o volver a zonas ya usadas. El segundo, minoritario, se caracterizó por una alta fidelidad espacial, describiendo dominios vitales compactos.

A pesar de que el comportamiento sedentario de los jabalíes ha sido ampliamente descrito (Calenge et al., 2002; Fischer et al., 2004; Saunders and Kay, 1996), también se han reseñado desplazamientos entre dominios vitales o centros de actividad causados por la actividad cinegética (Scillitani et al., 2010) y por la estacionalidad en la búsqueda de los recursos tróficos (Keuling et al., 2008a).

No todos los animales responden de igual manera ante la caza. Mientras que unos actúan desplazándose, otros permanecen más estáticos. En todo caso, los grandes desplazamientos representarían una respuesta minoritaria (Scillitani et al., 2010; Thurfjell et al., 2013). En nuestro estudio, el comportamiento mayoritario fue el de los jabalíes que realizaron desplazamientos entre centros de actividad, incluso fuera de la época de caza.

En relación con la distancia media entre lugares consecutivos de reposo, los jabalíes recorrieron las mayores distancias durante los meses de invierno (época de caza) y primavera. De las dos zonas donde se capturaron los jabalíes, en la del refugio de fauna silvestre los animales distanciaron más sus lugares de reposo que en la zona de caza controlada, especialmente en la época de actividad cinegética. Sin embargo, fuera de ésta fue a la inversa. La explicación de estos fenómenos podría ser la mayor diversidad de recursos tróficos disponibles en el refugio de fauna silvestre y, especialmente, la baja frecuentación humana durante la época de veda, que causaría menos molestias y, por tanto, menos desplazamientos. Dicha hipótesis también se encuentra en estudios sobre el comportamiento espacial y temporal de los jabalíes producido por las actividades humanas (Ohashi et al., 2013; Podgórski et al., 2013).

Los marcados desplazamientos estacionales, en cambio, cuentan con pocos estudios que los hayan puesto de manifiesto (Gabor et al., 1999; Keuling et al., 2008a; Lemel et al., 2003; Singer et al., 1981) y han sido descritos en otros tipos de hábitats en los que los cambios de clima drásticos en las estaciones afectan la disponibilidad de alimento. En nuestro estudio se detectó que los desplazamientos más importantes se realizaron durante la primavera y el otoño, y que su direccionalidad siguió mayoritariamente el eje nordeste-sudoeste. En los ambientes mediterráneos, debido a la manifiesta estacionalidad existe heterogeneidad espacial y temporal en la disponibilidad de los recursos tróficos, la cual puede causar importantes desplazamientos entre los centros de actividad, que dibujan MPC extremadamente alargados. Así, la presencia de mayores zonas con agua y cultivos en el norte, principalmente en verano, condicionarían el desplazamiento hacia esas zonas siguiendo la orografía, marcada por torrentes en esta dirección, tal y como se comentará en el apartado dedicado a la selección de hábitat.

El uso del espacio de los jabalíes en nuestra área de estudio podría describirse como un cambio frecuente de lugares de reposo consecutivos, separados entre sí 400 metros de media, alternando este comportamiento con fases de elevada fidelidad a una ubicación concreta (11 % del total de movimientos) y fases de grandes desplazamientos de más de 2.000 metros (9 % del total). A una escala mayor, existió cierta fidelidad espacial, pues el número de centros de actividad en los que los animales estuvieron más de una semana fue pequeño (entre uno y tres) y su superficie, relativamente grande (450 ha).

Estos aspectos de la ecología de los jabalíes contribuyen a tener un conocimiento esencial para la gestión de la especie, puesto que aportan la visión espacial y temporal de las poblaciones.

4.3.3. Selección de hábitat

El análisis de selección de hábitat a diferentes escalas ha permitido conocer en detalle los factores que condicionan los movimientos descritos. El jabalí, a pesar de ser una especie generalista en cuanto a los requisitos tróficos, en el Parque Natural de Sant Llorenç del Munt i l'Obac ha usado ciertas categorías de hábitat con más frecuencia de lo que se esperaba al azar, y dicha selección también se ha evidenciado a escala temporal (estacionalmente).

A escala de área de estudio, los jabalíes mostraron preferencia por los hábitats forestales, tanto los encinares como los pinares. También por los torrentes y los puntos de agua. Dicho comportamiento respondería a que los ambientes forestales son utilizados por la especie como lugares de refugio y, estacionalmente, como lugares de alimentación.

A escala de dominio vital, el análisis composicional mostró la importancia de los campos de cultivo, tanto los herbáceos como los arbustivos, y de los bosques de encinas. Los primeros representan una importante fuente de recursos en algunos periodos del año, en concreto los cultivos herbáceos, principalmente de cereal, en primavera-verano y los arbustivos (principalmente viñedos) en invierno (Herrero et al., 2006; Keuling et al., 2009; Schley and Roper, 2003; Thurfjell et al., 2009).

Los torrentes, por su exuberante vegetación, su estructura ideal para los desplazamientos y su disponibilidad de agua, fueron seleccionados de manera generalizada en todas las estaciones del año.

Por otro lado, los jabalíes rechazaron la proximidad de las construcciones e infraestructuras humanas en todos los periodos del año, excepto en otoño, época que coincide con el inicio de la actividad cinegética y la frecuentación humana, lo cual puede explicar que los animales busquen refugio cerca de las construcciones donde está prohibida la caza. Las urbanizaciones laxas ofrecen a los jabalíes refugio respecto a la caza y grandes oportunidades alimenticias, tanto por las bellotas de las encinas que forman la matriz de las urbanizaciones, como por los alimentos de origen humano.

Nuestros resultados describen desplazamientos en la época de cría hacia áreas cultivadas, puesto que representan zonas de alimentación. Durante el otoño e invierno, cuando los campos habían sido ya cosechados y empezó la época de caza, los jabalíes volvieron a los ambientes forestales.

Teniendo en cuenta las variables de hábitat y las escalas temporales y espaciales que condicionan la distribución de los jabalíes, se pueden orientar las estrategias de gestión, principalmente la caza y las medidas disuasorias para disminuir o prevenir los conflictos con las actividades humanas. Específicamente, los modelos estadísticos de la distribución estacional de los jabalíes permitirían explicitar a una escala espacial y temporal las áreas con elevada probabilidad de conflicto y, por tanto, orientar y evaluar las acciones de gestión de la especie.

4.4. Observaciones finales

Para avanzar en el conocimiento y la gestión del jabalí es necesario integrar diversas disciplinas, como la epidemiología, la genética, la etología y la ecología. El siguiente paso, para poder disponer de datos útiles en la gestión adaptativa, es aplicar los conocimientos puntuales y generar modelos para escalas mayores. Además de los factores mencionados, aspectos como la estructura poblacional, el uso de alimentación suplementaria (para distraer a los jabalíes y, así, evitar daños a cultivos o para la caza) y los factores ambientales, especialmente en el marco de cambio climático, deberían nutrir los modelos para mejorar la precisión y exactitud de sus estimaciones y, por tanto, su utilidad. Además, para la correcta aplicación de los modelos matemáticos, no solo debemos prestar atención a las variables implicadas, sino también a la relación entre ellas y a su evolución temporal.

Conocer los movimientos estacionales causados por las actividades humanas (tipos de cultivos, época de cosecha, caza, actividades turísticas, etc.) y la heterogeneidad espacial tiene una gran importancia en las decisiones de gestión de la especie en un espacio natural protegido. Especialmente, en un marco general en el que una enfermedad infecciosa, la peste porcina africana, amenaza con extenderse por el continente europeo y diezmar las poblaciones de jabalí y cerdo doméstico.

5. Conclusiones

1. El uso del trampeo fotográfico se ha mostrado eficaz para la obtención de estimaciones de abundancia de las poblaciones de jabalí en ambientes mediterráneos.

2. La aplicación de cebo es recomendable, porque incrementa la precisión de las estimaciones MR de abundancias poblacionales de jabalíes. Además, el tamaño medio de grupo en los periodos con cebo es más fidedigno, aspecto que también condiciona las estimaciones poblacionales finales.

3. Los índices de abundancia relativa, tanto en los periodos de trampeo fotográfico en los que se aplicó cebo como en los que no, se correlacionan significativamente con las estimaciones de abundancia absoluta, lo cual sugiere que son una aproximación útil para evaluar los cambios poblacionales de jabalíes.

4. El uso de kernels y el establecimiento de un valor de factor de amortiguación a escala de población e intensidad de muestreo, mediante la mediana de los valores *likelihood cross validation* (LCV) individuales, permite estandarizar las estimaciones de los dominios vitales.

5. Los kernel 50 % deben emplearse con cautela, pues solo aportan estimaciones similares entre las aproximaciones menos intensivas y solapamientos menores que en el punto anterior.

6. Los tamaños de los dominios vitales no se ven afectados por la edad o el género en la población de jabalíes estudiada. Sin embargo, estos resultados están sujetos a una elevada variación individual, aspecto especialmente relevante en esta especie.

7. La estacionalidad en la distribución de los recursos tróficos de los ambientes mediterráneos condiciona el uso del espacio y los desplazamientos de los jabalíes. Este aspecto facilitará la elaboración de modelos de distribución estacionales que, a una escala espacial mayor, indicarán la probabilidad de conflictos con la especie.

8. La marcada selección de cultivos de cereales durante la primavera-verano y de encinares durante el otoño-invierno permite focalizar los esfuerzos de gestión orientados a minimizar los conflictos, tanto en áreas de espacios naturales protegidos como fuera de ellas.

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