Spatial Ecology of the European Wildcat in the Iberian Peninsula

Maria Teresa Almeida Oliveira

Mestrado em Biodiversidade, Genética e Evolução
Departamento de Biologia
Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO)
2016

Orientador
Pedro Monterroso, Investigador Doutorado, Faculdade de Ciências da Universidade do Porto, Centro de Investigação em Biodiversidade e Recursos Genéticos

Coorientador
Pablo Ferreras, Investigador Doutorado, Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM), Ronda de Toledo, Ciudad Real, España

U.PORTO

FC FACULDADE DE CIÊNCIAS
UNIVERSIDADE DO PORTO

Todas as correções determinadas pelo júri, e só essas, foram efetuadas.
O Presidente do Júri,

Porto, ______/______/_________

MSc

Fotography Credits: Jorge Tobajas

Acknowledgments

First and foremost, I would like to thank my supervisor, Dr. Pedro Monterroso, and my co-supervisor, Dr. Pablo Ferreras, for giving me the opportunity to work with them. I am very grateful for all their guidance, teachings, motivation and patience throughout this master course, most especially during this last year.

I would like to thank to Organismo Autónomo de Parques Nacionales (Project OAPN 352/2011), the Spanish National Plan (project CGL2009-10741, funded by the Spanish Ministry of Science and EU-FEDER funds), the technical staff from Parque Nacional de Cabañeros and Parque Natural do Vale do Guadiana, J. M. Gil-Sánchez, J. M. López-Martín, Fermín Urra, Paulo Célio Alves, José Luis Robles Prieto, Aritz Ruiz-González (UPV-HU), Juan Luiz Ortega Arranz (ACENVA), Xosé Pardavila and Héctor Ruiz Villar for providing the wildcat data used in this study (telemetry data, scats and camera trapping records, hair and skin samples).

I am very grateful to all researchers who helped me to better understand several methodological processes behind home ranges and resource selection. I am particularly indebted to John Benson for everything he taught me, always with such patience, and for the many suggestions and recommendations.

I owe a huge acknowledge to all my friends and colleagues who contributed in some way or another to the realization and conclusion of this thesis. I wish to thank Ana Serronha, Andreola Velleryd, Elisa Maio, Filipe Rocha and Marisa Rodrigues for all laughs, jokes, advices and availability during the last two years. I want to thank Rafael Campos for all his support and readiness to help me, and for the interest he always showed in my work. Thanks are also due to André Ferreira for his help, suggestions and support. I am very grateful to Liliana Silva for the amazing friendship, which made everything easier during this master course. I owe Patrícia Ferreira and Andreia Pereira many thanks for their constant incentive and sheer friendship throughout the last years, in all situations. And finally, I want to express my gratitude to Mariana Rafaela, Catarina Rebelo and Daniela Brandão, who have been the best roommates I could ever have, giving me incredible support and friendship. To Mariana Rafaela I also owe very, very special thanks for her endless help with R, without which this thesis would not be finished yet.

Last but not least, I am deeply grateful for the continuous support and encouragement that I received from my family, especially my parents and brothers, not only during this master course but in every other moment.

Resumo

O uso do espaço pelos animais é um tema crucial em ecologia, e pode ser investigado com enfoque em duas perspectivas complementares: espaço geográfico e ambiental. Perceber como um animal usa o ambiente que lhe está disponível é um requerimento básico para a elaboração de estratégias de conservação. O gato-bravo apresenta uma distribuição fragmentada na Europa, principalmente devido a factores antropogénicos, e suspeita-se que as populações Ibéricas estejam a sofrer um declínio. A contínua destruição de *habitats* naturais e as elevadas taxas de hibridação na Península Ibérica (20%) levam a uma maior necessidade de compreender os padrões ambientais que influenciam a distribuição de gato-bravo nesta região. Assim, o principal objectivo deste estudo é examinar a selecção de *habitat* (considerando tipos de cobertura do solo, distância a zonas humanizadas/fontes de água e variáveis topográficas) ao nível da paisagem pelo gato-bravo, dentro dos limites geográficos da Península Ibérica. Para alcançar este objectivo, foi desenvolvida uma função de selecção de recursos, através do uso de modelos lineares generalizados mistos, num desenho experimental de uso-disponibilidade, usando dados de rádio-telemetria obtidos de 26 animais, distribuídos por cinco áreas de estudo. Este tipo de modelos foi também desenvolvido para cada género para investigar possíveis diferenças na selecção de *habitat* entre machos e fêmeas. Foram ainda realizadas análises com índices de selecção para avaliar que características do *habitat* eram seleccionadas ou evitadas no interior dos domínios vitais. As análises aos domínios vitais foram realizadas com estimadores de densidade *kernel*, delimitados na isolinha de 90% de probabilidade. Os machos apresentaram domínios vitais superiores aos das fêmeas, embora sem significância estatística. Os modelos de selecção de recursos mostraram que o gato-bravo selecciona preferencialmente áreas com maior cobertura vegetal, como florestas decíduas e zonas de matos, e evitam áreas abertas e humanizadas na Península Ibérica. Identificou-se um padrão de selecção de *habitat* diferenciada entre géneros, no qual as fêmeas demonstraram uma intensa selecção das variáveis de cobertura do solo, enquanto os machos não apresentaram fortes padrões de selecção para estas variáveis. Ambos os géneros seleccionam áreas com maior declive em zonas com baixa altitude, independentemente da posição topográfica. A qualidade de ajuste dos modelos mostrou que o conjunto de variáveis considerado explica com maior sucesso a variabilidade da variável de resposta para as fêmeas (80%) do que para os machos (39%). Isto indica que, enquanto as fêmeas parecem ser influenciadas principalmente por estas variáveis, existem outros factores não considerados a afectar a selecção de *habitat* por parte dos machos. A validação do modelo geral com dados independentes de presença de gato-bravo reflectiu uma boa capacidade de predição de presença desta espécie na Península Ibérica. Os índices de selecção revelaram um padrão geral de uso proporcional à disponibilidade dentro das áreas vitais, bem como uma elevada variação inter-individual. Contudo, verificou-se uma tendência para a selecção de zonas com maior cobertura vegetal e evitar áreas abertas, no interior dos domínios vitais. A análise combinada dos padrões de selecção pelo gato-bravo ao nível da paisagem e do domínio vital sugere que a mesma ocorre preferencialmente ao nível da paisagem. No entanto, são necessárias análises futuras para compreender este processo de uma maneira mais completa. Os resultados deste estudo revelam padrões particulares do uso do espaço pelo gato-bravo na Península Ibérica. Esta informação é relevante para uma adequada definição e implementação de estratégias de conservação na Península Ibérica. Estudos futuros devem focar no efeito conjunto da disponibilidade de presas e *habitat* na distribuição do gato-bravo na Península Ibérica e modelar o uso do espaço considerando também a dinâmica das populações e relações inter-específicas.

Palavras-Chave: Gato-bravo, *Felis silvestris silvestris*, Península Ibérica, Uso do espaço, Domínio vital, Selecção de *habitat*, Função de selecção de recursos, Proporção de selecção

Abstract

Animal space use is a central topic in ecology and can be addressed by focusing in two complementary perspectives: geographic and environmental space. Understanding how an animal uses the available environment is a basic requirement to wildlife conservation planning. The European wildcat presents a fragmented distribution across its range, mainly due to anthropogenic factors, and the populations in the Iberian Peninsula are suspected to be declining. The continuous habitat destruction and high hybridization rates in the Iberian Peninsula (20%) call for a better understanding of the patterns influencing wildcat's distribution in this region. The main goal of this study is to examine habitat selection of European wildcats at the landscape within the Iberian Peninsula. To achieve this purpose, a resource selection function (RSF) was developed, using generalized linear mixed models, in a use-availability framework with radio-telemetry data collected from 26 animals, distributed across five study areas. RSFs were also used to assess potential differences between males and females regarding habitat selection patterns. In addition, selection ratios were used to evaluate the environmental characteristics that were selected and avoided within home ranges. Home range analyses were conducted using kernel density estimators with a 90% isopleth. Males presented higher home ranges than females, although without statistical significance. Resource selection models showed that wildcats preferentially selected areas with higher vegetation cover, such as deciduous forests and scrubland areas, and avoided open and humanized areas in the Iberian Peninsula. A sex-biased habitat selection pattern was identified in Iberian wildcats. Females exhibited strong selection patterns for habitat covariates, while males did not. Both genders selected steeper areas at low altitudes, regardless of the topographic position. The models' goodness-of-fit showed that the set of the considered covariates had a higher success in explaining the variability in the response variable for females (80%) than for males (39%). This suggests that, while females seem to be mainly driven by these covariates, unaccounted factors are influencing males' spatial patterns. Model validation with independent wildcat presence data indicated that the developed RSF has a good ability to predict wildcat presence within the Iberian Peninsula. Selection ratios showed an overall proportional use within home ranges, but exposed high diversity patterns between individuals. Nevertheless, wildcats have a tendency to select areas with higher vegetation cover and to avoid open areas, within their home ranges. The combined analyses of European wildcats' selection patterns at the landscape and home range levels suggests that it preferentially occurs at a landscape level. However, further research to better understand this process is required. These results reveal particular patterns of space use of European wildcats in the Iberian Peninsula. This information is relevant for an accurate definition of European wildcat conservation strategies in the Iberian Peninsula. Future research should focus on investigating the joint effect of prey availability and habitat features, as well as modelling space use incorporating population dynamics and inter-specific relations.

Key words: European wildcat, *Felis silvestris silvestris*, Iberian Peninsula, Space use, Home range, Habitat selection, Resource selection function, Selection ratios

Index

List of Tables

Table 1. Covariates extracted and tested in the models for European wildcats' habitat selection in the Iberian Peninsula.

Table 2. Generalized Linear Models (GLMs) for each variable (ordered by AICc values).β– covariate estimate; SE – Standard Error.

Table 3. Model set of the top-ranked mixed-effect resource selection models at the landscape level, with AICc, delta AICc and AICc weights for the top-ranked models.

Table 4. Model averaged coefficients (β), standard errors (SE), confidence intervals (CI; 95%) and effect sizes from the top-ranked mixed-effect resource selection models for European wildcats in the Iberian Peninsula. * - Significant estimate values.

Table 5. Spearman rank correlation values of the *k*-fold cross validation procedure (with the correspondent p-value), and marginal and conditional R^2 values for each of the top models.

Table 6. Model set of the top-ranked mixed models for male and female European wildcats , with AICc, delta AICc and AICc weights for ech model.

Table 7. Coefficients estimate value (β), standard errors (SE), confidence intervals (CI; 95%) and effect sizes from the top-ranked mixed-effect resource selection models for male (model-averaged) and female (top model) European wildcats in the Iberian Peninsula. * - Significant estimate values.

Table 8. Spearman rank correlation values of the *k*-fold cross validation procedure (with the correspondent p-value), and marginal and conditional R^2 values for each of the top models for male and female wildcats.

List of Figures

List of Acronyms

AIC - Akaike’s Information Criteria

AICc - Akaike’s Information Criteria corrected to small sample sizes

DEM – Digital Elevation Model

GIS - Geographic Information System

GLM - Generalized Linear Model

GLMM - Generalized Linear Mixed effect Model

GPS - Global Positioning System

KDE - Kernel Density Estimator

LoCoH - Local Convex Hull

MCP - Minimum Convex Polygon

MMDM - Mean Maximum Distance Moved

PDF - Probability Density Function

RSF - Resource Selection Function

SE – Standard Error

SP - Sampling Protocol

TPI - Topographic Position Index

VHF - Very High Frequency

Part 1. General Introduction, Study Areas and Wildcat Telemetry Data

General Introduction

Animals perceive the environment around them through two main dimensions, space and time, and the behavioral decisions based on how they explore these two dimensions will affect fitness. Space use is a crucial topic in animal ecology and can be addressed by focusing in two complementary perspectives: geographic and environmental space (Moorter *et al.* 2016). While a geographic approach deals mainly with patterns, i.e. home ranges and species distributions (Moorcroft 2012), studies focusing on the environmental scale intend to identify the factors behind resource use and selection, i.e. the process behind the choice of these patterns (Manly *et al.* 2002).

Spatial Ecology: Home Range

The home range concept seems intuitive, but in fact it is unclear and variable among researchers. Burt (1943) defined home range as the area traversed by the animals during their daily activities, such as food gathering, mating and caring for young, among others, and occasional sallies outside the area should not be considered as part of the home range. This definition is the foundation of the general concept used nowadays, but it presents limitations mainly because it does not consider places known and recognized by the animals but not visited frequently (Boitani & Powell 2012). Conversely, according to Boitani & Powell (2012), an animal’s home range is the result of a dynamic process, since the way each animal perceives its own home range may change according to its cognitive map. Hence, a home range may be defined as the part of an animal’s cognitive map that it chooses to keep up-to-date with status of available resources and where it is willing to go to meet its requirements (Powell & Mitchell 2012).

Quantifying an animal´s home range is a key subject in ecological research, and several available estimators try to understand how an animal perceives its own home range. An efficient home range estimator should provide insights into how an animal values space, and should include places that are important but not necessarily frequented (Powell & Mitchell 2012). Several home range estimators have been developed and upgraded in order to obtain increasingly accurate results. Two main approaches are available: geometric techniques (such as Minimum Convex Polygon, MCP; Mohr 1947), which lack an underlying probabilistic model; and statistical techniques, such as KDEs (Kernel Density Estimators, Worton 1989; Fleming *et al.* 2015). MCP is one of the most widely used methods. However, as it considers only the extreme points, it discards most of the data, hence providing little information about home range's internal structure (Boitani & Powell 2012; Seaman *et al.* 1999).

Therefore, more complex methods, such as KDEs, are applied to get a deeper insight of home ranges. Contrarily to MCP, KDEs consider the internal structure of the data by producing a utilization distribution (calculated as probability density functions, PDFs), which describe the intensity of use within a home range. Other estimators, such as local convex-hull method (LoCoH; Getz *et al.* 2007) and Brownian bridge movement models (BBMM; Horne *et al.* 2007), have been recently developed, and allow the identification of sharp features in the environment and the identification of travel routes, respectively. From the myriad options regarding home range analyses, one must chose a methodology based on the hypothesis being tested and on previous knowledge of the data to be used, in order to reduce bias and to obtain more accurate information (Powell 2012).

Since species' distribution depends on the resource availability, and the later usually does not have a homogeneous distribution on the environmental space, some level of selection, at different scales and/or levels, is usually required (Manly *et al.* 2002; McGarigal *et al.* 2016).

Spatial Ecology: Habitat Selection

Habitat selection is the process by which an animal chooses a resource from the available environment based in behavioral decisions, which are basically a result of several demands and motivations, such as food gathering, reproduction and finding shelter (Johnson 1980; Krausman & Cain 2013; Manly *et al.* 2002; Moorcroft & Barnett 2008). Habitat use reflects the proportion of time an animal spends in a particular habitat, and "use" is considered selective if a particular habitat is used disproportionately when comparing to its availability (Beyer *et al.* 2010; Krausman & Cain 2013). Although habitat selection and preference are terms often used synonymously, habitat preference is the likelihood that a given resource will be selected if the availability of that resource is offered on an equal basis with the others (Johnson 1980; Manly *et al.* 2002).

Selection is a binary process which can occur at different levels, and a hierarchy behind this process was proposed by Johnson (1980): resource selection studies can be performed at the level of a species geographic range (first order selection); at the level of home range characteristics within a landscape within the species' geographic range (second order selection); at the level of habitat use within the individuals' home range (third order selection); and at the level of particular elements, such as food items (i.e. microhabitat), within the general features (i.e. habitat), such as feeding site (fourth order selection).

Resource selection can be assessed by combining any 2 of 3 possible sets of data (use, nonuse and available), which provides three sampling protocols: SP-A, available *vs* used units; SP-B, available *vs* unused units; SP-C, unused *vs* used (Manly *et al.* 2002). Use-availability (SP-A) is the most common (especially in studies using telemetry data), mainly due to the difficulties that arise when trying to define "nonuse" in ecology studies (Beyer *et al.* 2010; Krausman & Cain 2013; Manly *et al.* 2002; Thomas & Taylor 2006).

However, determining the available sample is a critical process and may cause interpretational bias if its size and spatial extent are not properly assessed (McGarigal *et al.* 2016; Northrup *et al.* 2013). These different sampling protocols can be applied at different levels (population or individual), and the combinations of both provide three general study designs to evaluate selection (Manly *et al.* 2002; Thomas & Taylor 1990):

Design I- Used, unused, or available resource units are sampled for the entire study area and for all animals within the study area; individual animal identification is not considered;

Design II- Individual animal identification is conducted and the use of resources is measured for each animal, but availability is measured at the population level (study area);

Design III- Individuals are identified or collected as in Design II, and at least two of the sets (used, unused or available resource units) are sampled for each animal.

Several analytical methods, such as selection ratios, can be used to understand resource selection. This can be further explored using Resource Selection Functions (RSF, Manly et al. 2002), which are spatially-explicit models that predict the relative probability of use by an animal at a given place during a given time, based on the environmental conditions that influence selection (Johnson *et al.* 2004). Although several models can be used to understand resource selection, the most widely used are the generalized linear mixed models (GLMM). This class of models provides a powerful tool to analyze habitat selection, mainly because these models allow the use of both fixed and random effects. The latest allow to have in account individual variation, as well as correlated and unbalanced sample sizes (Gillies *et al.* 2006).

These resource selection models have been widely implemented to provide insights into the variables affecting selection patterns at similar or multiple spatio-temporal scales (Benson *et al.* 2015b; Hinton *et al.* 2015; Mancinelli *et al.* 2015; Welch *et al.* 2016) or to understand how a given species select habitats in human modified landscapes (Dellinger *et al.* 2013; Benson *et al.* 2015a; Bouyer *et al.* 2015; Poessel *et al.* 2016), among others. Most of these studies include only habitat-related variables, but there may be varying ecological processes that influence resource selection and are usually not considered, such as population density and predation (McLoughlin *et al.* 2010) or population features, for example state of development (adult, juvenile) or gender (male/female) (Cassini 2011). When these possible dynamics are not considered nor included in the analyses, resource selection may provide misleading results which may, by turn, jeopardize the utility and application of the resource selection function (McLoughlin *et al.* 2010). Although it may not always be possible to incorporate these factors, an effort should be made in this direction to increase our understanding about these ecological interactions (McLoughlin *et al.* 2010).

The methodology chosen to evaluate selection must be carefully considered, from the sampling protocol to the study design, as well as the modeling technique, since it will influence the development and interpretation of resource selection functions, which may by themselves have strong implications on wildlife management and ecology studies (Johnson *et al.* 2006). In a quickly changing environment, with anthropogenic disturbances as major force, animal populations must either adapt to new conditions or limit their distribution to the decreasing areas of natural habitat. Understanding how animals use the available environment is a basic requirement for wildlife conservation planning. However, this task is not easy when dealing with elusive species, such as carnivores (Boitani & Powell 2012).

Spatial Ecology: Radio-telemetry data

Radio-telemetry methods are often used for studying elusive species, since its behavior is difficult to observe directly. This technique allows collecting information on individual movements and assessing space use, which would be neither practical nor possible to obtain with other wildlife research techniques (Boitani & Powell 2012). Animal radio-tracking started with the use of VHF (very high frequency) technology and although it is still frequently used, it presents some disadvantages, such as low spatial precision (when performing triangulation) and the need for a researcher to be in the field relatively close to the animal, which may affect its behavior (Cagnacci *et al.* 2010). The recent advances in technology have allowed a faster development of monitoring techniques, such as GPS (Global Positioning System) collars with higher precision and battery life, which allow researchers to obtain more and more accurate data with minimal animal disturbance (Tomkiewicz *et al.* 2010). Additionally, remote sensing data and the increased use of Geographic Information Systems (GIS) also provide more alternative methods to explore animal spatial ecology (Thomas & Taylor 2006). These fine-scale data combined with appropriate statistical treatment provide information which is undoubtedly useful to study and manage cryptic species (Moorcroft 2012).

The European Wildcat

The European wildcat (*Felis silvestris silvestris*, Schreber, 1777) is a mesocarnivore widely distributed through Europe, ranging from the Iberian Peninsula to Eastern Europe (Yamaguchi *et al.* 2015). However, its current distribution is severely fragmented as a result of sharp declines and local extinctions that occurred across Europe between the 18th and the 20th century, mainly due to habitat loss (Stahl & Artois 1994). While some populations are increasing in Central Europe (Hartmann *et al.* 2013; Nussberger *et al.* 2014), Iberian populations appear to be decreasing, with declines of over 30% on the past three generations (Palomo & Gisbert 2002; Cabral *et al.* 2005). Therefore, while the European wildcat's conservation status is considered Least Concern in its global distribution range (Yamaguchi et al., 2015), it is Vulnerable in Portugal (Cabral *et al.* 2005) and Near Threatened in Spain (López-Martín *et al.* 2007). Another threat to the conservation of the European wildcat concerns the hybridization with its domestic counterpart: the domestic cat (*Felis silvestris catus*). Habitat destruction and fragmentation led to an increased contact with feral individuals of the domestic form, which may promote genetic exchanges between both subspecies (Oliveira *et al.* 2008; Mattucci *et al.* 2016). Although hybridization occurs throughout Europe, it does not occur with the same frequency everywhere. For instance, Scottish and Hungarian populations present high admixture levels, while hybridization rates are lower in Germany, Italy and in the Iberian Peninsula (Oliveira *et al.* 2008; Gil-Sánchez *et al.* 2015; Mattucci *et al.* 2016). However, a recent study showed an hybridization rate of 20% within the Iberian Peninsula, highlighting the importance of monitoring the Iberian populations (Ramos 2014).

Even though European wildcats can be found in a wide variety of habitats, they are primarily associated with forested areas with low human population densities in central Europe (Klar *et al.* 2008), and with scrublands in Mediterranean environments, often avoiding areas of intensive agriculture and human settlements (Lozano, 2010; Monterroso et al., 2009). The species is considered to be a facultative specialist predator on European rabbits (*Oryctolagus cuniculus*), although also preying upon several different prey items (mainly small mammals), according to their availability (Malo *et al.* 2004; Lozano *et al.* 2006).

The Iberian Context

The Iberian Peninsula presents a remarkable set of diverse conditions for its relatively small area, mainly because it includes three distinct biogeographical regions: Alpine, Atlantic and Mediterranean (Rivas-Martínez *et al.* 2004). It is also included in the Mediterranean Basin hotspot (Myers *et al.* 2000). Because of its climatic and physiographical complexity, the Iberian Peninsula has a high environmental heterogeneity, which provides an enormous variety of habitats, as well as prey diversity and abundances (Blondel & Aronson 1999). However, human activity and its effect on the natural landscape is notorious, reflected in the intensification of agriculture and in the presence of human settlements, among other changes (Cuttelod *et al.* 2008).

Although a wide habitat diversity is available for wildcats in the Iberian Peninsula, these conditions are different from those in Central and Northern Europe, thus strategies for population management and conservation must be different (Ferreira 2010). Several studies regarding habitat selection of European wildcats have been developed in Central Europe (Germain *et al.* 2008; Klar *et al.* 2008) and some measures regarding management and conservation have been proposed (Klar *et al.* 2012). In the Iberian Peninsula, a number of studies regarding wildcat spatial ecology (Sarmento *et al.* 2006; Monterroso *et al.* 2009; Lozano 2010) have been conducted. However, these studies were conducted for local areas, so the information available is sparse. So far, no study has analyzed the regional habitat choices within the Iberian Peninsula. An Iberian approach would reveal a selection pattern considering the existent environmental diversity, which may provide useful insights for management and conservation of this species, especially in a scenario with increasing hybridization rates.

Objectives

This study intends to understand how Iberian wildcats adjust their patterns of habitat selection in response to a set of variables reflecting human impact and land cover type, at a fine scale, considering different levels. Telemetry data collected in five different study areas along different bioclimatic regions of the Iberian Peninsula will be used to address two specific topics:

1) How European wildcats select different habitat features at two different levels (landscape and home range), within the Iberian Peninsula;

2) To understand if there are differences in habitat selection between males/females, within the Iberian Peninsula.

These approaches are useful to characterize habitat selection patterns of European wildcats in the Iberian Peninsula, contributing to inform wildlife conservation strategies aimed at reversing the current declining trends of the Iberian populations.

Study Areas

The study areas considered in this study were distributed across the Iberian Peninsula, covering several ecosystem types (Figure 1). A total of five areas were considered, one located in Portugal (Guadiana Valley Natural Park) and four located in Spain (Izagaondoa, Navarre; Lleida, Catalonia; Cabañeros National Park, Castille La-Mancha; Sierra Arana, Andalusia) (Figure 1).

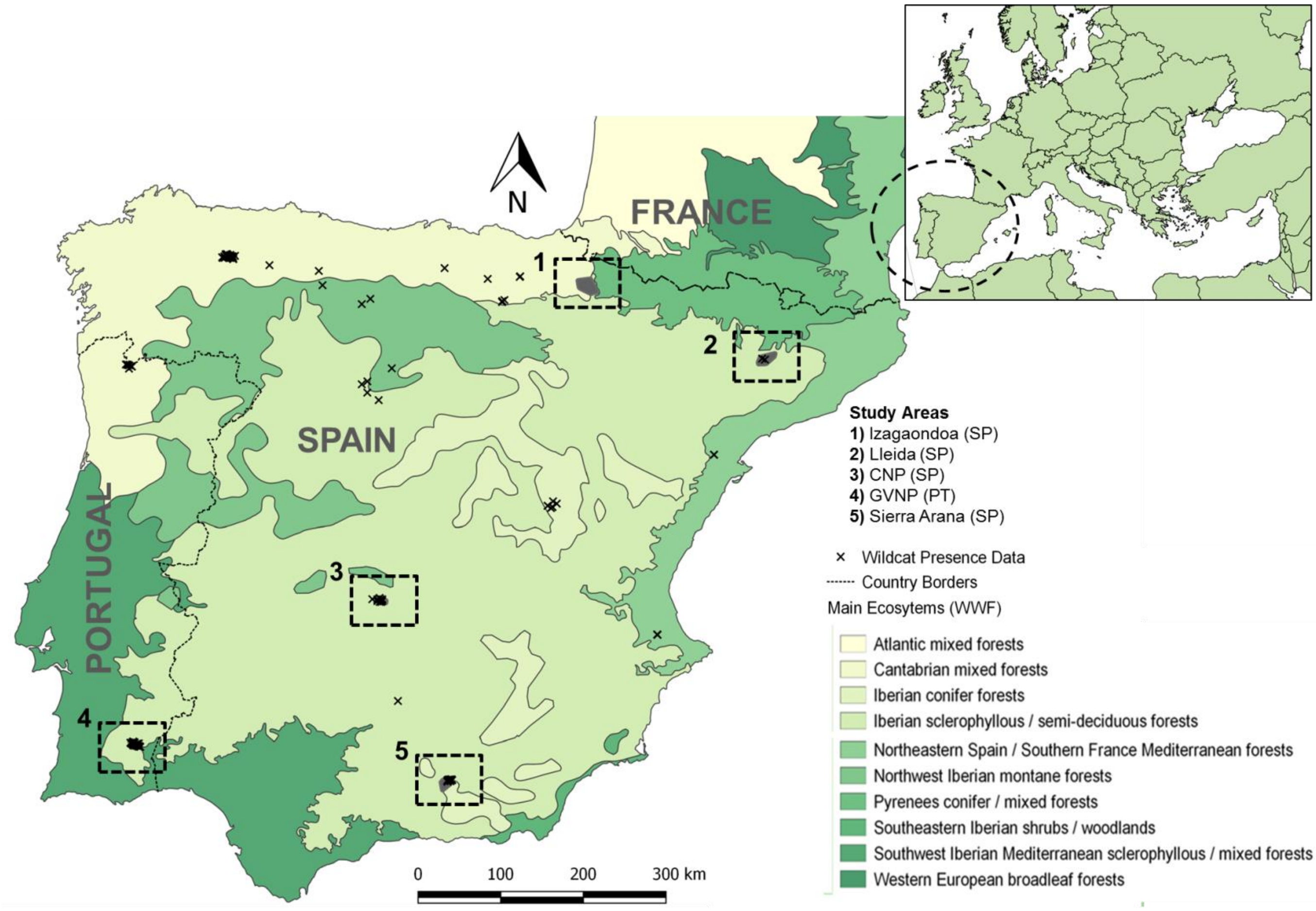

Figure 1. Locations of the five study areas and wildcat presence data considered in this study, within the Iberian Peninsula, and spatial distributions of the main ecoregions (source: WWF; accessible at: http://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world). CNP- Cabañeros National Park; GVNP- Guadiana Valley Natural Park; SP- Spain; PT- Portugal.

Guadiana Valley Natural Park (Southern Portugal)

The Guadiana Valley Natural Park (hereafter, GVNP) is a protected area located in Southern Portugal (37º 69’ N, -7º 76’ E). It has a typical Mediterranean climate regime, marked by hot dry summers and cold winters with low precipitation (Valente 2011). Typical landscapes are constituted by cereal croplands and agroforestry systems of *P. pinea* and *Q. ilex* (“Montado”). Scrubland patches are also present, mainly associated with steeper slopes and elevation ridges, with series of *Myrto communis–Q. rotundifoliae* dominating the vegetation (Monterroso 2013). Hunting activity is extremely important in this region, with the red-legged partridge (*Alectoris rufa*) and the wild rabbit (*Oryctolagus cuniculus*) being the main game species. The red fox (*Vulpes vulpes*), Egyptian mongoose (*Herpestes ichneumon)*, stone marten (*Martes foina*) and European wildcat (*Felis silvestris silvestris*) are the most common mammalian mesocarnivore species present (Monterroso, 2013). The first two are legally hunted, for predator control purposes.

Cabañeros National Park (Castilla-La Mancha, Spain)

The Cabañeros National Park (hereafter, CNP) is a protected area that lies in Montes de Toledo, Spain (hereafter, SP) (Castilla-La Mancha; 39º 33’ N, -4º 39’ E), and it is located in the Mediterranean pluviseasonal continental bioclimate region (Rivas-Martínez et al., 2004). The park has two dominant and contrasting habitats: (1) a large continuous Mediterranean montane forest dominated by holm and cork oak (*Quercus ilex* and *Quercus suber* respectively) and a dense shrub layer dominated by the tall sclerophyllous evergreens *Cistus ladanifer* and *Phyllirea angustifolia*; and (2) a large continuous Mediterranean oak savanna (plane grassland with scattered oaks) and a nearly absent shrub layer (Smit *et al.* 2009) in the central lower part of the study area. The red fox, stone marten and common genet are the most abundant mammalian carnivore species, but European wildcats, European badgers (*Meles meles*) and Egyptian mongooses are also found, although in lower densities (Guzmán 1997). There is a high density of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) (Smit et al., 2009). Hunting activity and predator control are not allowed in this area.

Sierra Arana (Andalusia, SP)

Sierra Arana is located east of the Subbaetic System, in the province of Granada (Andalusia, SE Spain; 37º 34’ N, -3º 49’ E), and it is characterized by a Mediterranean environment. This mountain range is dominated by forest areas of Aleppo pine (*Pinus halepensis*) with patches of two oak species (*Quercus rotundifolia* and *Quercus faginea*). Higher areas are dominated by forest pactches with scrubland vegetation alternated with areas composed by dense scrubland vegetation, mainly with juniper (*Juniperus oxicedrus*), rosemary (*Rosmarinus officinalis*), furze (*Ulex parviflora*) and grey-leaved cistus (*Cistus albidus*). These scrubland areas are alternated with agricultural areas (mainly olive groves and cereal plantations). At lower elevations until plain areas, the landscape is characterized by small ravines with high vegetation and rock cover. Ecotones of agricultural areas with forests/scrublands are an important habitat for the wild rabbits, which are abundant in these areas. Carnivore species present in Sierra Arana include the red fox, stone marten, genet and the European wildcat.

Lleida (Catalonia, SP)

Data from this area was collected in Lleida, a Spanish province located in western Catalonia (NE Spain; 41º 52' N, 1º 8' E). The study area is mainly composed by agricultural areas, dominated by dry-farmed cereal crops. Farms, houses and small villages have a scattered distribution across the area. Next to agricultural areas, scrublands are the most common habitat, and deciduous and coniferous forests are distributed with similar proportions.

The wildlife is highly diverse with a good population of small game species, mostly red-legged partridge and rabbit. Common carnivore's species present in the area are the red fox, the stone marten, badgers and weasels (*Mustela erminea*), as well as house cats (*Felis s. catus*) living near the households.

Izagaondoa (Navarre, SP)

The Izagaondoa Valley is located in the North of the Iberian Peninsula, in the autonomous community of Navarra (42º 78' N, -1º 42' E). The valley is located in a transitional area: it embraces both Atlantic and Mediterranean biogeographic regions. Higher areas in this valley are characterized for a strong presence of the common beech (*Fagus sylvatica*) (Urra, 2003). As elevation decreases, there is a stronger presence of pubescent oak's forests (*Quercus pubescens*), with holm oak predominating in xeric areas (Urra, 2003). Scrubland areas are dominated by boxwood (*Buxus sempervirens*) and *Genista scorpius* bushes, sometimes intercalated with patches of herbaceous vegetation and former agricultural areas (Urra, 2003). An intensive agricultural matrix is present, with reduced vegetation cover, and hunting activity is common in this area, with wild boar, hares, wild rabbits and common wood pigeon as main game species (Urra 2003). Carnivore's species present in Izagaondoa

Valley are mainly represented by the presence of the red fox, genets, badgers and stone martens (Urra 2003).

Wildcat Data

Wildcat telemetry data used in this study was provided by several researchers, collected in the five areas referred above (Figure 1). For GVNP, data was obtained from Monterroso and collaborators (2009). For Izagaondoa Valley (Navarre, SP), data was obtained from Urra (2003). Data from Catalonia was provided by J. M. López-Martín (pers. comm). Data from Castille-La Mancha was obtained from Ferreras and collaborators (2015). Data from Sierra Arana was provided by J.M. Gil-Sanchéz (pers. comm.).

Wildcat presence data, genetically identified as *F. s. silvestris* (scats and hair samples), obtained opportunistically or from ongoing projects was available at CIBIO (Research Center in Biodiversity and Genetic Resources). Camera-trapping data was provided by the Spanish National Plan (CGL2009-10741), Organismo Autónomo de Parques Nacionales (OAPN 352/2011) and by J.M Gil-Sanchéz (from Sierra Arana).

References

Benson JF, Mahoney PJ, Patterson BR (2015a) Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape. *Oikos*, **124**, 1664–1673.

Benson JF, Mills KJ, Patterson BR (2015b) Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation*, **182**, 223–232.

Beyer HL, Haydon DT, Morales JM *et al.* (2010) The interpretation of habitat preference metrics under use-availability designs. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **365**, 2245–54.

Blondel J, Aronson J (1999) *Biology and wildlife of the Mediterranean region*. Oxford University Press, USA.

Boitani L, Powell RA (2012) *Carnivore ecology and conservation: a handbook of techniques*. Oxford University Press.

Bouyer Y, San Martin G, Poncin P *et al.* (2015) Eurasian lynx habitat selection in human-modified landscape in Norway: Effects of different human habitat modifications and behavioral states. *Biological Conservation*, **191**, 291–299.

Burt WH (1943) Territoriality and home range concepts as applied to mammals. *Journal of mammalogy*, **24**, 346–352.

Cabral MJ, Almeida J, Almeida PR *et al.* (2005) Livro vermelho dos vertebrados de Portugal. Instituto de Conservação da Natureza. Lisboa. 659p.

Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 2157–2162.

Cassini MH (2011) Ecological principles of species distribution models: the habitat matching rule. *Journal of Biogeography*, **38**, 2057–2065.

Cuttelod A, García N, Abdul Malak D, Temple HJ, Katariya V (2008) The Mediterranean: a biodiversity hotspot under threat. In: J.-C. Vié, C. Hilton-Taylor and S.N. Stuart (eds). *The 2008 Review of The IUCN Red List of Threatened Species*.

Dellinger JA, Proctor C, Steury TD, Kelly MJ, Vaughan MR (2013) Habitat selection of a large carnivore, the red wolf, in a human-altered landscape. *Biological Conservation*, **157**, 324–330.

Ferreira JPSM (2010) Integrating anthropic factors into wildcat *Felis silvestris* conservation in Southern Iberia landscapes. PhD Thesis, University of Lisbon, Portugal.

Ferreras P, Díaz-Ruiz F, Alves PC, Monterroso PS (2015) Factores de la coexistencia de mesocarnívoros en parques nacionales de ambiente mediterráneo. *In: Proyectos de Investigación en Parques Nacionales 2011-2014. Amengual, P. (Ed.). Madrid: Organismo Autónomo Parques Nacionales, MAGRAMA.*

Fleming CH, Fagan WF, Mueller T *et al.* (2015) Rigorous home range estimation with movement data: A new autocorrelated kernel density estimator. *Ecology*, **96**, 1182–1188.

Germain E, Benhamou S, Poulle ML (2008) Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. *Journal of Zoology*, **276**, 195–203.

Getz WM, Fortmann-Roe S, Cross PC *et al.* (2007) LoCoH: Nonparameteric Kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, **2**.

Gillies CS, Hebblewhite M, Nielsen SE *et al.* (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.

Gil-Sánchez JM, Jaramillo J, Barea-Azcón JM (2015) Strong spatial segregation between wildcats and domestic cats may explain low hybridization rates on the Iberian Peninsula. *Zoology*, **118**, 377–385.

Guzmán JN (1997) Mamíferos. *GARCÍA-CANSECO, V. & ALONSO-VALERO, L.*

coordinadores. Parque Nacional de Cabañeros. Ecohábitat, 225–267.

Hartmann S a., Steyer K, Kraus RHS, Segelbacher G, Nowak C (2013) Potential barriers to gene flow in the endangered European wildcat (*Felis silvestris*). *Conservation Genetics*, **14**, 413–426.

Hinton JW, Van Manen FT, Chamberlain MJ (2015) Space use and habitat selection by resident and transient coyotes (*Canis latrans*). *PLoS ONE*, **10**, 1–17.

Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. *Ecology*, **88**, 2354–2363.

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65–71.

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. *Journal of wildlife Management*, **70**, 347–357.

Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology*, **41**, 238–251.

Klar N, Fernández N, Kramer-Schadt S *et al.* (2008) Habitat selection models for European wildcat conservation. *Biological Conservation*, **141**, 308–319.

Klar N, Herrmann M, Henning-Hahn M *et al.* (2012) Between ecological theory and planning practice: (Re-) Connecting forest patches for the wildcat in Lower Saxony, Germany. *Landscape and Urban Planning*, **105**, 376–384.

Krausman PR, Cain JW (2013) *Wildlife management and conservation: contemporary principles and practices*. JHU Press.

López-Martín JM, García FJ, Such A *et al.* (2007) *Felis silvestris. in: Atlas y libro rojo de los mamíferos terrestres de España*. Organismo autónomo parques nacionales.

Lozano J (2010) Habitat use by European wildcats (*Felis silvestris*) in central Spain : what is the relative importance of forest variables ? *Animal Biodiversity and Conservation*, **2**, 143–150.

Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: Factors affecting the trophic diversity. *Journal of Biogeography*, **33**, 1076–1085.

Malo AF, Lozano J, Huertas DL, Virgós E (2004) A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? *Journal of Zoology*, **263**, 401–407.

Mancinelli S, Peters W, Boitani L, Hebblewhite M, Cagnacci F (2015) Roe deer summer habitat selection at multiple spatio-temporal scales in an Alpine environment. *Hystrix, the Italian Journal of Mammalogy*, **26**, 132–140.

Manly BFJ, McDonald LL, Thomas DL (2002) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. *Kluwer Academic Publishers*, xiii + 177.

Mattucci F, Oliveira R, Lyons LA, Alves PC, Randi E (2016) European wildcat populations are subdivided into five main biogeographic groups: consequences of Pleistocene climate changes or recent anthropogenic fragmentation? *Ecology and evolution*, **6**, 3–22.

McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, 1–15.

McLoughlin PD, Morris DW, Fortin D, Vander Wal E, Contasti AL (2010) Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, **79**, 4–12.

Mohr CO (1947) Table of equivalent populations of North American small mammals. *The American Midland Naturalist*, **37**, 223–249.

Monterroso PS (2013) Ecological interactions and species coexistence in Iberian mesocarnivore communities. PhD Thesis, University of Porto, Portugal.

Monterroso P, Brito JC, Ferreras P, Alves PC (2009) Spatial ecology of the European wildcat in a Mediterranean ecosystem: Dealing with small radio-tracking datasets in species conservation. *Journal of Zoology*, **279**, 27–35.

Moorcroft PR (2012) Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *Journal of Mammalogy*, **93**, 903–916.

Moorcroft PR, Barnett A (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, **89**, 1112–1119.

Moorter B Van, Rolandsen CM, Basille M, Gaillard J (2016) Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology*, ***85*(1)** , 21–31.

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Northrup JM, Hooten MB, Anderson CR, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, **94**, 1456–1463.

Nussberger B, Wandeler P, Camenisch G (2014) A SNP chip to detect introgression in wildcats allows accurate genotyping of single hairs. *European journal of wildlife research*, **60**, 405–410.

Oliveira R, Godinho R, Randi E, Alves PC (2008) Hybridization versus conservation:

are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian Peninsula? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 2953–61.

Palomo LJ, Gisbert J (2002) Atlas de mamíferos terrestres de España.[Spain mammals' atlas] Dirección general de conservación de la Naturaleza-SECEM-SECEMU. 564pp.

Poessel SA, Breck SW, Gese EM (2016) Spatial ecology of coyotes in the Denver metropolitan area: influence of the urban matrix. *Journal of Mammalogy*, **97**, 1414–1427.

Powell RA (2012) Movements, home ranges, activity, and dispersal. *Carnivore ecology and conservation: a handbook of techniques (L. Boitani and RA Powell, eds.). Oxford University Press, London, United Kingdom*, 188–217.

Powell RA, Mitchell MS (2012) What is a home range? *Journal of Mammalogy*, **93**, 948–958.

Ramos L (2014) Assessing hybridization between wildcat and domestic cat: the particular case of Iberian Peninsula and some insights into North Africa. MSc Thesis, University of Porto, Portugal.

Rivas-Martínez S, Penas A, Díaz TE (2004) Bioclimatic and Biogeographic maps of Europe. León: Cartographic Service, University of León.

Sarmento P, Cruz J, Tarroso P, Fonseca C (2006) Space and Habitat Selection by Female European Wild Cats (*Felis silvestris silvestris*). *Wildlife Biology in Practice*, **2**, 79–89.

Seaman DE, Millspaugh JJ, Kernohan BJ *et al.* (1999) Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, **63**, 739–747.

Smit C, Díaz M, Jansen P (2009) Establishment limitation of holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) in a Mediterranean savanna–forest ecosystem. *Annals of Forest Science*, **66**, 1–7.

Stahl P, Artois M (1994) Status and conservation of the wildcat *(Felis silvestris)* in Europe and around the Mediterranean rim. Council of Europe.

Thomas DL, Taylor EJ (1990) Study designs and tests for comparing resource use and availability. *The Journal of wildlife management*, 322–330.

Thomas DL, Taylor EJ (2006) Study Designs and Tests for Comparing Resource Use and Availability II. *National Wildlife*, **70**, 322–330.

Tomkiewicz SM, Fuller MR, Kie JG, Bates KK (2010) Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2163–2176.

Urra F (2003) El gato montés en Navarra distribución, ecología y conservación. PhD Thesis, Universidad Autonóma de Madrid, Spain.

Valente SBP (2011) *Eliomys quercinus*: Distribution and regulating factors in “Baixo Alentejo”. MSc Thesis, University of Aveiro, Portugal.

Welch RJ, Tambling CJ, Bissett C *et al.* (2016) Brown hyena habitat selection varies among sites in a semi-arid region of southern Africa. *Journal of Mammalogy*, **97**, 473–482.

Worton ABJ (1989) Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies Stable. *Ecology*, **70**, 164–168.

Yamaguchi N, Kitchener A, Driscoll C, Nussberger B (2015) *Felis silvestris*. *The IUCN Red List of Threatened Species 2015*, **8235**, e.T60354712A50652361.

Part 2. Spatial Ecology of the European Wildcat in the Iberian Peninsula

[*Manuscript in preparation*]

Abstract

Animal space use is a central topic in ecology and can be addressed by focusing in two complementary perspectives: geographic and environmental space. Understanding how an animal uses the available environment is a basic requirement to wildlife conservation planning. The European wildcat presents a fragmented distribution across its range, mainly due to anthropogenic factors, and the populations in the Iberian Peninsula are suspected to be declining. The main goal of this study is to examine habitat selection of European wildcats at the landscape within the Iberian Peninsula. To achieve this purpose, a resource selection function (RSF) was developed, using generalized linear mixed models, in a use-availability framework with radio-telemetry data collected from 26 animals, distributed across five study areas. RSFs were also used to assess potential differences between males and females regarding habitat selection patterns. In addition, selection ratios were used to evaluate the environmental characteristics that were selected and avoided within home ranges. Home range analyses were conducted using kernel density estimators with a 90% isopleth. Males presented higher home ranges than females, although without statistical significance. Resource selection models showed that wildcats preferentially selected areas with higher vegetation cover, such as deciduous forests and scrubland areas, and avoided open and humanized areas in the Iberian Peninsula. A sex-biased habitat selection pattern was identified in Iberian wildcats: females exhibited strong selection patterns for habitat covariates, while males did not. Both genders selected steeper areas at low altitudes, regardless of the topographic position. The models’ goodness-of-fit showed that the set of the considered covariates had a higher success in explaining the variability in the response variable for females (80%) than for males (39%). Model validation with independent wildcat presence data indicated that the developed RSF has a good ability to predict wildcat presence within the Iberian Peninsula. Selection ratios showed an overall proportional use within home ranges, but exposed high diversity patterns between individuals. Nevertheless, wildcats have a tendency to select areas with higher vegetation cover and to avoid open areas, within their home ranges. The combined analyses of European wildcats' selection patterns at the landscape and home range levels suggests that it preferentially occurs at a landscape level. However, further research to better understand this process is required. These results provide relevant information for an accurate definition of European wildcat conservation strategies in the Iberian Peninsula.

Key words: European Wildcat, *Felis silvestris silvestris*, Iberian Peninsula, Space Use, Home Range, Habitat Selection, Resource Selection Function, Selection Ratios

Introduction

The European wildcat (*Felis silvestris silvestris*, Schreber, 1777) is a widely distributed mammalian mesocarnivore, ranging from the Iberian Peninsula to Eastern Europe (Yamaguchi *et al.* 2015). However, its current distribution is scattered, mainly due to severe population declines, which led to local extinctions in some areas (Stahl & Artois 1994). While a reverse in the declining trend has been reported in some populations in Central Europe (Hartmann *et al.* 2013; Nussberger *et al.* 2014), the same is not being reported in the Iberian Peninsula. In fact, a decreasing trend (>30%) was reported over the last three generations (Palomo & Gisbert 2002; Cabral *et al.* 2005), so its conservation status has been assessed as "Vulnerable" in Portugal (Cabral *et al.* 2005), and "Near Threatened" in Spain (López-Martín *et al.* 2007).

The European wildcat distribution through different biogeographic regions is achieved by this species' ecological flexibility, which allows it to adopt ecological adaptations to local conditions along several dimensions of their ecological niche, varying from prey selectivity to habitat selection. According to their feeding strategy, although some authors considered the wildcat to be a rodent specialist (Nowell & Jackson 1996), recent studies report European wildcats to be facultative specialists on European rabbits (*Oryctolagus cuniculus*), a keystone species in Mediterranean ecosystems (Delibes-Mateos *et al.* 2008), preying upon them whenever they are present (Malo *et al.* 2004; Lozano *et al.* 2006).

Regarding habitat selection patterns, European wildcats show a tendency to select areas dominated by deciduous forests in central-European temperate climates (Schauenberg 1981; Klar *et al.* 2008), while in Mediterranean ecosystems scrubland areas are selected over other land cover types (Ragni 1978; Monterroso *et al.* 2009; Lozano 2010). Due to its geographic position, the Iberian Peninsula provides a variety of ecological conditions, which may lead to different intra-specific selection patterns within a relatively small geographic area. Additionally, anthropogenic interferences may affect the selection process and have a negative effect on wildcat populations, mainly due to habitat destruction and increased contact with feral/domestic cats, which consequential increases in hybridization rates. Hybridization rates between European wildcats and domestic cats were considered to be low in the Iberian Peninsula (Oliveira *et al.* 2008; Gil-Sánchez *et al.* 2015). However, a recent study (Ramos 2014) found this rate to be 20%, suggesting that genetic introgression could be a serious threat for Iberian wildcat conservation. Therefore, there is an increasing need to evaluate not only population status but also which factors and environmental conditions are necessary to support stable European wildcat populations.

Like most mammalian carnivores, European wildcats have an elusive behavior which, coupled with low population densities, makes it difficult to collect a representative amount of ecological data. Non-invasive methods, such as scat collection or camera trapping, are commonly used to study cryptic species, since they provide reliable information that can be used in a myriad of studies. However, in the case of the European wildcat, camera-trapping data may not be an effective tool to distinguish between “pure” wildcats, its domestic counterparts, and their hybrids, due to the potentially similarity in coat patterns, which would difficult a correct identification, especially in areas with high hybridization rates. Also, these data may have limited use when it comes to obtain information regarding individual movement or selection patterns (Klar *et al.* 2008; Boitani & Powell 2012), although, for the latter, camera traps can be applied when considering, for instance, occupancy models in a grid-based design (ex.: Silva *et al.* 2013b). Nevertheless, to understand selection patterns, the use of radio- and/or satellite telemetry is most common, and it allows acquiring geographic locations of the collared individuals (usually representing a subsample of a given population; Aarts *et al.* 2008), thus it provides useful information to answer questions related with individuals’ and/or population’ spatial organization and exploitation of the available resources.

Habitat selection reflects the probability of a resource unit being used by the animal when it is available, thus allows one to understand which environmental characteristics are favorable to a given species (Manly *et al.* 2002; Lele *et al.* 2013). When modelling habitat selection, a common approach is to apply a use-availability design, which compares the obtained (use) data with data collected randomly across the considered study area (availability) (Manly *et al.* 2002). The comparison of use/available habitats is usually performed using logistic regression models, which can be used to construct resource selection functions (RSF), which provide values for relative probability of habitat selection. This can be applied at different levels, such as regional (Design I), landscape (Design II) and/or home range level (Design III) (Manly *et al.* 2002). This information is crucial for population management, and it is useful to, for example, define protected areas and to identify conservation corridors (Chetkiewicz & Boyce 2009; Klar *et al.* 2012), or to project the impact of habitat change (Manly *et al.* 2002). This approach can also allow understanding if we are in the presence of a population that follows a habitat matching rule (Pulliam & Caraco 1984; Cassini 2011), especially when facing, for instance, different levels of disturbances in natural habitats and intra- or inter-competition. This rule states that the occurrence of a given species in a habitat is directly related to habitat quality (Cassini, 2011). Several factors can interfere with this, such as populations' dynamics and structure (such as adult/young, or male/female), which may lead to differences in habitat selection. Carnivore species frequently show distinct social behaviors and spacing patterns between genders (Crook *et al.* 1976), and inferences about habitat selection without considering these possible differences may lead to biased interpretations (Conde *et al.* 2010). Therefore, when testing for the presence/absence of this resource matching rule in a given population, deeper insights can be obtained about habitat requirements and dynamics of given specie's population.

Considering the poorly known status of Iberian wildcat populations and their habitat requirements, it is relevant to gain insights about which environmental characteristics are selected, in order to apply management measures with feasibility. Until now, wildcat habitat studies within the Iberian Peninsula have been conducted at a small range (eg. Urra 2003; Sarmento *et al.* 2006; Monterroso *et al.* 2009; Lozano 2010). These studies are useful to understand habitat selection at a local landscape but they do not provide means to understand regional patterns of selection, unless the environmental conditions are very similar to those of the local landscape. A study considering several environments at a fine scale would provide insights into the environmental characteristics driving general habitat selection by wildcats and which of those are required to maintain wildcats within their natural range, with the purpose of reducing contact between wild/domestic forms.

Therefore, the main goals of this study are: i) to identify the environmental variables related to habitat selection at the landscape and home range levels within the Iberian Peninsula; and ii) to assess if the selection identified patterns vary between according to animals' gender. To achieve these goals, we combined radio-telemetry data obtained from radio-tracked European wildcats in five study areas distributed across the Iberian Peninsula, and employ RSFs and selection ratios under a Design II and Design III experiment, respectively, in a use-availability framework (Manly *et al*. 2002).

Additionally, gender-specific RSFs are compared between males/females, to evaluate if sex-biased habitat-matching is present in Iberian populations.

Methods

Study Areas

The telemetry data used in this study was provided by several researchers for five areas within the Iberian Peninsula. 1) Guadiana Valley Natural Park (GVNP) is a Mediterranean protected area located in southeastern Portugal (37º 69' N, -7º 76' E). GVNP is located in the Guadiana River basin, which is the most important ecological corridor in southern Portugal (Monterroso *et al.* 2014). Agricultural areas are present, and hunting activities are allowed, as well as predator control towards red foxes (*Vulpes vulpes*) and Egyptian mongooses (*Herpestes ichneumon*). 2) Izagaondoa Valley, located in Northern Spain (Navarre) (42º 78' N, -1º 42' E), is a transitional climacteric area which embraces both Mediterranean and Atlantic biogeographic regions, with higher areas characterized by deciduous species and, as elevation decreases, scrubland areas, sometimes with patches of herbaceous vegetation, become more common. Intensive agriculture is present. 3) Lleida, located in Catalonia, northeastern Spain (NE Spain; 41º 52' N, 1º 8' E), is characterized by a Mediterranean climate, with agricultural areas predominating in the landscape, as well as scattered houses and small villages. Hunting activities are present. 4) Cabañeros National Park (CNP) is a protected area located in central Spain (39º 33' N, -4º 39' E) with a typical Mediterranean environment. This park has two main contrasting landscapes, a savannah-like system and scrubland areas mainly associated with steeper slopes and higher elevations. No hunting activities are allowed. 5) Sierra Arana, located within the province of Granada (Andalusia, southern Spain) (37º 34' N, -3º 49' E), belongs to the Subbaetic System, and it is characterized by a Mediterranean environment. Higher areas are dominated by forest patches with scrubland vegetation and at lower elevations the landscape is characterized by small ravines with high vegetation and rock cover.

Field Data

Individual wildcats were trapped with box-traps, placed in areas with wildcat presence recorded previously or in suitable areas to the occurrence of this species. Traps were lured with live animals (partridges (*Alectoris rufa*) or house pigeons (*Columba* sp.), unavailable to captured animals) or Iberian lynx (*Lynx pardinus*) urine. Traps were checked daily and soon after sunrise, to reduce animal stress. Captured animals were chemically immobilized, and samples were taken to evaluate general health status and to perform genetic confirmation. Each individual was fitted with a radio-collar, with several models and brands (VHF system, n= 26; GPS system, n= 2) and, in order obtain each location, triangulation was performed, with the use of portable antennas and receivers (several models and brands).

Additional wildcat presence data from GVNP, CNP and Sierra Arana, and other areas across the IP (Table S2, Supplementary Material), was obtained from other methods: genetically confirmed scats, tissue and hair; and camera-trapping records individuals that exhibited European wildcat coat pattern characteristics (Ballesteros-Duperón *et al.* 2015). Data from five captured wildcats (but not radio-tracked) were also included (Table S1). These data was used as independent presence data to validate the RSFs models developed for Iberian populations of the European wildcat.

Covariate Selection

Three sets of variables potentially related to European wildcat distribution in the Iberian Peninsula were selected: land cover type, distance to humanized areas, distance to permanent water sources, and topographic characteristics (Table 1).

Landscape data was obtained from two vector-based land cover datasets: SIOSE 2005/2011 (Sistema de información de ocupación del suelo en España, www.siose.es) for Spain, and COS2007 (Carta de Ocupação e Uso do Solo, level 5, http://www.igeo.pt) for Portugal. The version of the land cover datasets was selected according to the period the wildcat data was collected, in order to use the most accurate land cover information for each study area. Therefore, SIOSE2011 was used for CNP, SIOSE2005 for the other three study areas located in Spain and COS2007 for GVNP.

The original datasets were then reclassified into 10 ecologically relevant classes for the European wildcat, based on the published literature (Ferreira 2003; Lozano *et al.* 2003; Sarmento *et al.* 2006; Monterroso *et al.* 2009): 1) humanized areas (inc. villages, farms, paved roads; H), 2) agricultural areas (AG), 3) agroforestry systems (AGF), 4) deciduous forests (DF), 5) coniferous forests (CF), 6) mixed forests (MF), 7) scrublands and transitional woodland scrub (SCL), 8) natural herbaceous vegetation areas (HRB), 9) open areas (OPEN) and 10) permanent water bodies (W; Table 1). Telemetry techniques have an associated error, which is variable between studies and felid species (ex.: 83m for *F. catus*, Norbury *et al.* 1998; 100m for *F. silvestris*, Klar et al., 2008; 373m (maximum) for *L. lynx*, Jędrzejewski *et al.* 2002). Therefore, we considered a 150m buffer (similar to Monterroso *et al.* 2009) around each location to obtain the area occupied by each of the land cover types (except H and W).

Table 1. Explanatory variables extracted and tested in the models for European wildcats' habitat use in the Iberian Peninsula.

Type	Variable	Description (Units)	Code
Land Cover	**Agricultural areas**	Areas mainly used for agricultural activities (>50%) (m^2)	AG
	Agroforestry systems	Areas mainly used for agriculture (≥50%), with forest cover higher than 10% [in Iberian ecosystems often named as "montado" and "dehesa"] (m^2)	AGF
	Deciduous Forest	Areas with a marked presence (≥30%) of deciduous forests, and undercover not used for agriculture (m^2)	DF
	Coniferous Forest	Areas with a marked presence (≥30%) of coniferous forests, and undercover not used for agriculture (m^2)	CF
	Mixed Forest	Areas with forests composed by deciduous and coniferous tree species (at least 25% for each forest type). Undercover not used for agriculture (m^2)	MF
	Scrublands and transitional woodland scrub	Areas mainly occupied (at least 25%) by scrubland cover and reduced percentages of tree cover (m^2)	SCL
	Natural herbaceous vegetation	Areas dominated by herbaceous species (≥25%), with small percentages of tree cover and scrublands (m^2)	HRB
	Open areas	Areas with reduced vegetation cover and higher presence of open areas (≥50%) (m^2)	OPEN
Distance	**Distance to humanized areas**	Distance to the edge of the nearest humanized area (villages, farms, paved roads, among others) (m)	DH
	Distance to permanent water bodies	Distance to the edge of the nearest permanent water body (m)	DW
Topography	**TPI**	Difference between a pixel's value and the mean value of the surrounding pixels (unitless)	TPI
	Roughness	The largest inter-pixel difference between a pixel and its surrounding pixels (unitless)	RGN
	Slope	Measure of the steepness of a line that connects two surrounding pixels (degrees)	SLP
	Elevation	Vertical distance between a pixel and the average sea level at its geographic location (meters)	ELV

Distances to the nearest permanent water source (DW) and humanized areas (DH) were estimated for each location. When a location was placed within the polygon, distance was set to zero (Klar *et al.* 2008). Because spatial data on small and local water sources was not available, we could only use the main and permanent water bodies (> 1 ha).

The topographic position index (TPI), roughness, slope and elevation were also included as potentially relevant variables for wildcat spatial ecology. The TPI describes the complexity of the landscape's topography and takes different values from concave (i.e. valleys) to steep slopes, and convex surroundings (i.e. ridges). This measure can provide additional information when it comes to understand the selection of topographic characteristics by a given species. The TPI, roughness and slope are derived from elevation data, which was obtained from ASTER-DGEM (Advanced Spaceborne Thermal Emission and Reflection Radiometer - Global Digital Elevation Model, downloaded from: http://gdex.cr.usgs.gov/gdex/) digital elevation models (DEM), with 30x30m resolution. The GDEM layer was recalculated with a neighborhood distance of 150m (Monterroso *et al*. 2009), where the final value for each pixel consisted on the average of pixels surrounding it.

All spatial analyses, including the reclassification of land cover datasets and estimation of the area occupied by each class, were performed using QGIS v2.14 vector tools (QGIS Development Team, 2013). Distances were obtained using GRASS GIS v7.0.3 vector tools (GRASS Development Team, 2016). Topographic conversions were performed with GRASS GIS v7.0.3 raster tools. Grids for TPI, roughness and slope were then created over the new DGEM layer with QGIS v2.14. DEM tools.

Data Analyses

Home range estimation

Kernel density estimators (KDEs) were used to estimate 90% home ranges for each radio-collared animal, using a fixed reference scaled bandwidth (*h_refscaled*; Kie 2013). Based on a preliminary analysis between four possible bandwidths (reference, least square cross validation, *plug in* the equation and reference scaled bandwidth), *h_refscaled* revealed to be the most appropriate for our dataset, since it provided the less fragmented home ranges (Kie 2013). Therefore, *h_refscaled* was estimated manually by reducing the reference bandwidth (*h_ref)* in 0.1 steps (following Kie, 2013) until the home range became fragmented or presented lacuna. *H_refscaled* was not allowed to be greater than *h_ref*. There is no standard value for the isopleth selection in home range estimation. Although the 95% isopleth is often selected, we defined the home range using the 90% isopleth, which has been argued to provide more accurate home range estimates (Börger *et al.* 2006; Boitani & Powell 2012).

The minimum number of fixes required for reliable home range estimation was determined following a bootstrap resampling procedure, a subsequent MCP estimation (Kenward 2000). The number of fixes was considered satisfactory when the MCP area would not increase with increasing number of fixes, i.e. the home range area achieved an asymptote.

For all analyses, data from all seasons was pooled together, since the different periods of monitoring did not allow for a separated analysis, although we acknowledge that there may be seasonal differences in wildcats' home ranges (Table S1, Supplementary Material). All home range analyses were performer using R software v3.2.5 (R Development Core Team, 2013) and the *rhr* v1.2.906 (Signer & Balkenhol 2015) package. A default output grid of 100x100 was used to perform home range analyses. Bootstrap analyses were performed using *move* v2.0.0 R-package, with 100 repetitions per step.

Habitat selection at the landscape level (Design II)

Habitat selection at the landscape level in the Iberian Peninsula was analyzed using a "use *vs* availability" approach to determine which habitat types had higher odds of being used by European wildcats, by developing generalized linear mixed models (GLMM) under a type II study design (Design II; Manly *et al.* 2002).

*S*tudies under designs I or II require the delimitation of an area that best defines the landscape "available" for a given population. Administrative boundaries in the definition of study areas lack biological meaning. Hence, following Dillon & Kelly (2008), we defined the area of availability in a similar way the effectively sampled area is defined for camera-trapping studies: by defining a polygon drawn by the outermost fixes for each studied population, and adding a buffer equal to the mean home range radius of our radio-tracked animals (estimated with the 90% KDE).

Habitat availability was estimated by taking a sample of points randomly generated within each study area. Because a high number of available locations is advisable to accurately assess habitat selection (Northrup *et al.* 2013), the number of available points for each animal was ten times the number of fixes obtained for that individual, taken randomly across the entire study area, following Koper & Manseau (2012).

Covariate's Exploratory Analysis

The first step in our modeling approach consisted in an exploratory analysis using Generalized Linear Models (GLMs) to assess the univariate effect of each of the potential explanatory variables in our dummy response variable (0 = available; 1 = used). GLM models were fitted using a logit link function. All tested variables were then ranked according to 1) AICc (Akaike's Information Criteria corrected to small sample sizes) values and 2) effect size (Burnham & Anderson 2002; Sullivan & Feinn 2012). In a logistic regression, the effect size is reported as an *odds ratio*, which corresponds to the value of the exponentiated coefficient. Next, a pairwise Spearman's rank correlation (r_s) was calculated between all explanatory variables. Variables with moderate to low correlation values ($r_s < 0.5$) were included in subsequent analyses (Hosmer & Lemeshow 2000; Hinton *et al.* 2015). When correlated variables are included in the same model, bias in coefficient estimation are likely to be introduced (Aarts *et al.* 2008; Northrup *et al.* 2013). If two variables presented a correlation value higher than 0.5, the one with lower AICc value and higher effect size was selected, since it presented a stronger relationship with the response variable.

All analyses were conducted using R v3.2.5. GLMs were fit using *stats* v3.2.5 package, and Spearman's rank values were obtained using *ltm* v1.0-12 package.

Modelling Approach

Generalized liner mixed effect models (GLMMs) were then used to model wildcat habitat preferences in the Iberian Peninsula. GLMMs were chosen due to the possibility of accommodating fixed and random effects, since the latter can account for unbalanced sample sizes and also control for correlation that arises from recording several locations per animal (Gillies *et al.* 2006). Prior to any modeling, all continuous variables were standardized to z-scores ($([x-\bar{x}]/\sigma_x)$) in order to facilitate a correct interpretation of model coefficients and to improve model convergence (Northrup *et al.* 2013; Bouyer *et al.* 2015).

GLMMs were fitted to our binary response variable for 26 individuals (CTF02, CTF03, CBM02, CBM03 and CBF02 were excluded since only one location was obtained; Table S1) using a logit link function. Random effects associated with individual animals and study areas were evaluated developing three sets of GLMMs, each with a different random effect (but considering the same set of fixed effects): 1) study area, 2) individual wildcats, and 3) individuals nested in study areas. The most parsimonious random effect will be considered.

After selecting the random effects to include, we built a set of models with all possible combinations between fixed effects (uncorrelated explanatory variables), which were then ranked in a hierarchical approach following AICc criteria (Burnham & Anderson 2002). We considered models with ΔAICc values ≤ 2 units of the lowest AICc to have equal support for being best models (Burnham & Anderson 2002). The coefficients of each variable included in the top models' set were assessed following a model averaging procedure (Burnham & Anderson 2002). Models that failed to converge (i.e.

estimation of their coefficients did not stabilize), were not included in the model averaging procedure.

The same modeling procedure was conducted to investigate possible differences in habitat selection between male and female wildcats, using gender-specific datasets.

All analyses were conducted using R version 3.2.5. Package *lme4* v1.1-12 (Bates *et al.* 2016) was used to fit GLMMs. *AICcmodavg* v2.0-4 (Mazerolle & Mazerolle 2016) was used to perform model averaging, and *MuMIn* v1.15.6 (Barton 2016) was used to create and rank all model combinations.

Model Evaluation

The coefficient of determination (R^2) was used to evaluate the models' goodness of fit. However, GLMMs require the estimation two parameters: the marginal R^2 and the conditional R^2 (Nakagawa & Schielzeth 2013). The first describes the proportion of variance of the fixed factors alone (that is, the explanatory variables), while the second describes the proportion of variance explained by both fixed and random factors (that is, the explanatory variables and the random effects) (Nakagawa & Schielzeth 2013). Additionally, the predictive performance of the best model was assessed in two ways: by 1) conducting a *k*-fold cross-validation (Boyce *et al.* 2002; Koper & Manseau 2012; Benson *et al.* 2015) and 2) using independent wildcat occurrence data in the Iberian Peninsula (Table S2). The *k*-fold cross-validation was conducted following Benson *et al.* (2015): 80% of the data was used to build a model, which was then used to predict the probability of use of the remaining 20%. This procedure was repeated five times until all data had been used. Spearman rank correlations were then run to evaluate the relationships between the frequency of cross-validated used locations and 10 probability bins of equal size, representing the range of predicted values. A model with good predictive performance should show a strong correlation ($r_s > 0.80$), with higher numbers of locations continually falling into higher probability bins.

An additional measure of model assessment consisted in estimating the probability of habitat selection with wildcat presence records obtained from across the Iberian Peninsula. These probabilities were then compared to the probabilities of selection of a set of points randomly distributed across the Iberian Peninsula (n=500 random points; pseudo-absence data). For each record and random point, variables were obtained using the same procedures described in section "Covariate Selection". Coefficients obtained from the general GLMM were projected to obtain the relative probability for each record and random point, applying the following resource selection formula:

$$w(x) = \frac{exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n)}{1 + exp(\beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n)}$$

, where β_0 is the intercept value from the global model, $\beta=(\beta_1, \ldots \beta_n)$ represents the coefficient values from the global model for variable "1,…,n" and $x=(x_1,\ldots,x_n)$ represents the value for each variable within each point. Since variables were rescaled to develop the global model, the values obtained for each point $(x_1,\ldots,x_n)$ were also rescaled. The two sets of probabilities were then square-root transformed to normalize data, and a Welch's *t*-test was performed to test for significant differences between both groups. Since the independent presence data includes records taken within three of our study areas (CNP, GVNP and Sierra Arana), a secondary analysis using only records outside the model's calibration range was conducted, to avoid potential lack of independence. Significant differences between presence and pseudo-absence data indicate that the model has good prediction ability in identifying areas for European wildcats in the Iberian Peninsula.

All analyses were performed using QGIS v2.14 and GRASS GIS v7.0.3 raster/vector tools and the R software v3.2.5. Coefficients of determination were obtained using *MuMIn* v1.15.6 R-package, *k*-fold cross-validation using *lme4* v1.1-12 R-package and Welch's *t*-test using *stats* v3.2.5 R-package.

Habitat selection at the home range level (Design III)

Selection ratios identify a general use of different habitat characteristics given their availability. In this study, these ratios were used to provide insights into habitat use within home ranges (Design III; Manly *et al*. 2002) of wildcats in the Iberian Peninsula, under a "use/availability" approach. For this analysis only fixes obtained within each defined home range (KDE-90%) were included, and a set of points representing availability ($n=10*N_{used}$) was randomly taken within each home range limit. For each used and available location, information regarding the three types of variables (land cover, distance to artificial areas/permanent water bodies, and topographic characteristics) was obtained as described in Section "Covariate Selection". Continuous variables (distance and topographic variables) were converted into six intervals, for comparative purposes. The use ratios for each variable type (land cover, distances and topography) were computed with the Manly selectivity measure (selection ratio = used/available; Manly *et al*. 2002). This measure tests the preference/avoidance of each interval or habitat type, where values above 1 reflect the selection of a given feature, while values below 1 represent avoided features. Habitat selection is tested using a Chi-square test, and Bonferroni's method is used to create confidence intervals. Whenever a given individual did not show a representative distribution (e.g. values limited to a single class), it was excluded from the analyses to avoid a biased interpretation of the selection index. Similarly, if humanized areas or permanent water sources were not present within an individual's home range, that individual was not considered in the estimation of selection ratios for distance to humanized areas/permanent water sources. We only included individuals for which we could estimate a reliable home range in these analyses.

All analyses were performed using QGIS v2.14 and GRASS GIS v7.0.3 raster/vector tools and the package *adehabitatHS* v0.3.12 (Calenge 2011) of R software v3.2.5.

Results

Wildcat Data

Telemetry data was obtained for 31 wildcats (16 males and 15 females), comprising a total of 2976 locations (Table S1, Supplementary Material), with 96 ± 28.05 (mean ± SE) locations per animal and 6.2 + 0.66 (mean ± SE) individuals per study area.

Home Range Analyses

From the 31 monitored European wildcats, we could achieve reliable home range estimates for 18 individuals (11 males and 7 females), distributed across all study areas (Table S1). From the remaining animals, nine (CTF02, CTF03, CTM04, GRF02, GRF03, GRF04, CBM02, CBM03, CBF02) were preliminarily excluded since the number of locations was lower than 10 (Seaman *et al.* 1999; Powell *et al.* 2000; Börger *et al.* 2006), and four (GRM01, GVF02, GVF04, GVM02) did not reach an asymptote in the bootstrap analyses. The KDE-90% home range areas showed high variability among individuals, and presented a median value of 13.68 km^2 [1.22 – 59.78] (Area (median) [Range]). Males present higher home range areas than females (HR_{males}=14.68 km^2 [1.22 – 43.01] vs. $HR_{females}$=4.59 km^2 [3.14 – 59.78]), although differences were not statistically different (Welch t=1.09, df=10.46, p=0.30; after a square-root transformation of the two sets).

Habitat Selection at the Landscape Level (Design II)

The home range radius for our sample was 2.11 ± 0.24 km (mean ± SE), therefore it was the distance chosen as buffer width to delimit study areas (Table S3, Supplementary Material).

All variables presented a low to moderate correlation between them ($r_s < 0.5$) (Table S4, Supplementary Material), except for the slope *vs*. roughness ($r_s > 0.9$). However, we found a stronger relation between the slope and our response variable, than roughness (Table 2). Therefore, slope was preferred for habitat selection analysis over of roughness.

Table 2. Generalized Linear Models (GLMs) for each variable (ordered by AICc values).β– covariate estimate; SE – Standard Error.

Univariate Model	*β*	SE	AICc	Effect Size
DF	0.45	0.01	19062.09	1.57
AG	-0.58	0.02	19194.58	0.56
SLP	0.42	0.02	19324.75	1.52
RGN	0.40	0.02	19339.27	1.50
DH	-0.05	0.02	19748.9	0.95
MF	0.15	0.01	19813.62	1.16
SCL	0.15	0.02	19843.94	1.16
OPEN	-0.38	0.08	19852.16	0.68
CF	-0.14	0.02	19866.2	0.87
DW	-0.65	0.03	19873.92	0.52
HRB	0.09	0.02	19880.67	1.10
TPI	0.09	0.02	19887.1	1.09
AGR	-0.09	0.03	19896.12	0.91
ELV	-0.03	0.02	19906.22	0.97

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; RGN- Roughness; SLP- Slope; ELV- Elevation

To evaluate habitat selection at a landscape level, a total of 2970 used and 29700 available locations, from 26 individuals, were used to fit GLMMs, with a set of 13 explanatory variables as fixed effects. Between the three possible random effects combinations (study areas, individual ID and individual ID nested in study areas), individual ID was considered the most appropriate. All random effects' combinations provided similar coefficients as well as AICc values. Following the principle of parsimony, the nested effect was excluded. The individual ID random effect was preferred over the study areas because it has a higher number of levels (n=26 individuals *vs*. n=5 study areas), which benefits the performance of GLMMs (Bolker *et al.* 2009), and because the effect of individuals already includes the study areas variation, since no individual is present in two study areas.

Table 3. Model set of the top-ranked mixed-effect resource selection models at the landscape level, with AICc, delta AICc and AICc weights for the top-ranked models.

Model	**Parameters**	**AICc**	**ΔAICc**	**Weights**
A) 1/2/3/4/5/6/8/9/10/11/12/13	14	17566.36	0	0.26
B) 1/2/3/4/5/6/7/8/9/10/11/12/13	15	17566.76	0.4	0.21
C) 1/2/3/6/7/8/9/10/11/12/13	13	17567.05	0.69	0.18
D) 1/2/3/5/6/7/8/9/10/11/12/13	14	17567.6	1.24	0.14
E) 1/2/3/4/6/7/8/9/10/11/12/13	14	17567.66	1.3	0.14

1-DH; 2-DW; 3- ELV; 4-AG; 5-AGF; 6-DF; 7-CF; 8-MF; 9-SCL; 10-HRB, 11-OPEN; 12-SLP; 13-TPI

The best model contained all variables (except for coniferous forests; Model A in Table 3) and had AICc weight of support of 0.26. The next four models (Models B-E in Table 3) also have substantial support of being best models (ΔAICc ≤ 2). None of these models failed to converge, hence their coefficients were successfully averaged (Table 4). The sum of AICc weights for the top five models is 0.93.

The coefficients for our general model are presented in Table 4 (see also Figures S1-S5, Supplementary Material). Deciduous forests were the land cover type with the stronger effect on wildcats' habitat selection patterns (Effect Size (hereafter, ES) = 1.82), with the higher odds of being selected, followed by scrublands (ES = 1.45). Herbaceous vegetation and mixed forests had 31% (ES = 1.31) and 27% odds (ES = 1.27) of being selected, respectively, while agricultural and open areas were avoided with odds of 11% (ES = 0.89) and 26% (ES = 0.74), respectively. Coniferous forests and agroforestry systems present lower odds of being selected and avoided (ES = 1.07 and ES = 0.95, respectively; Table 4). Agricultural areas, agroforestry systems and coniferous forests 1) have high standard errors, when comparing to the estimate values, and 2) are the only variables that are not present in every top model, which may indicate that the importance of these variables is moderate when comparing to the others.

Wildcats avoided both humanized areas (including buildings, villages and paved roads, among others) and permanent water sources (ES = 1.39 and ES = 1.08, respectively), although the latter with lower odds. Regarding topographic variables, wildcats selected steeper areas with high odds (ES = 1.53), while the topographic position had lower influence (ES = 1.07). Areas with high elevation are avoided with odds of 74%, indicating that wildcats prefer areas with low to moderate elevation, within a given range (Table 4).

Table 4. Model averaged coefficients (β), standard errors (SE), confidence intervals (CI; 95%) and effect sizes from the top-ranked mixed-effect resource selection models for European wildcats in the Iberian Peninsula. * - Significant estimate values.

Coefficient	*β*	SE	Upper CI	Lower CI	Effect Size
(Intercept)	-2.60*	0.36	-1.89	-3.31	0.07
DF	0.60*	0.06	0.73	0.50	1.82
SLP	0.42*	0.03	0.47	0.37	1.53
SCL	0.37*	0.07	0.52	0.24	1.45
DH	0.33*	0.02	0.38	0.29	1.39
HRB	0.27*	0.04	0.36	0.20	1.31
MF	0.24*	0.03	0.30	0.19	1.27
DW	0.08*	0.02	0.12	0.03	1.08
TPI	0.07*	0.02	0.11	0.03	1.07
CF	0.07	0.07	0.23	0.002	1.07
AGF	-0.05	0.04	0.01	-0.13	0.95
AG	-0.12	0.09	0.002	-0.29	0.89
OPEN	-0.30*	0.08	-0.14	-0.47	0.74
ELV	-1.36*	0.06	-1.24	-1.48	0.26

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; SLP- Slope; ELV- Elevation

Regarding the performance of the general model, the marginal R^2 values were the same for all top-ranked models (0.25; Table 5), and the conditional R^2 values were very similar among them (0.63 ± 0.004, mean ± SE; Table 5).

The *k*-fold cross validation provided high correlation values ($r_s > 0.80$ in all five models; mean ± SE: 0.85 ± 0.01; Table 5), which indicates that these models have a good predictive ability of wildcat presence in the Iberian Peninsula.

Table 5. Spearman rank correlation values of the *k*-fold cross validation procedure (with the correspondent p-value), and marginal and conditional R^2 values for each of the top models.

Model	Spearman rank (p-value)	Marginal R^2	Conditional R^2
A	0.82 (p<0.0050)	0.25	0.63
B	0.87 (p<0.0025)	0.25	0.63
C	0.82 (p<0.0050)	0.25	0.61
D	0.88 (p<0.0025)	0.25	0.63
E	0.88 (p<0.0025)	0.25	0.63

Effects of Gender on Wildcat's Habitat Selection

The female dataset included data from 12 individuals, with a total of 1698 used and 16980 available locations, and the male dataset included data from 14 individuals, with a total of 1272 used and 12720 available locations.

The best model for male wildcats included all but three variables - mixed forests, areas with scrublands and natural herbaceous vegetation -, and had a weight of support of 0.19 (Table 6). The following four models (models B to E; Table 6) had a ΔAICc ≤ 2, indicating that the support for these models is not statistically distinguishable. The five top-ranked models' AICc weights sum up to 0.60. None of the models failed to converge, therefore their coefficients were successfully averaged (Table 7).

The top ranked model for females included all 13 variables, and had weight of support of 0.66 (Table 6). The next model presented a ΔAICc > 2, therefore only model A was considered and model averaging was not performed.

Table 6. Model set of the top-ranked mixed models for male and female European wildcats , with AICc, delta AICc and AICc weights for ech model.

	Model	**Parameters**	**AICc**	**ΔAICc**	**Weights**
Males	A) 1/2/3/4/5/6/7/11/12/13	12	7956.53	0	0.19
	B) 1/2/3/4/5/6/7/9/11/12/13	13	7957	0.47	0.15
	C) 1/2/3/4/5/6/7/8/9/11/12/13	14	7957.93	1.4	0.1
	D) 1/2/3/4/5/6/7/8/11/12/13	13	7958.26	1.73	0.08
	E) 1/2/3/4/5/6/7/10/11/12/13	13	7958.27	1.74	0.08
Females	A) 1/2/3/4/5/6/7/8/9/10/11/12/13	15	9058.22	0	0.66

1-DH; 2-DW; 3- ELV; 4-AG; 5-AGF; 6-DF; 7-CF; 8-MF; 9-SCL; 10-HRB, 11-OPEN; 12-SLP; 13-TPI

The coefficients obtained with the GLMMs developed for males and females revealed different patterns between genders (Table 7).

Land cover was generally more important for females than for males, with deciduous forests being the vegetation type with higher odds of being selected by females ($ES_{females}$ = 4.21 *vs* ES_{males} = 1.17). The other land cover types have high odds of being selected as well, with agroforestry systems with the lower odds of selection ($ES_{females}$ = 1.16). Within land cover variables, only open areas are avoided by females, with odds of 41% (ES_{males} = 0.59). Land cover was less important for males. Still, as for females, deciduous forests were the category with higher odds of being selected. Mixed forests, scrubland habitats and areas with natural herbaceous vegetation 1) have high standard errors, 2) are the only variables not present in all top models (as happened with the general model), and 3) have effect size values closer to one, suggesting a low importance of these variables. Males avoided more land cover types than females: agricultural areas (avoided with odds of 28%, ES_{males} = 0.72), open areas (ES_{males} = 0.81), agroforestry systems (ES_{males} = 0.84) and coniferous forests (ES_{males} = 0.86) (Table 7).

Table 7. Coefficients estimate value (β), standard errors (SE), confidence intervals (CI; 95%) and effect sizes from the top-ranked mixed-effect resource selection models for male (model-averaged) and female (top model) European wildcats in the Iberian Peninsula. * - Significant estimate values.

	Coefficient	*β*	SE	Upper CI	Lower CI	Effect Size
MALES	(Intercept)	-2.67*	0.27	-2.13	-3.20	0.07
	DH	0.57*	0.03	0.64	0.51	1.77
	SLP	0.26*	0.04	0.33	0.18	1.29
	DF	0.16*	0.04	0.24	0.08	1.17
	TPI	0.07*	0.03	0.13	0.01	1.07
	HRB	0.00	0.01	0.09	-0.05	1.00
	MF	-0.01	0.03	0.05	-0.11	0.99
	SCL	-0.03	0.05	0.03	-0.17	0.97
	DW	-0.09*	0.03	-0.03	-0.16	0.91
	CF	-0.15*	0.05	-0.05	-0.25	0.86
	AGF	-0.18*	0.06	-0.06	-0.30	0.84
	OPEN	-0.21*	0.08	-0.05	-0.25	0.81
	AG	-0.33*	0.06	-0.21	-0.44	0.72
	ELV	-1.04*	0.09	-0.86	-1.22	0.35
FEMALES	(Intercept)	-2.59*	0.84	-0.95	-4.23	0.07
	DF	1.44*	0.12	1.67	1.20	4.21
	SCL	1.35*	0.15	1.65	1.05	3.85
	CF	0.86*	0.15	1.15	0.56	2.37
	HRB	0.79*	0.08	0.95	0.63	2.21
	AGRIC	0.73*	0.19	1.12	0.35	2.08
	MF	0.60*	0.05	0.71	0.50	1.83
	SLP	0.53*	0.03	0.59	0.46	1.69
	DW	0.19*	0.03	0.24	0.13	1.21
	AGF	0.15*	0.05	0.25	0.05	1.16
	DH	0.10*	0.03	0.17	0.04	1.11
	TPI	0.05*	0.03	0.10	0.002	1.05
	OPEN	-0.54*	0.25	-0.05	-1.02	0.59
	ELV	-1.72*	0.08	-1.55	-1.88	0.18

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; SLP- Slope; ELV- Elevation

While females avoided humanized areas with 11% of odds ($ES_{females}$ = 1.11), males had higher odds of selecting spaces farther away from these areas, and it was also the most important variable for male wildcats (ES_{males} = 1.77). Regarding permanent water sources, while males selected areas with lower distances from these places, females avoided areas near these water sources (ES_{males} = 0.91 *vs* $ES_{females}$ = 1.21) (Table 7).

Regarding topographic variables, their selection was similar between genders: slope was the most relevant variable, with a selection of steeper areas with odds of 29% and

69% by males and females, respectively (ES_{males} = 1.29 *vs* $ES_{females}$ = 1.69) (Table 7). Elevation had the same effect for males and females (ES_{males} = 0.35 *vs* $ES_{females}$ = 0.18), as did slope and TPI (Table 7). For both genders, elevation is the variable with lower odds of selection.

Regarding the performance of these models, all of the top-ranked male models had a marginal R^2 of 0.21, whereas the top model for females' was 0.29 (Table 8). The conditional R^2 for male wildcats suggests that 39% of the variability observed in the response variable is explained our models (0.39 ± 0.002, mean ± SE; Table 8). By contrast, the conditional R^2 for female wildcats was 0.80 (Table 8), indicating a good model fit.

The Spearman rank values of *k*-fold cross validation procedure were similar for males (0.88 ± 0.01, mean ± SE; Table 8) and females (0.87), supporting a good predictive ability of our models for male and female wildcats in the Iberian Peninsula.

Table 8. Spearman rank correlation values of the *k*-fold cross validation procedure (with the correspondent p-value), and marginal and conditional R^2 values for each of the top models for male and female wildcats.

	Model	**Spearman rank (p-value)**	**Marginal R^2**	**Conditional R^2**
Males	A	0.92 (p<0.0005)	0.21	0.40
	B	0.84 (p<0.0025)	0.21	0.39
	C	0.85 (p<0.0025)	0.21	0.39
	D	0.89 (p<0.0010)	0.21	0.39
	E	0.91 (p<0.0010)	0.21	0.39
Females	A	0.87 (p<0.0025)	0.29	0.80

Model Validation

A total of 127 samples and 6 animals, captured only once, were used as wildcat presence data to perform model validation (n_{total}= 133; Figure 1; Tables S1 and S2, Supplementary Material). Since our independent wildcat data did not specify the animal's gender for all registers, this information was only used to evaluate the general model. When projected on the locations of independent wildcat records, our model predicted a mean (relative) probability of occurrence of P = 0.14 ± 0.01 (mean ± SE; median: 0.12), which were significantly higher than the probabilities obtained for the set of random points (P = 0.10 ± 0.006; median: 0.06; t=-3.59, df= 194.58, p-value < 0.001; Figure 2). These significant differences were similar when considering only the samples located outside the model's calibration range (n=85) (t=-2.30, df= 117.12, p-value = 0.02), although with a slightly lower probability P = 0.11 ± 0.01 (median: 0.09).

These values represent a relative probability of use, instead of the absolute probability (Thomas & Taylor 2006). Therefore, they cannot be directly interpretable, and should only be used for relative comparisons.

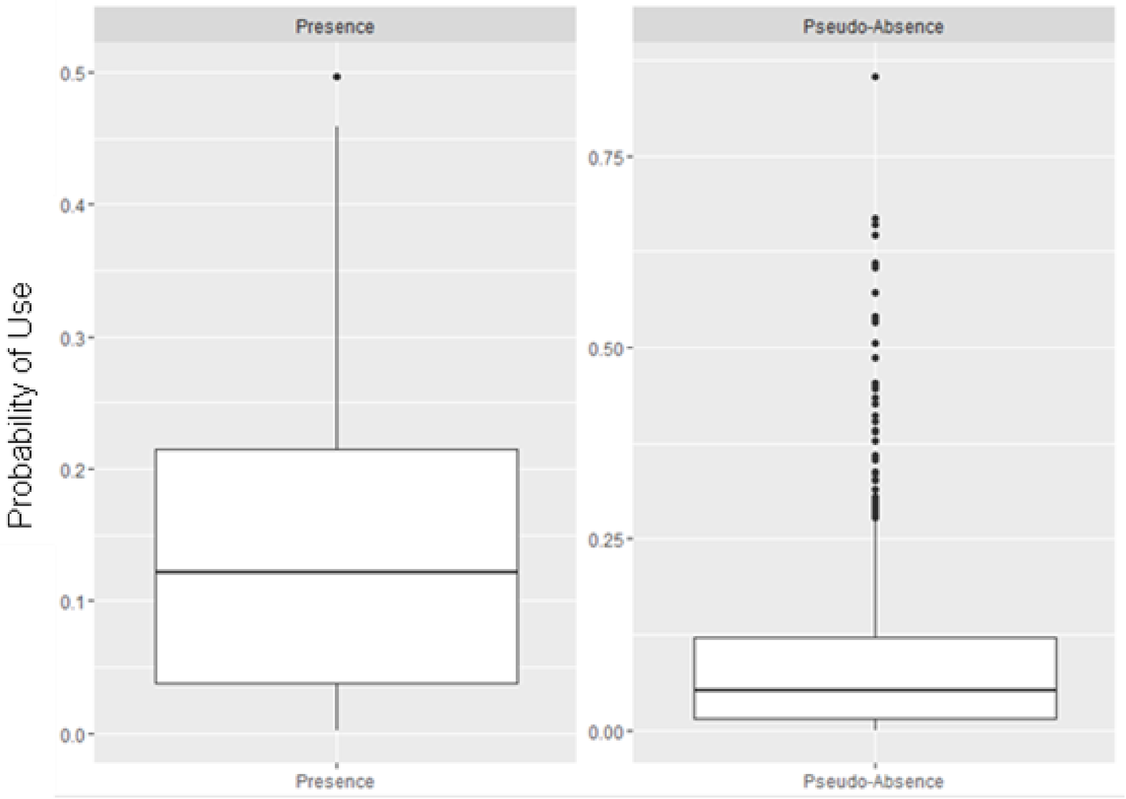

Figure 2. Boxplot representing the predicted relative probabilities (median, quartiles and 95% confidence intervals) of wildcat occurrence for the two datasets: independent wildcat records and randomly generated pseudo-absences in the Iberian Peninsula.

Habitat Selection at the Home Range Level (Design III)

Although without statistical significance, deciduous and coniferous forests obtained an average selection ratio higher than 1, suggesting a tendency for wildcats to select these land cover types in higher proportions than their availability (Figure 3A; Table S5, Supplementary Material). Mixed forests, however, presented selection ratio of 1.09 ± 0.40 (Wi ± SE), with a wide confidence interval (CI = 0.00 - 2.15). Deforested areas with natural vegetation (scrublands and patches with natural herbaceous vegetation) had selection ratios close to 1 (SR_{SCL}= 0.96 ± 0.08; SR_{HRB}= 0.98 ± 0.20; Table S5; Figure 3A). By contrast, agricultural and open areas were significantly avoided (SR_{AG}= 0.88 ± 0.06; SR_{OPEN}= 0.41 ± 0.17). European wildcats presented a tendency for avoiding agroforestry system, although this tendency was not statistically significant (SR_{AGF}= 0.70 ± 0.24; CI = 0.03 - 1.36).

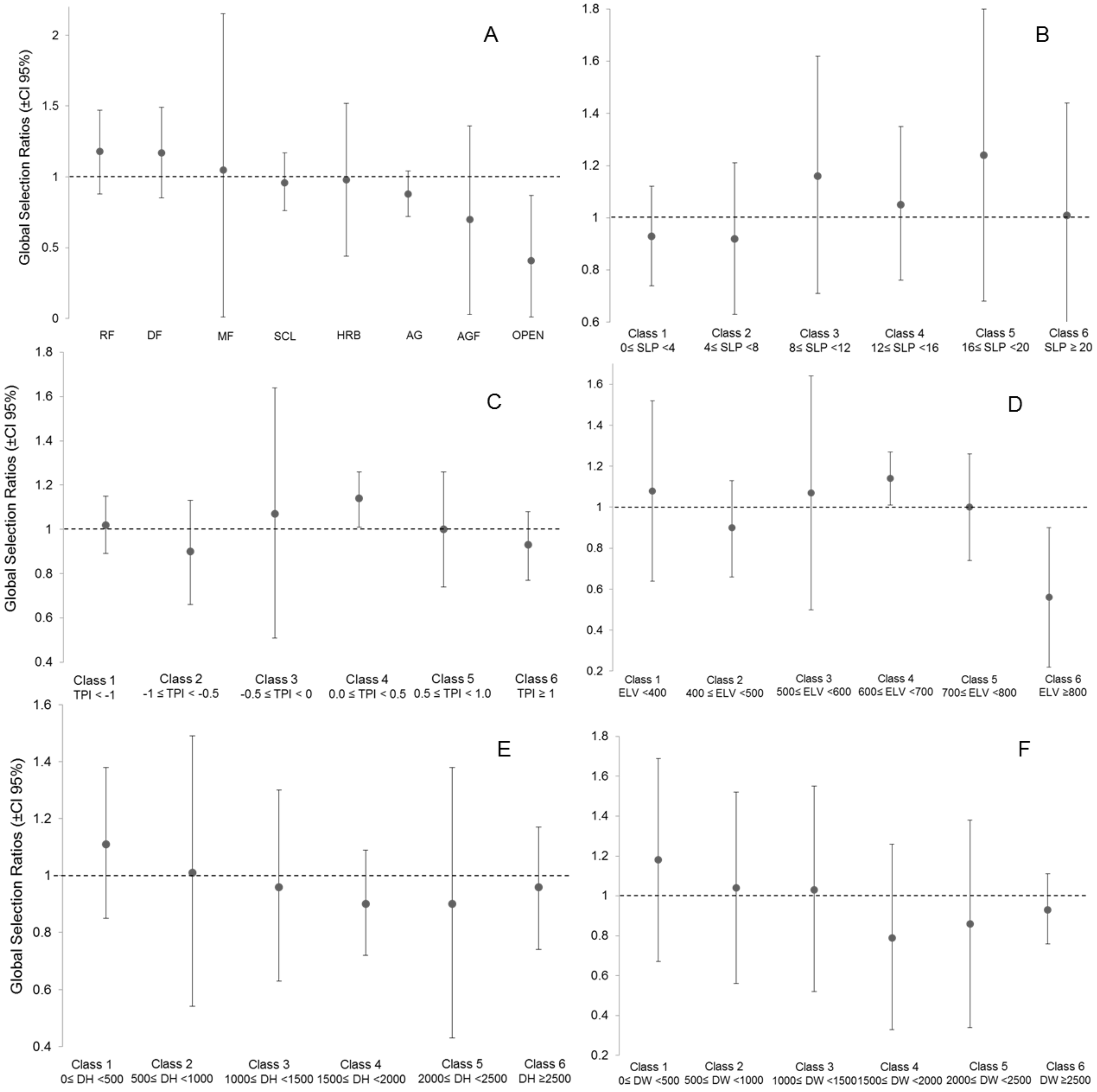

Figure 3. Selection ratios (Design III) and 95% confidence intervals for land cover type (A), slope (B, values in degrees), TPI (C), elevation (D, values in meters), distance to humanized áreas (E, values in meters) and distance to permanente water sources (F, values in meters). Dashed line represents the proportional use (Selection ratio = 1). AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; SLP- Slope; ELV- Elevation

Thirteen out of 18 individuals were considered for the analyses of altitudinal preferences, since those five animals only had available areas with elevation ranges bellow 400m and above 800m (Class 1 and 6, respectively; Figure 3D). Wildcats significantly avoided higher elevations (>800m, Class 6), and selected areas with mid-range altitude (Class 4; Figure 3D, Table S5). All remaining altitudinal classes were selected according to their availability (SR between 0.90 and 1.08).

When considering slope, wildcats presented a tendency to select steeper areas (Class 5; Figure 3B, Table S5), but it was not detected any particular selection tendency in the other classes. Regarding Topographic Position Index (TPI), the areas with higher selection indexes belong to class 4 (Figure 3C, Table S5), which is the only class selected significantly. The other classes (Figure 3C, Table S5) obtained selection ratios near 1, except for class 2, indicating that wildcats use these areas according to their availability, although no significant differences were found. A combined interpretation of the TPI and slope selection ratios suggests a general tendency of wildcats to select areas with moderate to high slopes and TPI values between 0 and 0.5, which indicates that, within home ranges, wildcats seem to prefer areas with some topographic complexity.

Regarding the selection ratios of distances to artificial areas and water sources within home ranges, only 14 and 10 individuals were used, respectively, since these areas were not presented within the other individual’s range. It is possible to see in Figures 3E-F that selection ratios are similar for both variables (check also Table S5). Wildcats seem to prefer, within home ranges, areas closer to human areas and water surfaces (< 500m). However, the obtained confidence intervals show that there is a high variability between individuals, and there is not a clear pattern in the selection or avoidance of both variables within home ranges.

Discussion

Home Range

Home range areas revealed a tendency to be larger for male than for female wildcats in the Iberian Peninsula. This pattern has been reported in other wildcat studies across Europe (France: Stahl et al., 1988; Switzerland: Liberek, 1996), and within other solitary felines (Iberian lynx (*Lynx pardinus*): Ferreras *et al.* 1997; Eurasian lynx (*Lynx lynx*): Herfindal *et al.* 2005; Bobcat (*Lynx rufus*): Litvaitis *et al.* 1986; Tucker *et al.* 2008). A higher home range area is expected for male wildcats, since it can increase their contact with females, thus maximizing reproductive success (Sandell 1989). By contrast, females tend to select areas with higher resource availability (prey availability and shelter), which can have a positive effect on the cubs' survival rate (Urra 2003; Sarmento *et al.* 2006; Monterroso *et al.* 2009). Since home range size is related to prey availability in mammalian carnivores, and females tend to select areas with higher habitat quality (sex-biased habitat matching), it is expected that they obtain smaller home ranges than males (Gittleman & Harvey 1982).

However, there was high variability in home range size even among individuals of the same gender (males: 1.22 km^2 to 43.01 km^2; females: 3.14 km^2 to 59.78 km^2). Such variability could result from different conditions within and across study areas, such as variable prey abundance, habitat quality, presence or absence of kittens, population density and also the presence/density of other potentially competing mesocarnivores (Nilsen *et al.* 2005; Powell 2012; Mattisson *et al.* 2013). If the general environment is sub-optimal, European wildcats may require larger areas to meet their daily needs, particularly their energetic requirements (Gittleman & Harvey 1982).

Habitat Selection in the Iberian Peninsula

Landscape level

Our modeling approach revealed that deciduous forests were the most important land cover type for European wildcats in the Iberian Peninsula, suggesting that it will be selected over the other land cover variables, if present. The selection for this habitat type is probably related to the fact that deciduous forests provide shelter and high prey availability (Stahl & Artois 1994; Klar *et al.* 2008), and this tendency has been reported in other wildcat studies within the Iberian Peninsula (Fernandes 1993; Urra 2003; Bárcena & Núñez 2005) and across Europe (Stahl & Artois 1994; Klar *et al.* 2008; Jerosch *et al.* 2010). This is particularly true in temperate bioclimatic region of the European wildcats distribution range, where it mainly feeds on rodents (Lozano *et al.* 2006). Scrubland areas were the second land cover type with higher odds of being selected. In Mediterranean areas, scrublands are a very common natural habitat and are closely associated with the presence of the European rabbit (*Oryctolagus cuniculus*) (Delibes-Mateos *et al.* 2008). Given the European wildcats' facultative specialization in this lagomorph (Malo *et al.* 2004; Lozano *et al.* 2006), scrublands provide a combination of vegetative cover and high prey availability, therefore they may be selected over deciduous forests, since prey availability strongly influences the European wildcats' distribution (Ferreira 2003; Monterroso *et al.* 2009; Lozano 2010; Silva *et al.* 2013a). Several studies report that scrubland areas are the most important habitat type for wildcats in the Iberian Peninsula (Ferreira 2003; Lozano *et al.* 2003;

Monterroso *et al.* 2009). However, Fernandes (1993) and Sarmento *et al.* (2006) found wildcats to prefer deciduous forests in Mediterranean environments. Nevertheless, the areas where these studies were conducted have already an influence of another biogeographic region (Atlantic) and are mountainous areas, where the density of European rabbits is low, thus it is expected that they would select deciduous forests and its edges, which have a higher availability of small mammals (Osbourne *et al.* 2005; Klar *et al.* 2008). Differences in the use of deciduous forests/scrubland areas may be related to 1) the availability of these areas at a landscape scale and/or to 2) the prey availability within each land cover type. Since we lack data on prey abundance, we could not consider its effects in our modeling approach. Regardless, both land cover types are important for wildcat's presence, but deciduous forests should be selected over scrubland areas, if both are similarly available. This study was conducted incorporating data from areas which have influence from different biogeographic regions, thus it is important to consider that the model incorporates the factors related to wildcat's presence in temperate and Mediterranean regions. European wildcats also select natural herbaceous vegetation, although with lower intensity than scrublands. Mediterranean landscapes, as well as temperate areas, are also characterized by mosaic areas, with patches of scrubland/forest vegetation and areas with natural herbaceous vegetation that can be used as resting sites and hunting areas, respectively, benefiting not only wildcat's presence (Lozano *et al.* 2003; García 2004; Klar *et al.* 2008; Monterroso *et al.* 2009) but other carnivores as well, such as the Iberian lynx (Fernández *et al.* 2003). Mixed forests are composed by similar proportions of deciduous and coniferous trees, and had positive, but lower, odds of being selected by wildcats. The presence of a given proportion of coniferous cover in this land cover type may influence these odds, since it usually provides lower prey density and a reduced cover, thus tend to be avoided by wildcats (Silva *et al.* 2013b). However, these results suggest that mixed forests may be selected if deciduous forests are absent or unavailable. Open areas, mainly characterized by patches without vegetation cover, were avoided by European wildcats. Such avoidance is probably related to the fact that, in those areas, prey density is lower, and there is higher exposure, which can reduce hunting success (Silva *et al.* 2013b). Our RSF suggests that coniferous forests alone, agricultural areas and agroforestry systems have no meaningful influence in wildcat selection at the Iberian scale. These variables estimates' suggest that the selection/avoidance of these areas varies across individuals, possibly related with local conditions, and have no strong influence in these animals' spatial patterns. Such results are coherent with studies elsewhere, which show that coniferous forests can be positively selected if not abundant and if associated with other forests types (Silva *et al.* 2013b). On the other side, larger areas of homogeneous coniferous forests, with lower vegetation and prey diversity/abundance, tend to be avoided (Silva *et al.* 2013b). Even though the overall tendency is for wildcats to avoid agricultural areas and agroforestry systems (areas used for agriculture, with the sparse tree cover), they may be used, since these areas have been shown to have a positive impact on wildcat distribution, if presented in mosaic areas with scrubland patches (Monterroso *et al.* 2009; Lozano 2010), as they provide both shelter and prey availability (Virgós *et al.* 2003; Calvete *et al.* 2004; Lombardi *et al.* 2007) Nevertheless, areas with intensive agricultural activities may be avoided (Lozano 2010).

Regarding topography, we found a positive effect of steeper slopes and negative effect of elevation for European wildcats. Areas with higher slope provide safety, with limited human access, and offer good resting sites (Ragni 1978). The importance of steep slopes for European wildcats has been reported in other studies (Lozano, 2010; Monterroso *et al.*, 2009; Pereira *et al.,* 2001 in Ferreira 2003). However, although preferring steeper slopes, European wildcats avoid high altitude areas within given range, probably because of harsher climacteric conditions and/or reduced prey availability. Other studies have reported this avoidance by wildcats (Dötterer & Bernhart 1996; Ferreira 2003; Bárcena & Núñez 2005; Silva *et al.* 2013a).

Our results show that areas mainly composed by artificial structures and with human activity are avoided by wildcats at a landscape scale. Humanized areas (including small villages and paved roads) are a source of disturbance, for they increase habitat destruction and roadkill rates (Bennett 1991; Kerr & Currie 1995; Collinge 1996). These disturbances have a negative impacts on wildcats, such as conditioning their space use or limiting reproduction success (Ferreira 2003; Klar *et al.* 2008; Piñeiro *et al.* 2012). Therefore, the inverse relation between distances to humanized areas the probability of European wildcat use in the Iberian Peninsula shown in our modeling approach is not surprising. We found a positive, but weak, relationship between the probability of wildcat use and the distance to permanent water sources, suggesting a limited effect on European wildcat distribution. The spatial distribution of water sources is a dynamic process in the dry Mediterranean environments, where many water holes and streams become increasingly dryer throughout the hotter season, until they become totally unavailable. Such dynamic system could be reflected in a dynamic use of this seasonally limiting resource, whose effects could be missed due to our dataset limitation.

All the above-discussed covariates explain 63% of variability of wildcat spatial use patterns, when accounting for the individual variance among animals (conditional R^2).

Inter-individual variability accounts for a great proportion of the models' effects, as only 25% of the variability is explained if these differences are not being considered (marginal R^2). Additionally, the fact that 37% of wildcat's spatial pattern of use remains unexplained suggests that there are other relevant factors not being considered. Prey availability is possibly the most relevant uncounted covariate in our modeling approach, as European wildcats are strongly bound to their feeding resources (Ferreira 2003; Monterroso *et al.* 2009). However, there are other factors that may influence this species distribution in the Iberian Peninsula, such as seasonality, the presence of potential competitors and/or direct human persecution (ex.: hunting, predator control).

Given that our modeling approach included data from wildcats tracked in five study areas across the Iberian Peninsula, representing its two main biogeographic regions, we expected the general global model to have a good predicting capacity. A usual method to evaluate the predictive capacity of a resource selection model is to project the model on independent datasets, and evaluating the estimated probabilities of occurrence (Klar *et al.* 2008). The projection of our general model to the independent dataset of wildcat occurrence in the Iberian Peninsula provided significantly higher relative probabilities of occurrence than those obtained on the randomly generated points. Even though that only the relative probabilities were obtained, this result suggests a good predictive ability of your general model.

Sex-biased Habitat-matching

The results of the RSFs for males and females independently showed distinct selection patterns between both genders within the set of selected environmental variables.

Females presented a strong selection of most land cover types, which suggests that spatial patterns are strongly influenced by land cover type, as they are particularly bound to deciduous forests and scrublands. Other land cover types, which are linked to high feeding resource availability (e.g. rodents and European rabbits; Brown et al., 2007; Calvete et al., 2004) and that were not clearly selected in the general model (e.g. agroforestry systems and agricultural areas), were strongly selected by females. On the other side, the most important land cover types for males were deciduous forests, however with an effect size lower than for females ($ES_{females} = 4.21$ *vs* $ES_{males} = 1.17$), and coniferous forests, agroforestry systems, open and agricultural areas were generally avoided. These results may indicate that male wildcats use mainly deciduous forests to access necessary resources, such as prey and shelter (Jerosch *et al.* 2010). Open areas are the only land cover type that is avoided by both genders, but its effect is stronger in females ($ES_{females} = 0.59$ *vs* $ES_{males} = 0.81$).The general higher odds of land cover selection by females may be related with a sex-biased habitat-matching in

European wildcats. A stronger dependence of good-quality habitats by females could be related to reproductive needs: while they require breeding sites to give birth and care for their young during weaning, female wildcats also have higher energetic requirements during pregnancy and weaning periods (Gittleman & Thompson 1988; Wade & Schneider 1992). Therefore, they require a habitat configuration that simultaneously provides protective cover (deciduous forests and scrublands; Klar et al., 2008; Stahl et al., 1988) in undisturbed places (higher distance to humanized areas and complex topography; Ragni, 1978), while maintaining access to prey (mosaic of forest/scrublands and agricultural/grassland areas, Lozano *et al.* 2003; Monterroso *et al*. 2009).

The topographic characteristics selected by male and female wildcats are similar. Both genders prefer areas with some degree of topographic complexity at mid-range altitudes. Taken together with the avoidance of close proximity to human settlements and other humanized areas, our results suggest that both sexes are affected by human disturbance, and require isolated low-disturbance areas, as suggested in the general model. Such avoidance has been reported in other species, such as the Eurasian lynx (Sunde *et al.* 1998) and cougars (*Puma concolor*) (Dickson & Beier 2002).

The differences between genders, when considering the importance of the explanatory variables, are also notorious when looking at the coefficient of determination. Although marginal values did not show a great difference between genders (Marginal R^2_{males}= 0.21 vs Marginal $R^2_{females}$= 0.29), it suggests that the selected variables may predict better the presence of females than of males. On the other side, the conditional values showed a low fit for the male's dataset and high for the female's dataset (Conditional R^2_{males}= 0.39 vs Conditional $R^2_{females}$= 0.80). This suggests that the set of the selected variables, along with the variability within each gender, has a greater influence in females' than in males' distribution.

Sex-biased habitat selection has been identified in other carnivores: jaguar (*Panthera onca*; Conde et al., 2010), cheetah (*Acinonyx jubatus;* Broomhall et al., 2004), and raccon (*Procyon lotor*; Gehrt and Fritzell, 1998), with a trend for females to select habitats based on resource distribution and males to select areas occupied by females. By analyzing differences in habitat selection between genders, not only deeper insights about populations' ecology and dynamics can be obtained, but measures regarding species management and conservation can be proposed with higher detail. These sex-biased differences in habitat use by European wildcats provide relevant information with implication for the conservation of this species in a scenario where the hybridization with its domestic counterpart is serious threat (Ramos 2014).

Home Range Level

Selection ratios at the home range level provided means to interpret how European wildcats use the space available in their cognitive map according to land cover and topographic characteristics in the Iberian Peninsula. Our results suggest that wildcats used coniferous and deciduous forests within their ranges, when present, in greater proportion than expected by chance, possibly due to shelter and prey availability. This tendency was found in other wildcat studies, although mainly for deciduous forests (Sarmento *et al.* 2006; Klar *et al.* 2008), and in other carnivore studies: bobcat (Tucker *et al*. 2008); leopard (*Panthera pardus*; Simcharoen *et al*. 2008). The positive selection of areas with coniferous cover, within home ranges, may be the result of poorer habitat quality, thus the animal would require additional areas to achieve its daily needs. Areas with reduced cover were used less than expected within their home ranges, a tendency found for other species as well (e.g. for cougar; Dickson & Beier 2002). All remaining habitats are used according to their availability, although with high inter-individual variability. Topographic and distance variables did not provide clear results about selection within home ranges, as most classes were used according to their availability, but again with high inter-individual variability.

Although these measures are not directly comparable to the results obtained with the general model, the tendency of most variables is similar between the general model and the selection indexes. This suggests that Iberian wildcats select these variables (land cover type, topographic characteristics and distances to humanized areas/permanent water sources) at a landscape level, with a less pronounced selection within home range, but with high individual variability. Influences of gender type, intra- and interspecific contact, seasonality and prey availability/abundance may also be influencing these selection ratios (Ballesteros-Duperón *et al.* 2005; Monterroso *et al.* 2009). Nevertheless, there is still a tendency to select areas with higher coverage within home ranges, and to avoid open areas. Sarmento and collaborators (2006) obtained similar results between selection indexes estimated at a landscape level and home range level, regarding land cover type.

Implications for European wildcat conservation

The results obtained in this study support a clear selection by Iberian wildcats of steeper habitats with high vegetation cover, and avoidance of open and humanized areas, at a landscape level. This study also suggests that wildcats may be selecting the considered variables (land cover type, topographic features and distance to humanized areas/ permanent water sources) preferentially at the landscape level, but further research is required to better understand these differences of selection between levels. This indicates that measures regarding management and conservation of wildcats in the Iberian Peninsula should focus on maintaining natural areas with lower human disturbances, which would also have a positive effect on reducing hybridization rates, since the contact between wild and feral/domestic forms would be expected to decrease.

This study shows a clear distinction in habitat selection by males and females, supporting a sex-biased habitat matching pattern. Another possible conservation approach would be to determine and maintain optimal areas for female wildcats, as males are more tolerant when it comes to habitat characteristics and will select areas occupied by females.

Future studies should try to include prey data and to obtain a more complete perception about sex-specific spatial ecology of Iberian wildcats, yet to be known.

References

Aarts G, Mackenzie M, Mcconnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data.*Ecography*, **31**, 140-160.

Ballesteros-Duperón E, Barea-Azcón JM, Moleón M *et al.* (2005) Preliminary results on habitat preferences of a wildcat (*Felis silvestris* Schreber, 1777) population in an area of south of Spain: influence of rabbit distribution and abundance. In: *Symposium - Biology and Conservation of the European Wildcat (Felis silvestris)*

Ballesteros-Duperón E, Virgós E, Moleón M, Barea-Azcón JM, Gil-Sánchez JM (2015) How accurate are coat traits for discriminating wild and hybrid forms of *Felis silvestris*? *Mammalia*, **79**, 101–110.

Bárcena F, Núñez IB (2005) Distribución y abundancia de gato montés (*Felis silvestris*) en el Parque Natural Os Montes do Invernadeiro (Galicia, NO de España): factores de hábitat implicados y relación con la presencia de zorro y marta. *Galemys: Boletín informativo de la Sociedad Española para la conservación y estudio de los mamíferos*, **17**, 29–40.

Barton K (2016) MuMIn: Multi-model inference. R package version 1.10. 0. 2014.

Bates D, Maechler M, Bolker B *et al.* (2016) Package “lme4.”

Bennett AF (1991) Roads, roadsides and wildlife conservation: a review. *Nature conservation 2: the role of corridors*.

Benson JF, Mills KJ, Patterson BR (2015) Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation*, **182**, 223–

232.

Boitani L, Powell RA (2012) *Carnivore ecology and conservation: a handbook of techniques*. Oxford University Press.

Bolker BM, Brooks ME, Clark CJ *et al.* (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127–135.

Börger L, Franconi N, De Michele G *et al.* (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.

Bouyer Y, Gervasi V, Poncin P *et al.* (2015) Tolerance to anthropogenic disturbance by a large carnivore: the case of Eurasian lynx in south-eastern Norway. *Animal Conservation*, **18**, 271–278.

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecological modelling*, **157**, 281–300.

Broomhall LS, Mills MGL, Du Toit JT (2004) Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *Journal of Zoology*, **261**, 119–128.

Brown PR, Huth NI, Banks PB, Singleton GR (2007) Relationship between abundance of rodents and damage to agricultural crops. *Agriculture, ecosystems & environment*, **120**, 405–415.

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed)*.

Cabral MJ, Almeida J, Almeida PR *et al.* (2005) Livro vermelho dos vertebrados de Portugal. Instituto de Conservação da Natureza. Lisboa. 659p.

Calenge C (2011) Analysis of habitat selection by animals. adehabitatHS Package for R. *Version 0.3*.

Calvete C, Estrada R, Angulo E, Cabezas-Ruiz S (2004) Habitat factors related to wild rabbit conservation in an agricultural landscape. *Landscape Ecology*, **19**, 531–542.

Cassini MH (2011) Ecological principles of species distribution models: the habitat matching rule. *Journal of Biogeography*, **38**, 2057–2065.

Chetkiewicz CLB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology*, **46**, 1036–1047.

Collinge SK (1996) Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape and urban planning*, **36**, 59–77.

Conde DA, Colchero F, Zarza H *et al.* (2010) Sex matters: Modeling male and female habitat differences for jaguar conservation. *Biological Conservation*, **143**, 1980–1988.

Crook JH, Ellis JE, Goss-Custard JD (1976) Mammalian social systems: structure and function. *Animal Behaviour*, **24**, 261–274.

Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in the conservation of the western Mediterranean Basin hotspot. *Conservation Biology*, **22**, 1106–1117.

Dickson BG, Beier P (2002) Home-range and habitat selection by adult cougars in southern California. *The Journal of Wildlife Management*, 1235–1245.

Dillon A, Kelly MJ (2008) Ocelot home range, overlap and density: Comparing radio telemetry with camera trapping. *Journal of Zoology*, **275**, 391–398.

Dötterer M, Bernhart F (1996) The occurance of wildcats in the southern Swiss Jura Mountains. *Acta Theriologica*, **41**, 205–209.

Fernandes ML (1993) Some aspects of the ecology and systematics of the wildcat (*Felis silvestris*) in Portugal. In: *Seminar on the biology and conservation of the wildcat (*Felis silvestris*)*, pp. 89–93.

Fernández N, Delibes M, Palomares F, Mladenoff DJ (2003) Identifying breeding habitat for the Iberian lynx: inferences from a fine-scale spatial analysis. *Ecological Applications*, **13**, 1310–1324.

Ferreira JPSM (2003) Análise dos factores condicionantes na distribuição de gato-bravo (*Felis silvestris*) no sitio Moura-Barrancos. Msc Thesis, University of Évora, Portugal

Ferreras P, Beltran JF, Aldama JJ, Delibes M, Aldama JJ (1997) Spatial organization and land tenure system of the endangered Iberian lynx. *Journal of Zoology*, **243**, 163–189.

García FJ (2004) El gato montés *Felis silvestris* Schreber, 1775. *Galemys: Boletín informativo de la Sociedad Española para la conservación y estudio de los mamíferos*, **16**, 1–14.

Gehrt SD, Fritzell EK (1998) Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. *Animal behaviour*, **55**, 1211–1227.

Gillies CS, Hebblewhite M, Nielsen SE *et al.* (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887–898.

Gil-Sánchez JM, Jaramillo J, Barea-Azcón JM (2015) Strong spatial segregation between wildcats and domestic cats may explain low hybridization rates on the Iberian Peninsula. *Zoology*, **118**, 377–385.

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, **10**, 57–63.

Gittleman JL, Thompson SD (1988) Energy allocation in mammalian reproduction.

American zoologist, **28**, 863–875.

Hartmann S a., Steyer K, Kraus RHS, Segelbacher G, Nowak C (2013) Potential barriers to gene flow in the endangered European wildcat (*Felis silvestris*). *Conservation Genetics*, **14**, 413–426.

Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoologie, London*, **265**, 63–71.

Hinton JW, Van Manen FT, Chamberlain MJ (2015) Space use and habitat selection by resident and transient coyotes (*Canis latrans*). *PLoS ONE*, **10**, 1–17.

Hosmer DW, Lemeshow S (2000) Introduction to the logistic regression model. *Applied Logistic Regression, Second Edition*, 1–30.

Jędrzejewski W, Schmidt K, Okarma H, Kowalczyk R (2002) Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). *Annales Zoologici Fennici*, **39**, 29–41.

Jerosch S, Götz M, Klar N, Roth M (2010) Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): Implications for its conservation. *Journal for Nature Conservation*, **18**, 45–54.

Kenward RE (2000) *A manual for wildlife radio tagging*. Academic Press.

Kerr JT, Currie DJ (1995) Effects of human activity on global extinction risk. *Conservation Biology*, **9**, 1528–1538.

Kie JG (2013) A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry*, **1**, 13.

Klar N, Fernández N, Kramer-Schadt S *et al.* (2008) Habitat selection models for European wildcat conservation. *Biological Conservation*, **141**, 308–319.

Klar N, Herrmann M, Henning-Hahn M *et al.* (2012) Between ecological theory and planning practice: (Re-) Connecting forest patches for the wildcat in Lower Saxony, Germany. *Landscape and Urban Planning*, **105**, 376–384.

Koper N, Manseau M (2012) A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models. *Rangifer*, **32**, 195–204.

Lele SR, Merrill EH, Keim J, Boyce MS (2013) Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology*, **82**, 1183–1191.

Liberek M (1996) Radiotracking the wildcat in Switzerland. *Cat News*, **25**, 18–19.

Litvaitis JA, Sherburne JA, Bissonette JA (1986) Bobcat habitat use and home range size in relation to prey density. *The Journal of Wildlife Management*, 110–117.

Lombardi L, Fernández N, Moreno S (2007) Habitat use and spatial behaviour in the

European rabbit in three Mediterranean environments. *Basic and Applied Ecology*, **8**, 453–463.

López-Martín JM, García FJ, Such A *et al.* (2007) *Felis silvestris. in: Atlas y libro rojo de los mamíferos terrestres de España*. Organismo autónomo parques nacionales.

Lozano J (2010) Habitat use by European wildcats (*Felis silvestris*) in central Spain : what is the relative importance of forest variables ? *Animal Biodiversity and Conservation*, **2**, 143–150.

Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: Factors affecting the trophic diversity. *Journal of Biogeography*, **33**, 1076–1085.

Lozano J, Virgós E, Malo AF, Huertas DL, Casanovas JG (2003) Importance of scrub – pastureland mosaics for wild- living cats occurrence in a Mediterranean area : implications for the conservation of the wildcat (*Felis silvestris*). *Biodiversity and Conservation Conservation*, **12**, 921–935.

Malo AF, Lozano J, Huertas DL, Virgós E (2004) A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? *Journal of Zoology*, **263**, 401–407.

Manly BFJ, McDonald LL, Thomas DL (2002) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. *Kluwer Academic Publishers*, xiii + 177.

Mattisson J, Sand H, Wabakken P *et al.* (2013) Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia*, **173**, 813–825.

Mazerolle MJ, Mazerolle MMJ (2016) Package “AICcmodavg.”

Monterroso P, Brito JC, Ferreras P, Alves PC (2009) Spatial ecology of the European wildcat in a Mediterranean ecosystem: Dealing with small radio-tracking datasets in species conservation. *Journal of Zoology*, **279**, 27–35.

Monterroso P, Rich LN, Serronha A, Ferreras P, Alves PC (2014) Efficiency of hair snares and camera traps to survey mesocarnivore populations. *European journal of wildlife research*, **60**, 279–289.

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

Nilsen EB, Herfindal I, Linnell JDC (2005) Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience*, **12**, 68–75.

Norbury GL, Norbury DC, Heyward RP (1998) Behavioral responses of two predator species to sudden declines in primary prey. *The Journal of wildlife management*, **62**, 45–58.

Northrup JM, Hooten MB, Anderson CR, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, **94**, 1456–1463.

Nowell K, Jackson P (1996) *Wild cats: status survey and conservation action plan*. IUCN Gland.

Nussberger B, Wandeler P, Camenisch G (2014) A SNP chip to detect introgression in wildcats allows accurate genotyping of single hairs. *European journal of wildlife research*, **60**, 405–410.

Oliveira R, Godinho R, Randi E, Alves PC (2008) Hybridization versus conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian Peninsula? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **363**, 2953–61.

Osbourne JD, Anderson JT, Spurgeon AB (2005) Effects of habitat on small-mammal diversity and abundance in West Virginia. *Wildlife Society Bulletin*, **33**, 814–822.

Palomo LJ, Gisbert J (2002) Atlas de mamíferos terrestres de España.[Spain mammals' atlas] Dirección general de conservación de la Naturaleza-SECEM-SECEMU. 564pp.

Pereira I, Ferreira JP, Grilo C, Santos-Reis M (2001) Estudos de Biologia e Ecologia de Mamíferos, bloco m) *Felis silvestris*. Programa de monitorização e Compensação das albufeiras de Alqueva e Pedrogão. Relatório Final, 96 pp.

Piñeiro A, Barja I, Silván G, Illera JC (2012) Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. *Wildlife Research*, **39**, 532–539.

Powell RA (2012) Movements, home ranges, activity, and dispersal. *Carnivore ecology and conservation: a handbook of techniques (L. Boitani and RA Powell, eds.). Oxford University Press, London, United Kingdom*, 188–217.

Powell R a., Boitani L, Fuller T (2000) Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, 65–110.

Pulliam HR, Caraco T (1984) Living in groups: is there an optimal group size. *Behavioural ecology: an evolutionary approach*, **2**, 122–147.

Quantum GIS (2013) Development Team, 2012. Quantum GIS geographic information system. Open source geospatial foundation project. *Free Software Foundation, India*.

Ragni B (1978) Observations on the ecology and behaviour of the wild cat (*Felis silvestris* Schreber, 1777) in Italy. *Carniv. Genet. Newsl*, **3**, 270–274.

Ramos L (2014) Assessing hybridization between wildcat and domestic cat: the particular case of Iberian Peninsula and some insights into North Africa. MSc Thesis, University of Porto, Portugal.

Sandell M (1989) The mating tactics and spacing patterns of solitary carnivores. In: *Carnivore behavior, ecology, and evolution*, pp. 164–182. Springer.

Sarmento P, Cruz J, Tarroso P, Fonseca C (2006) Space and Habitat Selection by Female European Wild Cats (*Felis silvestris silvestris*). *Wildlife Biology in Practice*, **2**, 79–89.

Schauenberg P (1981) Éléments d'écologie du chat forestier d'Europe *Felis silvestris* Schreber, 1777.

Seaman DE, Millspaugh JJ, Kernohan BJ *et al.* (1999) Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*, **63**, 739–747.

Signer J, Balkenhol N (2015) Reproducible home ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin*, **39**, 358–363.

Silva AP, Kilshaw K, Johnson PJ, Macdonald DW, Rosalino LM (2013a) Wildcat occurrence in Scotland: food really matters. *Diversity and Distributions*, **19**, 232–243.

Silva AP, Rosalino LM, Johnson PJ *et al.* (2013b) Local-level determinants of wildcat occupancy in Northeast Scotland. *European Journal of Wildlife Research*, **59**, 449–453.

Simcharoen S, Barlow ACD, Simcharoen A, Smith JLD (2008) Home range size and daytime habitat selection of leopards in Huai Kha Khaeng Wildlife Sanctuary, Thailand. *Biological Conservation*, **141**, 2242–2250.

Stahl P, Artois M (1994) Status and conservation of the wildcat *(Felis silvestris)* in Europe and around the Mediterranean rim. Council of Europe.

Stahl P, Artois M, Aubert MFA (1988) Organisation spatiale et déplacements des chats forestiers adultes (*Felis silvestris*, Schreber, 1777) en Lorraine. *Revue d'Ecologie*, **43**, 113–132.

Sullivan GM, Feinn R (2012) Using Effect Size - or Why the P Value Is Not Enough. *Journal of graduate medical education*, **4**, 279–82.

Sunde P, Stener SO, Kvam T (1998) Tolerance to humans of resting lynxes *Lynx lynx* in a hunted population. *Wildlife Biology*, **4**, 177–183.

Team RC (2013) R: A language and environment for statistical computing.

Thomas DL, Taylor EJ (2006) Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management*, **70**, 324–336.

Tucker SA, Clark WR, Gosselink TE (2008) Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. *The Journal of Wildlife Management*, **72**, 1114–1124.

Urra F (2003) El gato montés en Navarra distribución, ecología y conservación. PhD Thesis, Universidad Autonoma de Madrid, Spain. Universidad Autónoma de Madrid.

Virgós E, Cabezas-Díaz S, Malo A, Lozano J, López-Huertas D (2003) Factors shaping European rabbit abundance. *Acta Theriologica*, **48**, 113–122.

Wade GN, Schneider JE (1992) Metabolic fuels and reproduction in female mammals. *Neuroscience & Biobehavioral Reviews*, **16**, 235–272.

Yamaguchi N, Kitchener A, Driscoll C, Nussberger B (2015) *Felis silvestris*. *The IUCN Red List of Threatened Species 2015*, **8235**, e.T60354712A50652361.

Part 3. Concluding Remarks and Future Directions

Concluding Remarks

The present study provides relevant information about the spatial ecology of wildcats in the Iberian Peninsula that was largely unexplored. Although the use of a small dataset limited the possible analyses, the work developed in this thesis allowed to draw the following main conclusions:

1) Wildcat's home range areas followed the common patterns of carnivores, with larger areas for males than for females. The high variability in home range size obtained for both genders suggests that local differences drive the geographical space use by this felid.

2) The selection of the considered covariates is likely to occur at the landscape scale, with a less selective habitat use pattern within home ranges. However, there is a high inter-individual variability, which suggests that individual preferences are important at a finer scale. Although there are covariates not considered in the analyses, this study shows that wildcat conservation in the Iberian Peninsula is closely dependent on the preservation of patches with natural vegetation that can offer both cover and prey availability, located in areas with topographic complexity, and low human disturbance.

3) This study demonstrates clear sex-biased habitat selection by wildcats in the Iberian Peninsula, probably related with the energetic requirements and reproduction areas, which are mandatory for females. On the other side, males proved to be less influenced by the environmental covariates, suggesting a higher tolerance to lower habitat quality and a possible selection of areas that maximize contact with females. Although they generally avoided humanized areas, a lower female density in a given area associated with a tolerance towards habitat quality may lead to the increasing of hybridization rates, which are already preoccupying in the Iberian Peninsula.

Future Directions

Elusive species, such as the European wildcat, present a challenge to wildlife conservation research, and several topics about the biology of these species are unexplored due to the limited access to ecological data. Obtaining information on space use is a crucial step to develop solid conservation measures. Information regarding wildcat's space use within the Iberian Peninsula is scattered, limited to small areas and conducted under different methodologies, which limits their utility when trying to understand general patterns across this area. By incorporating data from several study areas in a single and unifying modeling analysis, this thesis takes a step in that direction, but there are questions that remain unanswered. Future studies should focus on:

1) Understanding how wildcats shape their home ranges and core areas within the Iberian Peninsula, by considering factors such as seasonality, animals' age and presence of competitors.

2) Developing mixed resource selection models considering interactions between two fixed effects and the use of random slopes (e.g. Benson et al., 2015; Godvik et al., 2009). For instance, interactions between different land cover types and/or prey type/availability/abundance would allow understanding if there are habitat characteristics used simultaneously and how the selection of a given land cover type is related with prey availability. Random slopes represent the interaction between a given fixed effect and a random effect (Johnson 2014), so the use of these approaches allows one to test more complex hypotheses, providing deeper insights into the factors that influence habitat selection, including individual variations.

3) Performing comparative multi-level and multi-scale studies between areas with confirmed hybridization and areas with no occurrences, considering the available resources, population density, and interspecific competition, among others, in order to understand which features lead to an increased contact between wild/feral/domestic forms.

4) Gathering data that can allow exploring additional factors regarding wildcat distribution and space use in the Iberian Peninsula, especially populations' features and inter-specific relationships. Telemetry studies are appropriate to address questions regarding resource use, and should be conducted especially in areas where space use hasn't been addressed. At the same time, obtaining data regarding prey availability/abundance that can be successfully incorporated in these studies is of major importance. A genetic monitoring of populations is also crucial to understand the population's tendency regarding hybridization rates. This information can be further incorporated in management strategies to conserve wildcat populations in the Iberian Peninsula.

References

Benson JF, Mahoney PJ, Patterson BR (2015) Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape. *Oikos*, **124**, 1664–1673.

Godvik IMR, Loe LE, Vik JO *et al.* (2009) Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, **90**, 699–710.

Johnson PCD (2014) Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes models. *Methods in Ecology and Evolution*, **5**, 944–946.

Supplementary Material

Table S1. Overview of the available telemetry data obtained for each study area. Individuals marked with (*) were considered for home range estimation; if marked with (**), a reliable home range estimate was achieved.

Study Area	**Gender**	**ID**	**Sampling Period**		**Number of locations**	**OBS**
			Beginning	**End**		
Izagaondoa (Navarre, SP)	F	NAF01**	27-09-1996	23-07-1998	786	
	F	NAF02**	30-01-1997	12-03-1998	403	
	M	NAM01**	01-02-1997	28-04-1998	173	
	M	NAM02**	30-01-1998	16-11-1998	346	
	M	NAM03**	18-06-1997	17-10-1997	118	
Overview					**1826**	
Lleida (Catalonia, SP)	F	CTF01**	13-04-1999	11-04-2000	128	
	F	CTF02	26-06-1999	-	1	Capture
	F	CTF03	02-09-2000	-	1	Capture
	M	CTM01**	11-07-1999	25-05-2000	92	
	M	CTM02**	13-08-1999	11-09-1999	39	
	M	CTM03**	05-08-2000	30-06-2000	38	
	M	CTM04	03-06-2000	20-07-2000	9	
	M	CTM05**	05-07-1999	30-06-2000	121	
	M	CTM06**	07-06-1999	04-10-2000	143	
Overview					**572**	
Sierra Arana (Andalusia, SP)	M	GRM01*	20-03-2003	23-08-2004	23	
	M	GRM02**	26-03-2003	26-01-2004	36	
	F	GRF01**	25-06-2003	01-05-2004	61	
	F	GRF02	14-05-2003	15-06-2003	9	
	F	GRF03	25-12-2003	30-09-2004	6	
	F	GRF04	03-08-2004	13-09-2004	4	
Overview					**139**	
GVNP (Southeastern PT)	F	GVF01**	22-07-2004	21-12-2004	38	
	F	GVF02*	11-08-2004	18-03-2005	90	
	F	GVF03**	13-07-2004	15-03-2005	68	
	F	GVF04*	05-08-2004	07-09-2004	17	
	M	GVM01**	16-08-2004	20-04-2005	73	
	M	GVM02*	29-07-2004	15-11-2004	21	
Overview					**307**	
CNP (Castille-La Mancha, SP)	M	CBM01**	27-03-2014	10-12-2014	40	
	M	CBM02	25-05-2014	-	1	Capture
	M	CBM03	11-06-2014	-	1	Capture
	F	CBF01**	28-03-2014	06-06-2014	88*	Includes GPS data
	F	CBF02	27-11-2014	30-11-2014	2	Capture
Overview					**132**	
TOTAL					**2976**	

Table S2. Overview of the additional wildcat data provided (Total number of registers – 127). Regarding camera trapping records, values between braces represent the number of camera traps in each area, while the number of registers represents the number of camera traps with at least one record of wildcat. NP- National park, NtP- Natural Park, NR- Natural Reserve

Data Type	Number of registers	Sampling Year	Country	Autonomous Community	Location	Protected Area
Camera-trapping Records	8 (44)	2007-2010	Spain	Castille-La Mancha		Cabañeros NP
	18 (39)	2009-2010	Portugal	-		Guadiana Valley NP
	10 (44)	2010-2011	Spain	Asturias		Muniellos NR
	5 (36)	2010-2011	Portugal	-		Peneda-Geres NP
	1 (20)	2012	Spain	Jaén		Sierra de Andújar NtP
	12 (16)	2013-2014	Spain	Andaluzia	Sierra Arana	
Hair	7	2004-2008	Spain	Basque Country	Alava/Vitoria/North Burgos	
	5	-	Spain	Castile León	Palencia/Valladolid/León	
	7	2011	Spain	Castille-La Mancha		
Skin/ Skin-Hair	5	2012-2014	Spain	Castile León	Palencia/Valladolid/León	
Scats	5	2014	Spain	Valencia	Albaida Valley	
	2	2014	Spain	Catalonia	Tarragona	
	32	2010-2011	Spain	Asturias		Muniellos NR
	6	2010-2011	Portugal	-		Peneda-Geres NP
	4	2009-2010	Portugal	-		Guadiana Valley NP

Table S3. Proportions (%) of each land cover tipe for each delimited study area, as well as range of topographic variables (Slope, Elevation, TPI). CNP- Cabañeros National Park; GVNP- Guadiana Valley Natural Park.

	CNP	**GVNP**	**Lleida**	**Izagaondoa**	**Sierra Arana**
AG	7.80	35.57	50.14	41.45	16.41
AGF	0.00	3.33	0.00	0.00	7.28
DF	20.51	3.81	17.02	10.11	6.15
CF	0.45	0.00	10.74	19.14	16.99
MF	0.90	1.02	0.10	2.13	5.01
SCL	33.56	46.99	18.87	20.25	34.45
HRB	36.64	7.06	0.55	2.18	8.92
OPEN	0.07	0.17	0.17	0.43	4.25
Total Area (km^2)	122.58	134.62	256.16	391.99	209.46
DH (m)	[0.00 - 9996.60]	[0.00 - 4222.32]	[0.00 - 5415.99]	[0.00 - 3870.86]	[0.00 - 7397.31]
DW (m)	[0.00 - 11105.71]	[0.00 - 4645.99]	[0.00 - 10362.61]	[0.00 - 9687.10]	[0.00 - 11863.47]
SLOPE (degrees)	[0.01 - 22.41]	[0.02 - 23.99]	[0.00 - 34.95]	[0.03 - 39.97]	[0.03 - 45.21]
ELEVATION (m)	[598.64 - 1049.65]	[13.83 - 331.17]	[289.36 - 757.07]	[419.03 - 1262.01]	[719.83 - 1976.07]
TPI	[-1.41 - 1.45]	[-1.40 - 1.57]	[-1.91 - 2.12]	[-1.75 - 1.86]	[-2.58 - 5.14]

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index

Table S4. Spearman rank correlation results between covariates.

	AG	**AGF**	**DF**	**CF**	**MF**	**SCL**	**HRB**	**OPEN**	**DH**	**DW**	**TPI**	**RGN**	**SLP**	**ELV**
AG	*****	-0.083	-0.308	-0.418	-0.142	-0.418	-0.182	-0.053	-0.327	-0.003	-0.098	-0.499	-0.511	-0.298
AGF	<0.001	*****	-0.020	-0.040	0.001	-0.042	-0.008	0.002	0.086	0.015	-0.001	-0.007	-0.013	0.060
DF	<0.001	0.001	*****	-0.116	-0.003	-0.155	-0.082	-0.044	0.151	-0.019	0.088	0.300	0.303	0.159
CF	<0.001	<0.001	<0.001	*****	-0.021	-0.232	-0.092	-0.023	0.032	0.100	0.057	0.347	0.369	0.248
MF	<0.001	0.853	0.549	<0.001	*****	-0.078	-0.028	-0.017	0.084	0.048	0.020	0.099	0.098	0.125
SCL	<0.001	<0.001	<0.001	<0.001	<0.001	*****	-0.105	-0.027	0.134	-0.068	0.028	0.105	0.104	-0.036
HRB	<0.001	0.15	<0.001	<0.001	<0.001	<0.001	*****	0.017	0.253	0.006	-0.006	-0.07	-0.082	0.033
OPEN	<0.001	0.769	<0.001	<0.001	0.004	<0.001	0.004	*****	0.078	0.000	0.056	0.084	0.072	0.175
DH	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****	0.294	0.029	0.152	0.142	0.374
DW	0.564	0.011	0.001	<0.001	<0.001	<0.001	0.273	0.943	<0.001	*****	0.001	0.04	0.041	0.340
TPI	<0.001	0.899	<0.001	<0.001	0.001	<0.001	0.337	<0.001	<0.001	0.896	*****	0.058	0.063	0.101
RGN	<0.001	0.227	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****	0.981	0.457
SLP	<0.001	0.028	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****	0.458
ELV	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; RGN- Roughness; SLP- Slope; ELV- Elevation

Table S5. Selection ratios (Wi) for wildcats in the Iberian Peninsula, considering design III. Standard error (SE) is presented, as well as the 95% confidence interval (IClower and ICupper).

Variable	**Class**	**Wi**	**SE**	**IClower**	**ICupper**
AG		0.88	0.06	0.72	1.04
AGF		0.70	0.24	0.03	1.36
DF		1.17	0.12	0.85	1.49
CF		1.18	0.11	0.88	1.47
MF		1.05	0.40	0.00	2.15
SCL		0.96	0.08	0.76	1.17
HRB		0.98	0.20	0.44	1.52
OPEN		0.41	0.17	0.00	0.87
TPI	TPI < -1	1.02	0.05	0.89	1.15
	-1 ≤ TPI < -0.5	0.90	0.09	0.66	1.13
	-0.5 ≤ TPI < 0	1.07	0.21	0.51	1.64
	0.0 ≤ TPI < 0.5	1.14	0.05	1.01	1.26
	0.5 ≤ TPI < 1.0	1.00	0.09	0.74	1.26
	TPI ≥ 1	0.93	0.06	0.77	1.08
Slope	0 ≤ SLP < 4	0.93	0.07	0.74	1.12
	4 ≤ SLP < 8	0.92	0.11	0.63	1.21
	8 ≤ SLP < 12	1.16	0.17	0.71	1.62
	12 ≤ SLP < 16	1.05	0.11	0.76	1.35
	16 ≤ SLP < 20	1.24	0.21	0.68	1.80
	SLP ≥ 20	1.01	0.16	0.59	1.44
Elevation	ELV < 400	1.08	0.17	0.64	1.52
	400 ≤ ELV < 500	0.90	0.09	0.66	1.13
	500 ≤ ELV < 600	1.07	0.22	0.50	1.64
	600 ≤ ELV < 700	1.14	0.05	1.01	1.27
	700 ≤ ELV < 800	1.00	0.10	0.74	1.26
	ELV ≥ 800	0.56	0.13	0.22	0.90
DH	0 ≤ DH < 500	1.11	0.10	0.85	1.38
	500 ≤ DH < 1000	1.01	0.18	0.54	1.49
	1000 ≤ DH < 1500	0.96	0.13	0.63	1.30
	1500 ≤ DH < 2000	0.90	0.07	0.72	1.09
	2000 ≤ DH < 2500	0.90	0.18	0.43	1.38
	DH ≥ 2500	0.96	0.08	0.74	1.17
DW	0 ≤ DW < 500	1.18	0.19	0.67	1.69
	500 ≤ DW < 1000	1.04	0.18	0.56	1.52
	1000 ≤ DW < 1500	1.03	0.20	0.52	1.55
	1500 ≤ DW < 2000	0.79	0.18	0.33	1.26
	2000 ≤ DW < 2500	0.86	0.20	0.34	1.38
	DW ≥ 2500	0.93	0.07	0.76	1.11

AG- Agricultural areas; AGF- Agroforestry systems; DF- Deciduous forests; CF- Coniferous forests; MF- Mixed forests; SCL- Scrubland areas; HRB- Natural herbaceous vegetation; OPEN- Open areas; DH- Distance to humanized areas; DW- Distance to permanent water sources; TPI- Topographic position index; SLP- Slope; ELV- Elevation

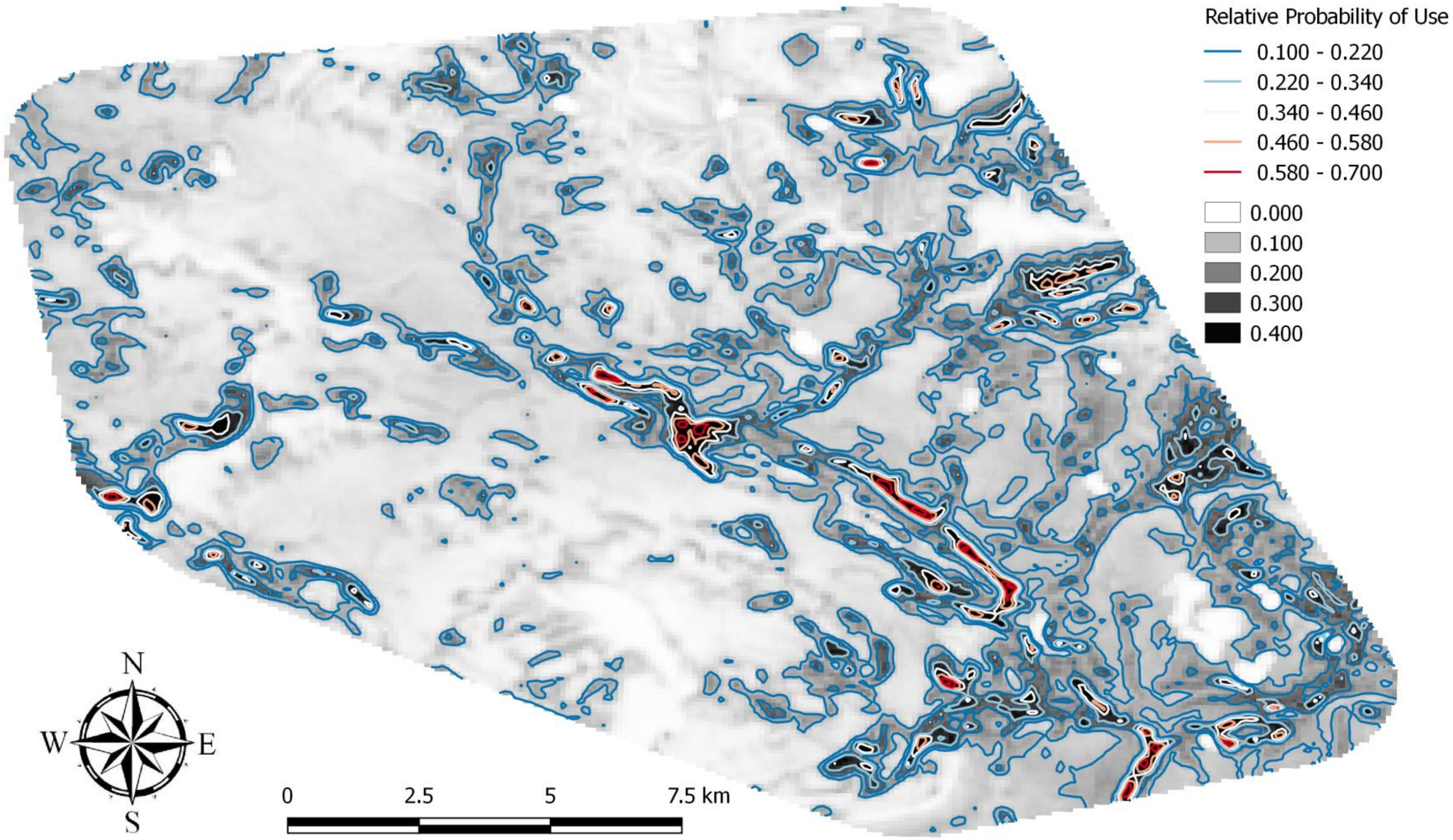

Figure S1. Relative probability of use in the study area of Izagaondoa Valley (Navarre, SP), predicted using the coefficients from the general generalized mixed model (Table 4, Part 2). Pixel size: 100x100m

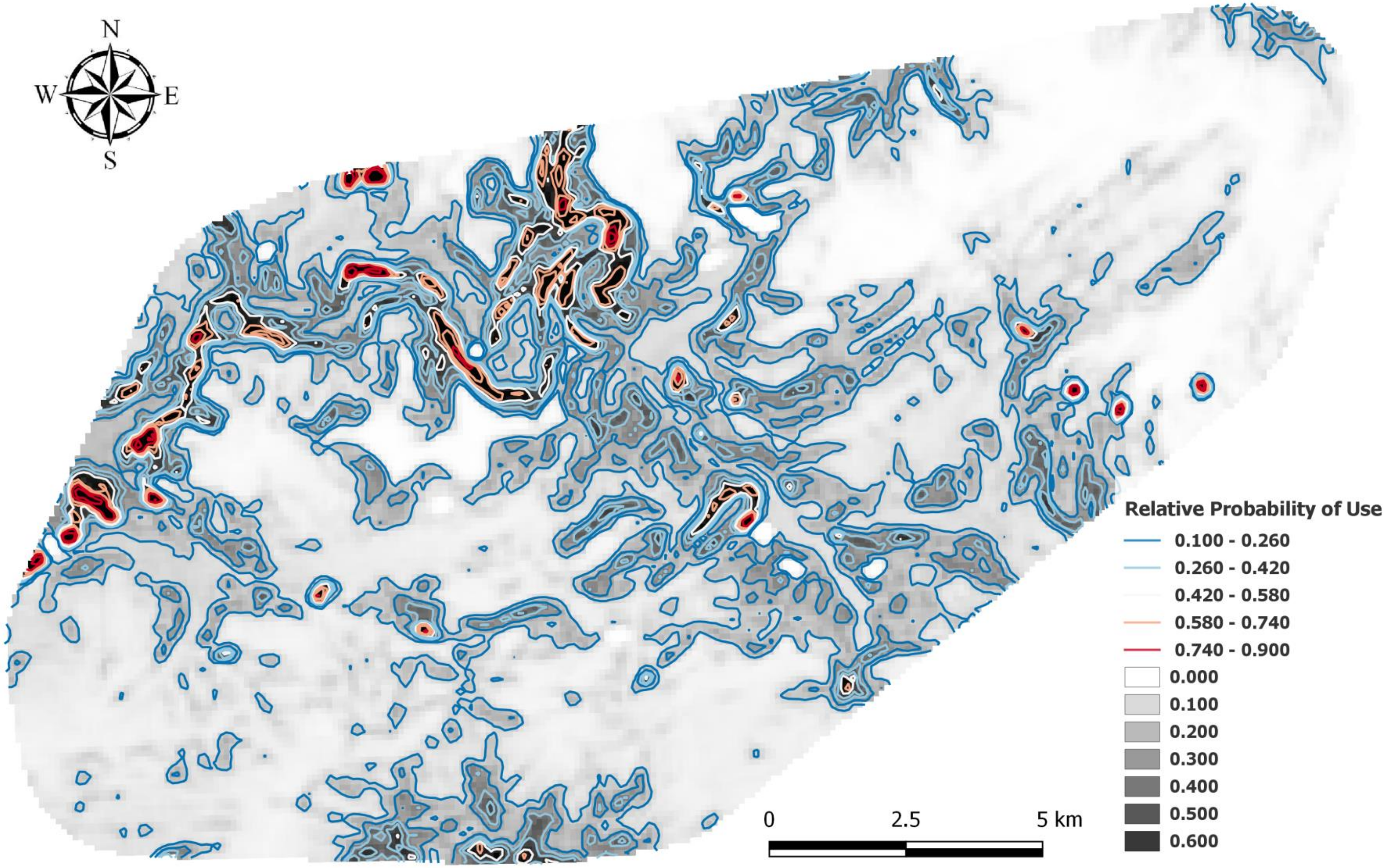

Figure S2. Relative probability of use in the study area of Lleida (Catalonia, SP), predicted using the coefficients from the general generalized mixed model (Table 4, Part 2). Pixel size: 100x100m

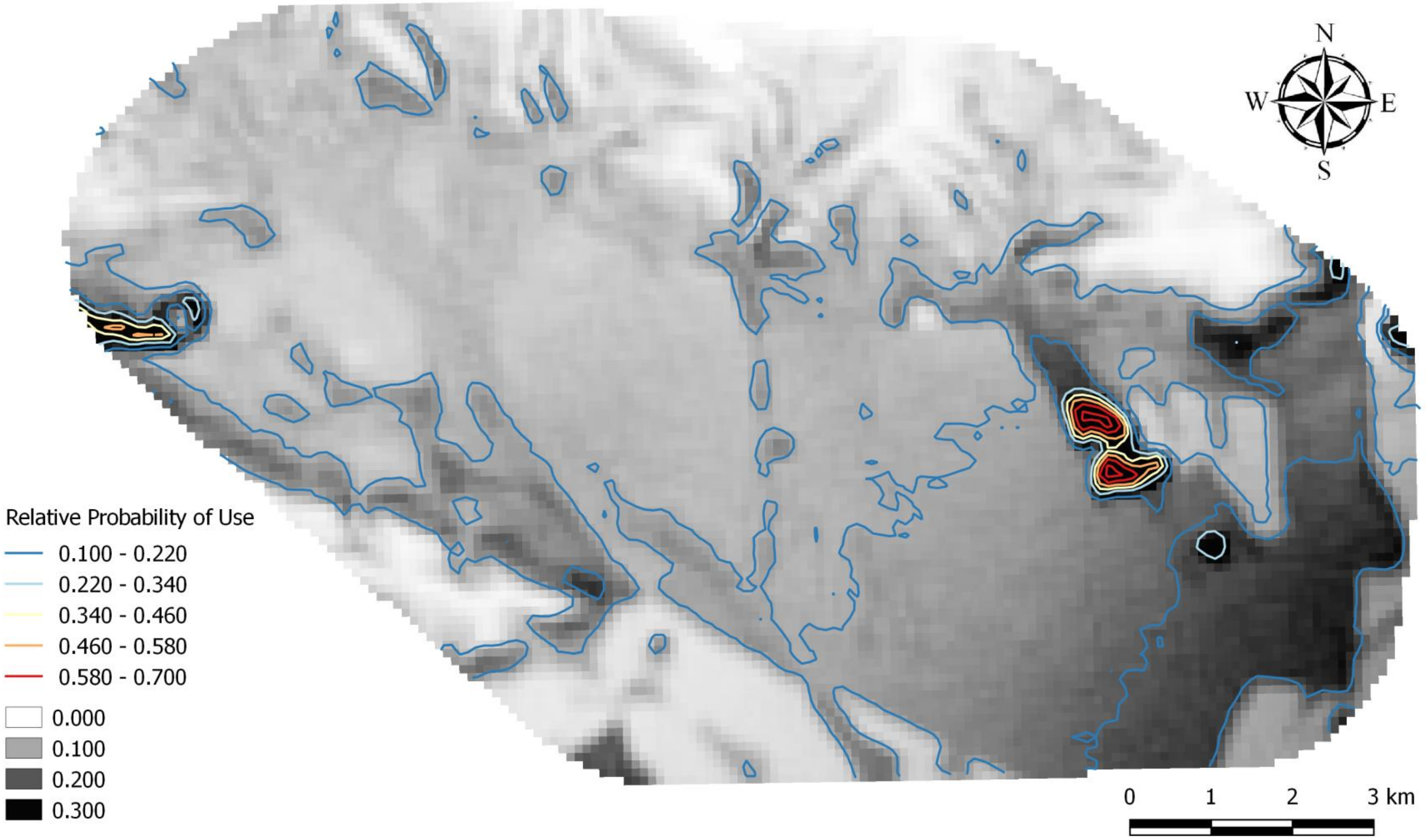

Figure S3. Relative probability of use in the study area of Cabañeros National park (Castille La-mancha, SP), predicted using the coefficients from the general generalized mixed model (Table 4, Part 2). Pixel size: 100x100m

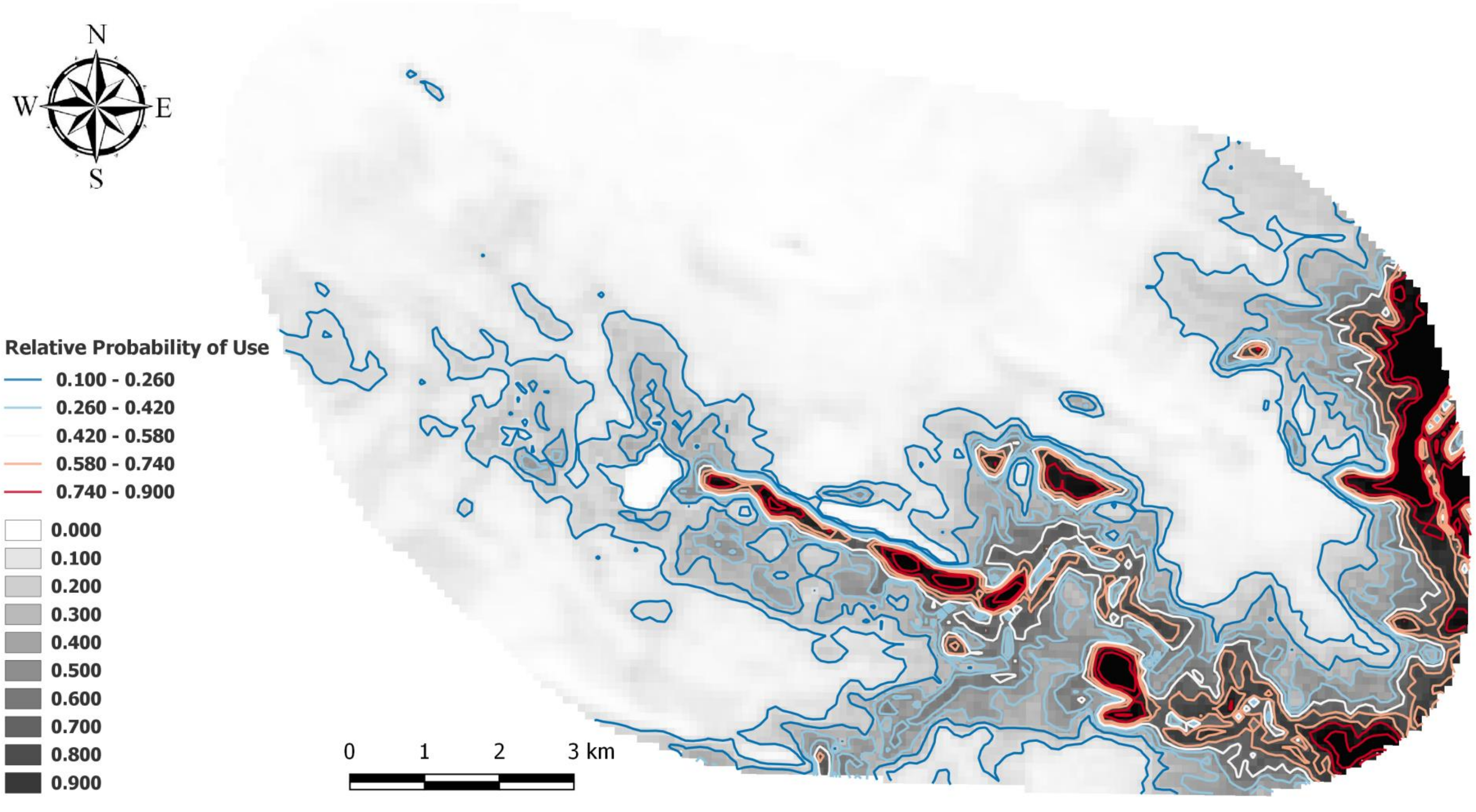

Figure S4. Relative probability of use in the study area of Guadiana Valley Natural Park (PT), predicted using the coefficients from the general generalized mixed model (Table 4, Part 2). Pixel size: 100x100m

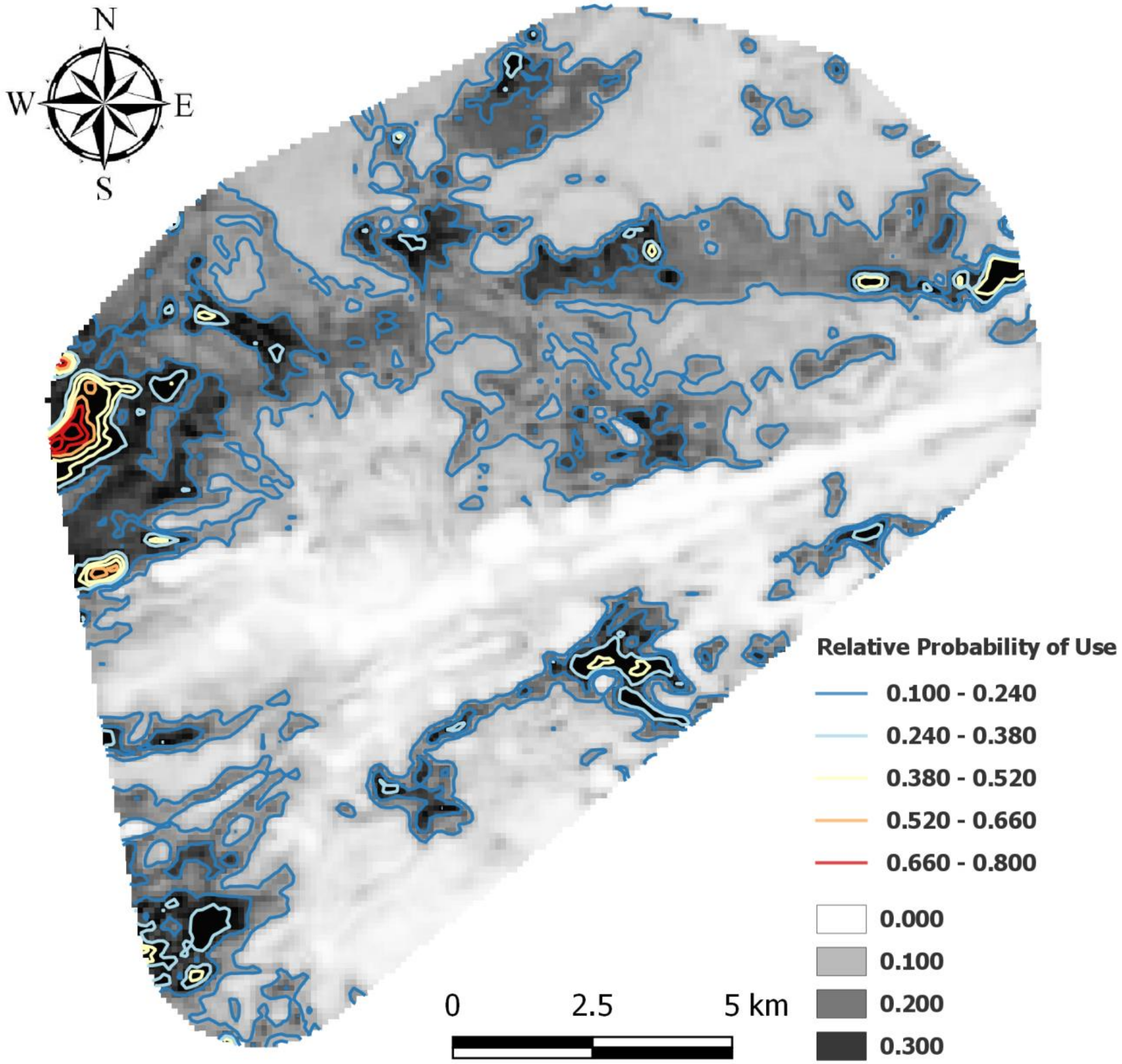

Figure S5. Relative probability of use in the study area of Sierra Arana (Andalusia, SP), predicted using the coefficients from the general generalized mixed model (Table 4, Part 2). Pixel size: 100x100m