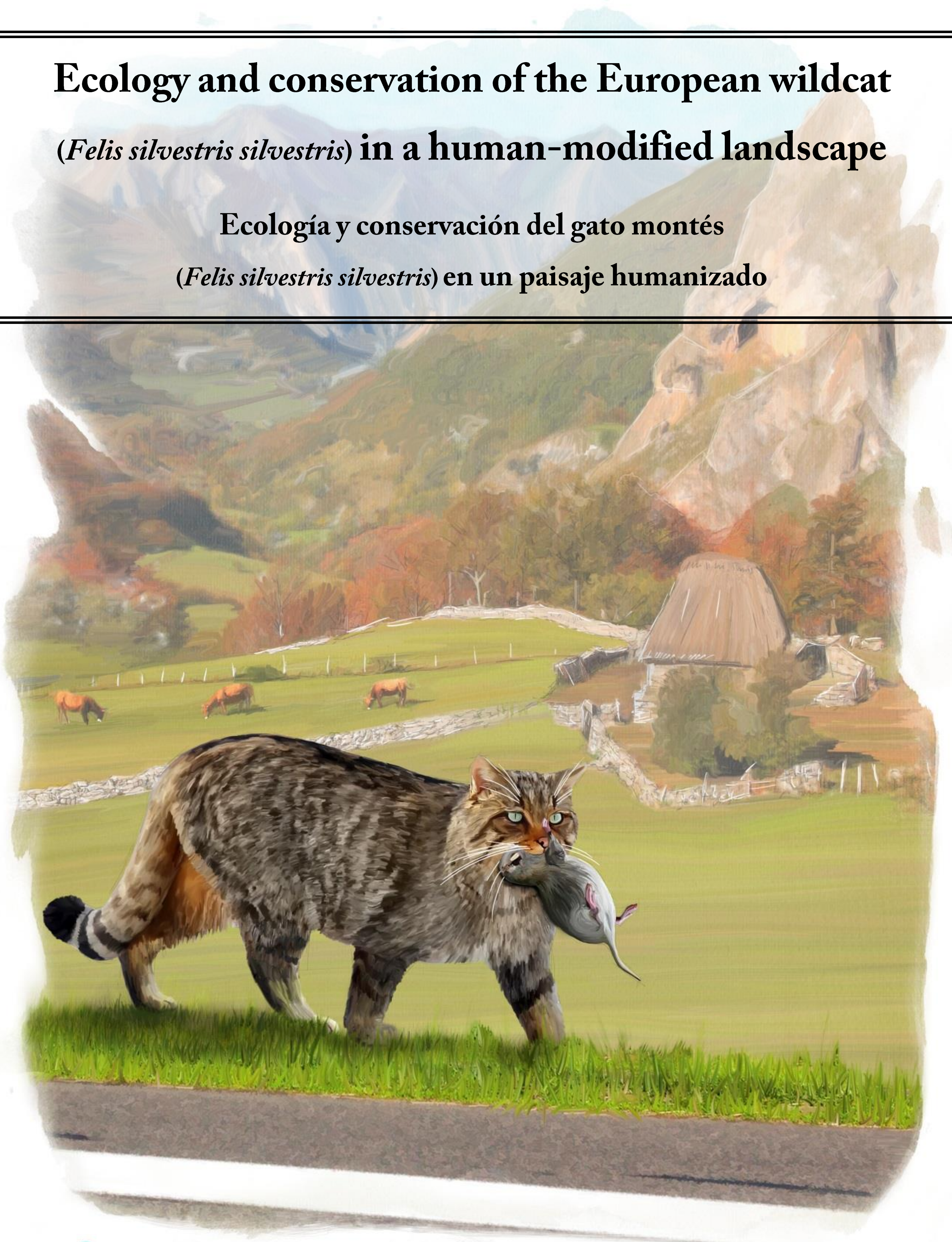
Ecology and conservation of the European wildcat (*Felis silvestris silvestris*) in a human-modified landscape

Ecología y conservación del gato montés (*Felis silvestris silvestris*) en un paisaje humanizado



Universidad de Oviedo

Héctor Ruiz Villar

Programa de doctorado en Biogeociencias - **PhD thesis** - Oviedo, 2023

Programa de doctorado en Biogeociencias

Línea de Investigación: Gestión y conservación de recursos biológicos

Departamento de Biología de Organismos y Sistemas

Instituto Mixto de Investigaciones en Biodiversidad

"Ecology and conservation of the European wildcat (*Felis silvestris silvestris*) in a human-modified landscape"

"Ecología y conservación del gato montés (*Felis silvestris silvestris*) en un paisaje humanizado"

Author

Héctor Ruiz Villar

Supervisors

José Vicente López Bao

Francisco Palomares Fernández

PhD Thesis

Oviedo, 2023

Universidad de Oviedo

Universidad de Oviedo

RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

1.- Título de la Tesis	
Español/Otro Idioma: Ecología y conservación del gato montés (*Felis silvestris silvestris*) en un paisaje humanizado	Inglés: Ecology and conservation of the European wildcat (*Felis silvestris silvestris*) in a human-modified landscape

2.- Autor	
Nombre: Héctor Ruiz Villar	DNI/Pasaporte/NIE:
Programa de Doctorado: Biogeociencias	
Órgano responsable: Centro Internacional de Postgrado	

RESUMEN (en español)

Las actividades humanas afectan al comportamiento de la fauna, sobre todo al de los carnívoros, que cumplen papeles fundamentales en los ecosistemas. El creciente contacto entre humanos y carnívoros requiere de una evaluación de los efectos de las actividades humanas sobre su comportamiento y un aumento en el conocimiento de su historia natural. El principal objetivo de esta tesis es detectar cambios comportamentales causados por las actividades humanas en un carnívoro, el gato montés, en paisajes humanizados. Además, pretende discutir los efectos ecológicos de dichos cambios y proponer medidas de conservación que promuevan la coexistencia entre humanos y gatos monteses. La tesis se divide en 6 capítulos.

El capítulo 1 trata los efectos de la agricultura intensiva y la configuración del paisaje en el tamaño de las áreas de campeo de los gatos monteses en Europa. Las áreas de campeo aumentaron en zonas con mayor presencia de agricultura intensiva y de bosques homogéneos, mientras que disminuyeron en zonas con alta densidad de borde de bosque, confirmando la preferencia de los gatos por paisajes en mosaico y destacando los posibles riesgos futuros asociados a la creciente intensificación de los usos.

El capítulo 2 analiza cómo la presencia y proporción de prados ganaderos afecta al consumo de presas en los gatos monteses, así como su variación estacional. Además explora la relación entre la abundancia y el consumo de presas. *Arvicola monticola* (un roedor pratense de gran tamaño) fue la presa principal siempre y cuando había prados ganaderos, destacando su papel como zonas de alimentación para los gatos. La dieta varió estacionalmente aunque no encontramos relación entre la abundancia y el consumo de presas.

El capítulo 3 evalúa los impactos de las molestias humanas en el tiempo dedicado por los gatos monteses a diferentes comportamientos y en el éxito en la caza. En presencia de humanos los gatos dedicaron más tiempo a estar alerta que a cazar, alimentarse o moverse que en escenarios sin molestias, lo cual supondría costes energéticos. Además, los gatos pasaron más tiempo cazando con más tráfico, cerca de carreteras y lejos de pueblos. También vigilaron más mientras se alimentaban en presencia de vehículos. Por último, aunque el efecto no fue significativo, el éxito en la caza disminuyó más en hembras que en machos de gato montés en presencia de vehículos, lo cual podría asociarse con mayor sensibilidad a molestias por parte de las hembras mientras cazan.

El capítulo 4 describe la ecología reproductiva de los gatos monteses en prados ganaderos. Las camadas durante el destete fueron de 1 a 3 crías, siendo 2 lo más habitual, con la mayoría de observaciones concentradas en verano. Las madrigueras auxiliares se encontraban en vegetación densa aunque los gatos utilizaron ocasionalmente construcciones humanas con fines reproductivos. Las hembras movieron a las crías con frecuencia y fueron exitosas en la caza.

El capítulo 5 investiga las interacciones entre gatos monteses y zorros. Los encuentros diurnos son escasos, lo cual podría asociarse con una evitación activa entre ambas especies. Los zorros actuaron de forma ofensiva mientras que los gatos mostraron intimidación defensiva, posiblemente acordes a su morfología. Ambas estrategias fueron exitosas en mantener la posición en las zonas de alimentación.

El capítulo 6 describe por primera vez el comportamiento de “almacenamiento de comida” en los gatos monteses. Un gato montés se comportó como un lince o un puma, visitando una carroña de corzo al menos 9 veces en 21 días, consumiendo los principales músculos y cubriendo la presa con pelo y vegetación.

En conclusión, los gatos monteses perciben tanto efectos positivos como negativos derivados de habitar paisajes humanizados. La Cordillera Cantábrica proporciona condiciones adecuadas en términos de presas, refugio y oportunidades reproductivas, aunque los gatos han de lidiar con los efectos negativos asociados a encuentros con humanos y sus actividades.

RESUMEN (en Inglés)

Human activities affect the behaviour of wildlife species, particularly of carnivores, which play fundamental roles in ecosystems. The growing contact between carnivores and humans urgently calls for increasing the knowledge on natural history of carnivores and studying the effects of human activities on their behaviour. The main aim of the present thesis is to detect behavioural alterations caused by anthropogenic activities in human-modified landscapes on a carnivore species, the European wildcat. Moreover, it pretends to discuss the ecological implications of such changes and propose effective conservation strategies that allow for coexistence between humans and wildcats. The present thesis is divided into six chapters.

Chapter 1 addresses the effects of intensive agriculture and landscape configuration on the home range size of wildcats across Europe. Home range size increased in areas with higher presence of intensive agriculture and in homogeneous forests, whereas it decreased when increasing forest edge density. This confirms the preference of wildcats for mosaic-structured landscapes and highlights the potential future risks associated to the current scenario of expanding land intensification.

Chapter 2 analyses how the presence and proportion of pastoral fields affect the consumption of different prey items by wildcats, as well as its seasonal variation. Additionally it explores the link between prey abundance and consumption. *Arvicola monticola* (a field-dwelling large rodent species) was the most consumed item as long as pastoral fields were present, remarking the role of pastoral fields as feeding ground for wildcats. Prey consumption varied seasonally although we found no relationship between inter-annual prey abundance and prey consumption.

Chapter 3 evaluates the impacts of human disturbance on wildcat time allocation to different behaviours and hunting success. Wildcats allocated more time to alert and less time to hunting, feeding and moving behaviours in the presence of humans than in undisturbed scenarios, which could add energetic costs for the species. Furthermore, wildcats spent more time hunting in scenarios with more traffic, closer to roads and further from villages. Similarly, they were more vigilant while feeding in the presence of vehicles. Finally, although the effects were not significant, hunting success decreased more in females than in male wildcats in the presence of vehicles which could be related with higher sensitivity to disturbance of females during hunting events.

Chapter 4 describes the breeding ecology of wildcats using pastoral landscapes. Litter size at weaning ranged from one to three, with two being the average and most observations occurred during summer. Most auxiliary dens were located inside thick vegetation close to pastoral fields, and human constructions were occasionally used with breeding purposes. Breeding females moved dens frequently and showed high hunting success.

Chapter 5 investigates the interspecific interactions occurring between wildcats and foxes. Diurnal encounters between these species are rare, which could result from the two species displaying active avoidance. Foxes showed offensive behaviours whereas wildcats displayed a defensive intimidation strategy, probably in relation to their morphology. Both strategies were equally effective for maintaining the position in feeding grounds.

Chapter 6 provides the first description of caching behaviour in wildcats. A wildcat behaved similar to lynx or pumas, and visited a roe deer carcass at least 9 days along a 21 day period, consuming the main muscles and covering it with hair and vegetation.

In conclusion wildcats may perceive both negative and positive effects derived from inhabiting human-dominated landscapes. The Cantabrian Mountains provide suitable conditions for wildcats in terms of prey, refuge and breeding opportunities, although wildcats need to deal with the detrimental effects associated to encounters with humans and their activities.

SR. PRESIDENTE DE LA COMISIÓN ACADÉMICA DEL PROGRAMA DE DOCTORADO EN BIOGEOCIENCIAS

Recommended citation:

Ruiz-Villar, H. (2023) Ecology and conservation of the European wildcat (*Felis silvestris silvestris*) in a human-modified landscape. PhD Thesis. Universidad de Oviedo.

Gobierno del
Principado de Asturias

This thesis was funded by a **“Severo Ochoa” predoctoral grant (BP17-65)** provided by the **Regional Government of the Principality of Asturias**. Field work was partially supported by M. Torres Diseños Industriales SAU and Land Rover Spain. Trapping of seven wildcat individuals in the Western Cantabrian Mountains was carried out by the Spanish Ministry of Science, Innovation and Universities and TRAGSATEC S.A.

This thesis, presented under the international mention from University of Oviedo, was assessed by three scientific experts from international research institutions:

-**Dr. Andrew Kitchener**: IUCN Cat Specialist Group Member and Principal Curator of Vertebrates, National Museums of Scotland.

-**Dra. Margarida Lopes-Fernandes**: Social Science Researcher at Centre for Research in Anthropology, NOVA-FCSH; Institute for Nature Conservation and Forests technician, Portugal; National Red Data Book on Mammals, editor; and IUCN Conservation Genetics Specialist Group member.

-**Dr. Maximilian L. Allen:** University of Illinois at Urbana-Champaign. Illinois Natural History Survey; and IUCN Cat Specialist Group Member.

A mis padres

A Ana

“Nature has been critical in fomenting science. But we’ve gotten lost along the way, forgetting about curiosity and pure love of discovery that should be driving our researches….it’s not too late to rediscover our connections to nature…we must stop and smell the flowers, despite the many pressing issues in the world waiting for resolution. We can do better. Understanding natural history is a first step.”

Joel Berger

2018

Extreme conservation: Life at the edges of the world

“The young wild-cats are by far the most intractable (small carnivores)*, perfect fiends of savage fury, quite unamenable to civilisation.”*

Abel Chapman and Walter Buck

1910

Unexplored Spain

Table of contents

General introduction

Human population has grown exponentially during the Holocene, going from 2.5 billion people in 1950 to 8 billion people in 2022, and expecting to reach 10.4 billion in 2100 (United Nations Population Data Portal consulted on 08/02/2023; https://pdp.unfpa.org/). As a consequence, natural habitats and landscapes around the globe have been modified aiming at satisfying the increasing human demands (Cumming et al., 2014; Khan et al., 2021; Milner and Boldsen, 2023). Specifically, the human activities related with production of energy (i.e. extraction and consumption of fossil and non-fossil resources; Khan et al., 2021) and food (livestock and agriculture; Alkemade et al., 2013; Milner and Boldsen, 2023; **BOX 1**), and construction of human settlements (Cumming et al., 2014) and infrastructures (e.g. roads, highways and railways; Spellerberg, 1998) are responsible for most of global destruction and alteration of habitats. Hence, increased human activities resulted in 77% of terrestrial landscapes being modified into what are broadly called anthropogenic or human-modified landscapes (Chase and Chase, 2016), while the truly unaltered environments continue to become scarce (Watson et al., 2016). In Europe wild ecosystems are virtually inexistent due to prolonged and intense human occupancy (Allan et al., 2017).

Human activities cause landscape modifications and exploitation of wildlife species, which are the principal causes of biodiversity loss and have profound impacts on ecosystems and species (Fischer and Lindenmayer, 2007). The effects span from dramatic and accelerated biodiversity losses involving the extinction of multiple taxons (Ceballos et al., 2015), to significant behavioural changes performed by the remaining species in order to coexist with humans (Tuomainen and Candolin, 2011). In brief, species suffer both lethal and non-lethal effects related to humans (Smith et al., 2021).

BOX 1. Human activities aiming at food production (i.e. agriculture and livestock rearing) probably increased at fastest rates than other activities to ensure food security (Thrall et al., 2011), resulting in half of the habitable earth's surface (46 million km^2) dedicated nowadays to agriculture (according to the United Nations Food and Agriculture Organization (FAO)). The agricultural surface has grown and contracted intermittently across the last millennia (Rabbinge and Van Diepen, 2000). However, during the last century, food production methods clearly transitioned from subsistence extensive practices to intensified and industrialized systems (Laurance et al., 2014), mainly fuelled by the appearance of machinery, and new crop and livestock varieties (Grassni, 2013). Traditional and sustainable farming and agriculture, defined as low-intensity practices which involve avoidance of overexploitation of natural resources, low use of machinery and chemicals, use of organic fertilizers and promotion of natural vegetation (Wezel et al., 2014; Wright et al., 2012) generate more progressive and less immediate changes in landscapes, partially allowing for the ecosystems and species to adapt (Wolff et al., 2001). On the contrary, intensive agricultural and farming practices cause drastic landscape modifications, which derive in landscapes with simpler structures and lower biological complexity than sustainable agricultural landscapes and, above all, than natural unaltered ecosystems (Henle et al., 2008; Moller et al., 2008).

Lethal effects allude to direct animal mortality caused by humans and their activities, e.g. hunting (Gosselin et al., 2014), poaching, road kills (Healey et al., 2020), and collision with infrastructures (Jenkins et al., 2010). Increased mortality can affect wildlife population demography, densities and, ultimately, even the behaviour of species (Carter et al., 2007), such as in the case of variations in vigilance patterns in social species (Gil et al., 2017). On the other hand, non-lethal effects refer to behavioural and ecological changes derived from the variation of the conditions in which animals make decisions (Wilson et al., 2020). For instance, humans can trigger antipredator responses in animals towards real or perceived threats (i.e. human disturbance (Frid and Dill, 2002)), which according to the "predation risk allocation hypothesis" could modify the allocation of time budget spent in each activity (Lima and Bednekoff, 1999) or the spatial and temporal ecology of animals aiming at avoidance of humans through e.g. nocturnality (Martin et al., 2010; Reilly et al., 2017; Sévêque et al., 2021, 2020; Tucker et al., 2018). Anthropogenic landscape modifications can either decrease or increase the availability and distribution of resources (Newsome et al., 2015), for example throughout habitat fragmentation (Doherty et al., 2019) or creation of suitable prey habitats (Briner et al., 2005) respectively. As a consequence, when resources become scarce or separate, animals may need to roam across larger areas to cover for their requirements (Riley et al., 2003; Schüttler et al., 2017) or, alternatively reduce their movements when exploiting predictable anthropogenic food resources (Šálek et al., 2015). Landscape fragmentation throughout the incorporation of linear structures such as roads or railways can create barriers that reduce wildlife movement (Holderegger and Di Giulio, 2010; Van Der Ree et al., 2011), or on the contrary, create conditions perceived as favourable by wildlife (e.g. increased prey availability; Northrup et al., 2012). Human activities can also modify the proximate environmental conditions (e.g. noise, pollution) ultimately affecting key behaviours such as feeding and moving (Davies et al., 2013; Pirotta et al., 2014).

Human-caused behavioural alterations on movement, feeding and breeding ecology can generate ecological changes such as variations on interspecific interactions or individual fitness and population dynamics (through e.g. changes in breeding success and offspring survival; **Fig 1**; Wilson et al., 2020). They can also affect fundamental processes involved in optimal ecosystem functionality including dispersal of seeds, nutrients and pathogens (Hawley and Altizer, 2011; Leroux and Schmitz, 2015; Russo et al., 2006). The severity and importance of these effects would depend on the intensity and distribution of human presence and activities (Wilson et al., 2020).

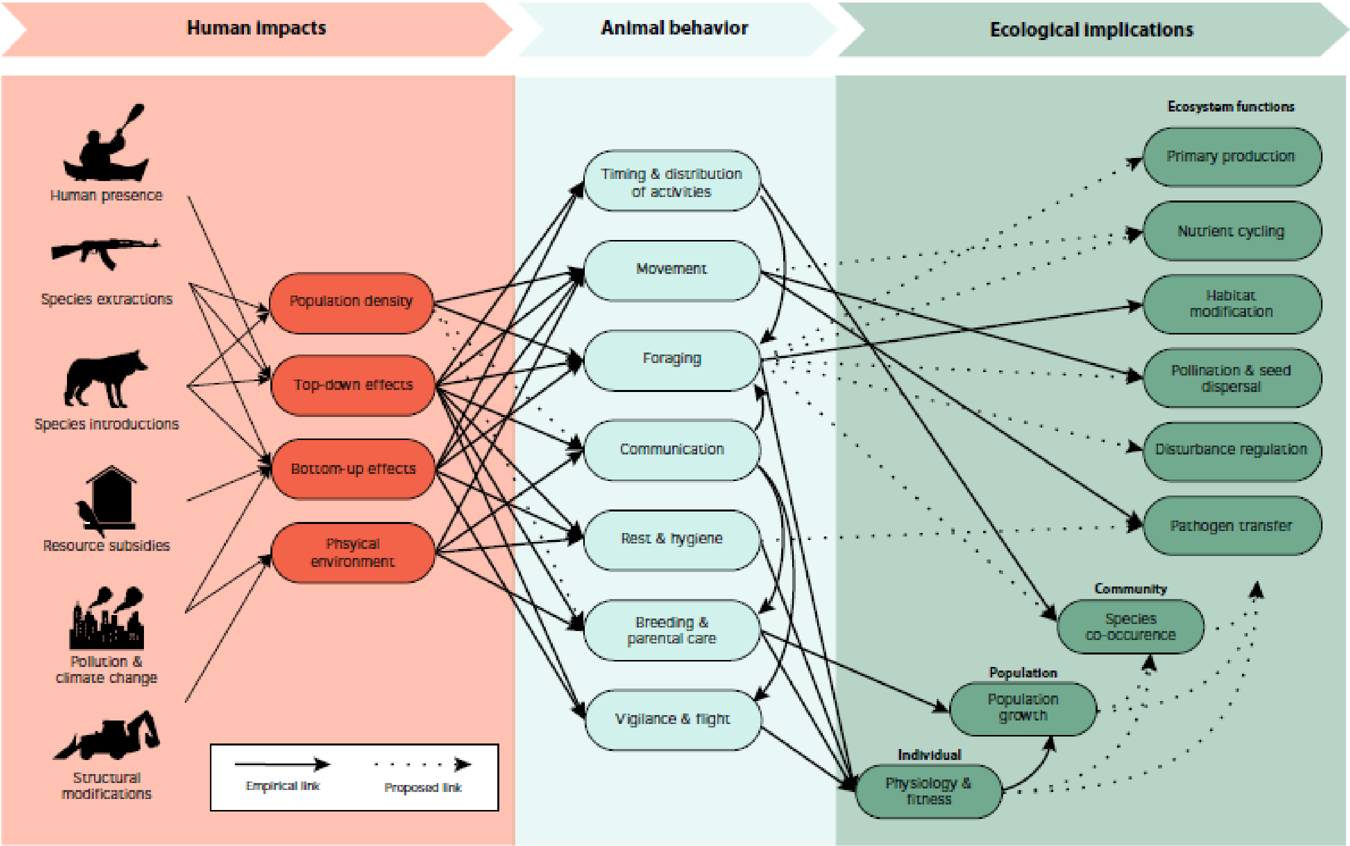


***Figure 1**. Different pathways in which human impacts could affect ecosystem functions throughout animal behaviour change. Solid arrows indicate links supported by empirical studies found by Wilson et al. 2020. Dashed arrows indicate proposed links not empirically documented. Adapted from Wilson et al. 2020.*

Among wildlife, predators are remarkably sensitive to human activities and can respond throughout behavioural changes with the potential to cascade down complete ecosystems (Suraci et al., 2019; Terborgh et al., 2001). Particularly, besides their scarcity in ecosystems, large carnivores can influence ecosystem functioning throughout their fundamental predatory role in regulating prey behaviour and populations, and its impact on the lower trophic levels (Suraci et al., 2019, 2016). On the other hand, medium and small-sized carnivores (i.e. mesocarnivores; carnivores with average body mass <15 kg ;Williams et al., 2018) are more abundant and widespread than large ones, but still highly fundamental for healthy ecosystem functioning, particularly in areas deprived from the presence of diverse large carnivore communities (Roemer et al., 2009). For instance, mesocarnivore predation upon small herbivores can regulate primary productivity in ecosystems (Estes et al., 1998), contribute to nutrient cycling (Ben-David et al., 2005), and alter soil fertility (Maron et al., 2006). Similarly, mesocarnivore absence could alter the composition of grass communities and structures and increase plant damage by rodents (Hambäck et al., 2004). Therefore, mesocarnivores play unique roles not covered by larger carnivores which mainly predate upon larger prey, as mesocarnivores control rodent populations (Ostfeld and Holt, 2004). This not only decreases the pernicious effects that an overpopulation of such species may cause in vegetation and seed production (Moreno et al., 2006; Williams et al., 2018), but also increases human health security by reducing the spread of diseases from rodents to humans (Levi et al., 2012; Ostfeld and Holt, 2004). In accordance, conservation of healthy mesocarnivore communities should be a priority in human-modified landscapes across the world (Marneweck et al., 2021).

Most large and medium carnivore species suffered a severe decline in Europe during the last centuries, mainly as a consequence of human activities involving habitat alterations related to agricultural practices (**BOX 2**) and direct persecution (Ripple et al., 2014; Sainsbury et al., 2019). In the last decades, however, several species are recovering throughout Europe as a consequence of multiple factors, including land abandonment, the implementation of different conservation laws and changes in social perception of wildlife (Chapron et al., 2014; Sainsbury et al., 2019). Nonetheless, prolonged past and present persecution altered carnivore behaviour favouring nocturnality, shyness and selection of habitats further from humans (Gaynor et al., 2018; Sévêque et al., 2020; Swenson, 1999; Theuerkauf, 2009). Whereas great effort has been invested in studying anthropogenic-associated effects on large carnivores (see Kuijper et al., 2016 and Ripple et al., 2014), probably due to their higher attractiveness and more evident role in ecosystems (Brooke et al., 2014; Mammola et al., 2020), comparatively little has been done regarding the effects of human activities on mesocarnivore behaviour (Brooke et al., 2014; Do Linh San et al., 2022). Indeed, many fundamental ecological traits of medium and small-sized carnivores, such as reproductive ecology or interspecific interactions, still remain poorly understood (Brooke et al., 2014; Do Linh San et al., 2022). Data deficiency on the ecology of wildlife species is generally linked with unfavourable conservation status (Bland et al., 2015; Jarić et al., 2016; Roberts et al., 2016) which urgently calls for gathering information on basic ecology of secretive species aiming at ensuring their persistence. Further, when ecological traits, such as foraging or movement ecology, have been studied, they have only occasionally been connected to human activities (Sévêque et al., 2021; Torres-Romero and Giordano, 2022).

BOX 2. Intensive agricultural practices first occupied those areas where labour costs, water and land availability, and transportation networks were more favourable (Laurance et al., 2014). On the contrary, areas with complex topography converted to intensified systems at lower speeds, which promoted the maintenance of more stable ecological conditions in mountains, that acted as wildlife ecological refuges and biodiversity hotspots (Buschke et al., 2020). Pastoral landscapes, defined as a mosaic of forest, shrub, meadows and pasturelands sustainably managed to produce livestock forage, derive from the appliance of extensive farming techniques mainly in mountain ranges across the world (Krauß and Olwig, 2018). Nevertheless, the originally sustainable pastoral landscapes are disappearing by two main reasons: i) they are progressively turning into intensive practices by increasing livestock pressure (that cause overgrazing in subalpine pasturelands) and by creating homogeneous landscapes through mechanized or fire-induced clearing of shrub patches (Blanco-Fontao et al., 2011; Papanastasis et al., 2002); and ii) the emigration of people to cities and the associated abandonment of rural areas and activities promote the natural evolution of ecosystems towards mature stages (Benayas et al., 2007).

Many human-related factors threaten the survival of carnivores in human-modified landscapes. For instance, 27% of carnivores (N=291 extant species) are listed as Critically Endangered, Endangered or Vulnerable by the International Union for the Conservation of Nature, and 48% species show declining population trends (IUCN Red List of Threatened Species consulted on 10/02/2023). Specifically, 23% of medium and small-sized carnivores (n= 229 species) are categorized as threatened and nearly 50% of the species showed decreasing population trends with Mustelidae, Felidae, Viverridae and Eupleridae being the most threatened (Marneweck et al., 2021; Torres-Romero and Giordano, 2022). Among the main threats, overhunting and poaching affects 96% of threatened small carnivore species, with Felids leading the list (**Fig 2**; Marneweck et al., 2021). In addition, land use change mainly driven by land conversion to intensified large-scale agriculture affects 85% of threatened small carnivore species (**Fig 2**; Marneweck et al., 2021).

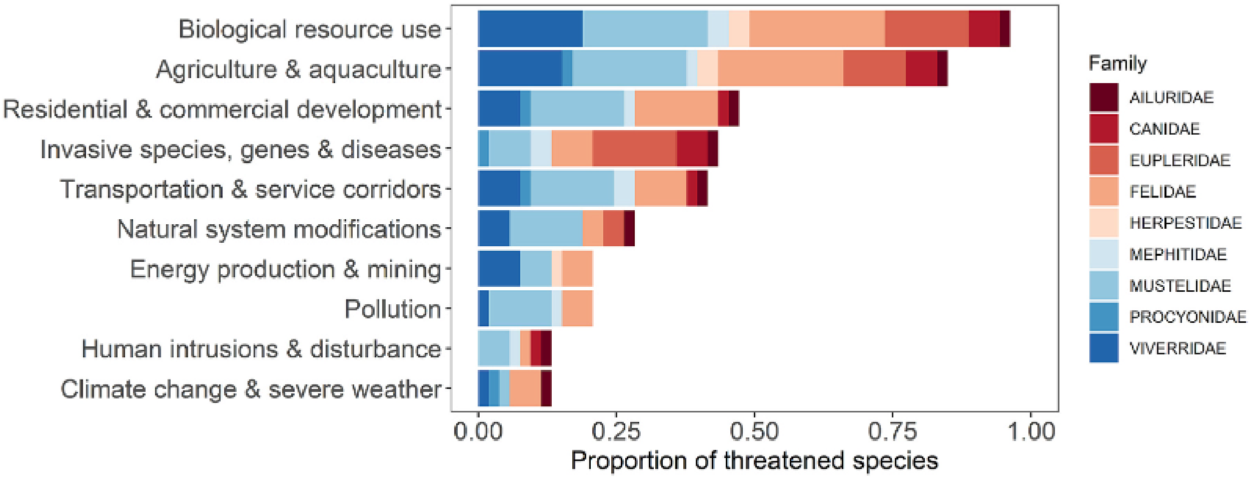


***Figure 2**. Threats affecting the 53 threatened (Critically endangered, Endangered or Vulnerable) species of carnivores < 15 kg. Adapted from Marneweck et al. 2021.*

Understanding how mesocarnivore species are affected by human activities is of paramount importance to ultimately design and apply effective conservation strategies ensuring the persistence and ecosystem functionality of these species (Jennings et al., 2015; Meijaard et al., 2007). For that aim, scientist must identify behavioural traits that can be used as indicators of altered ecology in relation to foraging, breeding and movement (Berger-Tal et al., 2011; e.g. home range size, prey consumption, or time allocation to foraging and vigilance behaviours) and discuss the potential individual and demographic outcomes of their variations. In addition, investigating those ecological aspects still poorly known to science is necessary to improve the assessment of the species situation and optimize their protection. Carnivores are mostly long-lived animals, so gathering the necessary data to approach this methodology requires the combination between: i) traditional long-term monitoring of ecological aspects collectable through direct observation of the species (e.g. behavioural observations of time allocation, breeding behaviour or interspecific interactions) or collection of biological samples (e.g. diet composition extracted from scat analyses; Smith et al., 2017); and ii) modern technologies (radio and GPS devices) that allow to obtain high resolution information on movement ecology related to habitat and home range use (Kays et al., 2020). Lastly, recent digitalization of global information on land use (e.g. presence and type of agriculture) and infrastructures provides the required information on human-related factors that could impact species ecological traits (Turner et al., 2003). By comparing behavioural data gathered in areas with different degrees of human-pressure we can study the impacts and potential consequences of increasing human activities on mesocarnivores.

Study species

Our study species is the European wildcat (*Felis silvestris*), a felid mammalian mesocarnivore (**BOX 3**), broadly encompassing 140000 individuals distributed across Europe in four continental metapopulations and a few insular populations (Sicily, Crete, and Scotland), through landscapes with different degrees of human pressures (Gerngross et al., 2022). Although previously considered a forest specialist, recent research highlights wildcat preference for mosaic-structured landscapes (either natural or anthropogenic) composed by interconnected areas providing refuge (e.g. forest and shrub), movement (e.g. vegetation stripes) and feeding opportunities (e.g. fields with rodents; Lozano et al., 2003; Monterroso et al., 2009; Portanier et al., 2022). Wildcats are hypercanivores, meaning that their diet is mainly composed by animal prey (Lozano et al., 2006; Moleón and Gil-Sánchez, 2006). Specifically, wildcats are considered facultative specialist, thus predating among different prey items according to their availability (Malo et al., 2004). For instance, wildcats mainly predate upon rabbits (*Oryctolagus cuniculus*) in the Mediterranean areas where this species is present, but show a rodent-based diet in the remaining areas inside their distribution area (Lozano et al., 2006). Consequently, and according to their ecological requirements, wildcats can regularly use human-modified landscapes that combine mosaic structures and abundance of their main prey items (Jerosch et al., 2018, 2017), although this may differ between sexes and study areas (Oliveira et al., 2018). Wildcats are mainly nocturnal and crepuscular animals, which combined with their shy nature may have propitiated that multiple key ecological traits such as wildcat breeding ecology or wildcats interactions with other mesocarnivores still remain poorly known (Ferretti et al., 2022; Migli et al., 2021a).

BOX 3. European wildcats present a series of pelage and morphological traits defined by Ragni and Possenti (1996) that can be used as considerably reliable cues to visually differentiate wildcats from domestic cats. The main features include a thick and blunt tail with a black tip and a few separate and rectangular rings, a dorsal black stripe going from the base of the neck to the base of the tail, three to five lines going down the back of the neck, lack of stripes on body sides, and black underfoot, among others. However, some individuals may still be misidentified in areas where hybrids occur (Devillard et al., 2014). Genetic analyses should be carried out to either determine the correct identification of a wildcat or the frequency of hybrids in the study area (Devillard et al., 2014). In our case, genetic identification of individuals was performed in chapter 1, as it involved several study areas across Europe. For the remaining chapters developed in the Cantabrian Mountains, recent research and analyses of individuals (n>30) showed a complete absence of hybrids (Tiesmeyer et al., 2020) increasing the confidence of low chances of wildcat misidentification in our research.

European wildcat showing its distinctive pelage traits. Photo by Héctor Ruiz-Villar

Contact with humans caused declines in wildcat populations across Europe during recent centuries, mainly due to habitat destruction and direct persecution of the species (Mueller et al., 2020; von Thaden et al., 2021). However, the global wildcat population seems to have recovered during the last decades probably thanks to reforestation of landscapes, reduced persecution, and human migration to cities (von Thaden et al., 2021). Nevertheless, this trend differs between wildcat metapopulations inhabiting most Eurosiberian biomes (i.e. northern Spain and the rest of wildcat European distribution) which show an increase or stabilization of their populations; and those existing in Scotland and Mediterranean environments (particularly most of the Iberian Peninsula) which are virtually extinct and show symptoms of severe decline, respectively (Gil-Sánchez et al., 2020; Senn et al., 2019). Therefore, the species still faces multiple human-related threats including intensification of landscape uses (Jerosch et al., 2018), road kills (Bastianelli et al., 2021), hybridization with domestic cats (something particularly relevant in Scotland, although also present in other wildcat populations; Senn et al., 2019), and disease load and transmission from domestic cats (Gerngross et al., 2022).

Aim, objectives and thesis structure

The principal aim of the present thesis is to assess the influence of anthropogenic activities in human-modified landscapes on the behaviour of European wildcats. Once the positive and negative behavioural alterations are evaluated, this thesis aims at discussing the potential ecological implications of such changes, and at proposing effective strategies facilitating wildcat conservation in human-modified landscapes. One of the main motivations of the current dissertation is to fill the knowledge gap about the effects of human activities on mesocarnivore behaviour at different scales, which should improve the conservation strategies aiming at safeguarding their functionality in humanized environments.

In particular, this thesis investigates the effects of intensive and extensive agriculture, changes in landscape structure, human presence and traffic on key behavioural traits such as movement, foraging and vigilance behaviours. Secondarily, this dissertation describes and analyses key ecological components (i.e. reproductive ecology, interspecific interactions, and exploitation of overlooked food sources) which knowledge is fundamental and necessary to improve demographic research and to establish adequate conservation and monitoring programs. For that purpose, we combined long-term traditional field data collection (e.g. diet analyses throughout scat collection and direct field behavioural observations of wildcats) with modern technologies such as GPS tagging of individuals and remote sensing information.

Hence, the current thesis is divided into two main sections (**Fig 3** for dissertation framework). In the first section, we use long-term monitoring data on behavioural indicators to study the potential effects of human-activities on European wildcats. Specifically, we analyse the influence of: agriculture intensity and landscape configuration on wildcat home range size at a European scale (Chapter 1); the presence of pastoral fields on wildcat prey consumption in the Cantabrian Mountains (Chapter 2); and the presence of humans and traffic on wildcat time allocation to different behaviours and hunting success in the Western Cantabrian Mountains (Chapter 3). In the second section, we describe fundamental and previously poorly known wildcat ecological parameters observed in the Cantabrian Mountains. Particularly we describe: the breeding ecology of European wildcats in the wild (Chapter 4); the interspecific interactions between wildcats and red foxes (*Vulpes vulpes*), which are potential competitors (Chapter 5); and the wildcat behaviour when exploiting an overlooked food resource, ungulate carrion (Chapter 6).

Each chapter corresponds to an already published or accepted scientific article composed by its fundamental sections: introduction, methodology, results and discussion; which may ultimately cause some information overlap between chapters. The main objectives of this thesis are elaborated in six chapters:

<u>Chapter 1.</u> The expansion and intensification of agriculture can alter the distribution of resources for wildlife consequently conditioning their movement ecology. This chapter aims at performing a broad scale evaluation of the effects of the proportion and intensity of agriculture (intensive vs. extensive practices) as well as its distribution in the landscape (i.e. landscape configuration) on the home range size of European wildcat across its distribution range. For that aim we analysed the variation on wildcat home range size obtained from tagging of wildcats using VHF and GPS devices in relation to land use and landscape structure information obtained with remote sensing procedures. Wildcat movement information was gathered across areas with different degrees of agriculture intensification and landscape fragmentation in Europe (specifically Portugal, Spain, Germany and Italy) during the last 20 years.

<u>Chapter 2.</u> Pastoral activities can promote the abundance of certain rodent species that can be exploited by carnivores. This chapter analyses the effects of the presence and proportion of pastoral fields on the consumption of different prey items by wildcats in the Cantabrian Mountains, as well as its seasonal variation. Additionally it explores the relationship between prey abundance and prey consumption. For that aim we determined prey

consumption through collection and macroscopic analysis of wildcat scats across seasons and obtained population estimates of prey items through direct and indirect approaches.

Chapter 3. Human disturbance can trigger antipredator responses in wildlife using human-modified landscapes which can ultimately affect their ecological performance. This chapter evaluates the impacts of human disturbance and traffic on wildcat time allocation to different behaviours and hunting success in the Western Cantabrian Mountains. Specifically, it investigates the time allocation to specific behaviours such as hunting or vigilance under different sources of human disturbance; it researches the effects of traffic on time allocation to hunting and vigilance during feeding events; and it analyses the effects of traffic intensity and presence on wildcat hunting success. For that purpose we combined wildcat individual and behavioural information obtained from direct observations and recordings in the western Cantabrian Mountains with data on traffic intensity and distance to human infrastructures.

Chapter 4. Information on breeding ecology is critical to understand wildlife demography and evaluate the effects of potential threats. This chapter describes reproductive parameters of European wildcats using pastoral landscapes in the Cantabrian Mountains. Specifically, we described size, date and location of litters, as well as den reutilization and feeding behaviours of females during the breeding period. To achieve this we performed observations of females during the pup rearing period.

Chapter 5. Interactions between carnivore species with partially overlapping niches can determine the spatial and temporal behaviour of the taxons involved. This chapter investigates the interspecific interactions occurring between two sympatric and similarly-sized mesocarnivores in the Cantabrian

Mountains: the wildcat and the red fox. Particularly we looked at behavioural responses of both species during direct encounters and discussed its potential consequences on their use of feeding grounds. For that aim we performed direct observations of interactions between wildcats and foxes, and categorized the responses of both species.

Chapter 6. Food caching involves the relocation and/or storage of food to create a predictable food resource to exploit during times of scarcity, which can determine food intake during critical periods. This chapter exhaustively describes for the first time a previously overlooked wildcat behaviour, the caching of food when consuming a roe deer carcass. This analysis results from the opportunistic detection and observation of caching behaviour in a GPS-tagged adult wildcat in the Western Cantabrian Mountains.

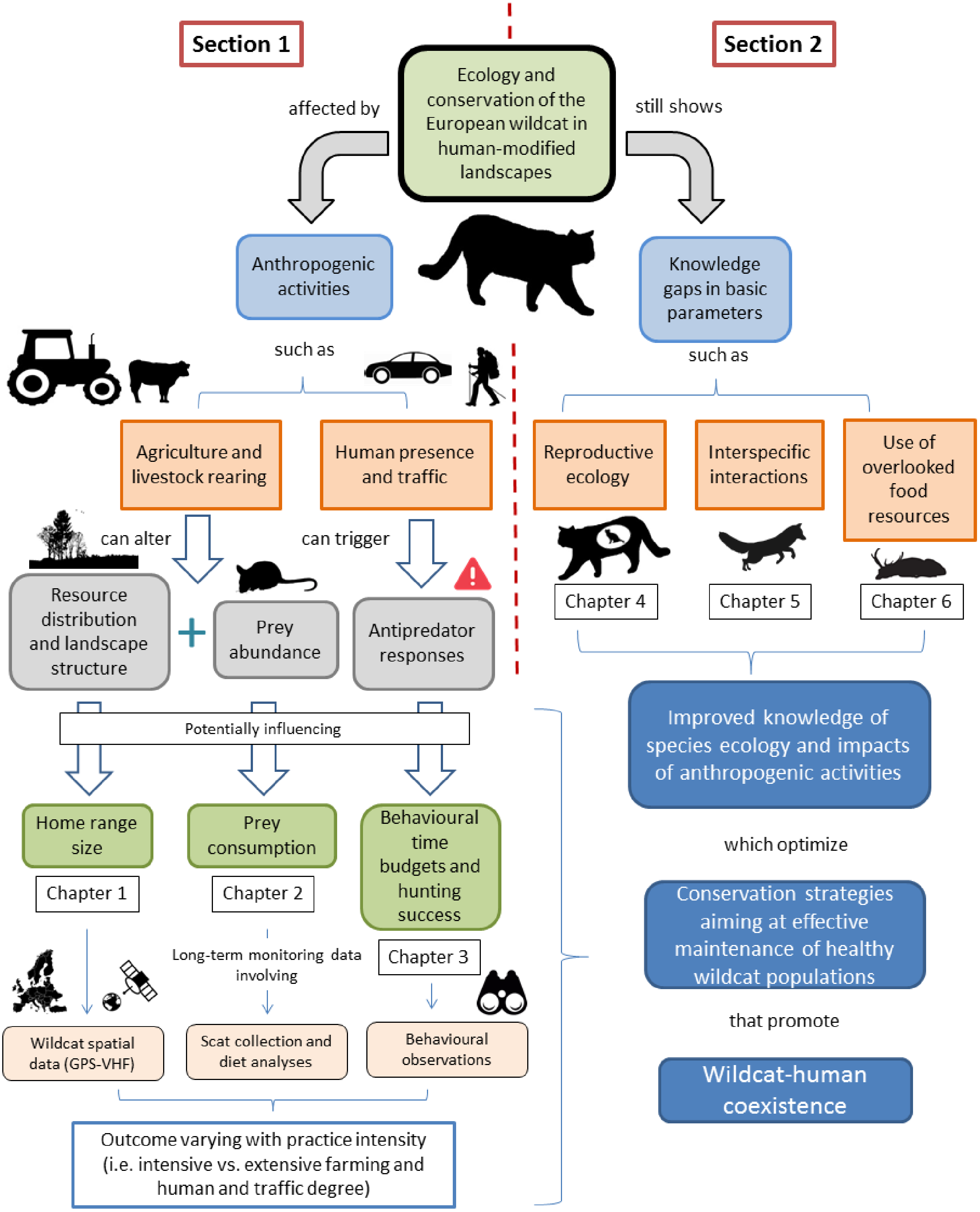


Figure 3. *Conceptual framework of the current thesis dissertation.*

Study area

The study area varies between different chapters according to the different objectives proposed. In chapter 1 the study area includes several locations across Europe. This is justified by the need of comparing wildcat home range sizes between areas with marked differences regarding the degree of presence and intensification of agriculture, as well as landscape configuration. Consequently, we included areas from Portugal, Spain, Germany and Italy to generate a gradient in the landscape characteristics of interest (**Fig 4**). Overview of the different study areas involved other than the Cantabrian Mountains appear in **Table 1**.

Table 1*. Overview of the European study areas other than the Cantabrian Mountains included in Chapter 1. To calculate the area the 95% MCP area of all individuals of the study area was joined. Core forest = forest pixels with no contact with other non-forest; edge forest = forest pixels contacting non-forest pixels. Adapted from Bastianelli et al., 2021.*

	Study area	Area [km^2]	Elevation [m]	Forest core	Non-forest	Forest edges
1	Guadiana Valley Natural Park	17	146	4%	91%	5%
2	Cabañeros National Park	35	686	3%	90%	7%
3	Izagaondoa Valley	78	584	17%	70%	12%
4	Lleida region	31	463	7%	77%	15%
5	Eifel	94	589	42%	48%	10%
6	Moselle Mountains/ Hunsrueck/Haardtwald	89	469	57%	29%	13%
7	Rheinauen Kaiserstuhl	139	230	25%	61%	14%
8	Soonwald	71	478	67%	24%	6%
9	Maremma Regional	44	119	51%	33%	15%

	Park					
10	Goldene Aue	80	194	12%	86%	2%
11	Paradiso di Pianciano Estate	43	863	38%	41%	22%

In chapters 2, 4 and 5 the area is narrowed down to two separate areas of the Cantabrian Mountains (NW Spain; **Fig 4**): Montaña Palentina Natural Park (MP; 190 km^2) in the central Cantabrian Mountains of Palencia; and the Western Cantabrian Mountains (WCM; 1800 km^2) between the provinces of Asturias and León. Both areas hold temperate oceanic bioclimatic conditions surrounded by a few submediterranean locations (Martínez and Arregui, 1999). Vegetation consists mainly of deciduous forests (*Quercus, Fagus* and *Betula* sp.), scrublands, and pastoral fields in the valley bottoms (Loidi, 2017). Both areas present low human population densities (<15 inhabitants/km^2; Goerlich and Cantarino, 2013) with economy mainly based on livestock farming. In this case, the area is large enough to effectively compare wildcat prey consumption between areas with contrasting landscape compositions regarding forest and pastoral fields, and for data compilation on poorly studied ecological traits such as breeding ecology and interspecific interactions.

Chapter 3 was performed in the Western Cantabrian Mountains described above (**Fig 4**). The area allows for comparisons of wildcat behaviour between sites with different degree of human presence and traffic. Finally, chapter 6 describes a single case of a wildcat consuming and caching a roe deer carcass also located in the Western Cantabrian Mountains (**Fig 4**).

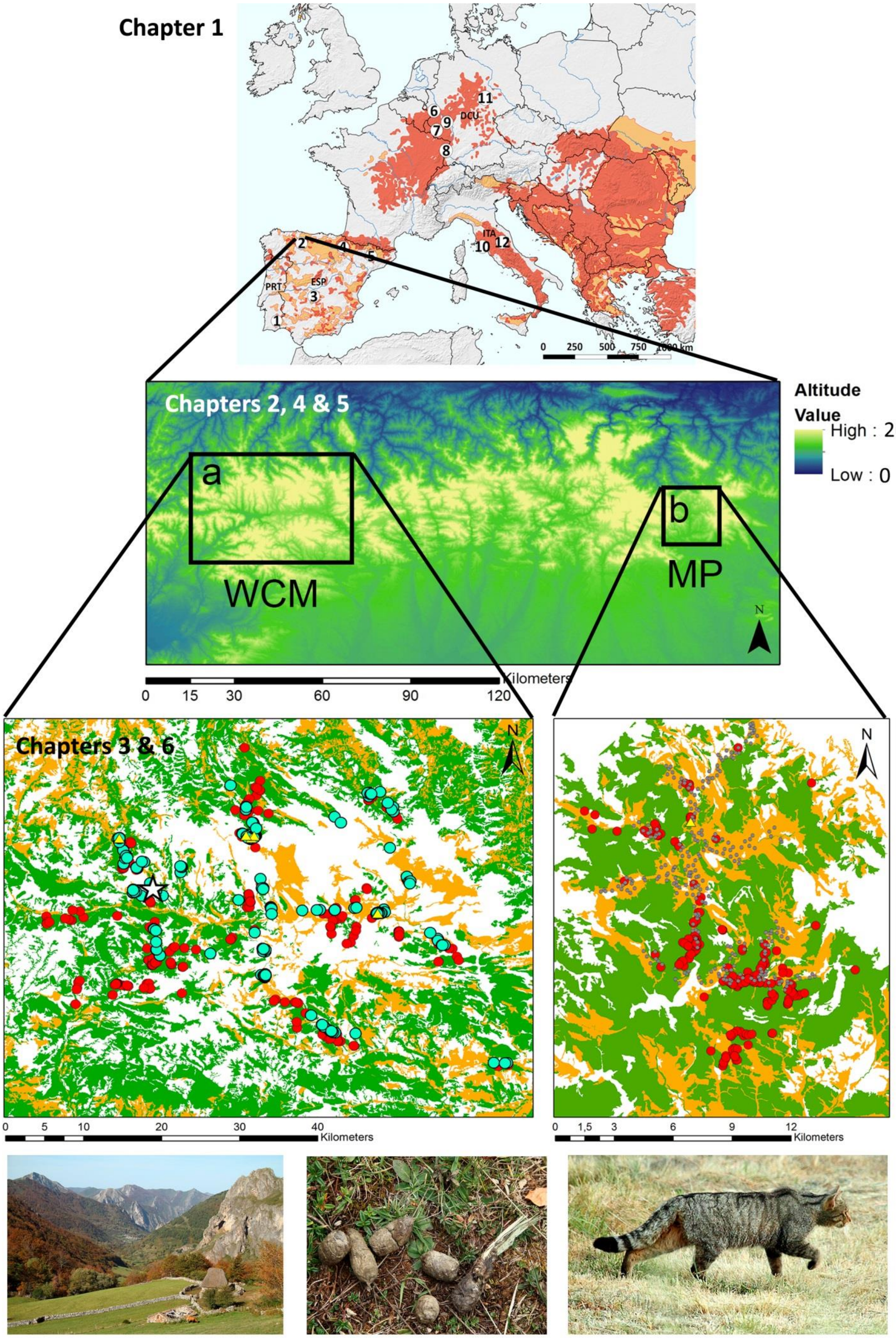

Chapter 1
11
6
9
DCU
7
8
ITA
10
12
2
4
5
PRT
ESP
3
1
0 250 500 750 1000 km
Chapters 2, 4 & 5
Altitude
Value
High : 2670
Low : 0
a
WCM
b
MP
N
0 15 30 60 90 120
Kilometers
Chapters 3 & 6
N
0 5 10 20 30 40
Kilometers
N
0 1,5 3 6 9 12
Kilometers

Figure 4 *(previous page)**.** Location of the different study areas considered in the current thesis. From top to bottom and from left to right: Study areas in Europe used in chapter 1 within the distribution range of the European wildcat described by Gerngross et al., (2022) and numbered from West to East: 1. Guadiana Valley Natural Park; 2. Cantabrian Mountains; 3. Cabañeros National Park; 4. Izagandoa Valley; 5. Lleida region; 6. Eifel; 7. Moselle Mountains/Hunsrueck/Haardtwald; 8. Rheinauen Kaiserstuhl; 9. Soonwald; 10. Maremma Regional Park; 11. Golden Aue; 12. Paradiso di Pianciano Estate. The red range represents the actual extent of the species, while the yellow range represents the possible extent. Bellow that is represented the location of the two study areas inside the Cantabrian Mountains (NW Spain): a) WCM (Western Cantabrian Mountains) and b) MP (Montaña Palentina). Red circles show the location of the wildcat scats, grey spots indicate the locations of* Arvicola monticola*, blue circles show the location of wildcat observations, yellow triangles show the location of wildcat-fox interactions and the white star shows the location of the caching event recorded for a wildcat individual. Green and orange blocks represent forest and pastoral field patches respectively (extracted from the Third Spanish Forest Inventory (1997-2007) of the Spanish Ministry of Agriculture, Fisheries and Food (https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx); Pictures at the bottom from left to right show the typical landscape of the Cantabrian Mountains with human-modified areas mixed with natural surfaces; a wildcat scat, and a wildcat individual photographed during one of the observations. Photos by Héctor Ruiz-Villar.*

SECTION 1

CHAPTER 1

Agriculture intensity and landscape configuration influence the spatial use of wildcats across Europe

Publication: Ruiz-Villar, H., Bastianelli, M.L., Heurich, M., Anile, S., Díaz-Ruiz, F., Ferreras, P., Götz, M., Herrmann, M., Jerosch, S., Jubete, F., López-Martín, J.M., Monterroso, P., Simon, O., Streif, S., Trinzen, M., Urra, F., López-Bao, J.V., Palomares, F., 2023. Agriculture intensity and landscape configuration influence the spatial use of wildcats across Europe. ***Biological Conservation*** 277, 109854.

DOI: https://doi.org/10.1016/j.biocon.2022.109854

1.1 Abstract

Land use intensification is increasing worldwide and affects wildlife movements, particularly of specialist carnivores. Resource availability and anthropogenic activities drive the extent and shape of home range size. Wildlife may respond to decreased resource availability under intensification scenarios by increasing their home ranges; however they may be less affected when inhabiting sustainable agricultural landscapes. We investigate whether agricultural practices and landscape configuration influence the spatial behaviour of wildcats, a medium-sized specialist carnivore inhabiting landscapes with different degrees of agricultural presence across Europe. We focus on the effect of the proportions of high impact and low impact agriculture, forest integrity and forest edge density on wildcat home range size. We found that wildcat home range increased along with the proportion of high impact agriculture and the forest integrity, whereas it decreased when forest edge density increased. Forest edge density buffered the detrimental effects caused by high impact agriculture. To enhance the long term conservation of wildcats in Europe it is crucial to protect the sustainable mosaic-structured landscapes and prevent its conversion to homogenous intensified agricultural landscapes.

1.2 Introduction

Land use intensification is increasing worldwide due to human population growth (Dobrovolski et al., 2011) and it is one of the main causes of biodiversity loss and habitat fragmentation worldwide (Tilman et al., 2001). Intensive agriculture alters the availability, predictability and distribution of resources (Beasley et al., 2007; Ullmann et al., 2018) consequently affecting the spatial ecology of wildlife (Kuefler et al., 2010).

The home range, defined as the environmental cognitive map of an individual that is regularly kept up to date (Powell and Mitchell, 2012) reflects the spatial use of animals aiming at maximizing their survival and reproduction (Börger et al., 2008; Nathan et al., 2008). The size of home ranges is shaped by the balance between the costs and benefits of inhabiting a certain area (Mattisson et al., 2013; Powell and Mitchell, 2012). This trade-off is determined by an array of factors: i) the energetic requirements of animals based on individual characteristics (e.g. sex; (Aronsson et al., 2016), reproductive (Edwards et al., 2013) and social status (Loveridge et al., 2009) ii) community-level factors related with intra- and interspecific interactions (Aronsson et al., 2016); iii) the environmental characteristics (e.g. food and shelter availability; (Mitchell and Powell, 2007; Šálek et al., 2015); and iv) the constraints in animal movement linked to anthropogenic activities (Riley et al., 2003) which may generate a cascade effect over the previously mentioned components (Sévêque et al., 2020).

In accordance with the *resource dispersion hypothesis* (MacDonald, 1983), smaller home-range sizes are exploited in heterogeneous habitats with high food and shelter availability (Newsome et al., 2015; Šálek et al., 2015). Due to their ecological requirements, carnivores are particularly sensitive to changes in resources and landscape configuration associated with intensive agricultural practices (Crooks et al., 2011; Zemanova et al., 2017). Landscapes intensively modified by humans, such as intensive crop fields or urban environments, may be rich in anthropogenic resources and benefit generalist carnivores (e.g. red fox (*Vulpes vulpes*) or racoon (*Procyon lotor*)), which may consequently exploit smaller home ranges (Bateman and Fleming, 2012; Šálek et al., 2015). However, species with some degree of specialisation regarding landscape configuration or resource availability might lose access to important resources in highly humanized landscapes. For example, specialised animals such as bobcats (*Lynx rufus*) , kodkods (*Leopardus guigna*), Eurasian lynxs (*Lynx lynx*) (Herfindal et al., 2005), and coyotes (*Canis latrans*) counteracted the loss of habitat and the restricted access to resources in humanized landscapes by exploiting larger home ranges (Riley et al., 2003; Schüttler et al., 2017). In addition, the cost of maintaining larger home ranges in anthropogenic landscapes might reduce the long-term survival of individuals due to increased human-caused mortality (Bastianelli et al., 2021; Bateman and Fleming, 2012; Poessel et al., 2014).

Extensive sustainable agriculture, however, appears less harming for carnivores as it promotes the maintenance of natural vegetation (Wright et al., 2012). The conservation of patches of original forest and scrubland, hedges, and edges of natural vegetation allow for higher landscape connectivity and diversity than intensified homogeneous agro ecosystems (Wezel et al., 2014). In addition, the use of pesticides is limited in sustainable extensive agriculture which favours the presence of prey species of multiple taxons (Wezel et al., 2014). All the above mentioned factors could modulate the impact of agricultural practices on carnivores and mitigate its negative effects on the home range size throughout enhanced resource availability (Ferreira et al., 2018; Jerosch et al., 2018). Therefore, the home range size of carnivores is expected to increase along a gradient of sustainability of agricultural practices – from extensive to intensive -, and would be modulated by landscape structure (i.e. the presence of different proportions and distributions of natural vegetation inside the agricultural matrix).

The European wildcat (*Felis silvestris*), a medium-sized carnivore specialised in capturing rodents and rabbits (Lozano et al., 2006), inhabits landscapes across Europe with different degrees of presence and intensification of agriculture (Jerosch et al., 2017; Oliveira et al., 2018). Although previously considered a forest specialist, recent research supports the wildcat preference for mosaic-structured landscapes (Lozano et al., 2003; Monterroso et al., 2009; Portanier et al., 2022). Landscape fragmentation associated to human activities and infrastructures, can reduce landscape connectivity (Westekemper et al., 2021), resource availability and ultimately impact wildcat survival (Bastianelli et al., 2021). To cope with such changes in the landscape, wildcats alter their habitat selection and spatial use (Jerosch et al., 2018, 2017; Oliveira et al., 2018). Similarly to other solitary carnivores, wildcat home range size is mainly determined by resource availability, particularly prey and space for females (Anile and Devillard, 2018) and mate availability for males (Sandell, 1989). These sex-specific differences result into different sensitivity of females and males to landscape modifications (Oliveira et al., 2018). Nevertheless, presence and distribution of patches and structures of natural vegetation inside the landscape matrix are key components in wildcat habitat selection and space use (Jerosch et al., 2017; Oliveira et al., 2018).

Although habitat selection and space use of wildcats in agricultural landscapes has been studied locally (Jerosch et al., 2018, 2017), the effects of different agricultural practices on wildcat home range size remain unexplored. As the area dedicated to agriculture is expected to increase in the following years to satisfy the needs of the increasing human population (Tilman et al., 2011), understanding the extent of different agricultural practices and how these affect the space use of wildcats is a matter of urgency for the conservation of wildcats and other sympatric species. With the advent of modern technologies (i.e. GPS collar devices) that provide high resolution data to study the spatial behaviour of animals tracked in agricultural landscapes (Kays et al., 2015) and with the accumulation of movement data collected in the last decades across researchers, such questions can be addressed at broader scales to provide effective recommendations on landscape management that ensure the future survival and functionality of species and ecosystems (Ferreira et al., 2018; Zemanova et al., 2017).

In this article, we examine how different agricultural practices influence the spatial behaviour of wildcats across the human-dominated landscapes of Europe. We expect i) wildcat home ranges to be larger when increasing the proportion of high impact (i.e. intensive) agriculture and the integrity of the remaining forest patches as prey availability for wildcats is expected to decrease in both scenarios. Nevertheless, the negative effect of high impact agriculture could be buffered by the presence of forest edges providing prey and shelter. On the contrary, we expect that ii) home ranges will be smaller when increasing the proportion of low impact (i.e. extensive) agriculture if integrated in landscapes with vegetation cover available (e.g. low impact agriculture intermixed with forest) as such mosaic-structured landscapes provide wildcats with abundant prey and shelter. Finally, we expect that iii) the proportion of high impact agriculture and artificial surfaces inside the home range will be higher for males than females whereas the proportion of refuge vegetation will be higher for females. Furthermore, the effect on the home range size of increasing proportion of high impact agriculture will be higher for females than for males.

1.3 Methods

Wildcat spatial data

We used wildcat tracking data from the collaborative EUROWILDCAT initiative (www.eurowildcat.org). We compiled data from 113 individuals (50 females and 63 males), in 12 study areas distributed across 4 different European countries (Fig 1.1; Table 1.A1). Each study area is thoroughly described in Bastianelli et al., 2021 and in Table 1 in the general introduction of this thesis. The majority of individuals were genetically identified as wildcats, with a few exceptions where only visual identification based on phenotypic pelage characters was applied (Ragni and Possenti, 1996). We did not include hybrids in the analysis to avoid potential behavioural differences between hybrids and wildcats (Germain et al., 2008). Our dataset contained 57056 tracking days (mean ± standard deviation=269.13 ± 185.23 days).

We aim at investigating the relationship between landscape composition and wildcat home range size. Therefore, we used wildcat home-range as the spatial unit for extracting the explanatory variables. We estimated home ranges using Autocorrelated Kernel Density Estimators 95% (AKDE95) because this method successfully addresses two main issues associated with working with large spatial datasets. Firstly, it accounts for spatial autocorrelation between fixes, which is common when working with tracking data (Fleming et al., 2015); and secondly it is little influenced by the length of monitoring periods, number of locations and technologies used (Fleming and Calabrese, 2017), consequently allowing for comparisons across datasets. AKDE95 home ranges provide a mean value and a confidence interval for each individual home range estimation (Fleming et al., 2015). For our purposes we used as a response variable only the mean value. We estimated the home ranges using the package 'amt' (Signer et al., 2019) from R statistical software (R Core Team, 2021).

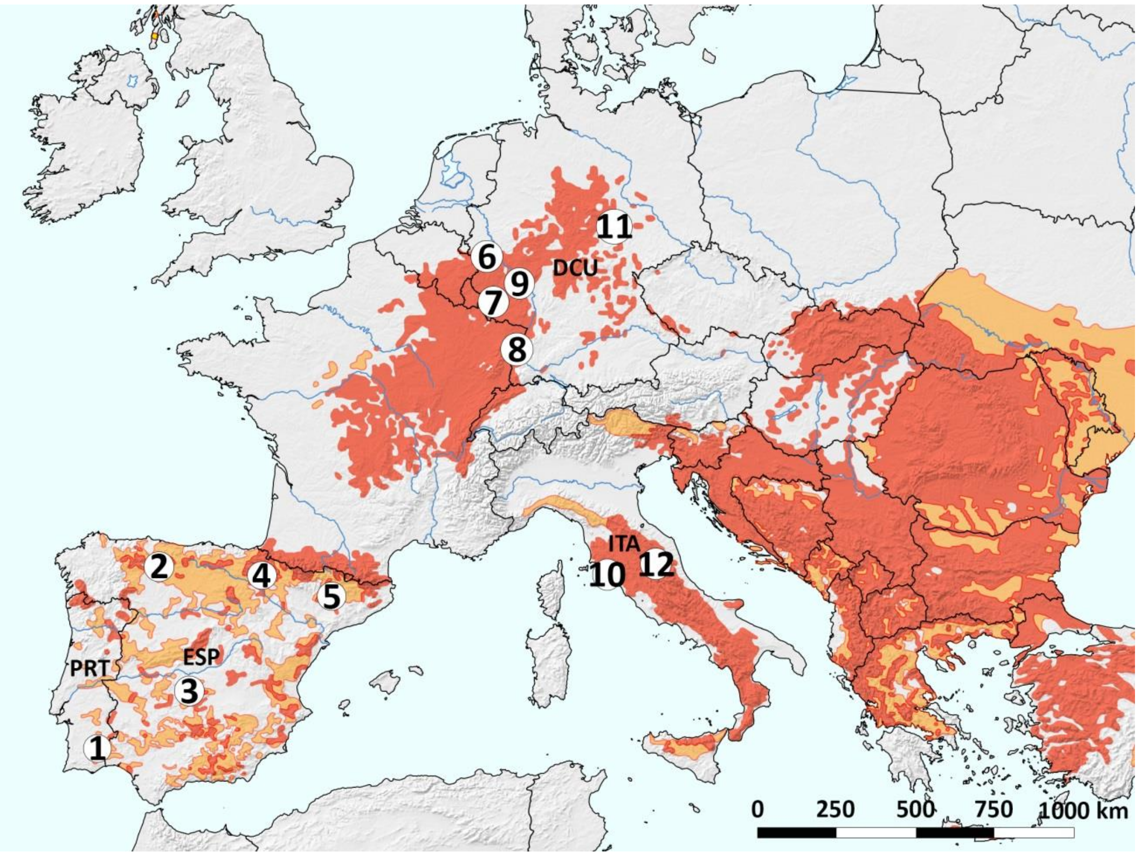


***Figure 1.1**. Location of the 12 study areas within the distribution range of the European wildcat described by Gerngross et al., (2022) and numbered from West to East: 1. Guadiana Valley Natural Park; 2. Cantabrian Mountains; 3. Cabañeros National Park; 4. Izagandoa Valley; 5. Lleida region; 6. Eifel; 7. Moselle Mountains/Hunsrueck/Haardtwald; 8. Rheinauen Kaiserstuhl; 9. Soonwald; 10. Maremma Regional Park; 11. Golden Aue; 12. Paradiso di Pianciano Estate. The red range represents the actual extent of the species, while the yellow range represents the possible extent.*

Environmental variables

We reclassified the Corine Land Cover (CLC) raster layers with 100 m resolution into High Impact Agriculture, Low Impact Agriculture, Refuge and Artificial according to the definitions of each category provided by CLC manuals (Table 1.A2). Afterwards, we extracted the proportion of each category inside each wildcat home range. High Impact Agriculture groups those agricultural categories in which intensive practices with significant environmental alteration occur. On the contrary, Low Impact Agriculture groups those extensive agricultural categories that maintain a significant proportion of natural vegetation. Finally, Refuge and Artificial respectively group categories associated with refuge vegetation (forest and scrubland) and human-created features. We followed Russo et al., 2020 and Bastianelli et al., 2021 and used different CLC layers according to the year in which a given individual wildcat was tracked (Table 1.A3).

We calculated Forest Edge Density (FED) and Forest Landscape Integrity Index (FLII) as proxies for landscape heterogeneity, configuration (Vinter et al., 2016) and forest intactness (Grantham et al., 2020) because they are directly related with prey and shelter availability. High FED values reflect higher landscape heterogeneity (Vinter et al., 2016) and are potentially associated with higher prey diversity and abundance. On the contrary, high FLII values represent homogenous forested landscapes (Grantham et al., 2020) with potentially lower prey availability for a carnivore preferring mosaic-structured landscapes (Benedek and Sîrbu, 2018). To calculate FED, we combined the broadleaved, conifer and mixed forest CLC categories into a single forest category, and then measured the edge length between forest and the remaining categories. This estimate was then divided by the home-range area, resulting in a FED (m/ha) for each wildcat home-range. FLII was extracted and averaged for each wildcat home range (300 m resolution; https://www.forestintegrity.com/home; Grantham et al., 2020).

Additionally, as wildcat occurrence is affected by snow cover (Mermod and Liberek, 2002), we extracted data on winter severity for each home range (500 m resolution) defined as the average number of days per year (from 2000 to 2019) with snow cover in each pixel obtained from MODIS snow data (http://dx.doi.org/10.5067/ACYTYZB9BEOS). Wildcat home ranges were calculated in a planar manner, so we included Terrain Roughness Index (TRI) as calculated by Riley et al., (1999) to account for potential differences in home-range sizes between flat and rough areas and to consider potentially higher shelter availability in rough terrains (Pedro Monterroso et al., 2013b; Oliveira et al., 2018).

Finally, to consider for potential differences in spatial use associated to different prey preferences by wildcats in each study area, we obtained information from the literature on the main prey consumed by wildcats in each or proximate study areas and created a categorical variable with two levels: rodents and rabbits (Table 1.A4).

Average and standard deviation of each continuous variable per study area and sex appear in Table 1.A1.

Statistical analysis

We fitted a generalized linear mixed model (GLMM) with a logarithmic link and gamma distribution with home range size area as response variable and the proportion of High and Low Impact Agriculture, FLII, and FED as explanatory variables. We further included additional covariates on sex (categorical variable with two levels: female and male), proportion of refuge vegetation, proportion of artificial features, winter severity, TRI and main prey to account for potentially factors that can influence wildcat home ranges other than agricultural and forest properties. The interaction terms between High Impact Agriculture and sex, High Impact Agriculture and FED and High Impact Agriculture and FLII were also included. We performed pairwise comparisons to test for significant differences on the proportion of the landscape categories described above between sexes performing Mann–Whitney U test using the wilcox.test function in the ‘stats’ package (R Core Team, 2021).

To account for non-independence of individuals followed within the same study area and with the same collar type (categorical variable with two levels: VHF and GPS), we included study area and collar type as random effects. Details on the biological relevance of the explanatory variables and interaction terms are given in Table 1.1. We did not include the age class of each wildcat as a variable for two reasons: i) a preliminary analysis yielded independence between home range area and age class (Kruskall-Wallis test, $p > 0.5$); and ii) age class information was not available for all individuals. Nevertheless, most individuals were adults (80% of individuals with known age). We did not include the length of each monitoring period for each wildcat because home range estimation using AKDE minimizes differences associated with monitoring time (Fleming and Calabrese, 2017).

We conducted all statistical analyses with the package lme4 (Bates et al., 2015) in the software R (R Core Team, 2021). We checked for collinearity between variables and kept those more related with our research questions (Appendix 1.A, Table 1.A5). We standardised continuous variables to allow for comparability among model coefficients. We selected the most supported model (top model) based on Akaike’s information criterion (AIC; Akaike, 1973) using the function dredge in the package MuMin (Barton, 2015). We compared the top model with a null model that only contained an intercept term. Details of model selection are provided in Table 1.2 while details of the full model are given in Table 1.A6. We explored the alternative of using model averaging but the direction and magnitude of the results did not differ greatly from those obtained by considering only the top model (Table 1.3, 1.A7 & 1.A8). All model assumptions were met and no influential outlying observations were detected (Appendix 1.A).

***Table 1.1**. Biological relevance and rationale for the inclusion of the variables and interaction terms in our model.*

Variable	**Description**
Sex	Included to account for larger home-ranges of wildcat males (Anile et al., 2017; Jerosch et al., 2017).
Proportion of High Impact Agriculture (*HI_Agric*)	We aimed at investigating the effect of the proportion of high impact agriculture on the home range size of wildcats. We expect resource availability to decrease in such conditions thus increasing wildcat home range size.
Proportion of Low Impact Agriculture (*LI_Agric*)	We aimed at investigating the effect of the proportion of low impact agriculture on the home range size of wildcats. We expect resource availability to increase in such conditions thus decreasing wildcat home range size.
Artificial	Anthropogenic structures can present constrains to wildcat movement in the landscape (Bastianelli et al. 2021) potentially influencing wildcat home range size.
Winter severity (*WintSev*)	Snow cover is a limiting factor in European wildcat presence (Mermod & Liberek 2002) and can influence their spatial use. We included this variable to account for potential effects of snow cover on wildcat home range size.
Forest landscape integrity index (*Forest_int*)	Home range size of animals is linked to resource availability (Herfindal et al 2005). We included forest integrity as a proxy for resource availability in forested environments, a key landscape component used by wildcats.
Terrain roughness index (*TRI*)	We calculated home ranges in a planar way so we included the terrain roughness index to account for potential differences between flat and rough areas (Monterroso et al. 2013).

Forest edge density (*Edge_dens*)	Wildcats select for mosaic structured landscapes (Oliveira et al. 2018). Forest edge density is a proxy for landscape heterogeneity and configuration (Vinter et al. 2016). Edges between forests and open lands are rich in prey species for wildcats (Jerosch et al. 2018). As resource availability influences home range size we included forest edge density in our models.
Main Prey	Wildcats select their preferred prey items according to availability and cost-effort balance in predation events (Lozano et al., 2006). Two main prey item types are described for wildcats in the literature: rabbits (*Oryctolagus cuniculus*) and several rodent species. We included this variable as prey type may influence home range size.
Interaction between proportion of high impact agriculture and sex	Resource requirements differ for male and female wildcats (Olveira et al. 2018) and thus the proportion of high impact agriculture inside the home range may affect home range size of males and females differently.
Interaction between proportion of high impact agriculture and forest edge density	The effects of proportion of high impact agriculture and forest edge density are expected to be opposite. It is possible that high forest edge densities compensate in terms of resource availability the lack of resources present in high impact agricultural landscapes consequently influencing home range size.
Interaction between proportion of high impact agriculture and forest landscape integrity index	Forests with high forest integrity may add their effect on wildcat home range size when combined with high impact agricultural landscapes as they create homogeneous landscapes that provide suboptimal conditions for wildcats.

Table 1.2. *Top model resulting from model selection based on Akaike's information criterion (model with the lowest AICc value). Other models with ΔAICc <2 are also shown. df, degrees of freedom; AICc, AIC for small sample sizes; ΔAICc, difference to best statistical model based on AICc; W, Akaike weights (based on all models). Variables are defined as follows: Sex, sex of the individual; HI_Agric, proportion of high impact agriculture; LI_Agric, proportion of low impact agriculture, Forest_int, Forest Lanscape integrity index; Edge_dens, forest edge density; TRI, terrain roughness index; WintSev, winter severity; MainPrey, main prey consumed by wildcats.*

	Variable	**df**	**AICc**	**ΔAICc**	**W**
HR_size	Sex + HI_Agric + Forest_int + Edge_dens + HI_Agric:Edge_dens + HI_Agric:Forest_int	10	805.89	0.00	0.09
	Sex + HI_Agric + Forest_int + Edge_dens + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	806	0.10	0.08
	Sex + HI_Agric + LI_Agric + Forest_int + Edge_dens + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	806.96	1.07	0.05
	Sex + HI_Agric + Forest_int + Edge_dens + TRI + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	807.53	1.63	0.04
	Sex + HI_Agric + Forest_int + Edge_dens + TRI + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.60	1.71	0.04
	Sex + HI_Agric + Forest_int + Edge_dens + WintSev + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.69	1.79	0.04
	Sex + HI_Agric + LI_Agric + Forest_int + Edge_dens + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.71	1.81	0.04
	Sex + HI_Agric + Forest_int + Edge_dens + MainPrey + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	807.83	1.94	0.03
	Null	4	885.52	79.62	$4.57*10^{-19}$

***Table 1.3**. Effects of the variables included in the best supported model on European wildcat home range size. For each variable, we report the estimate (Est), standard error (SE), and significance (P). ΔAICc shows the effect of removing each variable from the top model on the AICc. Significant values are based on Wald statistics with bold font indicating significant effects. Baseline level for Sex is Female.*

	Variable	**Est**	**SE**	**P**	**ΔAICc**
HR_size	Intercept	2.12	0.18	**<0.001**	
	Sex(Male)	1.03	0.19	**<0.001**	36.79
	HI_Agric	0.53	0.16	**<0.001**	30.93
	Forest_int	0.28	0.13	**0.029**	18.29
	Edge_dens	-0.24	0.11	**0.031**	11.45
	HI_Agric:Forest_int	0.47	0.12	**<0.001**	16.89
	HI_Agric:Edge_dens	-0.29	0.11	**0.007**	7.74

1.4 Results

Overall, the proportion of High Impact Agriculture [estimate (Est) = 0.53, standard error (SE) = 0.16, $P < 0.001$; Figure 1.2a, 1.2b, 1.2c; Table 1.3] and FLII [Est = 0.28, SE = 0.13, $P < 0.05$ Figure 1.2b; Table 1.3] were positively correlated with home range size, whereas FED was negatively correlated with range size [Est = -0.24, SE = 0.11, $P < 0.05$; Figure 1.2c; Table 1.3]. Furthermore, we observed an effect of the interactions between the proportion of High Impact Agriculture and FED and FLII. The increment of home range size with the proportion of High Impact Agriculture was significantly reduced when FED increased [Est = -0.29, SE = 0.11, $P < 0.01$; Figure 1.2c; Table 1.3] and turned negative at high FED values (Figure 1.2c). On the contrary, the increase in home range size with the proportion of High

Impact Agriculture was significantly enhanced when increasing FLII values [Est = 0.47, SE = 0.12, P < 0.001; Figure 1.2b; Table 1.3]. We did not detect a significant effect of the proportion of Low Impact Agriculture on wildcat home range size.

Home range size was significantly larger for males than for females [Est = 1.03, SE = 0.19, P < 0.001; Table 1.3], regardless of the proportion of High Impact Agriculture [Figure 1.2a]. Home range of males ranged from 1.3 to 121.6 km^2 (mean=24.1 ± 2.8 SE) while female home range ranged from 0.97 to 155.8 km^2 (mean = 10.5 ± 3.8 SE). The proportion of landscape categories associated with refuge was significantly larger for females than for males (pairwise comparison; p < 0.01; Fig 1.3). On the contrary, the proportion of landscape categories associated with high impact agricultural practices was significantly larger for males than for females (pairwise comparison; p < 0.01; Fig 1.3). We found no difference in the proportion of landscape features related to low intensity agricultural practices (pairwise comparison; p>0.05; Fig 1.3).

The proportion of artificial features, winter severity, terrain roughness and main prey did not influence wildcat home range size significantly.

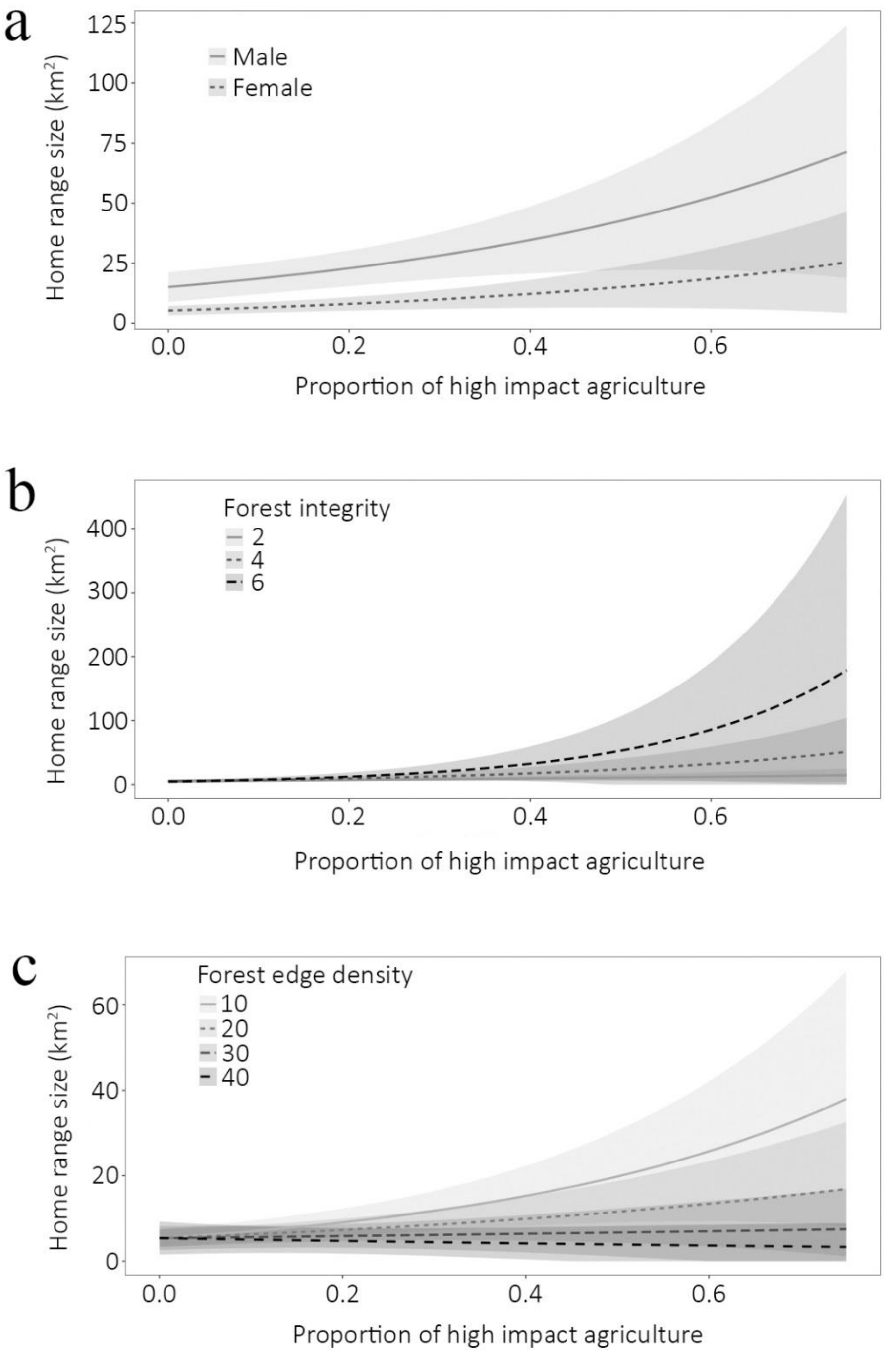


Figure 1.2. *Effects of the proportion of high impact agriculture on European wildcat home range size depending on:* ***a****. Sex (male vs. female);* ***b****. Forest integrity; and* ***c****. Forest edge density. Shown are model predictions with 95% confidence intervals. Predictions were calculated from the top model and by setting all other variables to their mean values.*

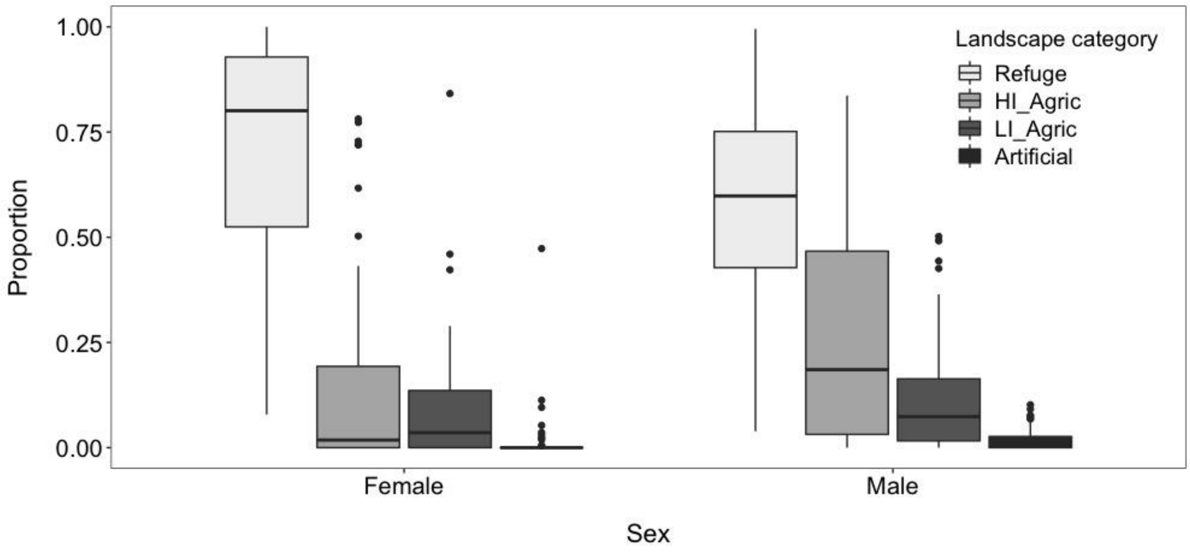


***Figure 1.3**. Variation in the proportion of the four analysed landscape categories (Refuge (pale grey); HI_Agric, i.e. proportion of High Impact Agriculture (medium grey); LI_Agric, i.e. proportion of Low Impact Agriculture (dark grey); Artificial (black)) between female and male wildcats.*

1.5 Discussion

Understanding how land use intensification and habitat transformation/destruction can influence carnivore populations, ecology and behaviour, is key to propose conservation actions that can promote carnivore persistence and functionality in such environments. Our results showed that the home range size of wildcats across Europe is influenced by the proportion of intensive agriculture, integrity of forest patches, and forest edge density. Landscape homogenization associated to land use intensification affect wildcat spatial behaviour by increasing foraging distances in highly fragmented landscapes, which may ultimately decrease individual fitness and trigger changes in population dynamics (Doherty and Driscoll, 2018). Increased movements through unsuitable habitat could also increase wildcat mortality (Bastianelli et al., 2021). The observed variation along gradients of landscape, agriculture-related variables and between sexes may reflect differences in resource availability and biological requirements (different for males and females) of wildcats inhabiting anthropogenic landscapes with varying degrees of agricultural presence (Beugin et al., 2016; Migli et al., 2021b; Oliveira et al., 2018; Portanier et al., 2022).

According to our expectations, wildcat home-range size increased significantly in areas with high proportions of intensive agriculture. The European wildcat is a facultative specialist in terms of diet (preferring rodents and rabbits; Lozano et al., 2006; Malo et al., 2004) and landscape configuration (preferring heterogeneous landscapes with mosaic-like structures; Lozano et al., 2003; Oliveira et al., 2018). Intensive agriculture generates homogeneous and simplified landscapes (Flohre et al., 2011), which generally translate into reduced prey diversity and abundance, the latter enhanced by pest control practices (Benedek and Sîrbu, 2018; Flohre et al., 2011). Consequently, in intensified scenarios, wildcats would need to roam across larger surfaces between the remaining patches of suitable habitat to meet their energetic requirements. Accordingly, lower prey abundance seemed to trigger an increase in wildcats’ home-range size in central Italy (Anile et al., 2017) and Spain (Oliveira et al., 2018), while smaller home ranges occurred in areas with high prey abundance (e.g. southern Portugal; Monterroso et al., 2009). Similarly, other felid species increased their home range size to counteract the loss of resources in human-dominated landscapes (Poessel et al., 2014; Riley et al., 2003; Schüttler et al., 2017).

On the other hand, low intensity and sustainable extensive agricultural practices did not affect wildcat home range size. Likely, such practices produce diverse and connected landscapes, similar to the mosaic landscapes that appear naturally in Europe (Hoffmann and Greef, 2003) and are preferred by wildcats (Lozano et al., 2003; Oliveira et al., 2018). Consequently, home range size of wildcats using sustainable agricultural landscapes should not differ significantly from those animals inhabiting natural mosaic-structured areas.

Following our expectations, home range size increased with increasing forest integrity. Forests with high integrity values are large and well connected, due to lower human pressures, which would be represented by very large homogeneous forest patches (Grantham et al., 2020). On the contrary, forests with medium and low integrity are smaller and fragmented, generally associated with higher human pressures, which would be represented by several forest patches with varying degrees of connectivity between them (Grantham et al., 2020). The first scenario may provide the necessary resources for a forest specialist (Zemanova et al., 2017). However, wildcats prefer mosaic-structured landscapes (Lozano et al., 2003; Oliveira et al., 2018) and could potentially perceive better conditions in slightly fragmented forests with medium to low forest integrity values. These heterogeneous landscapes could provide higher prey and shelter diversity than homogeneous landscapes (Cramer and Willig, 2002). Consequently, wildcats inhabiting large homogeneous forests would probably show larger home ranges. Our results show that the detrimental effects for wildcats associated to intensive agricultural landscapes are enhanced by increasing forest integrity of the surrounding wooded patches. This would be represented by blocks of forest and agricultural lands larger than the average wildcat home range size, so wildcats would not find adequate heterogeneity in small areas and would exploit larger home ranges to survive.

According to our predictions, increasing forest edge density resulted in smaller wildcat home ranges. Forest edge density is a proxy for landscape heterogeneity (Vinter et al., 2016), thus higher values represent more heterogeneous landscapes. Furthermore, as found in previous studies, forest edges are highly suitable habitats for wildcats, offering abundant prey and widespread shelters (Jerosch et al., 2018; Rodríguez et al., 2020), leading to smaller home-range sizes.

Our study reveals that high forest edge density can buffer the detrimental effects of intensive agriculture on wildcats. Indeed, when comparing scenarios characterized by high proportions of high impact agriculture, home range size decreased along with an increase in edge density. This finding corroborates that wildcats can find a more suitable habitat in agricultural landscapes rich in edge structures and forest patches than in large homogeneous agricultural landscapes. However, it is important to note that intensive agricultural landscapes that maintain forest patches with high edge densities are rare as land use intensification generally results in large simplified and homogeneous landscapes that avoid edge promotion (Ekroos et al., 2010).

Consistently with the space use reported in felids, we observed larger home ranges for male than for female wildcats, which corroborates other local studies on the same species (Anile et al., 2017; Jerosch et al., 2017). Our findings are in line with the social structure of felids in which females exploit smaller home ranges in resource-rich habitats to maximize offspring survival, whereas males maintain larger home ranges to include multiple females (Riley et al., 2003; Sandell, 1989).

Finally, wildcat females assume the full costs of the cub rearing process, which may explain why their requirements are generally stricter and choose areas with higher habitat quality than males (Jerosch et al., 2018; Oliveira et al., 2018). Our results reflect such differences between sexes, as female home ranges included a higher proportion of refuge habitats than males, whereas male home ranges included higher proportions of high impact agricultural and artificial categories than females. It is hence possible that males need to move through unsuitable habitats (e.g. agricultural fields) during the mating season to find females (Jerosch et al., 2018). Despite such differences suggest sex-associated sensitivity to habitat modifications, both sexes responded similarly to variations in the proportion of high impact agriculture. Nonetheless, we studied wildcat space use based on home range size variation, and such an approach might not capture variations in habitat selection between males and females at the micro scale.

1.6 Conclusion

Our study corroborates that wildcats find suitable conditions in heterogeneous mosaic landscapes with high presence of natural vegetation such as the extensive and sustainable agricultural landscapes (Lozano et al., 2003; Monterroso et al., 2009; Portanier et al., 2022). On the contrary, it is unlikely that wildcats can thrive in intensive and homogeneous agricultural landscapes, particularly the females, unless there is some degree of heterogeneity. For instance, linear microstructures like hedges and tree lines seemed crucial for wildcat survival in such environments (Jerosch et al., 2018). Future research should investigate the importance of such micro-scale features for wildcats space use in intensified landscapes across Europe.

The current trend of increasing land use intensification worldwide and the associated landscape simplification presents a threat for the European wildcat and for other species inhabiting natural mosaic landscapes (Anile et al., 2019). To favour the long term conservation of wildcats in the highly humanized European landscapes it is crucial to protect the remaining sustainable mosaic-structured landscapes (either natural or anthropic) and to prevent, or at least mitigate, its conversion to homogenous intensified agricultural landscapes. We recommend the promotion and monitoring of Agricultural policies that encourage and reward farmers to employ sustainable agricultural practices across Europe to preserve the mosaic-structured and sustainable agricultural landscape preferred by multiple species like the wildcat.

1.7 Acknowledgements

This paper was conceived and written within the collaborative EUROWILDCAT project (paper no. 002 of the EUROWILDCAT series; https://eurowildcat.org/). The co-authors are grateful to all members for their support for the initiative. The EUROWILDCAT spatial database is hosted by Fondazione Edmund Mach. HRV is beneficiary of a PhD scholarship “Severo Ochoa” from the Regional Government of Principality of Asturias. JVLB was supported by a Ramón y Cajal research contract (RYC-2015-18932) from the Spanish Ministry of Economy, Industry and Competitiveness. F. Díaz-Ruiz was supported by a postdoctoral contract from the University of Málaga (I Plan Propio de Investigación y Transferencia, call 2020).

1.8 Supplementary material

Appendix 1.A – Supplementary information on methods

Model assumption and outlier detection

We checked model assumption through visual inspection of the residuals. We plotted the fitted values against the residuals of the model and residuals greater than two were considered outliers (Atkinson, 1994). In decreasing order, we dropped each outlier from the data and again performed the top model. Outlier removal did not change the direction and magnitude of the effect of the response variables of interest. Furthermore, outliers did not meet the requirements for exclusion. Consequently, all outliers (n=6) were considered valid observations and should not be removed from the analysis (Cousineau and Chartier, 2010).

Collinearity

To avoid using highly correlated predictor variables (|r|>0.7; Dormann *et al.*, 2013), we calculated their correlation matrix (Table A5). The proportion of refuge vegetation inside the home range was correlated with the proportion of High Impact Agriculture (|r| = -0.80). Our research questions are related with the proportion of High Impact Agriculture and we consequently removed the proportion of refuge vegetation for further analyses.

***Table 1.A1**. Average and standard deviation of the variables considered in our model for male and female wildcats from different study areas across Europe. M refers to males and F to females. Brackets shows number of individual wildcats from each sex monitored in each study area. Definitions of variables appear in Table 1.*

Study area	Sex	HR_size	Artificial	Refuge	HI_Agric	LI_Agric	WintSev	Forest_int	TRI	Edge_dens
Guadiana Valley Natural Park	M (2)	28.03 ± 7.53	0 ± 0	0.53 ± 0.04	0.31 ± 0.15	0.16 ± 0.11	0.91 ± 0.18	0.16 ± 0	1.8 ± 0.4	0.83 ± 1.05
	F (4)	4.58 ± 1.07	0 ± 0	0.57 ±0.32	0.09 ± 0.17	0.33 ± 0.35	1.32 ± 0.58	0.31 ± 0.31	2.55 ± 0.54	2.42 ± 3.04
Cabañeros National Park	M (1)	47.53 ± NA	0 ± NA	0.45 ± NA	0.49 ± NA	0.03 ± NA	1.22 ± NA	6.66 ± NA	1.48 ± NA	14.81 ± NA
	F (1)	121.27 ± NA	0 ± NA	0.48 ± NA	0.43 ± NA	0.02 ± NA	1.50 ± NA	7.33 ± NA	1.8 ± NA	12.85 ± NA
Izagandoa Valley	M (3)	39.19 ± 18.85	0 ± 0	0.49 ± 0.17	0.1 ±0.14	0.05 ± 0.07	12.21 ± 3.54	2.83 ± 1.20	3.76 ± 0.54	12.27 ± 2.55
	F (2)	5.33 ± 1.75	0 ± 0	0.8 ±0.25	0.45 ± 0.12	0.01 ± 0.01	13.25 ± 4.81	2.80 ± 0.44	5.93 ± 0.85	24.8 ± 14.32
Lleida Region	M (6)	24.68 ± 23.01	0.004 ± 0.01	0.28 ± 0.13	0.63 ± 0.11	0.08 ±0.06	1.51 ±032	0.63 ± 0.73	2.35 ± 0.57	10.85 ± 8.63
	F (1)	6.83 ± NA	0 ± NA	0.34 ± NA	0.62 ± NA	0.04 ±NA	1.29 ± NA	0.16 ± NA	2.08 ± NA	14.49 ± NA
Eifel	M (6)	30.19 ± 44.81	0.01 ± 0.01	0.09 ± 0.02	0.02 ± 0.01	0.42 ± 0.09	60.49 ± 2.46	3.32 ± 0.64	1.79 ± 0.31	10.08 ± 4.4
	F (6)	3.88 ± 2.3	0 ± 0	0.75 ± 0.18	0.01 ± 0.03	0.24 ± 0.16	63.42 ± 7.88	2.97 ± 0.55	1.74 ± 0.18	11.95 ± 7.31
Haardtwald	M (6)	9.4 ± 4.43	0.01 ± 0.01	0.76 ± 0.16	0.1 ± 0.12	0.13 ± 0.07	50.84 ± 8.9	3.63 ± 2	2.62 ± 0.55	12.75 ± 10.92
	F (6)	3.49 ± 1.41	0 ± 0	0.88 ± 0.14	0.03 ± 0.04	0.09 ± 0.11	63.14 ± 11.39	3.59 ± 1.62	2.46 ± 0.6	12.21 ± 10.05
Rheinauen Kaiserstuhl	M (8)	30.88 ± 25.08	0.05 ± 0.02	0.47 ± 0.13	0.36 ± 0.16	0.01 ± 0.01	9.86 ± 1.55	1.35 ± 0.43	1 ± 0.62	16.75 ± 4.43
	F (11)	4.11 ± 2.53	0.02 ± 0.03	0.71 ± 0.17	0.14 ± 0.14	0.02 ± 0.06	10.62 ± 3.03	1.48 ± 0.54	1.16 ± 1.13	19.33 ± 4.78
Soonwald	M (6)	12.98 ± 5.35	0.04 ± 0.04	0.73 ± 0.18	0.08 ± 0.06	0.15 ± 0.09	42.2 ± 7.01	3.9 ± 1.06	1.96 ± 0.39	7.46 ± 2.53
	F (6)	4.33 ± 2.66	0.02 ± 0.04	0.92 ± 0.14	0.01 ± 0.03	0.04 ± 0.07	43.91 ± 10.37	3.83 ± 1.39	2.16 ± 0.54	5.56 ± 5.68
Maremma Regional Park	M (3)	47.09 ± 47.09	0.01 ± 0.01	0.58 ± 0.17	0.17 ± 0.09	0.08 ± 004	9.55 ± 1.67	1.45 ±0.26	2.61 ±0.18	11.9 ± 4.54
	F (1)	10.19 ± NA	0 ± NA	0.91 ±NA	0 ± NA	0.05 ± NA	9.95 ± NA	0.96 ±NA	3.85 ± NA	20.84 ± NA
Golden Aue	M (7)	23.42 ± 7.11	0.06 ± 0.03	0.11 ± 0.11	0.73 ± 0.11	0.09 ± 0.05	36.79 ± 1.15	1.55 ± 1.22	1.16 ± 0.34	15.96 ± 14.46
	F (9)	28.77 ± 62.30	0.01 ± 0.02	0.20 ± 0.15	0.70 ± 0.10	0.08 ± 0.07	37.87 ± 2.57	0.7 ± 0.99	1.74 ± 0.32	3.23 ± 1.06
Paradiso di Pianciano Estate	M (8)	10.98 ± 17.69	0.002 ± 0.005	0.72 ± 0.09	0.17 ± 0.14	0.05 ± 0.06	19.01 ± 4.96	4.49 ± 1.09	7.38 ± 0.51	19.2 ± 3.27
	F (1)	29.89 ± NA	0 ± NA	0.82 ± NA	0.03 ± NA	0.07 ± NA	21.15 ± NA	4.65 ± NA	7.99 ± NA	19.22 ± NA
Cantabrian Mountains	M (9)	19.38 ± 9.07	0.01 ± 0.02	0.79 ± 0.14	0.02 ± 0.02	0.07 ± 0.09	57.51 ± 15.32	5.91 ± 1.18	6.88 ± 2.41	30.78 ± 4.75
	F (5)	7.74 ± 11.05	0.09 ± 0.21	0.81 ± 0.25	0.003 ± 0.01	0.04 ± 0.04	54.53 ± 18.49	5.55 ± 1.57	8.34 ± 3.27	32.22 ± 13.86

Table 1.A2. *Reclassification of Corine Land Cover categories*

Original Corine Land Cover category	Reclassified category
Non-irrigated arable land	**HI_Agric (High Impact Agriculture)**
Permanently irrigated land	
Vineyards	
Fruit trees and berry plantations	
Olive groves	
Complex cultivation patterns	
Pastures	**LI_Agric (Low Impact Agriculture)**
Land principally occupied by agriculture, with significant areas of natural vegetations	
Agro-forestry areas	
Broad-leaved forest	**Refuge**
Coniferous forest	
Mixed forest	
Sclerophyllus vegetation	
Transitional Woodland-shrub	
Continuous urban fabric	**Artificial**
Discontinuous urban fabric	
Industrial or commercial units	
Road and rail networks and associated land	
Port areas	
Airports	
Mineral extraction sites	
Dump sites	
Construction sites	
Green urban areas	
Sport and leisure facilities	

Table 1.A3. *Corine Land Cover Databases used for the period each individual wildcat was monitored.*

Corine Land Cover Database	Wildcat monitoring period
1990	1990-1998
2000	1999-2003
2006	2004-2009
2012	2010-2014
2018	2015-2020

***Table 1.A4**. Main prey item (rodents vs. rabbit) of European wildcats in the different study areas.*

Study Area	Main prey item	References
Guadiana Valley Natural Park	Rabbit	Monterroso *et al.*, 2009
Cabañeros National Park	Rabbit	Ferreras *et al.*, 2021
Izagandoa Valley	Rodents	Urra, 2003
Lleida Region	Rabbit	Lozano et al., 2006
Eifel	Rodents	Sládek, 1973
Haardtwald	Rodents	
Rheinauen Kaiserstuhl	Rodents	
Soonwald	Rodents	
Maremma Regional Park	Rodents	Ragni, 1981
Golden Aue	Rodents	Sládek, 1973
Paradiso di Pianciano Estate	Rodents	Ragni, 1981
Cantabrian Mountains	Rodents	Ruiz-Villar *et al.*, 2022

***Table 1.A5**. Results of the correlation matrix between the considered continuous variables. Variables are defined as follows: HI_Agric, proportion of high impact agriculture; LI_Agric, proportion of low impact agriculture; Refuge, proportion of refuge vegetation; Artificial, proportion of anthropogenic CLC categories; WinterSev, Winter Severity; Forest_int, Forest Lanscape integrity index; TRI, Terrain Roughness Index; Edge_dens, forest edge density. Bold numbers show values between highly correlated variables (|r|>0.7).*

	HI_Agric	LI_Agric	Refuge	Artificial	WinterSev	Forest_int	TRI	Edge_dens
HI_Agric	1.00	-0.10	**-0.80**	0.26	-0.56	-0.54	-0.34	-0.14
LI_Agric		1.00	-0.25	-0.03	0.26	0.00	0.02	-0.29
Refuge			1.00	-0.33	0.43	0.56	0.43	0.21
Artificial				1.00	0.03	-0.06	-0.37	-0.03
WinterSev					1.00	0.57	0.24	0.06
Forest_int						1.00	0.48	0.21
TRI							1.00	0.28
Edge_dens								1.00

***Table 1.A6**. All parameters included in the full model of the GLMM investigating variation in home range size (km^2) of European wildcats. CLC refers to Corine Land Cover databases.*

Response	Fixed	Variable description	Random
HR_size	*Sex*	Sex of the individual: Male, Female	*Study_area*
	HI_Agric	Proportion of high impact agriculture CLC categories inside the home range	*Collar_type*
	LI_Agric	Proportion of low impact agriculture CLC categories inside the home range	
	Artificial	Proportion of artificial CLC categories inside the home range	
	WintSev	Winter Severity. Average number of days per year with snow cover	
	Forest_int	Mean Forest Integrity values for each Home range (from 0 to 10)	
	TRI	Terrain Roughness Index	
	Edge_dens	Forest edge density (m/ha)	
	MainPrey	Main prey item of wildcats for each Home range: Rabbits, rodents.	
	Sex:HI_Agric	Interaction between proportion of high impact agriculture and sex	
	HI_Agric:Edge_dens	Interaction between proportion of high impact agriculture and forest edge density	
	HI_Agric:Forest_int	Interaction between proportion of high impact agriculture and forest landscape integrity index	

***Table 1.A7**. Effects of individual, agricultural and forest variables on European wildcat home range size resulting from model averaging procedures. For each variable, we report the estimate (Est), standard error (SE), and significance (P). ΔAICc shows the effect of removing each variable from the top model on the AICc. Significant values are based on Wald statistics with bold font indicating significant effects. Baseline level for Sex is Female and for Main Prey is Rabbits.*

	Variable	**Est**	**SE**	**P**	**ΔAICc**
HR_size	Intercept	2.11	0.21	**<0.001**	
	Edge_dens	-0.25	0.11	**0.032**	11.45
	Forest_int	0.28	0.14	**0.041**	18.29
	HI_Agric	0.58	0.18	**0.002**	30.93
	Sex(Male)	1.00	0.19	**<0.001**	36.79
	HI_Agric:Edge_dens	-0.30	0.11	**0.007**	7.74
	HI_Agric:Forest_int	0.44	0.13	**<0.001**	16.89
	Sex(Male):HI_Agric	-0.12	0.18	0.526	
	TRI	-0.03	0.10	0.748	
	WintSev	-0.01	0.05	0.852	
	LI_Agric	0.02	0.07	0.733	
	MainPrey	0.02	0.12	0.880	

***Table 1.A8**. Set of models resulting from model average based on Akaike's information criterion (model with ΔAICc <2 are retained). df, degrees of freedom; AICc, AIC for small sample sizes; ΔAICc, difference to best statistical model based on AICc; W, Akaike weights (based on all models with ΔAICc < 2). Variables are defined as follows: Sex, sex of the individual; HI_Agric, proportion of high impact agriculture; LI_Agric, proportion of low impact agriculture; Forest_int, Forest Lanscape integrity index; Edge_dens, forest edge density; TRI, Terrain Roughness Index; Artificial, proportion of anthropogenic CLC categories.*

	Variable	**df**	**AICc**	**ΔAICc**	**W**
HR_size	Sex + HI_Agric + Forest_int + Edge_dens + HI_Agric:Edge_dens + HI_Agric:Forest_int	10	805.89	0.00	0.22
	Sex + HI_Agric + Forest_int + Edge_dens + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	806	0.10	0.21
	Sex + HI_Agric + LI_Agric + Forest_int + Edge_dens + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	806.96	1.07	0.13
	Sex + HI_Agric + Forest_int + Edge_dens + TRI + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	807.53	1.64	0.1
	Sex + HI_Agric + Forest_int + Edge_dens + TRI + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.60	1.71	0.09
	Sex + HI_Agric + Forest_int + Edge_dens + WintSev + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.69	1.79	0.09
	Sex + HI_Agric + LI_Agric + Forest_int + Edge_dens + Sex:HI_Agric + HI_Agric:Edge_dens + HI_Agric:Forest_int	12	807.71	1.81	0.09
	Sex + HI_Agric + Forest_int + Edge_dens + MainPrey + HI_Agric:Edge_dens + HI_Agric:Forest_int	11	807.83	1.94	0.08
	Null	4	885.52	79.62	

CHAPTER 2

Presence of pastoral fields in mountain landscapes influences prey consumption by European wildcats.

Publication: Ruiz-Villar, H., Urra, F., Jubete, F., Morales-González, A., Adrados, B., Revilla, E., Rivilla, J.C., Román, J., Seijas, J., López-Bao, J. V., Palomares, F., 2022. Presence of pastoral fields in mountain landscapes influences prey consumption by European wildcats. ***Journal of Zoology***. 319, 63–75.

DOI: https://doi.org/10.1111/jzo.13027

2.1 Abstract

Traditional agro-pastoral practices are more beneficial for biodiversity than intensified agricultural systems. Promotion of growth of natural herbaceous vegetation in pastoral fields can enhance rodent populations and consequently influence ecological aspects of carnivores with rodent-based diets, like prey consumption in the European wildcat (*Felis silvestris*). In this article, we investigated the effects of pastoral field extent, season and prey abundance on wildcat consumption of several prey species in the Cantabrian Mountains (NW Spain). Prey consumption in areas with presence of pastoral fields (even in low proportions) was dominated by profitable field-dwelling rodent species such as *Arvicola monticola*. Consumption of *Arvicola* was not correlated with its abundance and was higher during summer and autumn. *Apodemus* dominated wildcat diet in areas with higher forest proportion and far from pastoral fields particularly during spring. Our results suggest that varying habitat use and seasonal changes in prey accessibility may determine wildcat prey consumption in pastoral landscapes. Our results can contribute to highlight the potential benefits of traditional and sustainable pastoral activities for the conservation of the European wildcat across its distribution range.

2.2 Introduction

Traditional agro-pastoral systems, characterized by low-intensity agricultural practices (i.e., avoidance of overexploitation of natural resources, low use of machinery and chemicals, use of organic fertilizers, and promotion of natural vegetation (Wezel et al., 2014; Wright et al., 2012)), lead to mosaic landscapes that provide multi-taxon benefits and preserve higher biodiversity levels than more intensified agricultural systems (Doxa et al., 2010; Jubete and Román, 2016; Mander et al., 1999).

Pastoral activities can affect demography and distribution of species. For instance, pastoral fields (i.e., meadows and pasturelands sustainably managed to produce livestock forage) provide open areas with high productivity of natural herbaceous vegetation that enhance populations and richness of rodents (Briner et al., 2005; Duhamel et al., 2000; Morilhat et al., 2007). Rodent abundance in pastoral fields may increase foraging opportunities for predator species with rodent-based diets aiming for the most profitable prey items in terms of biomass, hunting effort, and abundance (Schoener, 1987). This can ultimately influence predator demographic performance through changes in habitat and prey selection (Millon and Bretagnolle, 2008; Moreira-Arce et al., 2015; Šálek et al., 2010). In addition, rodent availability and accessibility varies annually and seasonally in pastoral fields (e.g., increasing after harvest when prey species are more abundant and exposed; Butler and Gillings, 2004; Jacob and Tkadlec, 2010), and predators are expected to adapt to changes according to their degree of specialization (Andersson and Erlinge, 1977; Ishii and Shimada, 2010; Molsher et al., 1999).

European wildcats (*Felis silvestris*) can adapt their diet based on prey abundance and availability (Apostolico et al., 2016; Lozano et al., 2006). The European rabbit (*Oryctolagus cinnuculus*) is the main prey item for wildcats in the Iberian Mediterranean region (Lozano et al., 2006), whereas in temperate areas where rabbits are absent, rodents become the majority of their diet (Apostolico et al., 2016; Lozano et al., 2006; Piñeiro and Barja, 2011). For instance, Mermod and Liberek (2002) research on agro-pastoral mosaic landscapes of Switzerland detected montane water voles (*Arvicola monticola;* a large rodent species subject to population cycles weighing between 66 to 183 g) as important prey items. These voles select for open areas, such as pastoral fields and meadows (Duhamel et al., 2000), where they can cause economic damages (Delattre and Giraudoux, 2009), and traditional pastoral activities can enhance their populations (Morilhat et al., 2007). Although wildcat diet and use of mosaic landscapes have been studied separately (Jerosch et al., 2018; Lozano et al., 2003), the relationship between pastoral field extent inside wildcat territories and the importance of the highly profitable montane water voles in the diet of wildcats remains unexplored. Research in this direction can contribute to highlight the potential benefits of traditional pastoral activities for conservation of medium-sized carnivores depending upon rodent prey species and mosaic landscapes.

Wildcats in the Cantabrian Mountains (NW Spain) occupy landscapes with varying proportions of pastoral fields intercalated among a matrix of natural vegetation of deciduous forests and scrublands (López, 2002), going from totally wooded areas lacking pastoral fields to wide valleys with an important area occupied by these fields. Such gradient creates a good opportunity to investigate how prey consumption by wildcats shifts in relation to variations in proportion of pastoral fields in the landscape, and to the abundance of main prey items. We addressed the following questions: 1) Does a higher consumption of field associated rodent species (e.g., *Arvicola monticola*) relate to higher presence of pastoral fields?; 2) Does consumption of *Arvicola monticola* increase during summer and autumn, when higher prey availability and accessibility in pastoral fields is expected?, and 3) Is wildcat annual consumption of main prey rodent species (*Arvicola monticola* and *Apodemus*) determined by their annual abundance?

2.3 Methods

Study area

Our study was conducted in two separate areas of the Cantabrian Mountains (NW Spain; Figure 2.1): Montaña Palentina Natural Park (MP; 190 km^2) in the central Cantabrian Mountains of Palencia; and the Western Cantabrian Mountains (WCM; 1800 km^2) between the provinces of Asturias and León. Both areas hold temperate oceanic bioclimatic conditions surrounded by a few submediterranean locations (Martínez and Arregui, 1999). Vegetation consists mainly of deciduous forests (*Quercus, Fagus* and *Betula* sp.), scrublands, and pastoral fields in the valley bottoms (Loidi, 2017). We selected two study areas to cover for a complete gradient of proportion of pastoral fields and forests in the landscape. On one hand, landscape diversity is higher in WCM, having areas with high forest and low field proportion (42.8 and 9.9 % respectively; western part of Figure 2.1a) and with low forest and higher field proportion (20.4 and 20.2 % respectively; eastern part of Figure 2.1a). Alternatively, MP lies in between, with higher proportions of both forest and fields, which together occupy most of the area (51.5 and 25% respectively; Figure 2.1b). MP is dominated by limestone soils whereas the WCM have both limestone and siliceous soils. Both areas present low human population densities (<15 inhabitants/km^2; Goerlich and Cantarino, 2013) with economy based on livestock herding of cows and horses.

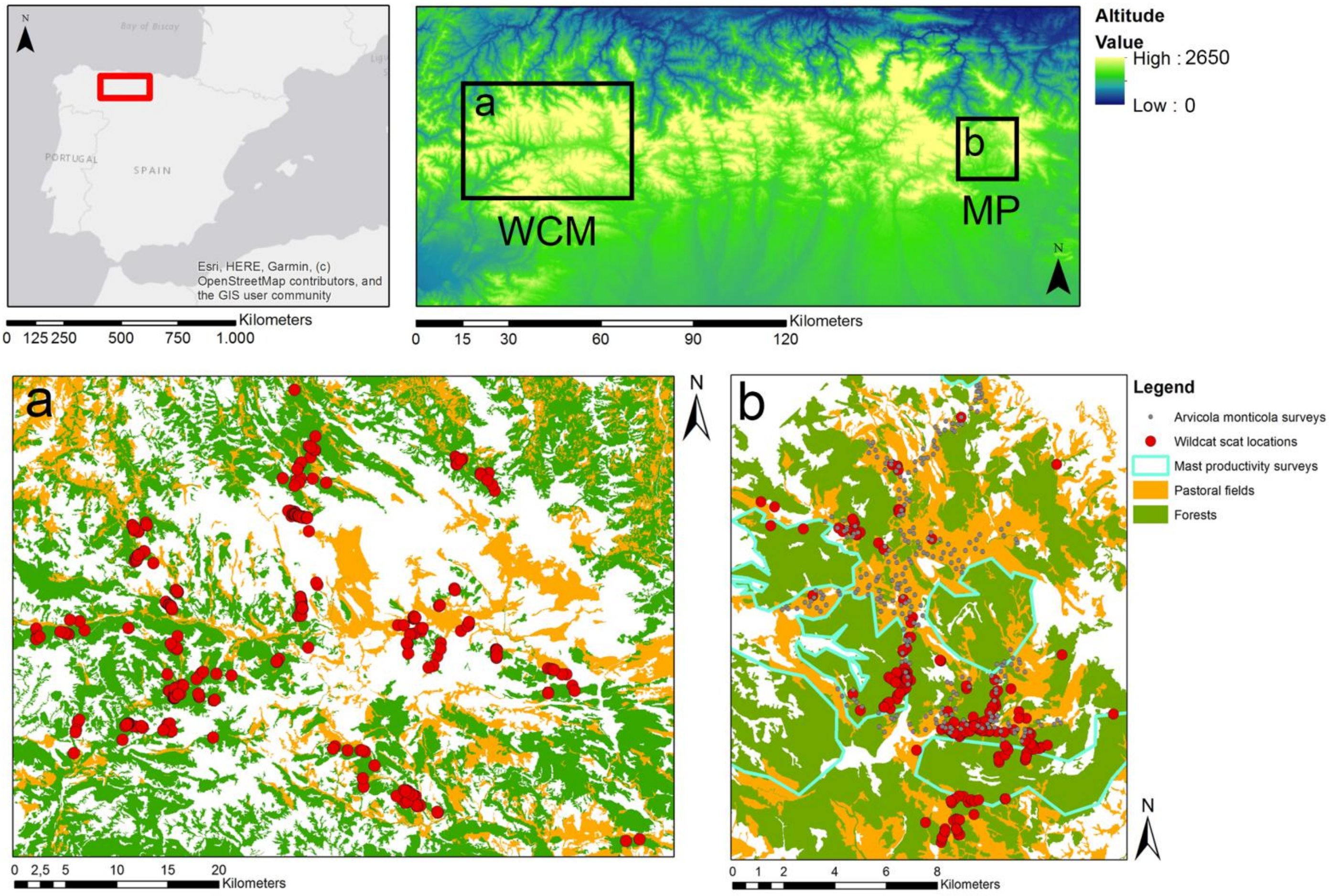


Figure 2.1. *Location of the two study areas inside the Cantabrian Mountains (NW Spain): a) WCM (Western Cantabrian Mountains) and b) MP (Montaña Palentina). Red circles show the location of the wildcat scats collected for the study period, grey spots and blue-lined polygons respectively indicate the locations of* Arvicola monticola *and mast productivity surveys. Green and orange blocks represent forest and pastoral field patches respectively (extracted from the Third Spanish Forest Inventory (1997-2007) of the Spanish Ministry of Agriculture, Fisheries and Food (https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx).*

Data collection

Scat sampling, identification and analyses of prey composition

European wildcat scats were collected both systematically in fixed transects and opportunistically, between Dec 2018 and Feb 2020 in WCM and between Nov 2014 and April 2020 in MP (Figure 2.1 and Supplementary File 2.1). Size of surveyed areas derives from landscape diversity, i.e. larger and smaller surveyed areas in WCM and MP associated to higher and lower landscape diversity respectively. Transects were repeated every three months aimed at collecting samples across meteorological seasons (hereafter referred to as seasons) in the same areas. We collected samples along the gradient of variables of interest to obtain a continuous and representative amount of samples inside each variable range (Figure 2.1 and Supplementary File 2.1). For each sample we recorded date, GPS location and estimated defecation season, the latter based on the degradation status of the scat and on the time passed from the previous transect in the same location. Very old-looking scats were never collected.

Scats were collected by experienced European wildcat researchers and assigned to European wildcat based on its morphology and smell. Although the certainty of assigning scats to carnivore species has been questioned (Monterroso et al., 2013), experimented researchers can accurately identify European wildcat scats (Barja et al., 2012). Nevertheless, to assess the researchers’ success in scat identification, a subsample of 135 scats was genetically analysed (Appendix 2.S1). From 123 scats that we could genetically identify, 107 (87%) were from the *Felis* genus, 15 from *Vulpes vulpes* and one from *Canis* sp. The proportion of misidentified fox scats was the same across study areas. We are confident that *Felis* scats belong to wildcats considering that: a) wildcats and domestic cats segregate in the

Cantabrian Mountains (Rodríguez et al., 2020) and other regions (Gil-Sánchez et al., 2015), and we consequently avoided scat collection in areas used by domestic cats; and b) no hybrids have been detected in the area so far (Tiesmeyer et al., 2020).

To determine the prey species consumed by wildcats we used macroscopic identification of bones, teeth, scales, feathers, and other identifiable prey remains extracted from washed scats. We determined the minimum number of individuals for each prey item in each scat based on repetition of identifiable remains. We used the identification guide by Román (2019) to identify Spanish rodents from bone and teeth remains, and compared reptile and bird remains with specimens preserved in Doñana Biological Station.

We described wildcat diet composition using both deterministic approaches (i.e. total count and relative frequency, and frequency of occurrence) to allow for comparisons with previous studies, and multinomial modelling (Morin et al., 2019) using Huggins closed population capture-recapture approaches (‘mra’ package in R; McDonald et al., 2018) to account for potential biases in sampling and prey detection.

Estimation of landscape composition surrounding wildcat scats

We created a buffer around each scat, estimated to include wildcat movements between the predation and defecation events. The mean time between predation and defecation (i.e., time that the food spends inside the gut from ingestion to defecation) for domestic cats and other medium felids is ca. 24h (23.78h) (Edwards et al., 2001; Loureiro et al., 2017). Consequently, we established a buffer with the size of the area potentially used by wildcats during 24h previous to defecation. We used data from 40 intensive GPS tracking datasets from 12 wildcats from the study area and period (6 individuals followed by the authors and 6 provided by TRAGSATEC S.A. (Ruiz-

Villar et al., 2023); further details on animal capture and handling are provided in Ruiz-Villar et al., (2020) and in Appendix 2.S2). Mean maximum distance between estimated predation and defecation sites was 1574.5 ± 1035.2m. Therefore, we created buffers with a radius of 1500m.

Within each buffer, we calculated the proportion of forest, shrub and pastoral fields, created after reclassifying the landscape categories obtained from the Third Spanish Forest Inventory (1997-2007) of the Spanish Ministry of Agriculture, Fisheries and Food (https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx ; see Supplementary File 2.2 for reclassification procedures). Distance from hunting grounds may also affect wildcat diet, and thus we calculated the minimum distance between each scat and the closest forest, shrub and pastoral field patch. We used ArcGis 10.1 (ESRI, 2012) for the analysis and extraction of landscape variables.

<u>Prey abundance estimates</u>

To study the influence of the abundance of the main prey rodent species on prey consumption by wildcats, we estimated the annual abundance of *Arvicola monticola* and forest dwelling species (i.e., *Apodemus* sp.) in MP, where forest and pastoral fields have wider representation in areas potentially used by the same wildcat individual.

We estimated the annual abundance of *Arvicola monticola* by surveying 278 fixed transects (100 m long; Figure 2.1b) during 4 consecutive days between 30th September and 14th October (2016-2019). To maintain constant soil and humidity conditions, we ran transects parallel to water courses. For transect selection, from a cloud of 500 sampling stations surrounding wildcat observations in pastoral fields during systematic wildcat count campaigns by

Rodríguez et al.(2020), we selected those with distance between sampling points greater than 100 m and distance to roads shorter than 500 m. We merged wildcat observations occurring closer than 100 m and discarded stations: located within 100 m from other wildcat observation, outside *Arvicola monticola*'s preferred habitats, and in inaccessible terrain. We subdivided each transect in 20 segments (5 m long and 5 m wide) where we counted for *Arvicola monticola* galleries identified by shape, entrance and disposition (Miñarro et al., 2012), obtaining an abundance index for *Arvicola monticola* ranging from 0 (no galleries found) to 20 (galleries present in all the segments). Gallery counts in *Arvicola* have been correlated with its abundance (Giraudoux et al., 1995).

Additionally, to estimate the annual abundance of *Apodemus* sp., we used mast productivity for the Fagacea family trees (*Fagus sylvatica*, *Quercus petraea* and *Quercus pyrenaica*) during autumn as a reliable proxy for delayed *Apodemus* abundance (from spring to autumn of the following year) (Pucek et al., 1993). For the period 2016 – 2020, between September and October just before acorn fall, we surveyed 880 tree individuals inside the main forest patches of MP (Figure 2.1b) counting the maximum number of fruits on each tree for 30 seconds (i.e., N30 productivity value; Koenig et al., 1994). To make productivity values representative of the forest patch, trees had to be: embedded in the forest patch (to avoid effects of abnormal insolation on productivity); under low competition stress with other trees; and in a mature fructification stage estimated from the normal diameter of each tree (> 40 cm). Visual productivity counts permit to rapidly survey large areas along years accounting for several branches of the same tree (Koenig et al., 1994). Finally, we averaged productivity values for the MP study area for each year.

Statistical analysis

Effects of landscape composition on prey consumption by wildcats

We used Multivariate Regression Trees (MRTs) to investigate the effect of landscape variables in the consumption of different prey items by European Wildcats. This method builds a hierarchical tree through successive dichotomies of the set of explanatory variables. The nodes establish thresholds in the explanatory variables organizing samples in groups that minimize and maximize dissimilarities on prey species composition within and between groups respectively (De'ath, 2002; Larsen and Speckman, 2004). MRTs are a robust method that efficiently analyse the relationship between multispecies data and environmental characteristics (i.e., between predated species and multiple landscape variables), tolerating certain degree of correlation between variables and efficiently accounting for many response variables (in our case, several ingested prey species) (De'ath, 2002; De'ath and Fabricius, 2000). However, to increase model predictability, we tested collinearity between variables using the Spearman correlation and excluded those with lower biological meaning between pairs with correlation values > 0.7 (Moore et al., 2010) (Supplementary File 2.3). Thus, we discarded percentage and distance to shrub, as they were less interesting for our analysis than the forest variables with which they were highly correlated. The final variables appear in Table 2.1. As our two study areas are ca. 100 km apart, we included study area location in our analysis to account for potential variation in prey composition and abundance between MP and WCM derived from subtle climatic and vegetation differences.

Table 2.1. *Codes, descriptions and rationale of the explanatory environmental variables included in the Multivariate regression tree (MRT) analysis. Forest-dwelling species refer to mice from the genus* Apodemus *and to* Myodes glareous*. Field-dwelling species refer to* Arvicola monticola*,* Microtus lusitanicus*,* Microtus arvalis *and* Microtus agrestis*.*

Predictor code	Type	Description	Rationale and associated hypothesis
Loc	Categorical	Study area location. Two levels: Montaña Palentina (MP) and Western Cantabrian Mountains (WCM)	Potential differences in wildcat diet may arise from sampling separated study areas.
Season	Categorical	Estimated meteorological season for scat deposition. Four levels: Autumn (Atmn), Winter (Wntr), Spring (Sprn) and Summer (Smmr)	Wildcat diet varies seasonally in other parts of the world (Lozano et al., 2006) and we expect the same to occur in our study.
PerFor	Continuous	Percentage of a 1500 m buffer surrounding each scat occupied by forest	Composition, abundance and availability of rodent prey species may change with varying proportions and distance to forest and fields (Cavia, Cueto & Suárez, 2009; Stevens & Tello, 2009). Wildcat prey consumption is expected to vary along a gradient of such variables: forest-dwelling species will dominate wildcat diet in areas with higher proportions and closer to forest and field-dwelling species will dominate wildcat diet in areas with higher proportions and closer to fields.
PerField	Continuous	Percentage of a 1500 m buffer surrounding each scat occupied by pastoral fields.	
Dist_For	Continuous	Distance in metres from the scat collection point to the closest forest patch. Distant is zero if the scat was collected inside a forest patch.	
Dist_Field	Continuous	Distance in metres from the scat collection point to the closest pastoral field. Distant is zero if the scat was collected inside a pastoral field.	

We used cross-validation to identify the tree size that optimized predictability (lowest Relative Error), which we selected because in our case it simultaneously allowed for reliable interpretation of results and included most of our variables of interest (Supplementary File 2.4). We calculated the overall fit of the model, i.e., the fraction of variance not explained by the tree (Error), and the predictive accuracy of the tree (CV Error) (De'ath, 2007). For MRT analysis we used mvpart (De'ath, 2007) and MVPARTwrap (Ouellette and Legendre, 2013) packages in R statistical software (R Core Team, 2021). We included prey species with > 100 individuals found in the overall scat examination. For the analysis, we used the estimated biomass for each consumed species to account for size variation between rodent species (after Palomo et al. (2007); Supplementary File 2.5). We standardized the biomass value for each prey item and scat as recommended for MRT analysis (De'ath, 2002) using normalization (i.e. making margin sum of squares equal to one).

There may be potential sources of non-independence between collected samples: scats belonging to the same individual or to individuals foraging in the same area, and individual prey remains appearing in several scats (Morin et al., 2019). Due to the overall small size of wildcat prey species (i.e. rodents) it is unlikely that macroscopic prey remains from the same prey item appear divided in several faecal samples (Wachter et al., 2012). On the other hand, we cannot assign scats to wildcat individuals as we lack individual genetic identification for each scat. Consequently, instead of randomly relating samples (e.g. based on proximity between them), we have assumed independence of samples for group comparison analyses (Lemons et al., 2010).

We used the indicator value (IndVal) for each species in each MRT group (Dufrêne and Legendre, 1997) to detect which species characterized certain environmental conditions. This method assigns indicative values to species which are both frequent and abundant (or in our case more consumed) in the studied group when compared to the whole dataset. For instance, the IndVal is the highest for a species when all its observations (or biomass consumed) appear in a certain group, without appearing in the rest of the groups. IndVal is calculated as the product of the relative frequency and the relative average abundance for each species in each cluster (Dufrêne and Legendre, 1997).

We performed pairwise comparisons to test for significant differences between: a) biomass consumption of the set of species between the MRT groups (i.e., multiple-group comparisons); b) biomass consumption of each species between the MRT groups; and c) biomass consumption of the different species inside each group. The latter two corresponded to single-group comparisons. For multiple-group comparisons we performed permutational multivariate analysis of variance using Bray-Curtis dissimilarity (PERMANOVA, vegan and RVAideMemoire packages in R-software) (Hervé, 2020; Oksanen et al., 2013). For single-group comparisons we performed Kruskall-Wallis test followed by Mann–Whitney U test with the correction of Holm (stats package; R Core Team, 2021). We set statistical significance levels at $\alpha < 0.05$.

Seasonal variation in wildcat prey consumption

We also performed multiple and single-group pairwise comparisons to test for significant differences between: a) biomass consumption of the set of species between seasons (i.e., multiple-group comparisons); and b) biomass consumption of *Arvicola monticola* and *Apodemus*, i.e., the prey items that characterized the two main branches of the MRT, between seasons (i.e., single-group comparisons). We used meteorological seasons (Autumn: September to November; Winter: December to February; Spring: March to May; and Summer: June to August) for two main reasons: a) they rely on earth temperature cycles that may be more biologically meaningful to species demographic cycles, and b) to allow for comparisons with results found in the existing wildcat literature (Malo et al., 2004; Mermod and Liberek, 2002; Piñeiro and Barja, 2011).

Prey consumption in relation to prey abundance

To test the relationship between annual prey abundance and annual wildcat prey consumption, for MP scats we represented annual variations in estimated prey abundance (for *Arvicola monticola* and *Apodemus)* together with annual variation of ingested biomass for both species by adding a locally weighted scattered plot smoothing (LOESS) curve for the data. We tested collinearity between estimated annual *Arvicola monticola* and *Apodemus* abundance and ingested biomass during the same year for both species using the Spearman correlation test. We extracted mean values of *Arvicola* abundance inside the 1500m buffers described previously corresponding to the year that the scat was collected. We obtained information on *Arvicola* abundance for 196 scats. As *Arvicola monticola* cycles last at least one year (Giraudoux et al., 1997), we considered the cycles (i.e. years) to last from spring to the end of winter of the next year. For instance, the abundance detected in the survey ran in autumn 2017 would represent the *Arvicola* abundance between spring 2017 and winter 2018. We used the mean annual N30 value for hard mast productivity surveys in MP as a proxy for *Apodemus* abundance the following year. We obtained information on mast productivity for 234 scats.

2.4 Results

Scat sampling, identification and analyses of prey composition

We collected 683 scats, and identified 3054 prey items of 35 different species (Table 2.2; Supplementary File 2.6). Wildcat diet was dominated by rodent species, particularly from the genus *Apodemus*, *Arvicola* and *Microtus*. Total counts showed that *Microtus lusitanicus*, mice of the genus *Apodemus* and *Arvicola monticola* were the main prey items of wildcats (Table 2.2). We included in the MRT analyses the following prey species: *Apodemus* sp. (combination of *Apodemus flavicollis, Apodemus sylvaticus,* and *Apodemus* sp.), *Arvicola monticola, Microtus agrestis, Microtus arvalis, Microtus lusitanicus,* and *Myodes glareolus*.

Table 2.2. *Diet composition of European wildcats in the Cantabrian Mountains calculated as total count (TC; total count of prey items found for each species/category), relative frequency (RF; number of items of each category divided per total number of items), frequency of occurrence (FO; number of samples with presence of each prey item divided per total number of samples), and CMR estimate (with Standard Error in brackets) calculated for the main prey items by Huggins closed populations capture-recapture models. Bold letters show the Class, Order and Family of the consumed species. N=Number of scats analysed.*

Wildcat prey consumption n=683				
	TC	RF	FO	CMR Estimate
Mammalia				
Rodentia. Muridae				
Apodemus sp.	595	19.48	0.45	0.43 (0.019)
Apodemus flavicollis	204	6.68	0.18	0.17 (0.014)
Apodemus sylvaticus	440	14.41	0.33	0.32 (0.018)
Rodentia. Cricetidae				
Arvicola monticola	461	15.09	0.39	0.37 (0.019)
Chionomys nivalis	19	0.62	0.02	
Microtus sp.	47	1.54	0.07	
Microtus agrestis	144	4.72	0.16	0.15 (0.014)
Microtus arvalis	166	5.44	0.12	0.12 (0.012)
Microtus lusitanicus	614	20.10	0.44	0.42 (0.019)
Myodes glareolus	110	3.6	0.11	0.11 (0.012)
Rodentia. Gliridae				
Glis glis	11	0.36	0.02	
Eliomys quercinus	2	0.06	0.003	
Insectivora				
Talpa occidentalis	6	0.2	0.01	
Crocidura russula	6	0.2	0.01	
Sorex coronatus	5	0.16	0.01	
Sorex minutus	4	0.13	0.006	
Other				
Capreolus capreolus	1	0.03	0.001	
Lepus castroviejoi	2	0.07	0.003	
Genetta genetta	1	0.03	0.001	
Unidentified rodent	17	0.56	0.02	
Unidentified mammal	3	0.1	0.004	
Reptilia				
Anguis fragilis	1	0.03	0.001	
Lacertidae	41	1.34	0.06	
Ophidia	6	0.19	0.01	
Unidentified reptile	5	0.16	0.01	
Aves				
Phyrrula phyrrula	1	0.03	0.001	

Anas platyrhynchos	1	0.03	0.001
Alectoris rufa	1	0.03	0.001
Turdidae	2	0.07	0.003
Unidentified passerine bird	31	1.01	0.04
Unidentified medium-sized bird	3	0.1	0.004
Arthropoda			
Coleoptera	9	0.29	0.007
Ortoptera	9	0.29	0.01
Und. Arthropod	2	0.07	0.001
Other			
Vegetation (purge)	84	2.75	0.12

Effects of landscape composition in prey consumption by wildcats

A MRT tree with six terminal nodes (Figure 2.2) was selected as the most predictive assemblage (Supplementary File 2.4), which explained 17.8% of the variation in the species normalized biomass data. The percentage of pastoral fields was the primer predictor (R^2=8.3) separating wildcat scats from areas with high (≥17.87%) and low (<17.87%) proportion of pastoral fields. *Arvicola monticola* characterized wildcat prey consumption in the former areas whereas *Apodemus* mice did so in the latter. Furthermore, areas with higher proportion of pastoral fields were divided in two clusters according to the season: summer and autumn (hereafter referred to as After Harvest), and winter and spring (hereafter referred to as Before Harvest). The first group was characterized by the consumption of *Arvicola monticola,* whereas the second was characterized by *Microtus arvalis*. Scats from areas with lower proportion of pastoral fields were split in those collected further (≥ 733m) and closer (< 733m) to such fields. *Apodemus* mice and *Myodes glareolus* characterized the diet in the areas further distanced from pastoral fields (Far From Fields). Scats collected closer to fields were divided between those with lower (< 24.96%) and higher proportion of forest (≥ 24.96%). Prey consumption in the former areas was characterized by the presence of

Microtus lusitanicus. Finally, the areas with higher proportion of forest were divided into two clusters, matching the two study areas: MP and WCM. Biomass consumption of the set of species varied between groups (PERMANOVA test; p = 0.01). In particular, differences aroused between Forests of WCM and Far From Fields group and all the other MRT groups, and between Before and After Harvest (pairwise comparisons; p<0.05).

Intergroup comparisons of biomass consumption of each species showed variation for all of them except for *Microtus agrestis* (Appendix 2.S3 for pairwise comparisons). *Arvicola* consumption was higher in most groups (p<0.001; Figure 2.2; Appendix 2.S3) than in the heavily forested WCM and Far From Field groups, in which case the consumption of *Myodes glareolus* and *Apodemus* was higher than for the other groups (p<0.0001; Figure 2.2; Appendix 2.S3). In field dominated areas, consumption of *Arvicola* was higher in summer and autumn (i.e., After Harvest) than in winter and spring (i.e., Before Harvest; p<0.001; Figure 2.2; Appendix 2.S3). Consumption of *M. arvalis* and *M. lusitanicus* was higher in Before Harvest and in Low Forested groups, respectively, than in most of the other groups (p<0.001; Figure 2.2; Appendix 2.S3).

Intragroup comparisons of biomass consumption between species showed that *Arvicola* was the most consumed species in terms of biomass in four out of six groups (i.e., all except WCM forests and areas Far From Fields; Table 2.3). *Arvicola* was more consumed than all the other species in After Harvest group and it was more consumed than some *Microtus* and *Myodes* species in Before Harvest, Forests of MP and Low Forested groups (Table 2.3). On the other hand, *Apodemus* was the most consumed species in Forests of WCM and areas Far From Fields (Table 2.3).

Table 2.3. *Mean normalized consumed biomass values for each species in each group derived from the MRT. Bold numbers indicate the most consumed species in each group. Asterisk shows the species with which differences in normalized biomass in relation to the most consumed species were significant according to Mann–Whitney U test (p<0.05). Codes for the group names are explained in Fig. 2.2.*

Group	*Arvicola monticola*	*Microtus agrestis*	*Microtus arvalis*	*Microtus lusitanicus*	*Myodes glareolus*	*Apodemus* sp.
After Harvest	**0.63**	0.05*	0.06*	0.12*	0.01*	0.22*
Before Harvest	**0.39**	0.06*	0.21	0.19	0.02*	0.25
Forests of MP	**0.38**	0.06*	0.08*	0.13	0.03*	0.32
Forests of WCM	0.25*	0.06*	0.01*	0.12*	0.07*	**0.67**
Low Forested	**0.54**	0.11*	0.01*	0.25	0.01*	0.25*
Far From Fields	0.06*	0.04*	0.01*	0.12*	0.11*	**0.87**

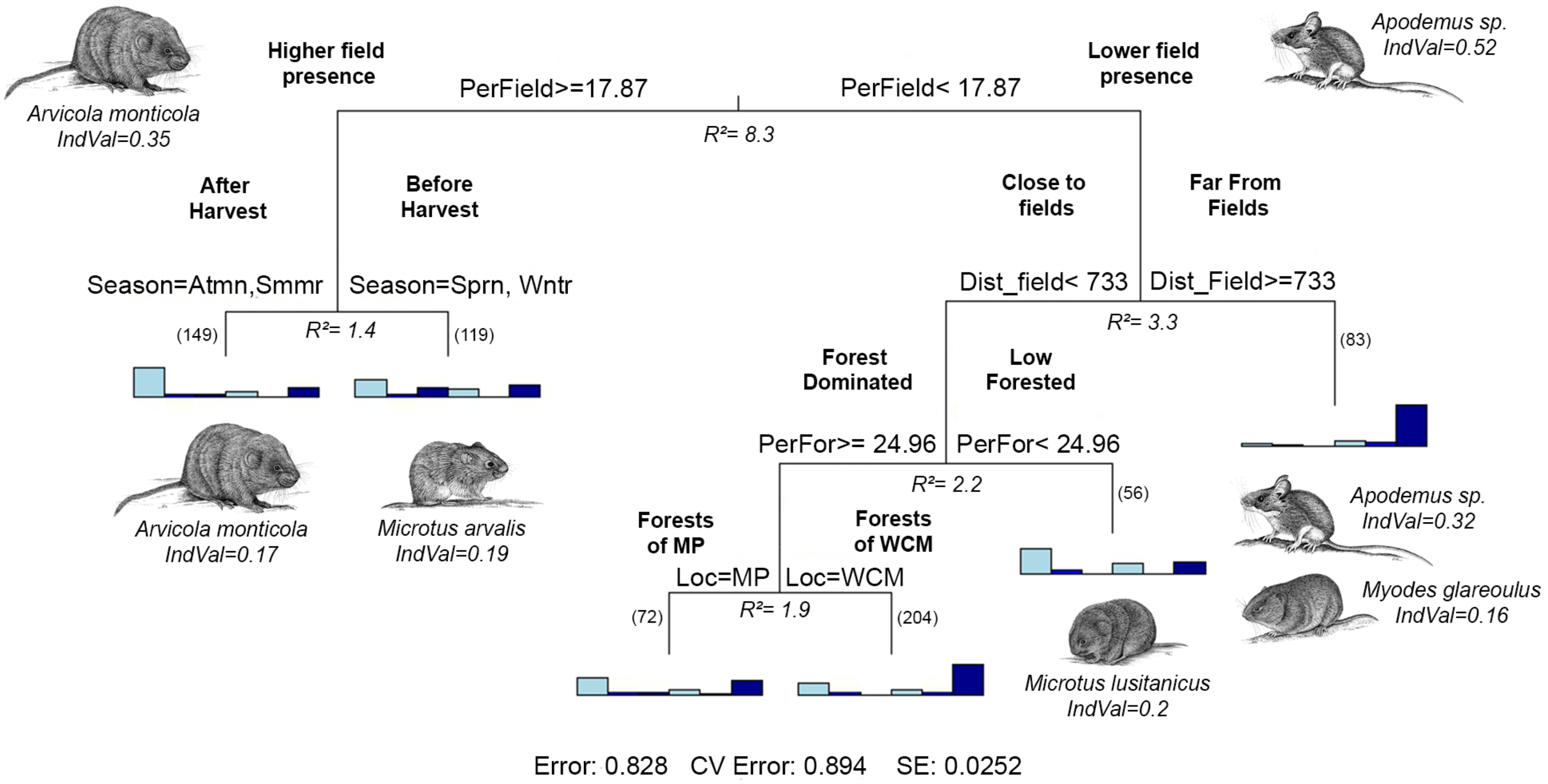


Figure 2.2. *Multivariate Regression Tree defining normalized biomass of rodent species consumed by European wildcats constrained by five environmental variables indicated in the tree (PerField, Season, Dist_Field, PerFor, and Loc) and defined in Table 1. Each terminal node represents the histogram corresponding to the mean normalize biomass values for each rodent species from left to right as follows: Arvicola monticola, Microtus agrestis, Microtus arvalis, Microtus lusitanicus, Myodes glareoulus and Apodemus sp. MP = Montaña Palentina and WCM = Western Cantabrian Mountains. Error, CV Error and Standard Error (SE) values are provided in the figure. Error represents the fraction of variance not explained by the tree and CV Error the predictive accuracy of the tree. The variance explained by each node (R2) is indicated and the number of scats is shown in parentheses. The silhouettes of the indicator species are shown for the first split and four out of six terminal nodes when IndVal test provided such information. Species illustrations by Jordi Mateos*, extracted from Palomo et al. (2007).

Seasonal variation in wildcat prey consumption

Biomass consumption of the set of species varied between seasons (PERMANOVA test; p = 0.01). Biomass consumption of *Arvicola monticola* was higher during summer and autumn (pairwise comparisons; p<0.02; Figure 2.3); whereas consumption of *Apodemus* was higher in spring (pairwise comparison; p=0.029; Figure 2.3).

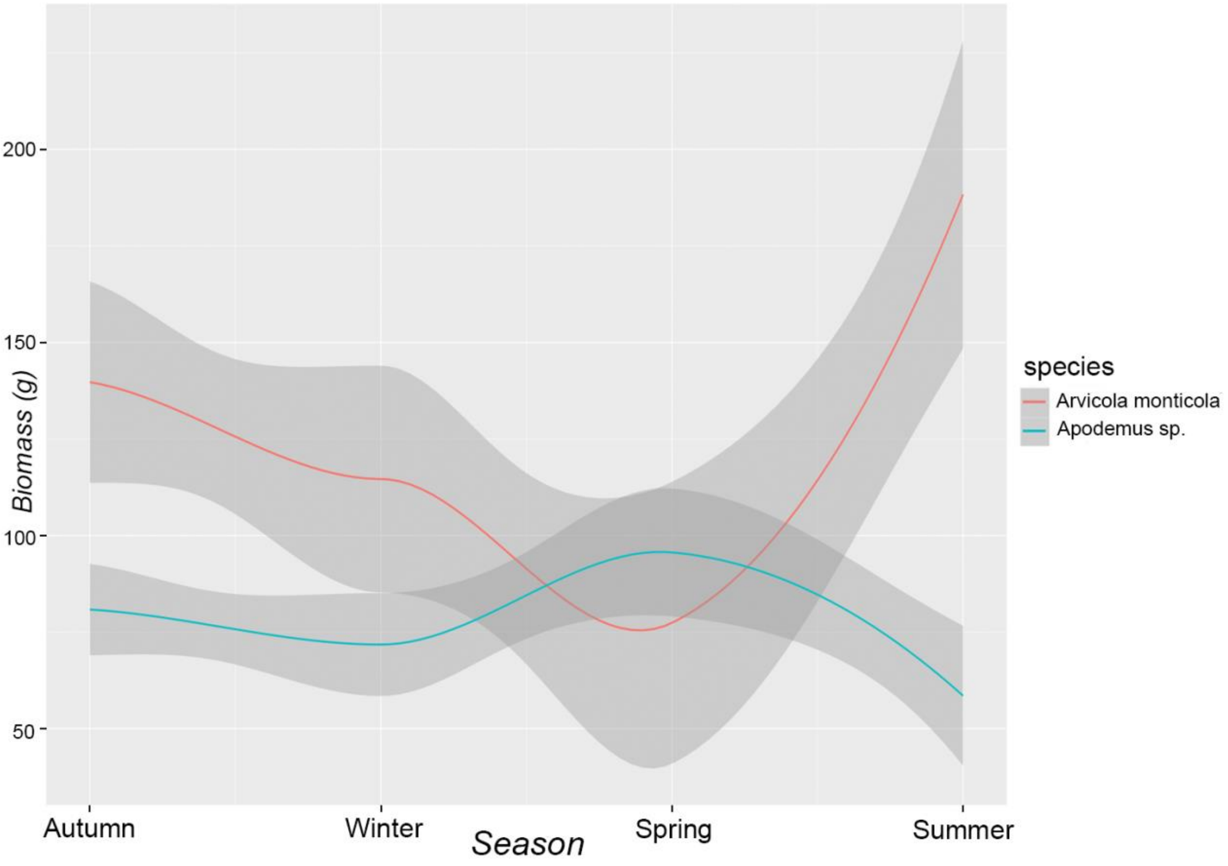


Figure 2.3. *Mean biomass consumed per scat of Arvicola monticola (red) and Apodemus sp. (blue), along meteorological seasons (autumn, winter, spring and summer) in the Cantabrian Mountains (n=683). Curves are smoothed by the LOESS method.*

Rodent consumption in relation to Arvicola and mast abundance

Annual abundance of *Arvicola monticola* and mast did not correlate with ingested biomass during the same year for *Arvicola monticola* ($p = 0.5$) or *Apodemus* ($p = 0.14$). The maximum and minimum ingested biomass of *Arvicola* and *Apodemus* respectively coincided with minimum *Arvicola* abundance values. On the contrary, a period with low and high consumption of *Arvicola* and *Apodemus* respectively coincided with a period of high abundance of *Arvicola monticola* (Figure 2.4a). 2016 and 2019 were years of high mast production whereas 2017 and 2018 had very low productivity values. The minimum consumption of *Apodemus* occurred one year after the minimum mast production year (Figure 2.4b).

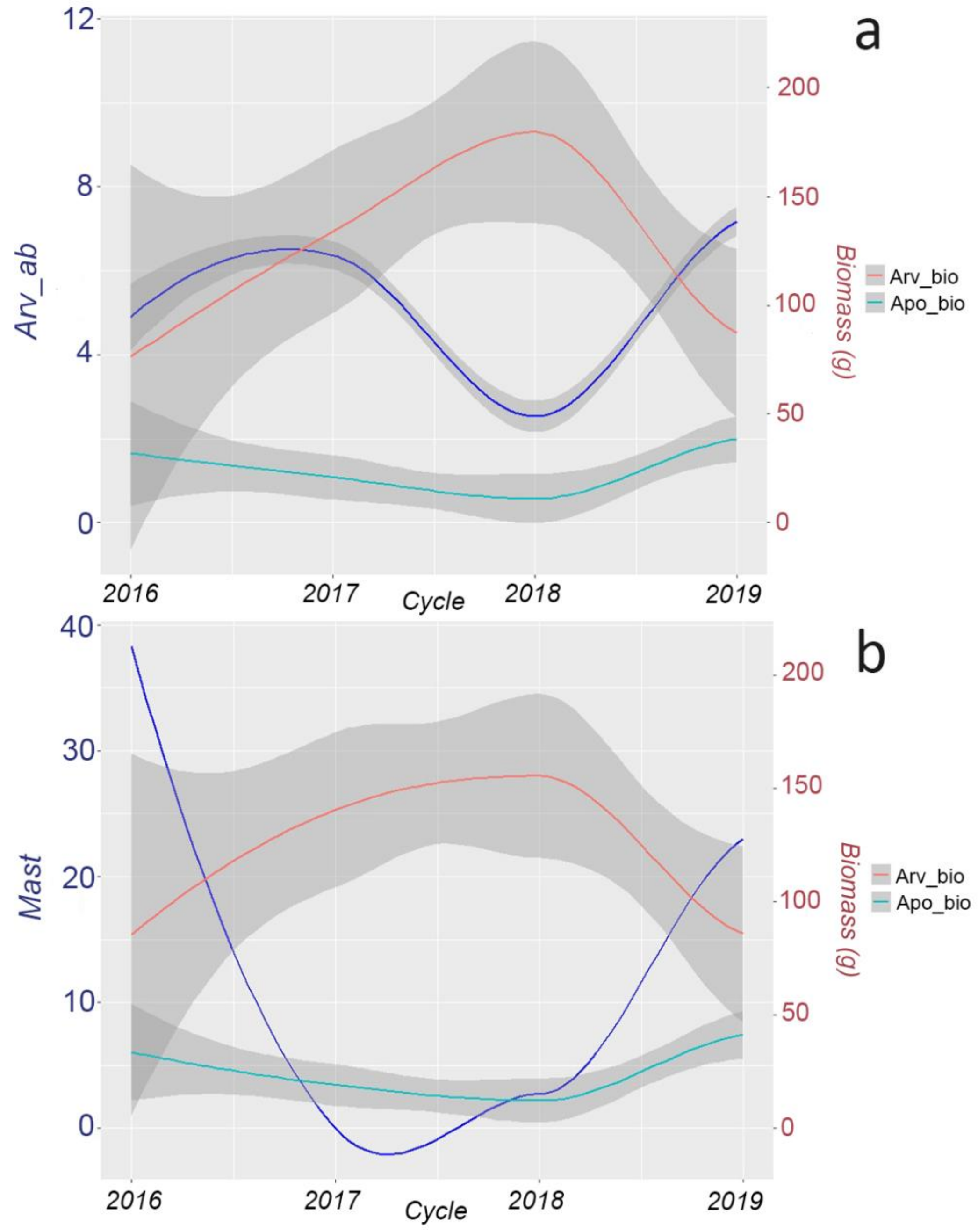


Figure 2.4. *Annual variation of* Arvicola monticola *biomass and* Apodemus biomass *(red (Arv_bio) and blue (Apo_bio) respectively and right y axis) consumed by European wildcats in relation to a)* Arvicola monticola *abundance (Arv_ab) (n= 196) or b) N30 mean values for mast production (Mast) (n=234) (dark blue line and left y axis). Curves are smoothed by the LOESS method.*

2.5 Discussion

Prey consumption by European wildcats in the Cantabrian Mountains is influenced by the proportion and distance to pastoral fields, season and possibly prey abundance. Regarding prey selection by wildcats, our results agree with (Lozano et al., 2006) and Mermod and Liberek, (2002) pinpointing rodents from the *Apodemus*, *Microtus* and *Arvicola* genus as wildcat main prey items in areas inside its Eurosiberian distribution range with absence of rabbits.

Wildcat prey consumption in areas with higher proportion of pastoral fields was dominated by field-dwelling rodent species. Specifically *Arvicola monticola* was the main prey consumed when pastoral fields were present and wildcats were using its proximities up to 733 m. Only when wildcats used highly forested and further distanced areas from pastoral fields did *Apodemus* mice become the main prey item. Mermod and Liberek (2002) and Piñeiro and Barja (2011) found *Arvicola* and *Apodemus* to be main prey items for wildcats in pastoral and forested environments respectively. Differences in prey consumption between MP and WCM forests may derive from contrasting vegetation characteristics between areas. WCM forests have higher diversity of fruit-producing trees (e.g., cherry and rowan trees) (Rivas-Martínez et al., 2017) which can produce different rodent communities.

The low predictable power of our MRT (17,8%) is expected for datasets including multispecies data (Cappo, De'ath & Speare, 2007; Espinoza *et al.*, 2014). Nevertheless, our MRT successfully detected the influence of proportion and distance to pastoral fields on wildcat prey consumption.

We expected rodent predation by wildcats to vary between habitats, as rodent communities may change accordingly (Cavia et al., 2009; Stevens and Tello, 2009). However, the proportion of pastoral fields necessary to influence wildcat diet was surprisingly low. This may be related with varying habitat use by wildcats in mosaic landscapes, preferring certain habitats in relation to prey and shelter availability regardless their proportion in the landscape (Lozano, 2010; Oliveira et al., 2018). As wildcats exploit predictable and profitable food resources (Krofel et al., 2021; Ruiz-Villar et al., 2020) they may frequently visit reliable feeding grounds such as the pastoral fields of the Cantabrian Mountains, where they predate upon *Arvicola monticola*. Our results agree with previous research on wildcats (Lozano, 2010; Oliveira et al., 2018) and other felid species (e.g. Iberian lynx, *Lynx pardinus;* Beaufoy, 1998) commonly using sustainably managed agro-pastoral components of the landscape as hunting grounds in relation to increased prey availability.

Following our expectations, prey consumption varied seasonally, with higher consumption of *Arvicola* during summer and autumn, when its abundance and accessibility to predators in pastoral areas may be higher (Butler and Gillings, 2004; Weber and Aubry, 1993). Seasonal variations in abundance of *Arvicola* respond to reproductive cycles of the species, with demographic peaks occurring between spring and the end of summer (Giraudoux et al., 1997). However, lower vegetation cover after the summer harvest may increase *Arvicola* vulnerability to wildcats, as rodents are easily detected and captured by predators in such conditions (Butler and Gillings, 2004). According to this, wildcats would mainly visit pastoral fields during summer and autumn when *Arvicola* is both abundant and vulnerable. This agrees with Rodríguez et al. (2020) explaining that summer accumulated the highest number of wildcat sightings hunting in pastoral fields. On the other hand, *Apodemus* dominated wildcat diet during spring, probably in relation to higher use of forested habitats by wildcats during the breeding season (Oliveira et al., 2018). Our results contrast with Piñeiro and Barja (2011), saying that *Apodemus* was mainly consumed in autumn. Nevertheless, *Arvicola monticola* was not present in their study area and the landscape structure and configuration may differ from ours.

We acknowledge some limitations in our study. Firstly, we assumed sample independence because we lack the sample relatedness information required when considering non-independence of samples in multivariate (quantitative) assessment of diet (Lemons et al., 2010). The low chances of masking occurring between prey items, of individual prey remains appearing divided in several scats, and the similarities between deterministic and multinomial diet estimates, indicate that our results would probably vary little if considering non-independence of samples. However, inferences should be made with caution as limitations of scat sampling (Klare et al., 2011) combined with the assumption of independence may lead to potential biases. Future research incorporating individual genetic identification of samples to account for sample relatedness may help addressing this issue. Secondly, wildcat scat identification success was not 100%, being possible that a few samples analysed belonged to red fox. The confusion rate may vary between seasons and areas where wildcat and fox diets overlap the most. Nevertheless, the high relative importance of *Arvicola monticola* in the diet may indicate that the effect of a 13% misidentified samples would probably not be substantial.

Contrary to our expectations, prey abundance was not correlated with prey consumption in the same year. Variation between years may suggest a potential delay on prey consumption after changes in population numbers similar to that observed in Australian feral cat populations, where cats switched from rabbits to mice one year after a rabbit demographic depression (Molsher et al., 1999). Authors linked this to predators switching prey preferences at different speeds according to their degree of specialization (Ishii and Shimada, 2010). Wildcats, as facultative specialists (Malo et al., 2004; Piñeiro and Barja, 2011), may adjust to such variations with some delay (Andersson and Erlinge, 1977). Nevertheless, our results may not be robust for two main reasons: the short monitoring period (4 years) and the use of mast production as a proxy for *Apodemus* abundance, as population numbers may be estimated with heterogeneous precision across the year (Pucek et al., 1993) potentially providing misleading results. Future research should prolong monitoring periods and incorporate actual abundance data obtained with more precise methods such as rodent surveys using live traps.

Although wildcats can perceive ecological benefits from using pastoral fields with presence of profitable prey (e.g. smaller home-range size (Šálek et al., 2015) and higher reproductive success (Sumasgutner et al., 2019)), detrimental effects associated to human modified habitats should be accounted for when evaluating potential advantages. For instance, wildcats frequenting human managed environments could suffer from higher road mortality (Bastianelli et al., 2021; Klar et al., 2009), increased hybridization and disease transmission from domestic cats (Tiesmeyer et al., 2020), and higher stress levels (Piñeiro et al., 2012).

In conclusion, traditionally and sustainably managed pastoral fields seem important landscape components for wildcats in the Cantabrian Mountains as the presence and consumption of wildcat main prey item in terms of biomass is linked to such ecosystems. Pastoral fields may provide predictable and profitable prey in terms of number, size and accessibility. Additionally, several anthropogenic and environmental factors may influence wildcat diet and its variation across years and seasons. We consequently encourage the maintenance of the current pastoral surface in the Cantabrian Mountains using traditional management methods (i.e. growth and maintenance of natural vegetation, use of natural fertilizers, avoidance of chemicals and low use of machinery) over the more intensive and nature damaging methods that are increasing worldwide (Dobrovolski et al., 2011). Preservation of sustainable pastoral landscapes may not only increase preying opportunities for rodent predator species like wildcats but also benefit multiple insect and bird species (Doxa et al., 2010; Jubete and Román, 2016; Mander et al., 1999). Besides, we recommend applying mitigation measures such as road underpasses, and neutering and vaccination of feral cats, aimed at reducing the potentially harmful effects for wildcats associated to presence of roads and feral cats respectively in human modified areas. The availability of prey in suitable habitat for wildcats fuelled by a positive perception from locals towards wildcats as controllers of rodent population outbreaks would create a favourable scenario for wildcat conservation in the Cantabrian Mountains.

2.6 Acknowledgements

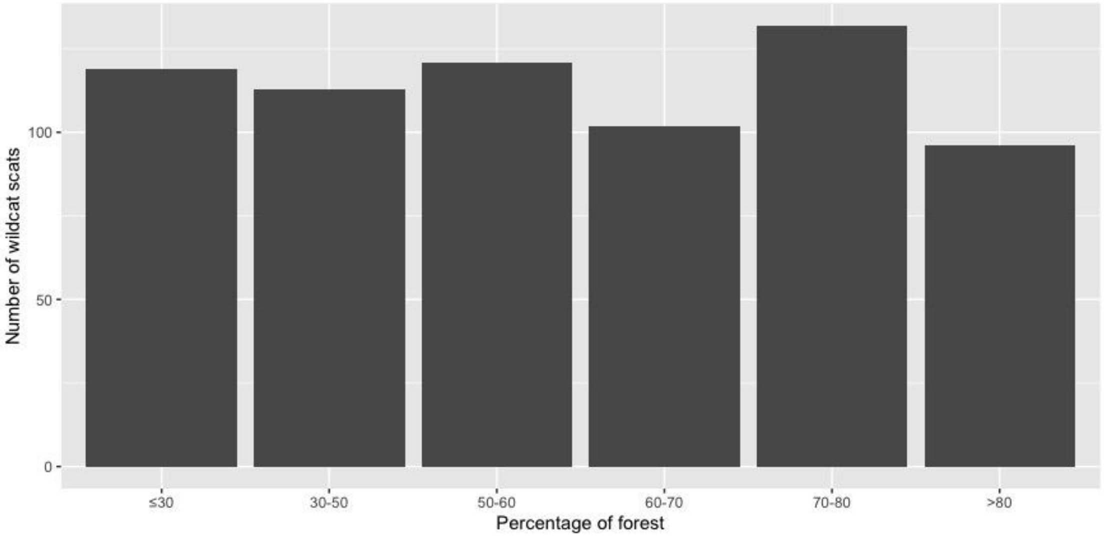
We thank the Regional Governments of Castilla y León and the Principality of Asturias for the permits to capture wildcats and collect wildcat scat samples (EP/P/128/2019 for CyL; AUTO/19/34, AUTO/2020/593 and AUTO/2019/3267 for Asturias). We thank the Spanish Ministry of Science, Innovation and Universities as well as TRAGSATEC S.A. for sharing the GPS spatial data of several intensive 24-h tracking periods of European wildcats. We thank M. Torres Diseños Industriales SAU and Land Rover Spain for their partial economic and logistic support. HRV is beneficiary of a PhD scholarship

“Severo Ochoa” from the Regional Government of Principality of Asturias. JVLB was supported by a Ramón y Cajal research contract (RYC-2015-18932) from the Spanish Ministry of Economy, Industry and Competitiveness.

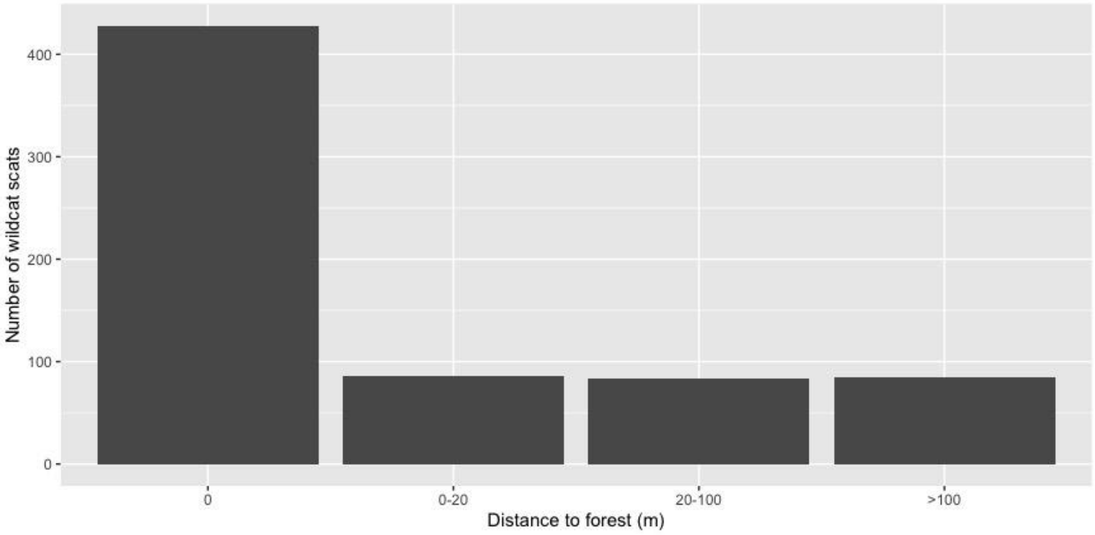
2.7 Supplementary material

***Appendix 2.S1**. Number of wildcat scat samples collected along horizons of the different variables considered for the multivariate regression tree (MRT): Percentage of a) forest and c) fields inside the 1500m buffer around each scat; Distance from each sample to the closest b) forest and d) field patch. Please notice that forest is present in most of the study area (Figure 2.1) which combined with wildcats rarely roaming at high distances from forests makes it difficult to find samples at great distance from forest patches.*

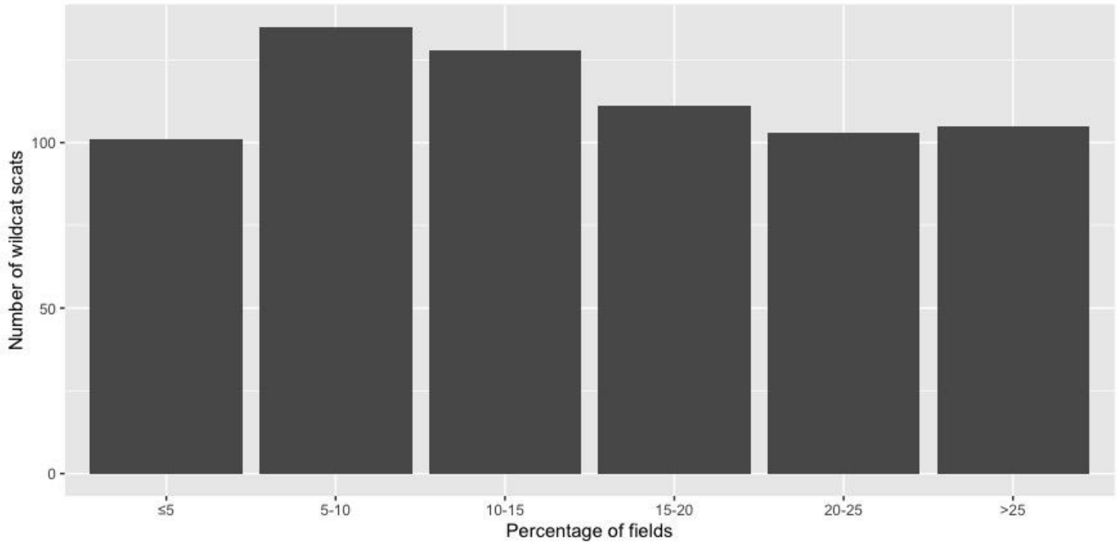
a



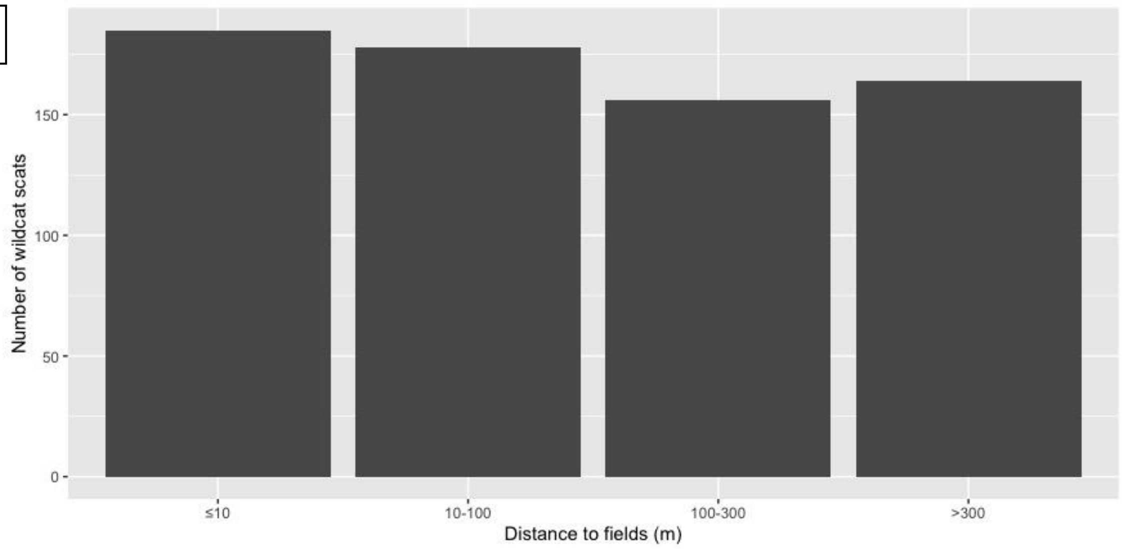
b



c


Number of wildcat scats
0
50
100
≤5
5-10
10-15
15-20
20-25
>25
Percentage of fields

d


Number of wildcat scats
0
50
100
150
≤10
10-100
100-300
>300
Distance to fields (m)

Appendix 2.S2*. Extended information on genetic analysis of collected scats:*

We sequenced a 126 base-pair fragment (oligos excluded) of the ATP6 mtDNA gen, using the primers ATP6DR1: 5’ CCAGTATTTGTTTTGATGTTAGTTG 3’ and ATP6DF3: 5’ AACGAAAATCTATTCGCCTCT 3’ (Chaves et al., 2012). We obtained sequences in both directions with an automatic sequencer (ABIprism-3130xl), and used Sequencher 5.0 (Genes Codes Corporation, Ann Arbor, MI, USA) for edition. We compared consensus sequences with those of the main carnivore species with potentially similar scat morphology present in the study area: *Felis silvestris*, red fox (*Vulpes vulpes*), and grey wolf (*Canis lupus*); along with sequences registered both in the GenBank (https://www.ncbi.nlm.nih.gov/), using the tool BLAST, and Carnivora databases (http://www.dna-surveillance.auckland.ac.nz/page/carnivora/science).

Appendix 2.S3. *Extended information on wildcat capture and handling:*

We captured and GPS collared twelve individual European wildcats using box-traps (permit EP/P/128/2019). Six individuals were lured by the authors using visual baits consisting on pigeon feathers nailed in a piece of cork. Traps were revised every morning and evening. Other six individuals were captured by workers from TRAGSATEC S.A. within the frame of the National Plan of Conservation of the Cantabrian Capercaillie (*Tetrao urogallus cantabricus*) using box traps lured with sardines. Box traps were equipped with a minkpolice device (MinkPolice, Alert House Aps, Copenhagen, DK) to monitor the presence of captured animals. In all cases a professional veterinary handled and anesthetized the individuals using 0.35 cc of ketamine (100 mg/ml) + 0.2 cc of dexmedetomidine (1 mg/ml). We equipped the wildcats with an 80 g GPS-GSM Followit collar (Followit Sweden AB, Lindesberg, SE) programmed to get one GPS location every 7 h, except on the first Saturday of every month when it took one point every half an hour for a full 24-h period (intensive tracking). Collars are equipped with a drop-off system that will be activated after one year and the collar will be released. After recovery, individuals were released immediately in the capture sites.

***Appendix 2.S4**. List of the landscape categories reclassified for the landscape composition analysis. The first column shows the original category found in the Third National Forest Inventory. Definitions in Spanish can be found in the excel file attached inside the following link: https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx. The second column shows the translation of the categories to English. The third column shows the category assigned to the previous categories when reclassifying the landscape categories. The categories related with artificial elements such as villages, roads, and mines, and the ones related with water masses such as rivers or lakes, had not been considered for the landscape analysis.*

Original National Forest Inventory Category Name (Spanish)	Category translation	Reclassified category
Bosque	Forest	Forests
Bosque de Plantaciones	Plantation Forest	
Complementos del bosque	Forest Complements	
Arbolado fuera del Monte (AFM) Riberas	Tress outside hills (TOH) River edges	
Arbolado fuera del Monte (AFM) Bosquetes	Tress outside hills (TOH) Small forest patches	
Matorral	Shrub	Shrubs
Prados con setos	Meadows with hedges	Fields
Mosaico desarbolado sobre cultivo y/o prado	Treeless mosaic landscape over crops and/or meadows	
Mosaico arbolado sobre cultivo y/o prado	Mosaic landscape with tree cover over crops and/or meadows	
Herbazal	Grasslands	
Cultivo con arbolado disperso	Crops with sparse tree cover	
Agrícola y prados art.	Artificial crops and meadows	

***Appendix 2.S5**. A) Correlation values obtained from studying correlation matrixes between continuous variables obtained by the Spearman method. Definitions of continuous variables appear in the table below (B). Shaded cells show the high correlation values between shrub variables and forest variables.*

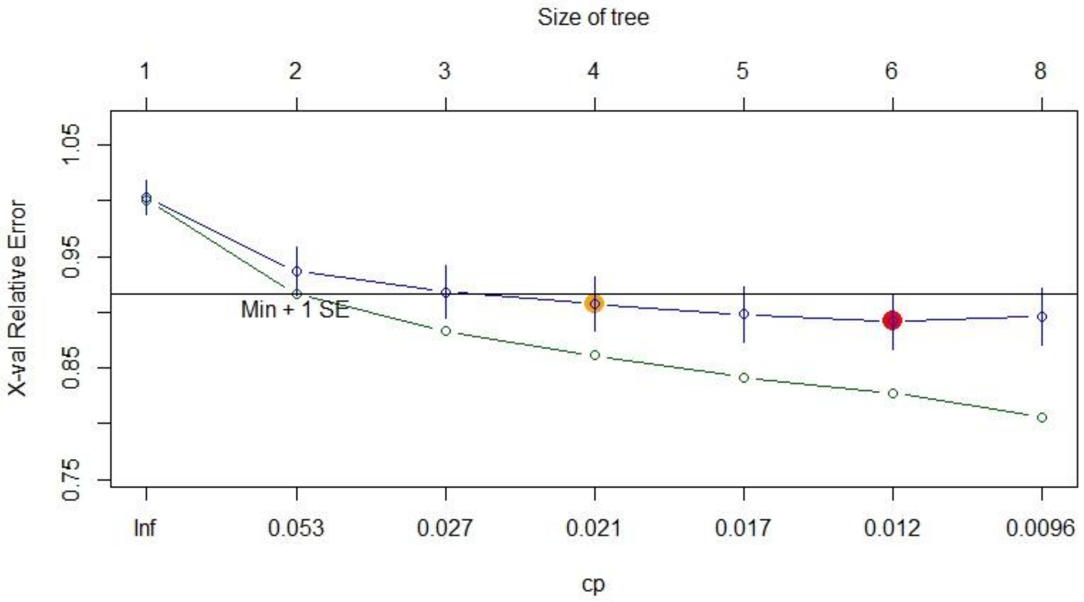
A

	PerFor	PerField	PerShr	Dist_For	Dist_Field	Dist_Shr
PerFor	1	-0.29	-0.79	-0.52	0.33	0.63
PerField	-0.29	1	-0.24	0.39	-0.66	-0.02
PerShr	-0.79	-0.24	1	0.32	0.03	-0.69
Dist_For	-0.52	0.39	0.32	1	-0.58	-0.48
Dist_Field	0.33	-0.66	0.03	-0.58	1	0.10
Dist_Shr	0.63	-0.02	-0.69	-0.48	0.10	1

B

Predictor code	Description
PerFor	Percentage of a 1500 m buffer surrounding each scat occupied by forest.
PerField	Percentage of a 1500 m buffer surrounding each scat occupied by pastoral fields.
PerShr	Percentage of a 1500 m buffer surrounding each scat occupied by shrub.
Dist_For	Distance in metres from the scat collection point to the closest forest patch. Distant will be zero if the scat was collected inside a forest patch.
Dist_Field	Distance in metres from the scat collection point to the closest pastoral field, managed meadow or pastureland patch. Distant will be zero if the scat was collected inside one of such.
Dist_Shr	Distance in metres from the scat collection point to the closest shrub patch. Distant will be zero if the scat was collected inside a shrub patch.

***Appendix 2.S6**. Result of the Cross-Validation method to assess optimum tree size for the multivariate regression tree (MRT). The red spot indicates the tree size that minimizes relative error and maximizes predictable power (which we selected for our MRT). The orange spot indicates the most parsimonious tree size with a relative value under the minimum + Standard Error threshold.*



Appendix 2.S7. *Biomass values (in g) assigned to the main prey items consumed by European wildcats in the Cantabrian Mountains according to the maximum weight values provided by Palomo et al 2007. Apodemus sp. weights were calculated as the mean between Apodemus flavicollis and Apodemus sylvaticus weights.*

Prey species	**Biomass (g)**
Apodemus flavicollis	50
Apodemus sylvaticus	35
Apodemus sp.	42.5
Arvicola monticola	183
Microtus agrestis	41.4
Microtus arvalis	41
Microtus lusitanicus	19
Myodes glareolus	30

Appendix 2.S8. *Frequency of different prey items found in European wildcat scats in the Western Cantabrian Mountains (WCM) and Montaña Palentina (MP) per year and season: A (Autumn), W (Winter), Sp (Spring) and S (Summer). Number in brackets represents the scat sample size analysed for each specific season. Bold letters show the Class, Order and Family of the consumed species.*

Western Cantabrian Mountains (n=421)						
Year	2018	2019				2020
Season	A(76)	W(109)	Sp(83)	S(55)	A(65)	W(33)
Mammalia						
Rodentia. Muridae						
Apodemus sp.	90	101	120	66	65	20
Apodemus flavicollis	44	49	50	18	26	13
Apodemus sylvaticus	104	102	97	48	60	22
Rodentia. Cricetidae						
Arvicola monticola	37	59	20	48	69	29
Chionomys nivalis	2	6	1	8		1
Microtus sp.	2	1	2	2		4
Microtus agrestis	27	34	12	25	16	7
Microtus arvalis	7	19	5	24	17	10
Microtus lusitanicus	87	127	87	68	67	39
Myodes glareolus	14	33	31	10	5	2
Rodentia. Gliridae						
Glis glis	4	1	1	5		
Eliomys quercinus			1	1		
Insectivora						
Talpa occidentalis	1	2				
Crocidura russula	1					
Sorex coronatus	1	1		1	1	
Sorex minutus	1	2				
Other						
Capreolus capreolus						1
Lepus castroviejoi		1	1			
Genetta genetta			1			
Unidentified rodent		2				
Unidentified mammal					1	1
Reptilia						
Anguis fragilis				1		
Lacertidae	6	4	5	1		
Ophidia	1		1	1		
Unidentified reptile		1		1		
Aves						
Phyrrula phyrrula			1			
Anas platyrhynchos					1	
Alectoris rufa					1	
Turdidae		2				
Passerine bird	8	6	4	1	2	1
Medium bird			2	1		
Arthropoda						
Coleoptera		1				
Ortoptera	3			1		
Und. arthropod		1				
Other						
Vegetation (purge)	9	7	5	4	3	3

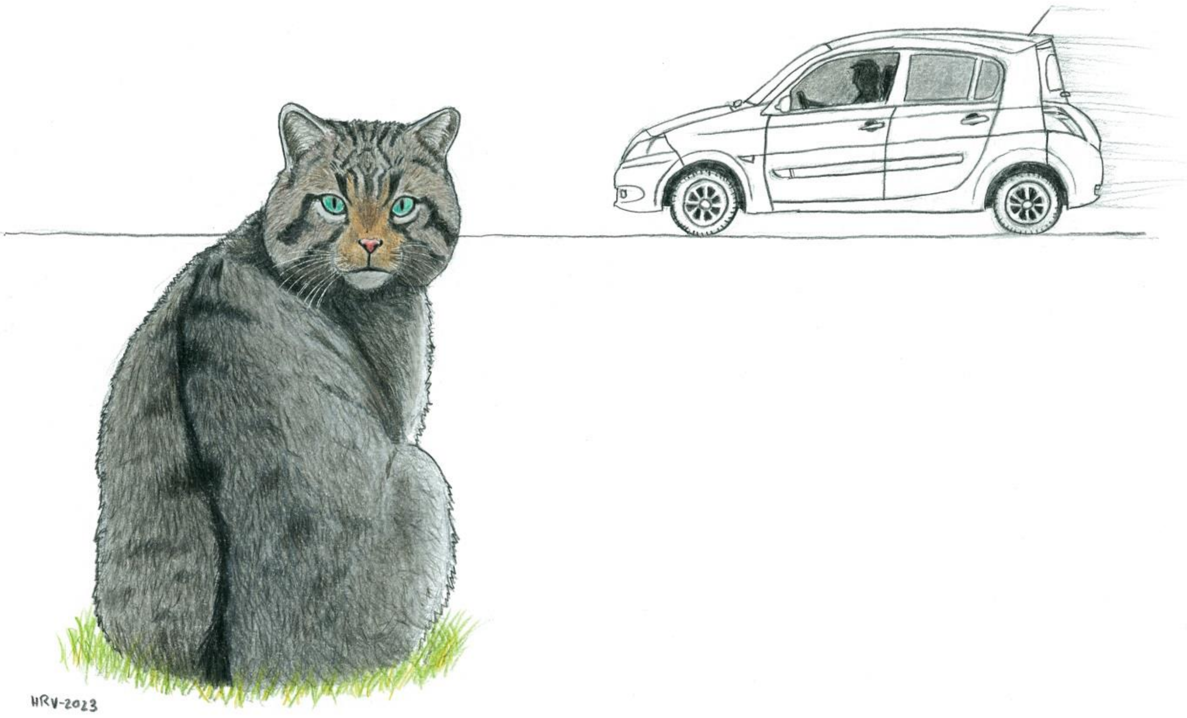
Montaña Palentina (n=262)																				
Year	2014	2015			2016			2017				2018				2019				2020
Season	A(3)	A(1)	W(5)	S(19)	A(4)	W(1)	S(10)	A(37)	W(2)	Sp(14)	S(11)	A(26)	W(19)	Sp(27)	S(2)	A(36)	W(10)	Sp(8)	S(8)	W(19)
Mammalia																				
Rodentia. Muridae																				
Apodemus sp.	2	5	1	3	4	1	6	13		10	4	9	7	6		48	5			9
Apodemus flavicollis										1						2			1	
Apodemus sylvaticus	1						1			1			1			2	1			
Rodentia. Cricetidae																				
Arvicola monticola	3		6	28	1		6	25	1	6	18	30	16	21	1	19	2	5	5	6
Chionomys nivalis		1																		
Microtus sp.				1	1			3		4	1	3	4	5		7	3	2	1	1
Microtus agrestis				1			1	1			2	1	1	4		2	1	1	2	6
Microtus arvalis	1		1		1			4	1	2	1		6	4		17	4	6	3	33
Microtus lusitanicus	3	2	9	8	2		8	33	1	9			12	17		5	8	6	2	14
Myodes glareolus							3	2		4		1	1			3				1
Insectivora																				
Talpa occidentalis									1					2						
Crocidura russula																	3	2		
Sorex coronatus												1								
Sorex minutus																		1		
Other																				
Unidentified rodent			1					3						4		1	1	2	2	1
Unidentified mammal														1						
Reptilia																				
Lacertidae				1	1			7			1	5		3		4	1	2		
Ophidia				1											1					1
Unidentified reptile										2								1		
Aves																				
Passerine bird				2							1	2	1			2			1	
Arthropoda																				
Coleoptera								4		1	2							1		
Ortoptera												3						2		
Und. arthropod										1										
Other																				
Vegetation (purge)	1			2			2	3		4	3	18	3	7		4	1	3	2	

Appendix 2.S9. *Results of the Mann–Whitney U test for pairwise comparisons to detect significant differences ($p<0.05$) in the normalized biomass values for each species between each MRT group. Shaded cells show cases for which differences were very significant ($p<0.001$). Codes for the group names: AH = After Harvest; BH = Before Harvest; FMP = Forests of Montaña Palentina; FWCM = Forests of Western Cantabrian Mountains; LF = Low Forested; and FF = Far From Fields.*

Pairwise comparison	*Arvicola monticola*	*Microtus agrestis*	*Microtus arvalis*	*Microtus lusitanicus*	*Myodes glareolus*	*Apodemus* sp.
AH-BH	0.00036	1	0.00015	0.121	1	1
AH-FMP	0.065	1	1	1	0.309	0.36
AH-FWCM	<0.0001	1	0.00043	0.973	0.00016	<0.0001
AH-LF	0.204	0.23	0.451	<0.0001	1	1
AH-FF	<0.0001	1	0.041	0.361	<0.0001	<0.0001
BH-FMP	0.911	1	0.051	0.234	0.850	0.74
BH-FWCM	0.011	1	<0.0001	0.503	0.007	<0.0001
BH-LF	0.353	0.59	0.00015	0.234	1	1
BH-FF	<0.0001	1	<0.0001	1	<0.0001	<0.0001
FMP-FWCM	0.006	1	0.00014	0.973	0.571	<0.0001
FMP-LF	0.911	0.51	0.241	0.0005	0.674	0.77
FMP-FF	<0.0001	1	0.015	0.4	0.002	<0.0001
FWCM-LF	<0.0001	0.81	1	0.00032	0.036	<0.0001
FWCM-FF	0.00043	1	1	0.973	0.008	0.04
LF-FF	<0.0001	0.15	1	0.036	<0.0001	<0.0001

CHAPTER 3

Humans and traffic influence European wildcat behaviour in pastoral landscapes.



Publication: Ruiz-Villar, H., Morales-González, A., López-Bao, J.V., Palomares, F. Humans and traffic influence European wildcat behaviour in pastoral landscapes. ***Animal Behaviour.*** *Accepted.*

3.1 Abstract

Human activities and infrastructures can disturb wildlife and alter their behaviour by triggering anti-predator responses such as changes in time allocation to different behaviours. For instance, disturbance sources like traffic can significantly vary allocation of time to vigilance and foraging behaviours, which can be used as sensitive measures of human disturbance on animals. Such changes may ultimately derive in physiological and ecological costs for the species. We used the unique opportunity to obtain direct behavioural observations of European wildcats in the Cantabrian Mountains (NW Spain) to investigate how different sources of anthropogenic disturbance influence time allocation of wildcats to specific behaviours. Furthermore, we analysed how traffic affects hunting and vigilance time budgets as well as hunting success. We found that wildcats allocated more time to alert and less time to hunting, feeding and moving behaviours in the presence of humans than in undisturbed situations. Furthermore, wildcats allocated more time to hunting in situations with higher traffic levels, in the proximities of roads and further from villages. Similarly, they dedicated more time to vigilance behaviours while feeding in the presence of moving vehicles. Finally, female wildcats seem to decrease hunting success in presence of vehicles more than males although such effect was not significant. In conclusion, humans and traffic influence behaviour of wildcats inhabiting pastoral anthropogenic landscapes, although it is difficult to know to which extent such changes may translate into wildcat demographic effects.

3.2 Introduction

Close coexistence between wildlife and humans may increase the risk for animals of suffering lethal and non-lethal impacts derived from regular encounters with humans and their activities (Morales-González et al., 2020; Smith et al., 2021). The most common non-lethal direct effect consists on humans triggering behaviours in animals aiming at avoiding attacks from predators, which occur in response to real or perceived predatory threats (i.e. antipredator behaviours; Humphreys & Ruxton, 2018; Ives & Dobson, 1987). Due to the role as super-predators displayed by humans in many animal communities (which includes killing carnivore species; Darimont, Fox, Bryan, & Reimchen, 2015), animals sensitive to human persecution can display different behavioural responses according to the intensity of the perceived risk towards diverse sources of anthropogenic disturbance (e.g. an approaching human; Moen et al., 2019, or the noise generated by road traffic; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014). This response generally fits the “predation risk allocation hypothesis”, and can consists on allocating the time budget spent in each activity (Lima and Bednekoff, 1999; J. A. Smith et al., 2017) or on displaying spatial and temporal avoidance of humans (Reilly et al., 2017).

Optimal foraging theory (Krebs et al., 2010) proposes that wildlife species finding food resources in the proximities of human-dominated environments, must find the balance between the energetic reward obtained from food acquisition and the risk associated to increased encounters with humans and their activities (Stankowich and Blumstein, 2005). They can regulate such balance by adjusting the intensity of their antipredator responses in relation to environmental (e.g. food availability or distance to perceived risk) and individual traits (Bonnot et al., 2017; Carrete and Tella, 2010; Wevers et al., 2020). When successfully displayed, this strategy allows for exploiting nutrient rich food resources while surviving in such environments. Nevertheless, when wrongly displayed, survival and health condition can remarkably suffer from increased contact with humans (Barja et al., 2012; Bastianelli et al., 2021).

One of the most widespread sources of human-disturbance with well-studied effects on wildlife behaviour are roads and the associated traffic (Coffin, 2007; Van Der Ree et al., 2011). Variables like traffic intensity (i.e. proportion of time with vehicles during observations) or distance to roads (Northrup et al., 2012) may change the response of wildlife towards roads. It has been suggested that wildlife may perceive roads as movement barriers (Van Der Ree et al., 2011); but they also may increase the use of road verges due to enhanced foraging opportunities (Northrup et al., 2012) to the point of getting habituated to oncoming vehicles and perceive them as low threatening (Brieger et al., 2022). In addition, traffic can significantly vary time allocation to vigilance and foraging behaviours (Shannon et al., 2014). Such behavioural alterations may ultimately derive in non-lethal physiological and ecological costs for the species such as increased stress levels or decreased reproduction (Lima, 1998; Smith et al., 2015; Wilson et al., 2020).

As animals need to optimize their behavioural time budgets to maximize reproductive success and survival, the intensity of behavioural changes provide a sensitive measure of human disturbance on animals (Berger-Tal et al., 2011). For instance, human activities can affect the time invested on alert and vigilance behaviours which are considered to be incompatible with other behaviours such as feeding, and may consequently present energetic costs for individuals (Ciuti et al., 2012; Pangle and Holekamp, 2010; Wang et al., 2011). Additionally, energy intake is directly related with kill rate and consumption of prey in predators, which can be influenced by human disturbance as observed in cougars (*Puma concolor*) and tigers (*Panthera tigris)* (Kerley et al., 2002; Smith et al., 2015). Nonetheless, linking changes in behaviour with its potential ecological consequences can be challenging (Beale and Monaghan, 2004; Gill et al., 2001).

Most analysis on time allocation in relation to human disturbance have been carried out with species easy to observe in large numbers, such as birds or mammalian herbivores (Beale and Monaghan, 2004; Li et al., 2011), and that spend large amounts of time foraging, which facilitates the identification of alert behaviours between feeding events (Bednekoff and Lima, 1998). Literature becomes, however, scarce when referring to threat-sensitive behaviours on elusive species, such as carnivores, through direct behavioural observations (Holcomb et al., 2009; Hunter et al., 2007; Pangle and Holekamp, 2010).

Research on carnivore responses to humans involve capturing the individuals for GPS collar deployment, sometimes running additional experimental encounters with animals to study their reaction through GPS data (e.g., Moen et al., 2019), or spatially linking the presence of anthropogenic structures, such as roads, with the indirect interpretation of wildlife behaviour inferred from GPS data (Kerley et al., 2002; Northrup et al., 2012). Alternative approaches such as camera trapping (Lovell et al., 2022; Oberosler et al., 2017) are expensive (Caravaggi et al., 2017), can become another source of anthropogenic disturbance (Caravaggi et al., 2020) and rarely provide detailed results on the behavioural reactions of animals to threats, mainly because of their stationary limitations in detecting complete wildlife responses towards immediate sources of disturbance in front of the camera (Caravaggi et al., 2017). In this regard, non-intrusive direct observations of animals aimed at studying their behavioural responses to human-disturbance factors may allow obtaining high resolution and precise information on behavioural cues causing no disturbance to the animals and with no necessity to infer potential behavioural responses from non-observational data.

The European wildcat (*Felis silvestris*) is a small felid species (<15 kg ;Williams et al., 2018) that inhabits mosaic-landscapes with different degrees of human presence across Europe (Jerosch et al., 2017; Oliveira et al., 2018). European wildcats are the only wild felid species in most of their distribution range, and as mesocarnivores they play fundamental roles in ecosystems, such as predation upon small herbivores regulating primary productivity in ecosystems (Estes et al., 1998), contributing to nutrient cycling (Ben-David et al., 2005), and altering soil fertility (Maron et al., 2006). Although wildcats may find abundant prey in anthropogenic environments (Ruiz-Villar et al., 2022) encounters with humans in such locations may impact wildcats negatively through e.g. increased road mortality (Bastianelli et al., 2021) and increased stress levels (Piñeiro et al., 2012). It is also possible that wildcat behaviour and hunting success are affected by human disturbance, as seen for other species (Kerley et al., 2002; Smith et al., 2015). In this regard, research mainly focused on habitat selection (including sexual differences) based on GPS data (Jerosch et al., 2018; Oliveira et al., 2018), and the selection of road crossing points across infrastructures which can act as movement barriers (Klar et al., 2009; Rodriguez et al., 1997). Although behavioural data on wildcats is hard to obtain as this species is rarely observed across its distribution range, wildcat behaviour can be directly recorded and analysed in pastoral fields of the Cantabrian Mountains (NW Spain), used by wildcats with predation purposes (Jiménez-Albarral et al., 2021; Rodríguez et al., 2020; Ruiz-Villar et al., 2022). This combined with the presence of several potential sources of disturbance for wildcats using such environments (roads and traffic, villages, humans or livestock) create a rare opportunity to study the effects of human disturbance on wildcat behaviour through direct observations, something required to ensure effective wildcat conservation in future scenarios with increasing human presence.

In this article, we examine behavioural responses of European wildcats using pastoral fields of the Cantabrian Mountains to different sources of human disturbance. Particularly, we investigate how the presence of humans and human-related noise, cyclists, vehicles, livestock and dogs in comparison with the disturbance generated by wildlife species and with undisturbed situations may affect time allocation of wildcats to hunting, grooming, alert, feeding, moving and stationary behaviours. Furthermore, we will look at how traffic and distance to roads influence hunting and vigilance behaviours as well as hunting success. We expect that: i) time allocation by wildcats to different behaviours varies depending on the source of disturbance and differs from undisturbed situations. Wildcat perception and tolerance towards different sources of disturbance may vary. For instance, wildcat alert response towards humans may always be high, as observed for other carnivores when experimentally approached (Ordiz et al., 2019; Wam et al., 2014). Something similar is expected to occur when interacting with potentially competing or disturbing wildlife species such as red foxes (*Vulpes vulpes;* Ruiz-Villar et al. 2021) or corvids (Verbeek, 2010). On the other hand, response to moving vehicles may be low, as species can become habituated to moving traffic by repetition of a harmless stimuli, thus decreasing their anti-predator response (Brieger et al., 2022; Lima et al., 2015). However, behavioural changes associated to traffic presence may be overlooked and consequently we aim at its specific research expecting that: ii) both the overall time allocation to hunting behaviours (model 1) and the specific time allocation to vigilance behaviours while feeding upon a recently captured prey (model 2) would increase in situations with higher traffic intensity; and iii) traffic presence would decrease wildcat hunting success (model 3) as they will be more distracted by a potential threat occurring in the surroundings. Traffic and the associated noise may reduce hunting performance in wildcats due to noise masking or disturbance during hunting events for which they need to compensate by spending longer periods hunting, as observed in other acoustic predators like bats (Siemers and Schaub, 2011). In addition the presence of a threat during prey consumption may trigger antipredator behaviours (in our case vigilance) in wildcats during such events (J. A. Smith et al., 2017). Finally, wildcat females generally use areas with lower human presence, which may be related with higher sensitivity to sources of human disturbance that may influence prey availability and kitten security (Beugin et al., 2016; Oliveira et al., 2018). We consequently expect that iv) behavioural responses to traffic would differ between sexes, with females showing a higher increase in the time invested in vigilance behaviours while feeding (model 2) and a higher decrease in hunting success (model 3) in comparison to males.

3.3 Methods

Study area

We recorded European wildcat behaviour inside an area of ca. 1,800 km^2 located in the western end of the Cantabrian Mountains (NW Spain; Fig. 3.A1). Landscape is characterized by a mosaic of broadleaf forests (oak (*Quercus* sp.), beech (*Fagus sylvatica*), birch (*Betula* sp.), etc.), broom and heather-like shrubs, and pasturelands. The valley bottoms are occupied by human settlements and fields derived from traditional farming activities (García et al., 2005).

Wildcat observations

Taking advantage of the regular use of open pastoral fields by European wildcats with hunting purposes in the Cantabrian Mountains (Rodríguez et al., 2020; Ruiz-Villar et al., 2021; Ruiz-Villar et al., 2022), we searched for wildcats between August 2012 and December 2020 combining two methods: opportunistic observations either along transects in cars on main and secondary paved roads or from stationary points. We used binoculars, a telescope and a bridge camera (Swarovski Habicht 7x42; Swarovski ATS 65HD + Zoom 20X60, Swarovski Optik KG, Austria; and Canon PowerShot SX60 HS (Canon Inc., Japan)) to locate and film wildcats from a minimum distance of 200 m (to eliminate disturbance and potential alterations on wildcat behaviour). We identified wildcats based on the external morphological and pelage characteristics described by Ragni and Possenti (1996). No hybrids with domestic cats have been previously detected in the study area (Tiesmeyer et al., 2020) which reduces the chances of wildcat-hybrid misidentification in the Cantabrian Mountains. Nevertheless, as morphology solely does not fully allow wildcat differentiation from hybrids (Devillard et al., 2014) and we did not genetically analyse each observed individual wildcat, we use the term wildcat or European wildcat referring to phenotypic European wildcats. We assigned each observation to a specific individual based on its particular pelage characteristics e.g. shape and number of tail rings, size of the white patch in the chest and other characteristics presented by Jiménez-Albarral et al. (2021). Sex was determined when possible through the observation of the genital area. For each observation, we determined the location as the point where the wildcat spent most of the time or, in case the animal was moving, the middle point. For long observations, the location was updated every 20 min.

Behavioural data collection

Wildcat video recordings ranged between a few seconds and 111 min (mean = 24 min; Standard deviation=±24 min); and observations < 10 min (n=113) were discarded for the analyses modelling time proportions allocated to specific behaviours inside complete observations. We considered feeding events as the defining behaviours of wildcat activity in open fields because the main goal of wildcats in such environments is to capture and feed upon prey. The maximum duration of a recorded feeding event was 455s. To maximize the chances of including full feeding events inside observations, we established 600s (10 min) as the minimum duration of observations that can be representative of wildcat behaviour. This is a conservative approach as the median duration of feeding events was 48s. By increasing the minimum observation time to 10 min, we increase the chances of including several feeding events combined with other behaviours in a single observation. On the contrary, observations shorter than 10 min will probably not include sufficient behavioural diversity.

We tagged the main wildcat behaviours (Table 3.1) as well as the presence and duration of disturbance sources in the proximate environment visible by wildcats (ca. <200 m without visual obstacles) using the software BORIS (Friard and Gamba, 2016). We tagged each behaviour with the source of disturbance with which it overlapped: vehicle, human, cyclist, livestock, wildlife, human noise, dog and none (absence of disturbance). We started recording the disturbance when it was detected by the observer. When several but not overlapping sources of disturbance occurred within a behaviour (e.g. first no disturbance occurred, second a vehicle drove by and third a cyclist passed by while the wildcat was moving) we tagged each corresponding proportion of the total time of the behaviour with the corresponding source of disturbance. In the cases when two sources of disturbance overlapped (e.g. a vehicle passed by while the wildcat was moving in a meadow where there were livestock) we only accounted for the source of disturbance that we considered more threatening. We created a hierarchy between sources of disturbance to decide which source was more influential on wildcat behaviour. In particular we ranked the mean proportion of time dedicated to alert behaviour during each source of disturbance when overlapping disturbances did not occur (Table 3.A1). From more to less threatening (higher to lower mean proportion of time invested in alert behaviour), disturbances were ordered as: human, wildlife, cyclist, dog, livestock, vehicle, and human-noise. Cyclist never overlapped with other sources of disturbance. We also calculated the proportion of the observation time allocated to each behaviour type.

To estimate traffic presence and intensity (models 1 to 3) we recorded every passing vehicle regardless its distance to the wildcat. We recorded traffic presence by detecting the noise produced by a car in the recordings (since we started hearing the car until the noise totally stopped) and calculated the traffic intensity as the proportion resulting from the observation time with vehicles divided by the total observation time with vehicles and without any kind of disturbance. We also recorded wildcat responses to different wildlife species with which we observed interactions: another wildcat, red fox, brown bear (*Ursus arctos*), roe deer (*Capreolus capreolus*) and corvids, particularly magpies (*Pica pica*) and crows (*Corvus corone*).

As time dedicated to vigilance in carnivores can sometimes be confounded with looking out for prey (both behaviours consist on looking around in a stationary position), we recorded vigilance behaviours occurring during feeding events (i.e. the time spent consuming a prey item since its capture until the prey is finished), as the possession of a prey item in that specific moment reduces the chances of "looking around behaviours" aiming at prey detection. We then calculated the proportion of the time in the feeding event dedicated to vigilance behaviours (model 2).

To estimate hunting success (model 3), we recorded wildcat hunting attempts, considered as an event of the wildcat jumping over a potential prey, and determined the outcome (success or failure), thus calculating the hunting success per attempt and observation.

Table 3.1. *Wildcat behaviours and disturbance sources tagged on wildcat recordings.*

Behaviour	Definition
Moving	Displacement through the environment. It includes walking, trotting, running and jumping.
Stationary	Motionless behaviours. It includes standing, sitting and laying.
Hunting	Behaviours part of the process of capturing prey. It includes approaching, stalking and leaping over prey. The outcome of the recorded attempt can be success – they prey is caught; or failure –the prey is not caught.
Feeding	Process of chewing and swallowing the prey.
Marking	Face rubbing, urination and defecation with marking purposes
Grooming	Process of licking the own pelage.
Alert	Tense behaviour in response to a threat. We recorded three alert behaviours with increasing intensity: vigilance – looking continuously in the direction of the threat; crouch – standing low next to the ground to avoid detection; and flight – running away from the threat.
Disturbance	Potential sources of disturbance were recorded from the moment they were detected by the observer (e.g. car sound approaching, farmer going into a field). The following disturbance sources were recorded: vehicle, human, cyclist, livestock, wildlife, human noise (e.g. saw machine), dog and none (absence of disturbance).

A number of additional covariates that may influence wildcat behaviour were included for each observation (Table 2): 1) weather – sunny, overcast, bad weather (rainy, snowy, and windy)-; 2) Sex – female, male or unknown-; 3)

Age – Adult, Juvenile, Kitten, Unknown -; 4) Distance (m) to the closest road; and 5) Distance (m) to the closest village. We calculated observation distances to the closest road and village on ArcGIS 10.1 (ESRI, 2012) using the layers of Transport Networks and Human Settlements made available by the Spanish National Geographic Institute (https://centrodedescargas.cnig.es/CentroDescargas/catalogo.do?Serie=CAANE).

Statistical analysis

To investigate the differences between sources of disturbance in time allocation to different behaviours, we calculated, for each observation and source of disturbance, the proportion of the total duration of the disturbance allocated to hunting, grooming, alert, feeding, moving, and stationary behaviours. Several behaviour types may occur simultaneously (e.g. stationary and alert) and consequently the sum of time allocation proportions can be larger than one.

We performed pairwise comparisons to test for significant differences on: (1) the proportion of time allocated to the set of behaviours between the different disturbance types (i.e. multi-group comparisons); (2) the proportion of time allocated to each behaviour type between the disturbance sources; and (3) the proportion of time allocated to each behaviour type for each disturbance type. The latter two corresponded to single group comparisons. For multi-group comparisons we performed permutational multivariate analysis of variance using Bray-Curtis dissimilarity followed by posthoc procedures (PERMANOVA, vegan and RVAideMemoire packages in R-software; Hervé, 2020; Oksanen et al., 2013). For single-group comparisons we performed the Kruskal-Wallis test followed by posthoc procedures (stats and pgirmess packages in R-software; Giraudoux, Antonietti, Beale, Pleydell,

& Treglia, 2018; R Core Team, 2021). We set statistical significance levels at < 0.05.

To investigate the effects of traffic on i) the proportion of time allocated to hunting (model 1) and ii) the proportion of time allocated to vigilance during feeding events (model 2) we fitted two generalized linear mixed model (GLMM) with a binomial zero-inflated distribution using 'logit link' with time invested to hunting / total observation time and time allocated to vigilance while feeding / total duration of feeding event as response variables, respectively. In both cases we used traffic intensity (or traffic presence in model 2), distance to road, and distance to village as explanatory variables. In model 2, we used traffic presence instead of intensity as the behavioural analyses correspond to a smaller time window (i.e. feeding event) which may be influenced by the presence of a vehicle in that specific moment. For the time invested hunting and total observation time we only considered time with vehicles and without disturbance. For model 2 we only considered feeding events occurring with presence of vehicles or without disturbance. In both models we further included sex (female and male), age (adult and juvenile), season (summer, autumn, winter and spring) and weather (sunny, overcast, bad weather) as additional covariates to account for factors that may influence time allocation to hunting and vigilance. The interaction term between traffic intensity and sex and between traffic presence and sex were also included in models 1 and 3, and model 2, respectively. We added subject as a random factor to account for non-independence of observations recorded for the same individual. In the first model and to make results representative we only considered observations with durations longer than 10 minutes. Details on the biological relevance of the explanatory variables and interaction terms are given in Table 3.2.

***Table 3.2**. Biological relevance of the variables and interaction terms included in our models. Unless specified, all variables were included in all models.*

Variable	Description
Traffic intensity	Included in models 1 and 3. Traffic intensity may influence time allocation to different behaviours (e.g. vigilance and hunting) and hunting success in carnivores (Northrup et al., 2012; Smith et al., 2015).
Traffic presence	Included in model 2. When working at narrow time scales (i.e. duration of a feeding event) the presence of a vehicle in the surroundings may trigger evasive responses which can influence behavioural time allocation (Lima et al., 2015; Zurcher et al., 2010).
Distance to road	Wildlife behaviour can vary in relation to road distance by, for instance, moving more and feeding less when closer to roads (Ciuti et al., 2012; Prokopenko et al., 2017).
Distance to village	Behavioural responses of wildlife to anthropogenic sources of disturbance can vary with distance to human settlements by, for instance, increasing tolerance to humans in the proximity of settlements (Bjørvik et al., 2015).
Sex	Wildcat females are considered to be more sensitive to human presence and disturbance to which they respond by selecting habitats with lower human presence (Oliveira et al., 2018; Ruiz-Villar et al., 2023). Consequently, behavioural responses to human-related disturbance are expected to differ between sexes.
Age	Previous exposure to disturbance and its accumulation with age affect the response towards vehicles (Thurfjell et al., 2017), for such reason behavioural responses can be different between adults and juveniles.
Season	As seen for other species, hunting success or time spent vigilant may be influenced by season (Hilborn et al., 2012; Quenette, 1990) as prey availability, landscape structure and traffic intensity may also change. We considered meteorological seasons: winter (Dec to Feb), spring (March to May), summer (June to Aug) and autumn (Sept to Nov).
Weather	Weather commonly influences wildlife behaviour (Lemel et al., 2003) as it determines body temperature or vulnerability to predation due to diminished detection capacities (e.g. in windy or rainy conditions). Accordingly we included three levels: sunny, overcast and bad weather.
Interaction between traffic intensity and sex	Included in models 1 and 3. Male and female wildcats respond differently to sources of human disturbance (Oliveira et al., 2018; Ruiz-Villar et al., 2023). It is possible that traffic intensity affects male and females differently regarding hunting success and time allocation to hunting and vigilance behaviours during feeding events.
Interaction between the traffic presence and sex	Included in model 2. The same as above.

In addition, to evaluate the effects of traffic intensity and the immediate presence of vehicles during a hunting attempt on the hunting success of European wildcats we performed a GLMM with a binomial distribution using 'logit link' with hunting success (number of successful hunting attempts / number of total hunting attempts per observation) as a response variable (model 3). We used observations with at least one hunting attempt and longer than 10 minutes, and not considered the time when disturbances other than vehicles occurred. The explanatory variables for model 3 were the same than for model 1 (Table 3.2). For the three models we did not consider observations with unknown sex and observations from kittens and individuals with unknown age.

We conducted all statistical analyses with the package lme4 (Bates et al., 2015) and glmmTMB (Brooks et al., 2017) in the software R (https://www.r-project.org/). For the three models we used the argument ´weights´ available in the glmer and glmmTMB functions of the above-mentioned packages, respectively, to account for the different dimensions of the denominators of the response variables. To avoid using highly correlated predictor variables ($|r|>0.7$; Dormann et al., 2013), we calculated their correlation matrix and found no correlated variables. We standardised continuous variables by subtracting their mean and dividing by the standard deviation to allow for comparability among model coefficients. We used model selection to test all combinations of the predictor variables; model selection was based on Akaike's information criterion (AIC; Akaike, 1973) using the library MuMin (Barton, 2015). All combinations of the included variables were biologically plausible. We calculated model averages using the "zero" method (Grueber et al., 2011). For models 1 and 2 we averaged models with $\Delta AIC<6$. This allowed us to be 95% sure that the truly most parsimonious model was retained within the confidence set (Richards, 2007; Richards et al., 2011). In the case of model 3 and to avoid the retention of an overly complex model (Richards, 2007), we only considered models with ΔAIC<2. To exclude potential differences arising from a more restrictive model averaging, we additionally evaluated model averaging including models with ΔAIC<6 for model 3 and found no remarkable differences in both the direction significance of our results (Table 3.A2). To improve inference and parameter accuracy during model averaging, we eliminated models from the top model set that were more complex versions of nested models with lower AIC (Richards et al., 2011). Details on model selection are provided in Table 3.3 while details of the full model are given in Table 3.A3. Similarly, details on the diagnostics of zero-inflated distribution, overdispersion, and assessment of residuals using the package DHARMa (Hartig, 2020) for all models are provided in Appendix 3.A, Fig. 3.A2, Fig. 3.A3, and Fig 3.A4. Full dredging tables for all models are provided in Supplementary Material 1. To make predictions we back-transformed the log odds to probabilities.

Table 3.3. *Set of models resulting from model selection based on Akaike's information criterion (model with the lowest AICc value). Models with ΔAICc < 6 (for models 1 and 2) and ΔAICc < 2 (for model 3) and that were more parsimonious versions of the top model are shown. Such models were used for model averaging procedures. df, degrees of freedom; AICc, AIC for small sample sizes; ΔAICc, difference to best statistical model based on AICc; W, Akaike weights (based on all models). Variables are defined as follows: HuntTime, proportion of time allocated to hunting (time invested hunting / total observation time); VigTime, proportion of time allocated to vigilance during feeding events (time allocated to vigilance / duration of feeding event since beginning to end); HSobs, hunting success at the level of observation (number of successful hunting attempts / number of hunting attempts per observation); Age, Age class of the individual; Weather, Meteorological conditions during*

observation; TraffInt, Proportion of the observation time with traffic divided per total observation time; TraffPres, Inmediate presence of a vehicle (Yes or No); Distance_road, Distance to the closest road (m); Distance_village, Distance to the closest village (m); Season, Meteorological season; Sex, sex of the individual; TraffInt:Sex, Interaction between traffic intensity and sex; TraffPres:Sex, Interaction between traffic presence and sex.

Model	Response variable	Variable	df	AICc	ΔAICc	W
1. GLMM binomial zero-inflated	*HuntTime*	Age + Weather + TraffInt + Distance_road + Distance_village + Season + Sex + TraffInt:Sex	14	32757	0.00	0.49
		Age + Weather + TraffInt + Distance_road + Distance_village + Season + Sex	13	32759	1.98	0.18
		Weather + TraffInt + Distance_road + Distance_village + Season + Sex + TraffInt:Sex	13	32759	2.21	0.16
		Age + Weather + TraffInt + Distance_road + Distance_village + Season	12	32761	3.71	0.08
		Weather + TraffInt + Distance_road + Distance_village + Season + Sex	12	32761	4.26	0.06
		Null	3	34385	1628	0
2. GLMM binomial zero-inflated	*VigTime*	Age + Weather + TraffPres + Season + Sex + TraffPres:Sex	12	2053.7	0.00	0.32
		Age + Weather + TraffPres + Distance_road + Sex + TraffPres:Sex	10	2057.3	3.54	0.05
		Age + Weather + TraffPres + Sex + TraffPres:Sex	9	2058.3	4.62	0.03
		Weather + TraffPres + Distance_road + Distance_village + Sex + TraffPres:Sex	10	2059.4	5.68	0.02
		Weather + TraffPres + Distance_road + Sex + TraffPres:Sex	9	2059.5	5.79	0.02
		Null	3	2147.6	93.88	$1.3*10^{-21}$
3.GLMM binomial	*HSobs*	Age + TraffInt+ Distance_road + Season + Sex + TraffInt:Sex	10	402.32	0.00	0.04

	Sex	3	403.08	0.75	0.03
	Season + Sex	6	403.08	0.76	0.02
	TraffInt + Distance_road + Season +Sex + TraffInt:Sex	9	403.20	0.88	0.02
	Age + Distance_road + Season + Sex	8	403.39	1.07	0.02
	Distance_road + Season + Sex	7	403.41	1.09	0.02
	TraffInt + Season +Sex + TraffInt:Sex	8	403.49	1.17	0.02
	Distance_road + Sex	4	403.68	1.36	0.02
	Season	5	404.20	1.88	0.01
	Null	2	404.73	2.41	0.01

Ethical note

This research involves passive observations of non-habituated wildcat individuals in the wild at large distances and therefore does not require from interactions or manipulations of the monitored wildcats. In this specific context, our country does not require from the expedition of any particular permit. We aimed at recording wildcat behaviour both in undisturbed conditions and in disturbed situations not provoked experimentally and caused by factors other than the observer. Accordingly, observations were obtained using optic material and bridge cameras with long zooms at distances greater than 200 m to eliminate the effect of the observer on wildcat behaviour.

3.4 Results

We obtained 279 observations (110.84 h in total) from 92 individual wildcats. The proportion of time allocated to the different behaviours varied between the sources of disturbance (PERMANOVA test; p = 0.001; Fig 3.1). In particular, differences aroused between human and none, human and vehicle, wildlife and none, and wildlife and vehicle (pairwise comparisons; p<0.05).

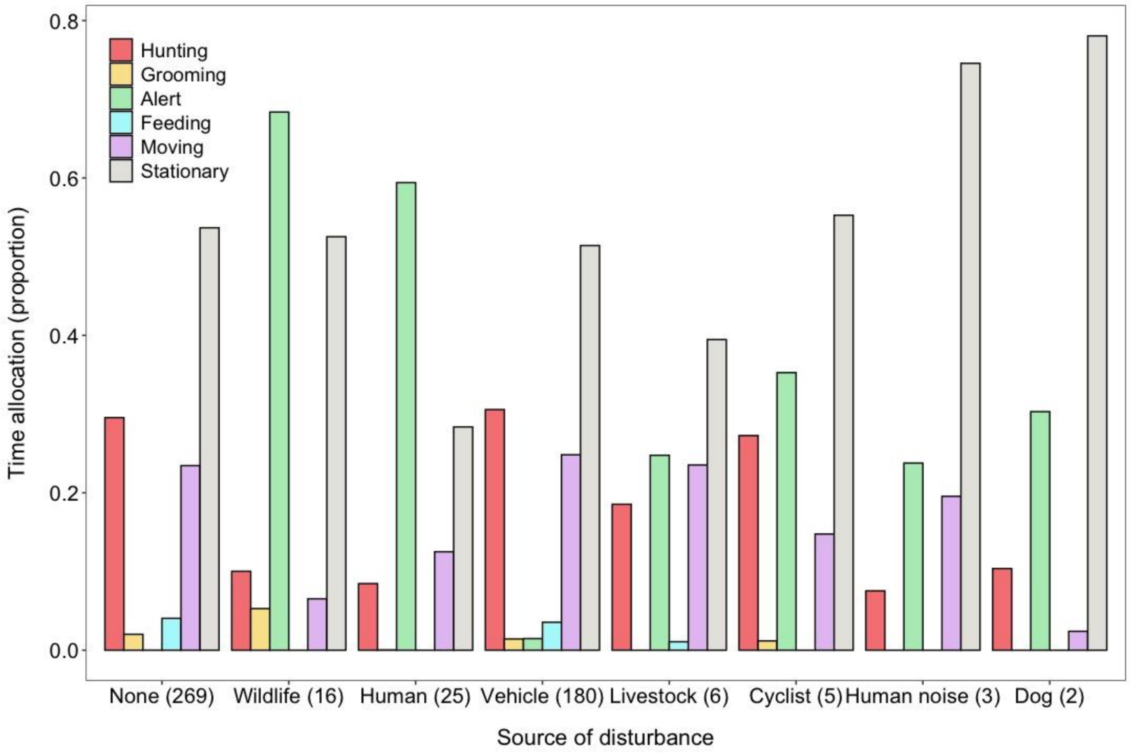


Figure 3.1. *Proportion of time allocated by European wildcats to different behaviours (hunting, grooming, alert, feeding, moving, and stationary) under different sources of human disturbance (x axis). Brackets show the sample size of behavioural recordings for each disturbance source. When two sources of disturbance overlapped in time we assigned the behavioural recording to that with higher potential of disturbance (Table 3.A1). Two behavioural categories may occur simultaneously and thus sum of proportions can be larger than 1.*

The proportion of time allocated to a specific behaviour varied between the sources of disturbance for all behaviours (Table 3.A4 for pairwise comparisons). Wildcats allocated significantly more time to alert behaviours under the presence of humans, livestock or wildlife than in the presence of vehicles or in the absence of disturbances (p<0.001; Table 3.4; Fig 3.1). Similarly, wildcats allocated less time to hunting and moving under human or wildlife presence than in presence of moving vehicles (p<0.001; Table 3.4; Fig

3.1). They also allocated less time to hunting, feeding and moving under human or wildlife presence than in the absence of disturbance (p<0.001; Table 3.4; Fig 3.1). Comparisons of the time allocated to each behaviour during a specific disturbance source showed that wildcats allocated more time to alert behaviours than to other behaviours under presence of humans and wildlife (Table 3.4; Fig 3.1). On the other hand, wildcats allocated more time to hunting, moving and stationary behaviours under the presence of vehicles or the absence of disturbance (Table 3.4; Fig 3.1).

Table 3.4. *Mean (± standard deviation) of the proportion of time allocated to each behaviour under each type of disturbance source. Bold numbers indicate the behaviour to which most behavioural time was allocated. Asterisk shows the behaviours for which significant differences were found in comparison to the absence of disturbances according to Kruskall-Wallis posthoc procedures (p<0.05). Brackets show the sample size of behavioural recordings for each disturbance source.*

Group	Hunting	Grooming	Alert	Feeding	Moving	Stationary
Human	0.08*	<0.01	**0.59***	0*	0.12*	0.28*
Livestock	0.18	0	0.25*	0.01	0.23	**0.39**
Cyclist	0.27	0.01	0.35	0	0.15	**0.55**
Wildlife	0.10*	0.05	**0.68***	0*	0.06*	0.52
Human noise	0.07	0	0.24	0	0.19	**0.75**
Dog	0.10	0	0.30	0	0.02	**0.78**
Vehicle	0.31	0.01	0.01	0.03	0.25	**0.51**
None	0.30	0.02	<0.01	0.04	0.23	**0.54**

To investigate the effects of traffic intensity on the proportion of time allocated to hunting (model 1) we used 161 observations from 50 individuals (124 from males and 37 from females). Time allocation to hunting increased with the traffic intensity [estimate (Est) = 0.62, standard error (SE) = 0.21, P < 0.001; Fig 3.2, Table 3.5], distance to village [Est = 0.72, SE = 0.03, P < 0.001; Table 3.5] and spring and winter seasons vs. autumn [Table 3.5]. On the other hand, time allocation to hunting decreased with distance to road [Est = -0.06, SE = 0.01, P < 0.001; Fig 3.2, Table 3.5] and with the overcast and sunny weather vs. bad weather (rainy, snowy and windy) [Table 3.5]. Males and females spent an average of 30% and 37% of the observed time hunting, respectively.

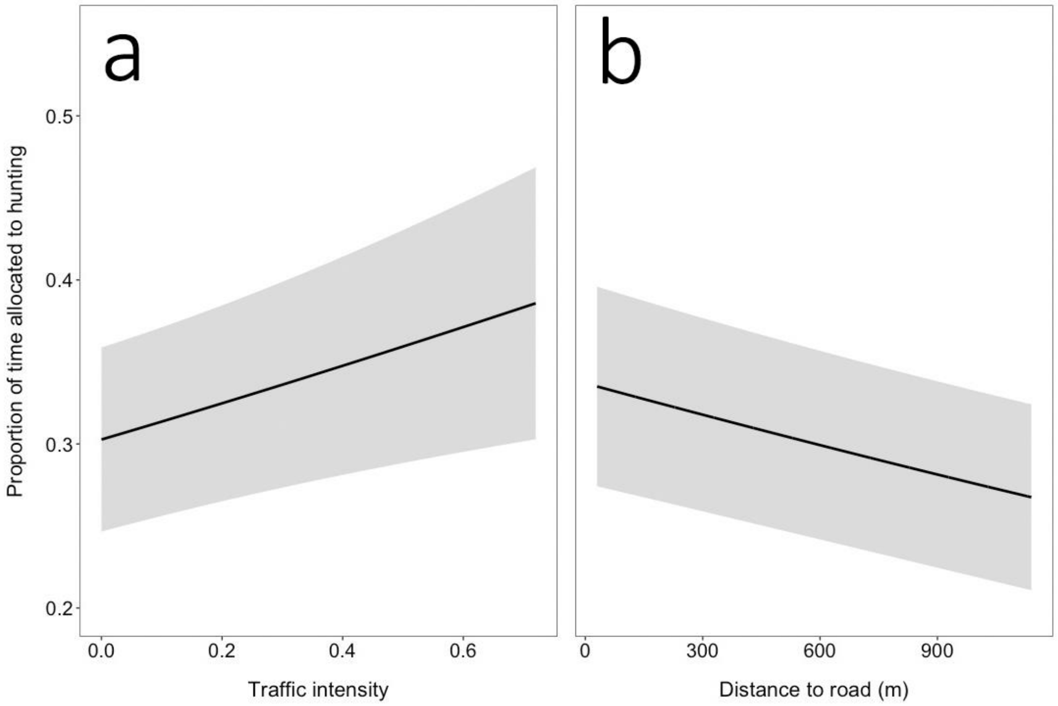


Figure 3.2. *Effects of traffic intensity (a) and distance to road (b) on the proportion of time allocated to hunting (time allocated to hunting / total observation time) in European wildcats. For total observation time we only considered time with vehicles and without disturbance. We considered observations longer than 10 min (n = 161). Shown are model predictions with 95% confidence intervals. Predictions were calculated from the top model (model 1) and by setting all other variables to their mean values.*

***Table 3.5**. Effects of the variables included in the model averages on: 1. time allocation to hunting; 2. time allocation to vigilance during feeding events; and 3. hunting success in European wildcats. For each variable, we report the estimate (Est), standard error (SE), significance (P), Odd Ratios (OR) and 95% Confidence Intervals of odds ratio (95% CI). ΔAICc shows the effect of removing each variable from the top model on the AICc. Significant values are based on Wald statistics with bold font indicating significant effects. The 95% CI of odds ratio is used as a proxy for the presence of statistical significance if it does not overlap 1. Baseline level for sex, age, weather, season and traffPress are female, juvenile, bad weather (rainy, snowy and windy), autumn and no respectively.*

	Variable	**Est**	**SE**	**P**	**ΔAICc**	**OR**	**95% CI**
1. HuntTime	Intercept	-0.82	0.14	**<0.001**		0.44	0.33-0.58
	TraffInt	0.62	0.21	**<0.001**	285.48	1.86	1.23-2.80
	Sex(Male)	-0.17	0.10	0.088	3.71	0.83	0.70-0.99
	Age(Adult)	0.07	0.05	0.193	2.21	1.09	1.01-1.19
	Distance_road	-0.06	0.01	**<0.001**	21.76	0.94	0.92-0.97
	Distance_village	0.72	0.03	**<0.001**	746.69	2.06	1.95-2.18
	Weather(Overcast)	-0.07	0.02	**<0.001**	196.74	0.93	0.89-0.97
	Weather(Sunny)	-0.22	0.02	**<0.001**	196.74	0.80	0.77-0.84
	Season (Spring)	0.65	0.05	**<0.001**	213.25	1.91	1.72-2.12
	Season (Summer)	0.02	0.01	0.060	213.25	1.02	0.99-1.05
	Season (Winter)	0.38	0.03	**<0.001**	213.25	1.46	1.37-1.56
	TraffInt:Sex(Male)	0.25	0.23	0.269	1.98	1.45	1.02-2.07
2. VigTime	Intercept	-2.89	0.46	**<0.001**		0.05	0.02-0.14
	TraffPres (Yes)	1.13	0.16	**<0.001**	71.88	3.11	2.26-4.28
	Sex (Male)	-0.28	0.25	0.270	28.82	0.75	0.46-1.24
	Age (Adult)	0.55	0.28	**0.048**	8.03	1.82	1.15-2.87
	Weather (Overcast)	1.14	0.31	**<0.001**	19.74	3.14	1.69-5.84
	Weather (Sunny)	1.29	0.32	**<0.001**	19.74	3.63	1.94-6.81

	Season (Spring)	-0.31	0.32	0.333	4.62	0.65	0.36-1.17
	Season (Summer)	-0.19	0.14	0.168	4.62	0.76	0.65-0.90
	Season (Winter)	-0.13	0.20	0.496	4.62	0.83	0.55-1.25
	TraffPres(Yes):Sex(Male)	-0.88	0.17	**<0.001**	27.43	0.41	0.30-0.58
3. HSobs	Intercept	0.12	0.48	0.803		1.13	0.44-2.87
	TraffInt	-1.25	1.87	0.505	1.07	0.04	0-1.06
	Sex(Male)	-0.70	0.42	0.093	5.97	0.47	0.22-1
	Age(Adult)	-0.17	0.34	0.608	0.88	0.54	0.26-1.10
	Distance_road	-0.12	0.14	0.391	2.34	0.81	0.63-1.05
	Season (Spring)	0.64	0.78	0.411	2.97	2.26	0.47-10.84
	Season (Summer)	0.44	0.30	0.136	2.97	1.75	1.16-2.66
	Season (Winter)	0.30	0.35	0.383	2.97	1.47	0.74-2.92
	TraffInt:Sex(Male)	1.46	2.12	0.492	3.24	42	1.37-1281

To investigate the effects of traffic intensity on the proportion of time allocated to vigilance during feeding events (model 2) we used 261 feeding events recorded during 132 observations of 57 individuals. Time allocation to vigilance during feeding events increased with the presence of a vehicle [Est = 1.13, SE = 0.16, P < 0.001], and such increase was significatively higher for females than males [Est = -0.88, SE = 0.17, P < 0.001; Fig 3.3, Table 3.5]. On average, both sexes spent a similar proportion of time vigilant while feeding (ca. 11.5%). In addition, time allocation to vigilance during feeding events increased with adult age [Est = 0.55, SE = 0.28, P < 0.05; Table 3.5] and overcast and sunny weathers [Table 3.5].

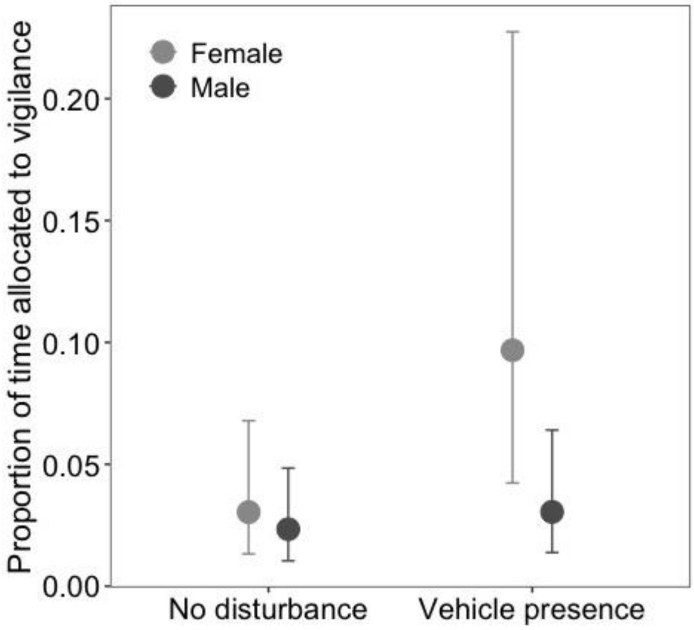


Figure 3.3. *Variation in the proportion of time allocated to vigilance behaviours while feeding (time allocated to vigilance during feeding events / duration of feeding event) according to the immediate presence of a vehicle and sex of the wildcat individual. We considered 261 feeding events. Shown are model predictions with 95% confidence intervals. Predictions were calculated from the top model (model 2) and by setting all other variables to their mean values.*

To investigate the effects of traffic intensity on the hunting success of wildcats (model 3) we used 147 observations of 47 individuals. We found that females decreased their hunting success more than males with traffic intensity (Fig 3.4) although such effect was not significant when considering the p-value [Est = 1.46, SE = 2.12, P >0.05; Table 3.5] and was marginal when considering the odds-ratio [CI: 1.37-1281; Table 3.5]. On average, females had higher hunting success than males (46 and 39% respectively). No significant effect was found for the rest of the variables considered.

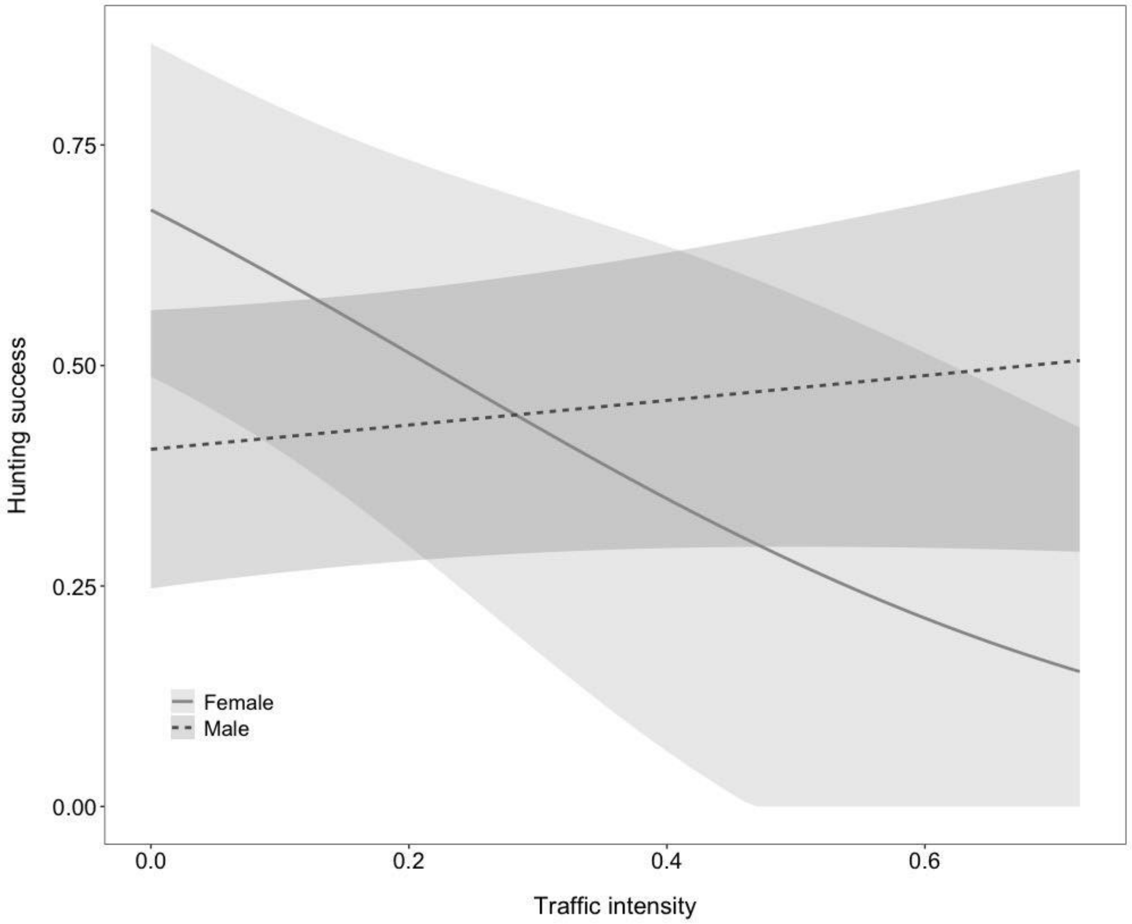


Figure 3.4. *Effect of the traffic intensity on the hunting success (number of successful hunting attempts per observation / total number of hunting attempts per observation) of male and female wildcats. We used observations with at least one hunting attempt and longer than 10 min, and not considered the time when disturbances other than vehicles were occurring (n=141). Shown are model predictions with 95% confidence intervals. Predictions were calculated from the top model (model 3) and by setting all other variables to their mean values.*

3.5 Discussion

Our results show that European wildcats changed their behaviour when exposed to different sources of human-related disturbance, and that such responses varied between males and females, with the latter suffering more remarkable behavioural changes than males. Specifically, a combination of different values of traffic intensity, vehicle presence and distance to roads determined the behaviour of wildcats in terms of time allocation to hunting, vigilance and hunting success. Although changes in behaviour and hunting success can be difficult to link with physiological consequences (Beale and Monaghan, 2004; Gill et al., 2001), the antipredator responses observed in European wildcats could potentially derive into energetic costs for the species (Ciuti et al., 2012; Pangle and Holekamp, 2010; Wang et al., 2011) which might ultimately influence demographic performance of wildcats through effects on individuals' fitness and breeding success (McHuron et al., 2017; Wilson et al., 2020).

According to our expectations, wildcats allocated most of their time to alert behaviours and reduced the time invested in hunting and feeding behaviours in the presence of humans, livestock, and wildlife (particularly larger carnivores like foxes, and corvids that regularly mob predators; Verbeek, 2010) in comparison to absence of disturbance. Importantly, wildcats did not allocate time to feeding when in presence of humans. Antipredator responses of carnivores towards approaching humans are common among European carnivores (e.g brown bears (*Ursus arctos* ; Ordiz et al. 2013, 2019), and wolves (*Canis lupus;* Wam et al. 2014)) that suffered persecution in recent times. Regarding livestock, other felid species have been shown to change their behaviour in relation to livestock presence (Cheetahs (*Acinonyx jubatus*; Broekhuis et al., 2019) and leopards (*Panthera pardus*; Pudyatmoko, 2017)). We observed livestock (mainly cows and horses) actively chasing wildcats when overlapping in pastoral fields, which may explain why wildcats display anti-predator responses when sharing fields with livestock. Whereas wildcats are prepared to display antipredator responses to wildlife species such as foxes (Ruiz-Villar et al., 2021), the presence of humans (which can display super-predator roles in animal communities; Darimont et al., 2015) and livestock in wildcat territory adds an additional load of time allocation to antipredator behaviours in the species, which could potentially increase their energetic cost throughout reduction of time invested in food obtainment (Williams et al., 2006), but also through enhanced stress levels (Arlettaz et al., 2015). In this regard, although wildcat exposure to some sources of human disturbance may be infrequent in our study area, as shown by the low sample size of wildcat responses to e.g. cyclist, dogs, or human associated noise, the sample size was larger to study wildcat reactions to humans, vehicles and absence of disturbance, allowing us to obtain more robust results. Consequently, we recommend the vigilance and persecution of undesirable human behaviours towards wildcats (e.g. disturbing approaches by wildlife photographers) that can certainly alter the behaviour of this protected species (Cui et al., 2021).

Although wildcat responses to high threatening sources of disturbance may vary with the distance to the threat, we did not include this in our first analysis because experimental approximations to individuals would have been a more suitable approach and we prioritized the non-disturbance on the species from our side. Future research should consider this variable to establish security distances around wildcats that reduce human impact on wildcat behaviour. Additionally, we must acknowledge that wildcats may detect threats earlier than we do due to their higher sensitive capacities (Kitchener et al., 2010) which may affect their behaviour in larger time windows than we perceive. However, our limited detection rate of threats successfully detected substantial changes in wildcat behaviour.

Time allocation of wildcats to basic behaviours (such as alert) did not greatly vary between instances without disturbance and situations with presence of moving vehicles. This may point to a certain level of habituation of wildcats to rolling traffic in the surroundings of their hunting areas, something observed for other mammals (Brieger et al., 2022; Marino and Johnson, 2012). However, and following our expectations, traffic showed initially overlooked effects on wildcat behaviour and hunting success. Wildcats allocated more time to hunting in situations with higher traffic levels, in the proximities of roads and further from villages. Similarly, they dedicated more time to vigilance behaviours while feeding in the presence of moving vehicles. Finally, traffic affected hunting success differently in males and females, with the latter decreasing more their hunting success in the presence of vehicles.

Our results may indicate that wildcat foraging efficiency is lower in high traffic situations as they need to spend more time hunting, consequently increasing the invested time to capture the minimum prey required. Traffic generally has considerable levels of associated noise (Barber et al., 2010). Like many felids, wildcats relay on acoustic cues to detect and capture subterranean prey (Kitchener et al., 2010). Thus, traffic and the associated noise may reduce hunting performance in wildcats due to noise masking or disturbance during hunting events. This has been observed in other predators relying on acoustic cues such as bats (Siemers and Schaub, 2011) and owls (Senzaki et al., 2016), where traffic noise increased the time invested in hunting and decreased foraging efficiency. It is also possible that road proximities are preferred hunting grounds for wildcats, where they spend more time hunting, as such environments are generally more favourable to rodents (Bellamy et al., 2000). Road proximities receive more solar radiation which favours primary productivity of herbaceous species and rodents (Bellamy et al., 2000); and rodents may use road proximities (and the associated traffic noise) as refuges from predators sensitive to human disturbance (Berger, 2007). Wildcats using road proximities are highly vulnerable to road mortalities, the highest source of mortality for wildcats in Europe (Bastianelli et al., 2021).

Wildcats were more vigilant in high traffic situations, thus being potentially more distracted from their “hunting goals”. Most behavioural analyses stated that time allocation to vigilance is incompatible with time allocation to other vital activities such as feeding (Ciuti et al., 2012; Pangle and Holekamp, 2010; Wang et al., 2011). So, in addition to the potential distracting effect of traffic while hunting, investing more time vigilant may also have energetic consequences for wildcats. Nevertheless, we should point that time allocation to specific behaviours may also depend on individual characteristics such as health condition or prey abundance (Beale and Monaghan, 2004; Gill et al., 2001), being possible that those individuals spending more time vigilant are those that can afford it for being in better condition.

Female wildcats were more influenced by traffic than males, both in terms of time invested in vigilance behaviours while feeding and in hunting success although the effect on the latter was not conclusive. Wildcat females tend to exploit areas further from human activities, potentially aiming at safeguarding their own and their kittens survival (Beugin et al., 2016). In this regard, female wildcats may be less familiar with human interactions, which may increase the intensity of their responses towards perceived anthropogenic threats. Females also responded more intensely than males to human disturbance in bottlenose dolphins (*Tursiops truncatus*; Symons et al., 2014), and Mediterranean mouflons (*Ovis musimon;* Benoist, Garel, Cugnasse, & Blanchard, 2013).

Wildcats use pastoral fields with hunting purposes as they provide prey abundance, particularly mountain water voles (*Arvicola monticola*; Ruiz-Villar et al. 2022). The risk of encountering humans in such environments is high, to which wildcats generally respond displaying antipredator responses, which minimizes the time dedicated to other critical activities such as hunting or feeding. Although wildcats may perceive certain advantages by hunting in road proximities they still have to be aware of human presence in such locations (higher vigilance with presence of traffic) which may cause energetic costs and increased mortality risk (Bastianelli et al., 2021).

This trade-off between prey availability and increased risk derived from encounters with humans has been assessed for other species around the globe. For instance, European lynx (*Lynx lynx*) selected areas with intermediate prey availability (roe deer, *Capreolus capreolus)* and human disturbance, thus avoiding both locations with higher roe deer densities that were generally very human disturbed and locations with very low human disturbance but coincident with very low roe deer densities (Basille et al., 2009). On the contrary other species can be completely displaced by super-predators leading to exploitation of the least favourable environments, as seen for cheetahs (*Acinonyx jubatus*) which were outcompeted by lions (*Panthera leo*) and hyenas (*Crocuta crocuta*). Other felid species found the balance by changing their temporal use of habitats to avoid overlapping with humans (Nisi et al., 2022). Wildcats exploit the prey-rich environments disturbed by humans in broad daylight (Ruiz-Villar et al., 2022) so there seems not to be temporal avoidance of human-dominated environments. Nevertheless, such areas could potentially act as attractive sinks where direct mortality and other detrimental behaviourally-related ecological effects due to human-related causes may occur (Bastianelli et al., 2021).

In conclusion, humans and traffic influence wildcat behaviour, although it is difficult to know to which extent such changes translate into demographical consequences for wildcat. Future research integrating wildcat observations, spatial data, breeding success and road mortality from wildcats using environments with different degrees of human presence may help to better address these questions.

3.6 Acknowledgements

HRV is beneficiary of a PhD scholarship “Severo Ochoa” from the Regional Government of Principality of Asturias.

3.7 Supplementary material

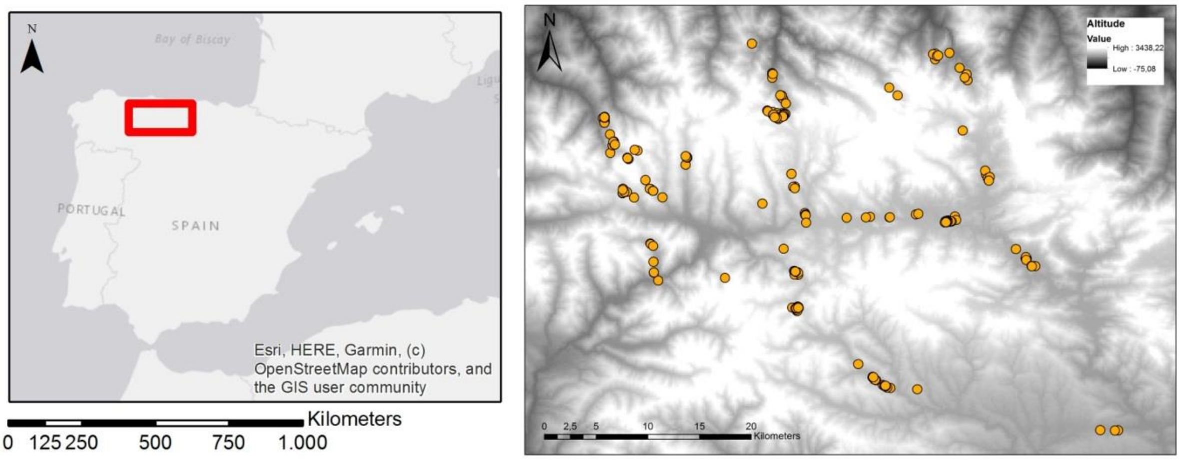


Fig 3.A1. *Location of wildcat behavioural observations (yellow circles) inside the study area (red square) located in the Western Cantabrian Mountains (NW Spain).*

Table 3.A1. *Mean (± standard deviation) proportion of time dedicated to alert behaviour during each source of disturbance when overlapping between disturbances did not occur. Brackets show the sample size of observations for each disturbance source.*

Disturbance type	Proportion of time dedicated to alert behaviour
Human (15)	0.651 (±0.265)
Wildlife (14)	0.558 (±0.294)
Cyclist (5)	0.312 (±0.366)
Dog (2)	0.234 (0.111)
Livestock (2)	0.213 (±0.166)
Vehicle (171)	0.006 (±0.029)
Human noise (1)	0

Table 3.A2. *Effects of the variables included in the model averages on hunting success in European wildcats (model 3) considering the models with ΔAICc < 6 and that were more parsimonious versions of the top model. For each variable, we report the estimate (Est), standard error (SE), significance (P), Odd Ratios (OR) and 95% Confidence Intervals of odds ratio (95% CI). ΔAICc shows the effect of removing each variable from the top model on the AICc. Significant values are based on Wald statistics with bold font indicating significant effects. The 95% CI of odds ratio is used as a proxy for the presence of statistical significance if it does not overlap 1. Baseline level for sex, age, weather, season and traffPress are female, juvenile, bad weather (rainy, snowy and windy), autumn and no respectively.*

Variable	**Est**	**SE**	***P***	**ΔAICc**	**OR**	**95% CI**
Intercept	0.09	0.49	0.851		1.09	0.42-2.88
TraffInt	-0.90	1.69	0.596	1.07	0.16	0-8.63
Sex(Male)	-0.60	0.44	0.179	5.97	0.48	0.23-0.99
Age(Adult)	-0.181	0.33	0.588	0.88	0.64	0.29-1.38
Distance_road	-0.10	0.13	0.457	2.34	0.82	0.64-1.06
Season (Spring)	0.47	0.72	0.517	2.97	2.17	0.46-10.31
Season (Summer)	0.34	0.32	0.286	2.97	1.75	1.15-2.65
Season (Winter)	0.23	0.33	0.485	2.97	1.46	0.73-2.92
TraffInt:Sex(Male)	1.09	1.89	0.567	3.24	32.66	0.98-1087

Table 3.A3. *Parameters included in the four full separate GLMMs models investigating variation in time allocation to hunting (HuntTime), time allocation to vigilance during feeding events (VigTime), hunting success at level of observations (HSobs) and hunting success at level of attempt (HSatt) in European wildcats. A full separate model was calculated for each response variable using the fixed and random variables.*

Response	**Fixed**	**Variable description**	**Random**
HuntTime	*TraffInt*	Observation time with presence of vehicles divided per total observation time. We excluded the time when a disturbance different from vehicles was occurring. Only for models 1 and 3.	*Subject*
VigTime	*TraffPres*	Immediate presence of a vehicle. Categorical with two levels: Yes or No. Only for model 2.	
HSobs	*Distance_road*	Distance to the closest road (m)	
HSatt	*Distance_village*	Distance to the closest village (m)	
	Sex	Sex of the individual: Male and Female	
	Age	Age class of the individual: Juvenile (less than 2 years excluding kittens) and Adult (more than 2 years)	
	Season	Meteorological season: Winter (Dec to Feb), Spring (March to May), Summer (June to Aug) and Autumn (Sept to Nov).	
	Weather	Weather conditions during observation: bad weather (windy, snowy, rainy), overcast or sunny.	
	TraffInt:Sex	Interaction between traffic intensity and sex. Only for models 1 and 3.	
	TraffInt:Sex	Interaction between traffic presence and sex. Only for model 2.	

Appendix 3.A. *Methods on evaluation of zero-inflated distribution, overdispersion, and normality of residuals.*

We used the package DHARMa in R software (Hartig, 2020) to test for zero-inflated distribution, overdispersion and normality of residuals in all the binomial GLMM models. Binomial GLMM models 1 and 2 showed a zero-inflated distribution and did not show overdispersion (Fig. 3.A2). Thus, we fitted a GLMM zero-inflated binomial model and tested that zero-inflation was corrected (Fig. 3.A3). Binomial model 3 neither showed zero-inflated distribution nor overdispersion (Fig. 3.A4) and we used a GLMM binomial model.

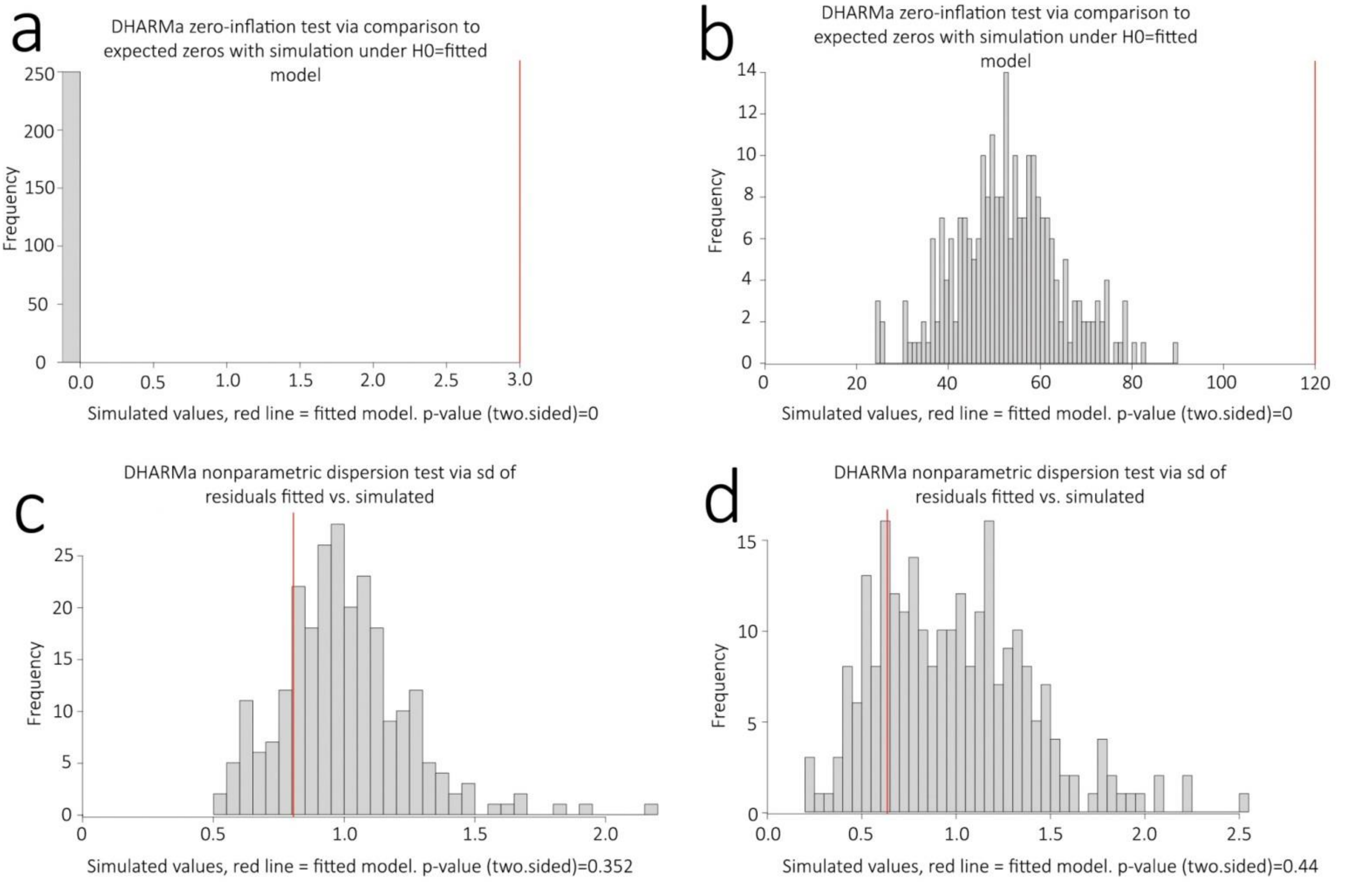


Fig 3.A2. *Results of the diagnostics for zero-inflated distribution (a and b) and overdispersion (c and d) in binomial models 1 and 2 (a and c; and b and d respectively). We used the package DHARMa. The red line far from the data indicates a zero-inflated distribution of the data. The model shows no overdispersion.*

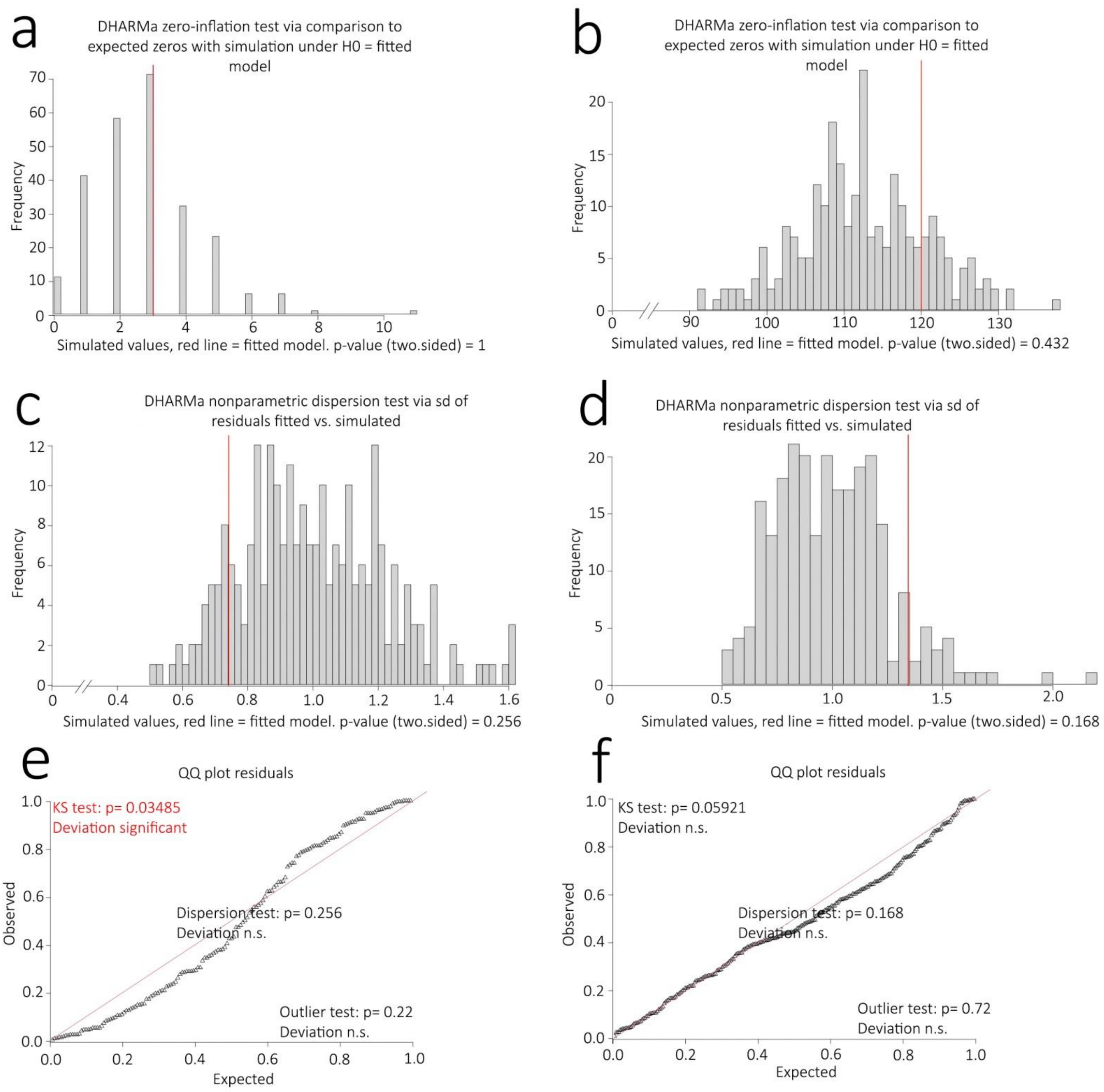


Fig 3.A3. *Results of the diagnostics for zero-inflated distribution (a and b), overdispersion (c and d), and normality of residuals (e and f) in zero-inflated binomial models 1 and 2 (a,c,e and b,d, f respectively). We used the package DHARMa. The models corrected zero-inflation issues observed in binomial models (Fig A2).*

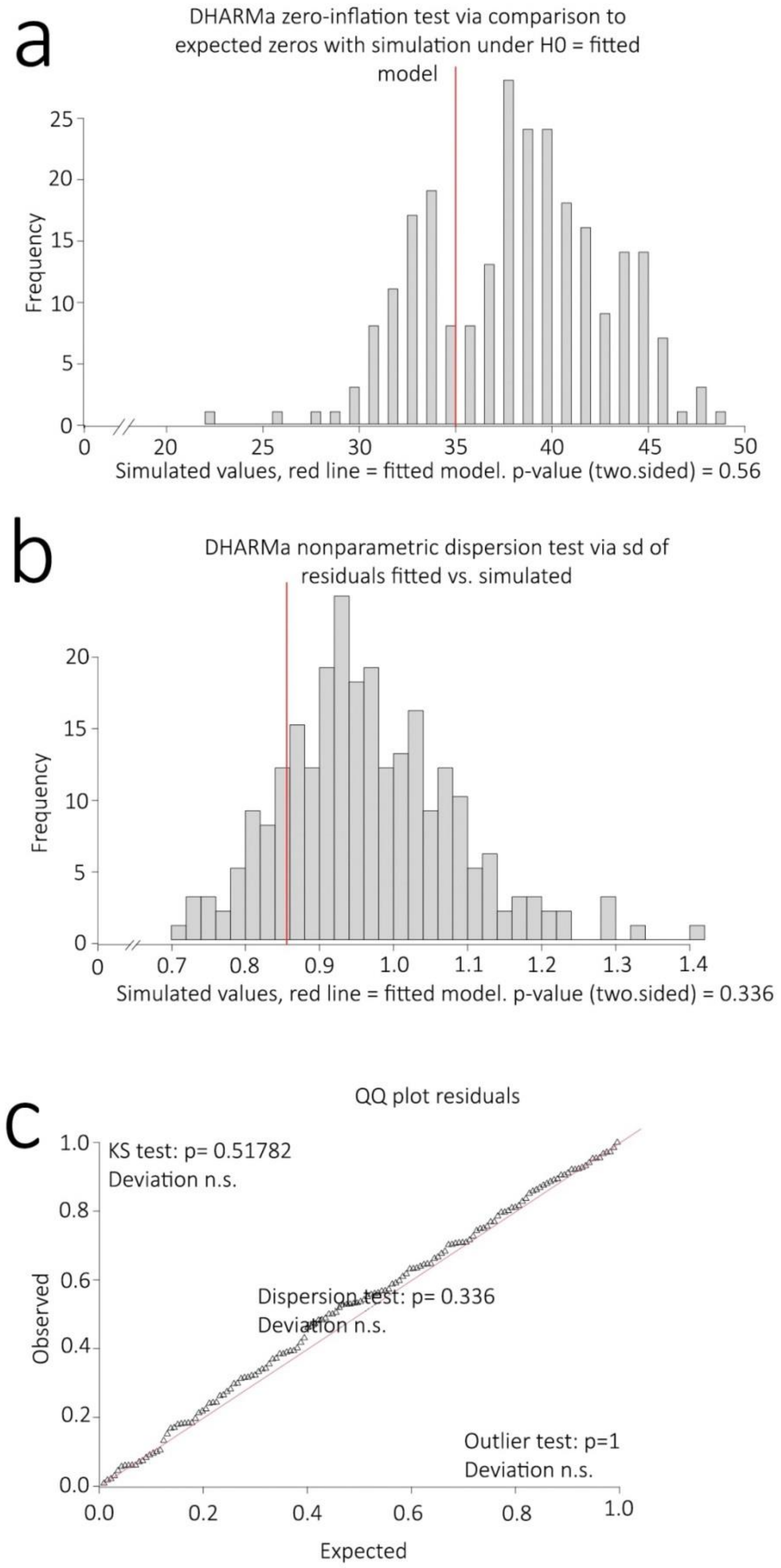


Fig 3.A4. *Results of the diagnostics for zero-inflated distribution (a), overdispersion (b) and normality of residuals (c) in binomial model 3. We used package DHARMa in R software. The model neither shows zero-inflation issues nor overdispersion.*

Table 3.A4. *Results of the Kruskall-Wallis post-hoc procedures for pairwise comparisons to detect significant differences (p<0.05) in the time allocated to each behaviour between the different sources of disturbance. The cells with an X show the pair of cases for which significant differences were detected.*

Pairwise comparison	Hunting	Grooming	Alert	Feeding	Moving	Stationary
Human-Livestock						
Human-Cyclist						
Human-Wildlife						
Human-HumanNoise						
Human-Dog						
Human-Vehicle	x		x		x	x
Human-None	x		x	x	x	x
Livestock-Cyclist						
Livestock-Wildlife						
Livestock-HumanNoise						
Livestock-Dog						
Livestock-Vehicle						
Livestock-None			x			
Cyclist-Wildlife						
Cyclist-HumanNoise						
Cyclist-Dog						
Cyclist-Vehicle						
Cyclist-None						
Wildlife-HumanNoise						
Wildlife-Dog						
Wildlife-Vehicle	x		x		x	
Wildlife-None	x		x	x	x	
HumanNoise-Dog						
HumanNoise-Vehicle						
HumanNoise-None						
Dog-Vehicle						
Dog-None						
Vehicle-None						

SECTION 2

CHAPTER 4

Insights into the breeding ecology of wild-living European wildcats in the Cantabrian Mountains, Spain.

Publication: Ruiz-Villar, H., López-Bao, J.V. & Palomares, F. Insights into the breeding ecology of wild-living European wildcats in the Cantabrian Mountains, Spain. ***Mammal Research***.

DOI: https://doi.org/10.1007/s13364-023-00708-z

4.1 Abstract

Gathering knowledge on the breeding ecology of species in wild-living conditions is critical to set baselines from which to analyse population trends and design appropriate conservation actions. This is particularly challenging when studying elusive animals like carnivores, as breeding events are difficult to detect and monitor. Based on direct sightings of wildcat, we provide the first scientific information on the breeding ecology in wild conditions of European wildcats as well as hunting success and provisioning rates of female wildcats. Mean litter size at weaning was two with most observations occurring between July and September. Auxiliary dens were mostly located inside thick vegetation in the proximities of pastoral fields, although anthropogenic constructions were occasionally used. Two cases of different female wildcats rearing their respective litters closer than 500 m were recorded. Hunting success of breeding females (66%) was higher than that of non-breeding females (33%) and males (40%). Breeding females provided around 80% of the captured prey to their kittens. In conclusion, direct observations of wild-living wildcats in the Cantabrian Mountains (NW Spain) allowed us to find that anthropogenic mosaic-structured landscapes combining open pastoral fields providing prey, and areas with thick vegetation such as shrub and forest patches providing shelter, encompass conditions required by the wildcats to successfully breed in human-dominated environments.

4.2 Introduction

The breeding ecology of species can be defined by a set of behavioural parameters, such as den selection (Fernández and Palomares, 2000; Sazatornil et al., 2016), prey provisioning rates (Nour et al., 1998) or spatial behaviour (Palomares et al., 2017), and fitness parameters, such as age at first and last reproduction (Krüger, 2005; Wikenros et al., 2021), probability of reproduction, litter size, or juvenile survival (López-Bao et al., 2019, 2010; Sikes et al., 1998). Variation in such parameters can determine fitness, ultimately influencing species demography (Anthony and Blumstein, 2000). Several environmental and human-related factors can constrain the outcomes of breeding events (Sazatornil et al., 2016; Steidl and Anthony, 2000) by altering the availability of prey (Sherley et al., 2013) and suitable breeding spots (Shamoon and Shapira, 2019). For instance, human activities can influence breeding processes negatively throughout enhanced mortality risk of offspring due to disturbances while rearing (Zuberogoitia et al., 2008) or positively throughout increased food availability (Šálek et al., 2015). In this context of increased human presence (Milner and Boldsen, 2023), primary knowledge on the natural history of the species, including breeding ecology, is critical to set baselines from which to analyse population trends and design appropriate conservation actions (Fernández and Palomares, 2000; Morales-González et al., 2022).

Despite the necessity of obtaining data on breeding parameters, research on breeding ecology in wild conditions is generally scarce, as breeding events are difficult to detect and monitor, particularly when studying elusive and nocturnal animals like carnivores (Swenson, 1999; Theuerkauf, 2009). Although research on captive carnivores can provide preliminary results on the breeding ecology of the species (Ruiz-Olmo et al., 2018), gathering information in wild-living individuals is crucial to obtain accurate results determined by individual and environmental factors, particularly in human-dominated scenarios.

The European wildcat (*Felis silvestris*) is a medium-sized carnivore that inhabits landscapes with different degrees of human presence across Europe (Gerngross et al., 2022). Although some of their populations recovered during the last decades, others show clear signs of decline (Gil-Sánchez et al., 2020; Senn et al., 2019). Due to its elusive behaviour, very little is known about wildcat breeding ecology, with the existing information obtained across Europe mainly based on captive or dead individuals (Daniels et al., 2002; Ruiz-Olmo et al., 2018) or published in grey literature (Stahl et al., 1992). In particular, information regarding behaviourally related reproductive parameters in wildcats, such as den selection and reutilization or food provisioning rates is mostly inexistent. Although several works have highlighted the importance of suitable breeding conditions for female wildcats, these conclusions are generally inferred from habitat selection approximations, instead of actual detection and monitoring of breeding dens (Monterroso et al., 2009; Oliveira et al., 2018).

Wildcats use open areas in the pastoral fields of the Cantabrian Mountains with hunting purposes, creating a good opportunity to observe their behaviour (Ruiz-Villar et al., 2021; Ruiz-Villar et al., 2022), which facilitates the detection and observation of breeding females and their offspring allowing for an approximation on describing reproductive parameters in a wild living population of this felid.

In this article, we aimed at providing the first scientific information on the breeding ecology of European wildcats in natural conditions. Specifically, we described the seasonality, number and size of kittens during weaning, den location and description of surrounding landscape, duration of den use and frequency of their reuse. Furthermore, we also studied the hunting success and provisioning rates of female wildcats and compared it with non-breeding females and males.

4.3 Methods

Study area

We observed European wildcats in the Western Cantabrian Mountains (NW Spain) inside an area of ca. 1800 km^2 between the provinces of Asturias and León (Fig 4.1), although additional information on wildcat reproduction from collaborators was gathered for the whole Cantabrian range (Fig 4.1). The Cantabrian Mountains, which experience rough winters with considerable snow cover (Arenillas et al., 2008), belong to the temperate oceanic bioclimatic region with a few Mediterranean locations (Martínez and Arregui, 1999) with altitudes ranging from 0 to 2650 m.a.s.l. The landscape is characterized by a mosaic of broadleaf forests (oak (*Quercus* sp.), beech (*Fagus sylvatica*), birch (*Betula* sp., etc.), broom and heather, and pasturelands. The valley bottoms are occupied by human settlements and fields derived from traditional farming activities (Fig 4.1; García et al. 2005). In these mountains, wildcats predate upon ten species of rodents, with *Arvicola monticola* encompassing most rodent consumption by wildcats in pastoral fields (Ruiz-Villar et al., 2022).

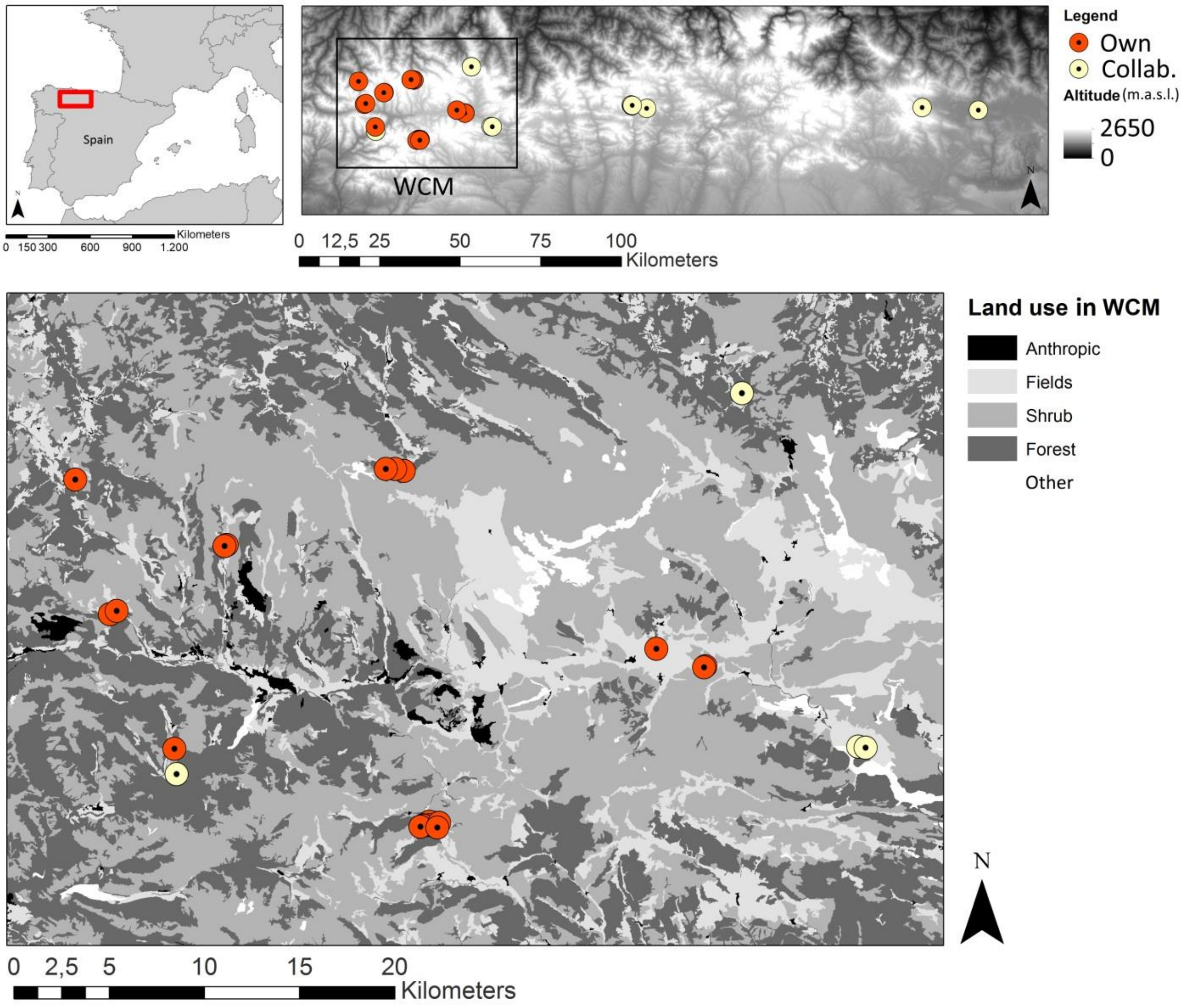


***Figure 4.1**. Location of the wildcat reproductive dens recorded in the Cantabrian Mountains (NW Spain; top right). Orange circles show location of own sightings and pale yellow circles show locations of dens recorded by collaborators. The bottom map shows the main land use categories found in the Western Cantabrian Mountains (WCM), where we actively searched and monitored wildcat breeding events. To facilitate map interpretation land use categories were reclassified from the Third Spanish Forest Inventory (1997–2007) of the Spanish Ministry of Agriculture, Fisheries and Food (https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas.htm.aspx). 'Anthropic' refers to human settlements, highways and mines. 'Fields' refers to anthropogenic meadows and pasturelands (i.e. pastoral fields). 'Shrub' and 'Forest' encompass all the shrub and forest types, respectively. 'Other' includes water bodies and bare ground.*

Wildcat observations

Based on the regular use of open fields, meadows and pasturelands by European wildcats with predation purposes in the Cantabrian Mountains (Rodríguez et al., 2020; Ruiz-Villar et al., 2021; Ruiz-Villar et al., 2022) we aimed at observing wildcats, at sunrise and sunset when they are more active and visible in pastoral fields (Jiménez-Albarral et al., 2021), during the mid and late breeding periods (July to November; Ruiz-Olmo et al., 2018) from 2014 to 2022. To optimize our efforts, we did not look for wildcats during the early breeding season (April to June) as very young kittens remain in the birthing den and are consequently very difficult to detect when following wildcat females without using any specific tracking system (e.g. telemetry). Moreover visits to birthing dens can be a source of disturbance to the studied individuals. We did not run night observations as the use of spotlights can alter wildlife behaviour (Wilson, 1999) and thermal viewers do not allow for reliable differentiation between wildcats and domestic cats. We detected wildcats through opportunistic surveys either along transects in cars on paved roads or from stationary viewing points. Once we detected the wildcat, we ran all observations from stationary viewing points using binoculars and a telescope (Swarovski Habitch 7x42 and Swarovski ATS 65HD + Zoom 20X60, Swarovski Optik KG, Austria) to observe wildcats from the distance (>200 m) without altering their behaviour, and recorded the individuals using a bridge camera Canon PowerShot SX60 HS (Canon Inc., Japan). Specifically, we were interested in observing wildcat breeding females but recorded all individuals seen across the mentioned period.

We identified wildcats based on diagnostic pelage characteristics presented by Ragni and Possenti (1996). The chances of misidentifying a wildcat with a hybrid in the Cantabrian Mountains are very low based on the lack of wildcat-domestic cat hybrids detected there by previous researchers (Tiesmeyer et al., 2020). Nevertheless, as morphology solely does not fully allow wildcat differentiation from hybrids (Devillard et al., 2014) and we did not analyse our focal animals genetically, we use the term wildcat or European wildcat referring to phenotypic European wildcats. We assigned each observation to a specific individual based on its unique pelage characteristics as presented by Jiménez-Albarral et al. (2021). Sex was determined when possible through the observation of the genital area. Observations of non-sexed individuals were discarded from the analysis.

Detection of breeding females and collection of breeding parameters

We determined the breeding status of females by observing wildcat females in the company of kittens. Accordingly, we considered as breeding females only those observed in the company of kittens. These observations stemmed from previous behaviours potentially indicating the presence of kittens in the surroundings. For instance, we confirmed the presence of kittens for all the cases, when undisturbed wildcat females repeatedly carried captured prey outside the field by leaving the meadow through the same area. Nonetheless, disturbed individuals could behave differently and leave the field with the captured prey for different reasons (e.g. to feed upon the captured prey hidden from potential threats (Ruiz-Villar et al. *under review*)). Our method allows gathering breeding-related information during the weaning period, when kittens are transitioning their diets from milk to solid prey (Gittleman, 1986).

To count kittens and estimate their size, we waited until late dawn when they could roam outside the auxiliary den into the open pastoral field more likely. Most litters were observed in multiple occasions and different environments, which reduced the chances of underestimating the number of kittens. We assigned three age categories to the kittens based on the wildcat size and other external traits that allowed for approximate age estimation based on the body growth rate established in the domestic cats (DiGangi et al., 2020): 1. Kittens 1/4 the size of the mother, with poor movement capabilities and very striped body sides; 2. Kittens half the size of the mother with good movement capabilities and maintaining the striped pattern characteristic of young kittens (Fig. 4.2b); and 3. Kittens 3/4 the size of the mother that have already developed the adult pelage lacking stripes on the sides (Fig. 4.2a and c).

We monitored den use by recording the minimum number of days spent using each den. To minimize disturbance, den description during breeding season was based on distant observations of the place used by the kittens, although dens were visited outside breeding season to determine if they were using enclosed structures inside vegetation and undetectable from the distance. We also recorded the type of den, i.e. birthing den: where the female gave birth (Fernández and Palomares, 2000); or auxiliary den: where the female moved the kittens after leaving the birthing site (Fernández and Palomares, 2000). As we did not use GPS tagging or radio-tracking of females to locate dens, most information obtained regarded auxiliary dens involved situations when the kittens were older, prey-fed and visible, although information on a few birthing dens was compiled as well. We included opportunistic observations of female wildcats moving the kittens (i.e. female kittens followed by already mobile kittens) despite they were not using any den to increase information of number of kittens with females. We only included observations, for which we were sure that we did not miss previous or later movement of kittens to minimize the risk of underestimating the number of kittens.

Finally, we collected information from collaborators regarding nine breeding events in relation to size and number of kittens, observation date, and litter location and type across the whole breeding period (May to November from 2009 to 2022).

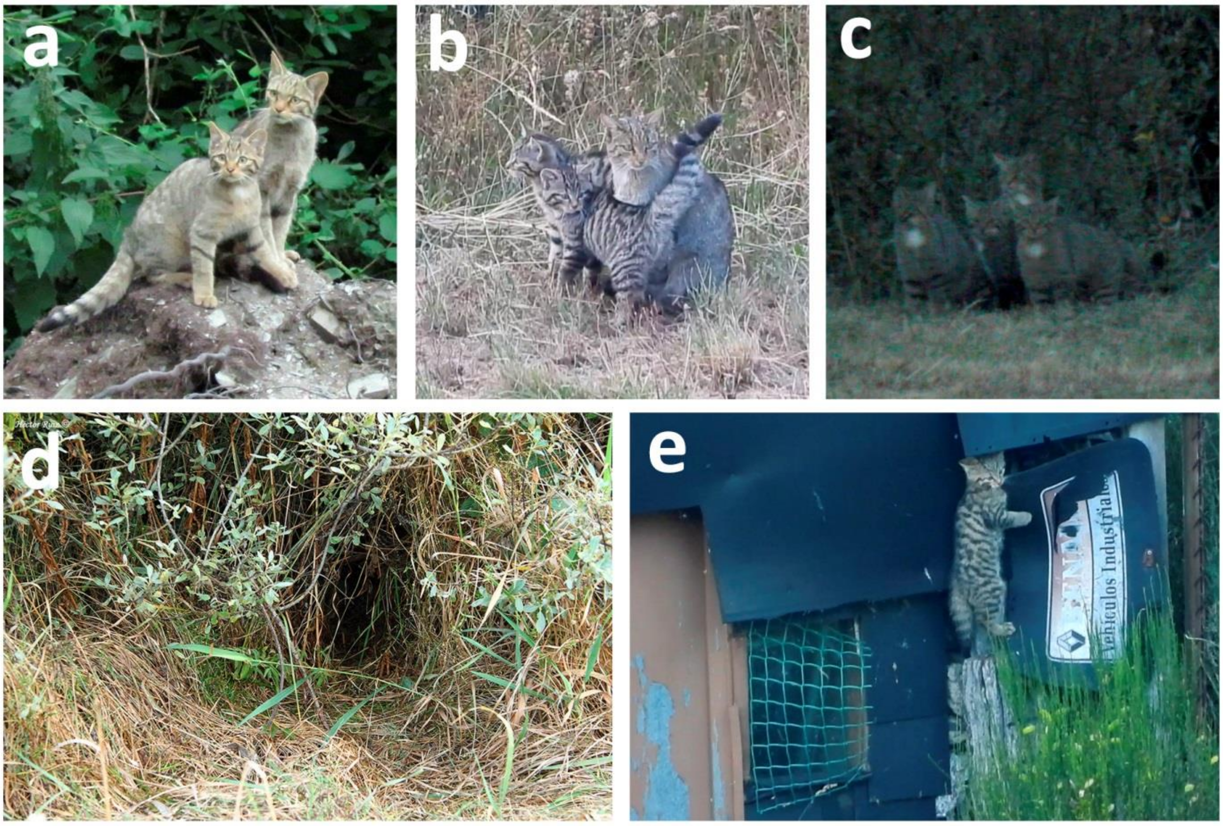


Figure 4.2. *Figures a to c show wildcat females with a varying number of kittens of different sizes: a) Female with one kitten of category 3 (3/4's of the mother); b) Female with 2 kittens of category 2 (1/2 of the mother); and c) Female with 3 kittens of category 3. As seen, kittens from category 2 present marked stripes on sides that are lost as they grow. Figure d shows the typical vegetation cover under riparian vegetation (Salix sp.) commonly used by European wildcats as maternal dens. Figure e shows a wildcat kitten in an abandoned hut used with breeding purposes by a female wildcat. Wildcat pictures were obtained by Héctor Ruiz-Villar from large distances without disturbing the individuals.*

Collection of hunting behaviour and provisioning rates

We recorded hunting behaviour of all observed wildcats and determined the hunting success per individual and observation (i.e. number of successful hunting attempts per observation divided by number of total hunting attempts per observation). We recognized hunting behaviours based upon the definition provided by Stanton et al. (2015) i.e. the cat actively pursues live prey including movements such as crouching, stalking, or any other species-specific behaviour. The main species captured by wildcats during our observations was *Arvicola monticola* (Ruiz-Villar et al., 2022), a large rodent species easy to identify from the distance due to its much larger size in comparison with the rest of rodent species. To determine the prey provisioning rates we recorded the number of captured prey provided by the female to the kittens divided by the total amount of captured prey by the female and represented it as a percentage. Similarly we calculated the percentage of captured prey consumed by the mother as the number of consumed prey divided per the total number of captured prey multiplied by 100.

Statistical analysis

To compare the hunting success of breeding females, non-breeding females and males during the mid and late breeding period (July to November) we fitted a Generalized Additive Mixed Model (GAMM; ‘mgcv’ package in R statistical software; Wood 2015) with a logarithmic link and binomial distribution with hunting success as a response variable and wildcat status (i.e. breeding female, non-breeding female and male) as an explanatory variable. To consider the effects associated to varying number and different durations of observation per individual we included such variables as smoothing term and offset respectively. To account for potential differences on hunting success associated to individuals and years (the latter potentially determined by different prey abundances) we included wildcat ID and year as random effects. We set statistical significance levels at $p < 0.05$.

4.4 Results

We obtained 40 observations of 10 breeding female wildcats (and their litters) using 19 different dens during the study period (Table 4.1). Additionally, we compiled information on the number of kittens and use of 10 dens by 8 female wildcat from collaborators (Table 4.1). Number of kittens varied from 1(16 %) to 3(16%), with 2 being the most frequent number (68 %) (Table 4.1, Fig. 4.3a). Most kittens observed were half (58 %) or 3/4 (37 %) the size of the mother (Table 4.1). Most observations of kittens occurred between July and September (Table 4.1). Observations in May correspond with very young kittens whereas observations in October and November correspond with late litters. Most auxiliary dens were located inside shrub (mainly broom (*Cytisus* sp.; 28 %)) and riparian vegetation (*Salix* sp.; 38%; Fig 4.2d and Fig 4.3b), although wildcats occasionally used anthropogenic constructions like huts or stone walls with breeding purposes (10%; Table 4.1, Fig 4.2e and Fig 4.3b). We compiled information on two birthing dens, which were inside enclosed structures (hollow trunk and rock crevice; Table 4.1). The majority of monitored dens were located in the proximities of pastoral fields (97 %; Table 4.1). Nonetheless, shrub patches and hedges were present in close proximity in all the cases females were using pastoral fields (Table 4.1). Duration of den use varied between 1 and 18 days, with the majority of dens being used during periods between 1 and 3 days (45 %; Table 4.1). Distance between observed dens used by the same female during the same breeding period varied between 35 and 507 m. Two cases of different female wildcats rearing their respective litters closer than

500 m from each other were recorded. 17% of the dens were reused either by the same female during the same breeding period or by the same or other female during consecutive breeding periods (Table 4.1). Length of monitoring periods varied between 1 and 27 days.

We obtained 40, 12 and 89 observations of 10 breeding females, 6 non-breeding females and 25 male individuals and recorded 189, 40 and 458 their hunting attempts respectively. Hunting success of breeding females (66%) was significantly higher than hunting success of non-breeding females (33%; $p<0.001$) and males (40%; $p<0.05$; Fig 4.3c). Regarding prey provisioning to kittens, females provided around 80% of the captured prey to the kittens and consumed the remaining 20%.

Table 4.1. *Summary of the recorded wildcat breeding events in the Cantabrian Mountains and the different dens used by females with kittens during each of them. The part above the blank line shows breeding events recorded by the author for which monitoring of females and use of dens was done. The part under the blank line shows wildcat reproduction events compiled from collaborators. Kitten size was classified into three categories: 1. Kittens 1/4 of the mother size; 2. Kittens ½ of the mother size; and 3. Kittens ¾ of the mother size. Den reuse refers to the reutilization of the same den by the same or other female in the same or in consecutive years. Unk=Unknown.*

Breeding event	Female ID	Number of kittens	Kitten size	Date	Den type	Den location	Landscape description	Min Days at den	Den reuse
1	F1	2	2	23/07/22	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	1	
				04/08/22	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river surrounded by shrub	Unk	Yes
2	F2	3	2	21/07/21	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with stream surrounded by shrub	3	
				27/07/21	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	1	
				17/08/21	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	1	
				17/08/21	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river surrounded by shrub	Unk	
3	F3	2	2	21/07/21	Auxiliary	Shrub vegetation and stone wall	Pastoral fields surrounded by shrub	6	
				28/07/21	Auxiliary	Inside abandoned hut	Pastoral fields surrounded by shrub	1	
				30/07/21	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	1	
				17/08/21	Auxiliary	Shrub vegetation and stone wall	Pastoral fields surrounded by shrub	Unk	Yes
4	F4	1	3	22/08/20	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river and vegetation stripes	1	
				29/08/20	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river and vegetation stripes	17	
				15/09/20	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river and vegetation stripes	Unk	Yes
5	F5	1	2	03/08/20	Moving	NA	Oak forest	NA	
6	F6	2	3	07/08/20	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	1	
				09/08/20	Auxiliary	Shrub	Pastoral fields	Unk	

						vegetation	surrounded by shrub		
7	F7	2	2	17/10/19	Unk	Shrub vegetation	Pastoral fields surrounded by forest and shrub	8	
				13/11/19	Auxiliary	Shrub vegetation	Pastoral fields surrounded by shrub	Unk	
8	F8	2	2	15/07/19	Auxiliary	Under fallen tree	Pastoral fields with vegetation stripes surrounded by shrub	18	
		2	3	19/08/19	Auxiliary	Under fallen tree	Pastoral fields with vegetation stripes surrounded by shrub	3	Yes
9	F9	2	3	11/09/14	Auxiliary	Isolated willow tree (*Salix* sp.)	Pastoral fields with vegetation stripes	1	
10	F10	3	3	01/09/14	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river and vegetation stripes	12	
Breeding events compiled from collaborators									
11	F11	2	3	16/08/22	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with vegetation stripes	Unk	
12	F12	2	3	16/08/22	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with vegetation stripes		
13	F13	3	1	05/07/20	Birthing	Under rock	Pastoral fields surrounded by shrub		
			2	11/08/20	Auxiliary	Riparian vegetation (*Salix* sp.)	Pastoral fields with river surrounded by shrub		
				13/08/20	Auxiliary	Young pine trees	Pine plantation next to pastoral fields		
14	F14	1	2	20/08/19	Auxiliary	Stone wall	Pastoral fields with vegetation stripes		
15	F13	2	2	06/08/19	Auxiliary	Under rock	Pastoral fields surrounded by shrub		Yes.
16	F15	2	3	30/09/17	Auxiliary	Young pine trees	Pine plantation		
17	F16	1	2	20/08/16	Moving	NA	Rocky slope with shrub		
18	F17	3	1	20/05/10	Birthing	Inside hollow tree (*Quercus* sp.)	Oak forest next to pastoral fields		
19	F18	2	2	08/07/09	Birthing	Rock crevice	Pastoral fields surrounded by shrub		

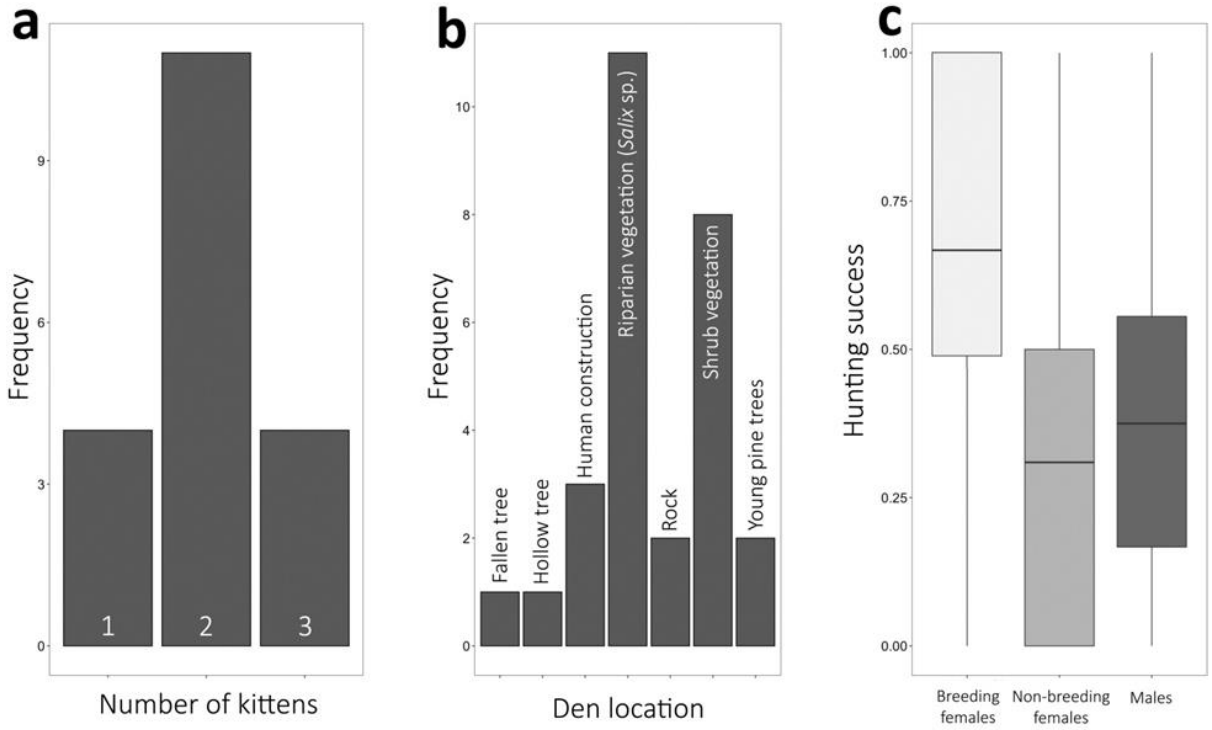


Figure 4.3. *Frequency of: a) litters composed by 1, 2 and 3 kittens (n = 19 litters); and b) different den locations (n = 29 dens) documented for breeding wildcat females using pastoral fields of the Cantabrian Mountains. Figure c represents the hunting success (number of successful hunting attempts divided by total number of attempts per observation) of breeding (n = 40 observations) and non-breeding (n = 12 observations) wildcat females, and males (n = 89 observations) during the mid and late breeding period (July to November). Only observations longer than 10 min were considered.*

4.5 Discussion

We provided the first scientific data on the breeding ecology of wild-living European wildcats as well as the first information on hunting success and prey provisioning rates of breeding females (i.e. percentage of the captured prey that was brought to the kittens by their mother).

The litter size of wildcats at weaning found in our study in the Cantabrian Mountains (mean = 2) fell within the range obtained in captive animals, which spanned from one to six kittens at birth (usually 3 - 4) and halved after weaning due to kitten mortality (Ruiz-Olmo et al., 2018). However, we don’t know whether litter size at birth in the wild differs from that recorded in captivity due to the difficulties of finding recently born kittens in untagged wildcat individuals. Furthermore, it is possible that mortality in the wild differs from that in captivity due to different sources of mortality recorded for both scenarios. For instance, wild kittens may be more vulnerable to interspecific predation or extreme weather conditions and captive individuals may be more susceptible to disease and infanticide, generally linked to the maintenance of dense and enclosed populations (Ruiz-Olmo et al., 2018).

Breeding seasonality was also similar to that recorded previously for the species based on other methods, which showed females to breed most litters between spring and summer (Daniels et al., 2002; García, 2006; Ruiz-Olmo et al., 2018; Stahl et al., 1992). Nonetheless, most litters in captivity were born in April (Ruiz-Olmo et al., 2018), and considering the size and dates of most kittens observed in the Cantabrian Mountains it is possible that most parturition in the wild occurs between May and June. This could be related with the climatic conditions of the Cantabrian Mountains as well as synchronization between parturition and peaks in prey availability. For instance, the snow cover can persist until late spring in medium to high elevations of the Cantabrian Mountains (Arenillas et al., 2008). Snow cover is a limiting factor for wildcat occurrence (Mermod and Liberek, 2002) and one would expect that females synchronize their parturition with more adequate snowless conditions. In addition, wildcats using pastoral fields mostly feed upon montane water voles (*Arvicola monticola*), which are more abundant and accessible after the grass harvest in July (Ruiz-Villar et al., 2022). It is thus likely that kitten rearing and weaning overlaps with prey abundance and favourable weather conditions in order to increase kitten survival as seen in other felid species (Jansen and Jenks, 2012). We recorded one case of a late litter in October. Late litters were recorded as replacement litters in captive wildcat females that lost their kittens or were in their first reproductive year (Ruiz-Olmo et al., 2018). Although literature says that kitten survival is higher in replacement litters in captivity (Ruiz-Olmo et al., 2018), this kind of litters in an environment with long and snowy winters like the Cantabrian Mountains are probably less likely to survive.

Auxiliary dens were mostly recorded inside thick vegetation like shrub (mainly broom (*Cytisus* sp.)) and willow (*Salix* sp.). This agrees with the literature on wildcats and other felids showing that females rely on availability of areas with dense vegetation for breeding purposes (Fernández and Palomares, 2000; Oliveira et al., 2018; White et al., 2015). Although adult wildcats may not suffer many predation in our latitudes, vegetation cover may protect kittens which are more vulnerable to attacks from potential predators or encounters and disturbance from humans, as seen in the Eurasian lynx (*Lynx lynx*; Andrén et al., 2006). We detected the use of anthropogenic constructions by wildcats with breeding purposes, including an abandoned hut and two stone walls. Such constructions may resemble cave or rock deposits naturally used by medium felids for breeding (Boutros et al., 2007). This contrasts with literature recorded for other felid species, generally selecting inaccessible areas to reduce encounters with humans (White et al., 2015). High prey availability in pastoral fields (Ruiz-Villar et al., 2022) may ensure prey provisioning to kittens which could promote the use by females of the available breeding spots in the surrounding environment, including human constructions. The two recorded birthing dens were inside a cavity (hollow tree and rock crevice) with one entrance. This is common in other felid species breeding in European landscapes and they may provide safety to the kittens during the first stages of life (Fernández and Palomares, 2000; White et al., 2015). However, when kittens are large enough, females move them to auxiliary dens following the increasing mobility of kittens and their requirements of space (Fernández et al., 2002).

Pastoral fields were present around most dens, although there is a bias in this regard as we monitored open areas were females could be visible when hunting. Shrub and wooded linear structures such as riparian vegetation or hedges were present around most dens. As previously stated for the species, such structures increase landscape heterogeneity and are crucial for wildcat survival in open and fragmented landscapes like agricultural central European areas (Jerosch et al., 2018; Ruiz-Villar et al., 2023). As a predator selecting for mosaic-structured environments, wildcats need simultaneous availability of open areas with prey abundance to hunt (such as pastoral fields) and vegetation cover (such as broom, willow and linear wooded structures; Lozano, 2010; Ruiz-Villar et al., 2023) to rest, breed or hide from potential threats. In this regard, the Cantabrian scenario of pastoral fields embedded in a matrix of large surfaces of shrub and forest interconnected by linear vegetation structures can encompass the requirements demanded by wildcats.

The use of auxiliary dens was generally short with most dens used between 1 and 3 days. As recorded for other felid species, females can move auxiliary dens regularly as a direct consequence of disturbance or to reduce probabilities of both detection by predators and parasite infestation of kittens (Fernández et al., 2002). It is also possible that breeding females move dens to avoid overexploitation of prey in a given point as they may use different hunting grounds around each den. The duration of den use seems generally shorter than that detected in the Iberian lynx (Fernández et al., 2002), although in some cases it was considerably long (up to 18 days). It is possible that the use of anthropogenic landscapes were sources of disturbance are widespread may push female wildcats to move their kittens more regularly, as seen in other carnivores (Thiel et al., 1998). Besides this, several dens were reused either during the same period or in successive breeding periods, which may point to a limited availability of suitable breeding spots in human-modified landscapes.

Wildcat females are highly territorial, very rarely presenting overlapping territories that are defended from neighbouring females (Beugin et al., 2016; Biró et al., 2004). In addition, female wildcats were shown to use home ranges of 7.74 km^2 in the study area (Ruiz-Villar et al., 2023), which makes it surprising that we detected females breeding their respective litters closer than 500 m from each other in two separate areas and occasions. Pastoral fields provide abundance of prey during pup rearing periods (Ruiz-Villar et al., 2022) and as a consequence it is possible that wildcat females relax their territoriality under such circumstances, as it was described in other territorial vertebrates (Maher and Lott, 2000).

We found that the hunting success of breeding females was significantly higher than that of non-breeding females and males. Breeding females become highly effective at capturing prey during the weaning period. Hunting success in vertebrates has been previously shown to increase during the breeding period, as for instance, hunting success was higher for red-backed shrikes (*Lanius colliuro*) during the nestling feeding period (Morelli et al., 2016). In this case, such increase was explained by a simultaneous increase in prey availability. In our study, however the prey availability was presumed to be the same for males, breeding and non-breeding-females during the same monitoring period. It is possible that wildcat females selected those micro-scale areas with higher prey availability during breeding periods thus increasing their hunting success. From the prey captured, females fed 79% to the kittens and ate the rest. This draws attention to the energetic costs for female individuals during the pup rearing process, which double the basic energetic requirements (Natural Research Council, 2006), making the selection of suitable sites a determining factor for a successful reproductive outcome.

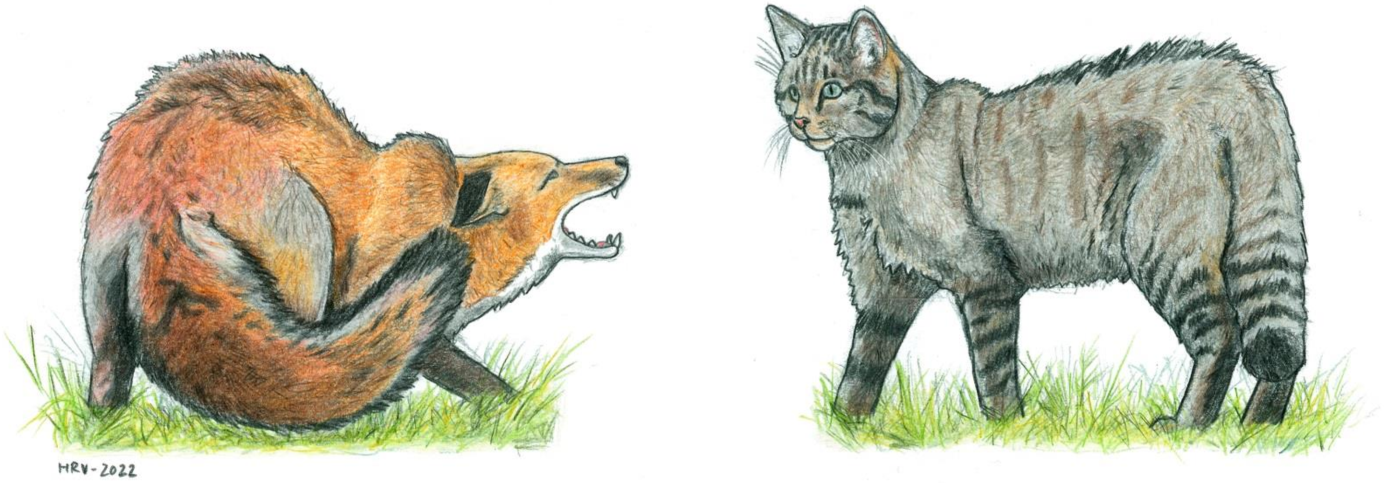
In conclusion, our study showed that pastoral fields embedded in a matrix of vegetation cover can provide both prey abundance to support the energetic requirements as well as the refuges for successful breeding by wildcats (Ruiz-Villar et al., 2022). Nevertheless, human-modified landscapes present multiple sources of risk and mortality that may compromise kitten survival. For instance, kittens may be vulnerable to road mortality while moving between dens or after independence (Bastianelli et al., 2021). In addition, they can suffer the consequences of frequent disturbance by humans (Barja et al., 2012). Direct non-intrusive observations of wild-living wildcats proofed efficient to acquire representative and unique data on the reproductive parameters of wildcats using human-modified landscapes in the Cantabrian Mountains (NW Spain). Future research should aim at studying differences in breeding ecology and success in wildcats using landscapes with different degrees of human presence to investigate to which extent and in which direction (positive or negative) humans are influencing the breeding ecology of wildcats.

4.6 Acknowledgements

We thank Bernardino López, Alberto Pola, Jonathan Rodriguez and Roberto Rodríguez for their collaboration by providing breeding data on European wildcats across the Cantabrian Mountains. HRV is beneficiary of a PhD scholarship “Severo Ochoa” from the Regional Government of Principality of Asturias.

CHAPTER 5

Like cat and fox: diurnal interactions between two sympatric carnivores in pastoral landscapes of NW Spain.



Publication: Ruiz-Villar, H., Jubete, F., Revilla, E., Román, J., Urra, F., López-Bao, J.V., Palomares, F., 2021. Like cat and fox: diurnal interactions between two sympatric carnivores in pastoral landscapes of NW Spain. ***European Journal of Wildlife Research***. 67, 1–6.

DOI: https://doi.org/10.1007/s10344-021-01469-3

5.1 Abstract

Felids and canids coexist along their ranges worldwide. Various interactions can occur between these carnivores, with multiple consequences such as demographic changes of competitors, or behavioural modifications in the use of the spatial, temporal or trophic niches. European wildcats (*Felis silvestris silvestris*) and red foxes (*Vulpes vulpes*) coexist across Europe using multi-use landscapes when hunting rodents. They commonly use open fields during the day in the Cantabrian Mountains (NW Spain). We collected 597 diurnal phenotypic wildcat observations between 2012-2019, during which we observed 14 encounters (2.34%) of wildcats and foxes. We compiled 11 more encounters from collaborators. Diurnal encounters between both species seem to be rare, which could result from the two species displaying active avoidance. During the encounters, foxes mainly showed offensive behaviours whereas wildcats showed a defensive intimidation strategy, probably in relation to their morphology. Both strategies were equally effective for maintaining the position in feeding grounds.

5.2 Introduction

Felids and canids coexist in most of their distribution ranges, and consequently different types of interactions occur between species of both groups. The most common interactions include: a. Intraguild predation: one species kills and eats a competitor (Polis et al., 1989) (felids over canids (FOC) (Helldin et al., 2006) and canids over felids (COF) (Fedriani et al., 2000)); b. Interference competition: one species prevents another from exploiting common resources through aggressiveness, sometimes killing the competitor (i.e. Interspecific killing) (Schoener, 1976) (FOC (Jiménez et al., 2019) and COF (Kortello et al., 2007)); c. Exploitation competition: a subordinate species reduces the access to common resources to minimize competitive stress (Creel and Creel, 1996; Jensen, 1987); d. Commensalism: one species feeds upon the bits of food leftovers from another species; and e. Kleptoparasitism: one species steals the food acquired by other species (FOC (van der Meer et al., 2011) and COF (Kortello et al., 2007)). In many occasions, canids and felid coexist but interactions between them are not obvious (Wikenros et al., 2010).

It is important to study interactions among both groups as they can explain variations in different ecological parameters. For instance, intraguild predation and interference competition generate multiple effects. Direct effects refer to the immediate displacement or mortality of the subordinate species, generally decreasing its abundance (Jiménez et al., 2019). On the other hand, indirect effects commonly derive in behavioural modifications on the subordinate species regarding the use of space, time, and diet (Kortello et al., 2007). Other effects derived from the demographic suppression of the subordinate species include, for example, variations in prey abundance (Jiménez et al., 2019). Factors such as body size ratio and number of individuals can determine the likelihood of predation or interference competition between carnivores (Palomares and Caro 1999).

Carnivore interactions have been studied using several methodologies. In Europe, where carnivores are mostly elusive, technologies like GPS telemetry and camera-traps have been applied to study interactions (López-Bao et al., 2016; Pedro Monterroso et al., 2013a). Nevertheless, when possible, modern technologies are generally combined with direct observations of the species, as the quality of the information obtained increases (Almeida and Grossman, 2012).

European wildcats (*Felis silvestris silvestris*) and red foxes (*Vulpes vulpes*), coexist along their European range sharing prey and habitat (Díaz-Ruiz et al., 2013; Lozano et al., 2006). Adult foxes are generally larger than wildcats (X > 5.5 kg in adult male red foxes from Spain (Gortázar et al., 2000) vs. X= 4.53 kg in adult male wildcats from the Cantabrian Mountains (Ruiz-Villar et al. *unpublished data*)). Although wildcat-fox interactions have been shortly studied in relation to use of space and time throughout the use of camera-traps (Monterroso et al., 2014), to our knowledge, no research has previously been done on wildcat-fox interactions based on direct observations of encounters. In the temperate biomes of Europe, both species use farmed pasturelands and meadows as hunting grounds, particularly aimed at capturing montane water voles (*Arvicola monticola*) (Lozano et al., 2006). Although generally considered as facultative nocturnal (Pedro Monterroso et al., 2013a), wildcats and foxes can be seen during the day in the Cantabrian Mountains (Rodríguez et al., 2020). The regular use of open areas by both species during daylight (Rodríguez et al., 2020) creates a good opportunity to study encounters between two elusive carnivores based on direct observations, providing valuable information about their behaviour during the encounters and partially contributing to discuss the potential causes and consequences for each species.

In this article we studied the diurnal interactions occurring between phenotypic European wildcats (hereafter referred to as wildcats or European wildcats) and red foxes in the Cantabrian Mountains (NW Spain) by addressing the following questions: 1. How frequent are diurnal interactions between wildcats and foxes?; 2. What species initiates the interaction?; 3. What are the behavioural responses of both species to the encounter?; and 4. Which species remains in the field?

5.3 Methods

Study area

The study area is located in the western end of the Cantabrian Mountains (NW Spain), between the provinces of Asturias and León (42º56’40.0’’N 6º18’54.7’’W) (Fig. 5.1). The area belongs to the temperate biome of the north of Spain and is characterised by a mosaic of broadleaf forests (oak (*Quercus* sp.), beech (*Fagus sylvatica*), birch (*Betula sp.*), etc.), broom and heather, and pasturelands. Human settlements are generally located in the valley bottoms creating traditional farmed landscapes with fields and pasturelands along such areas (García et al., 2005). In our study we included observations collected by collaborators from similar areas within the Cantabrian Mountains (Fig. 5.1).

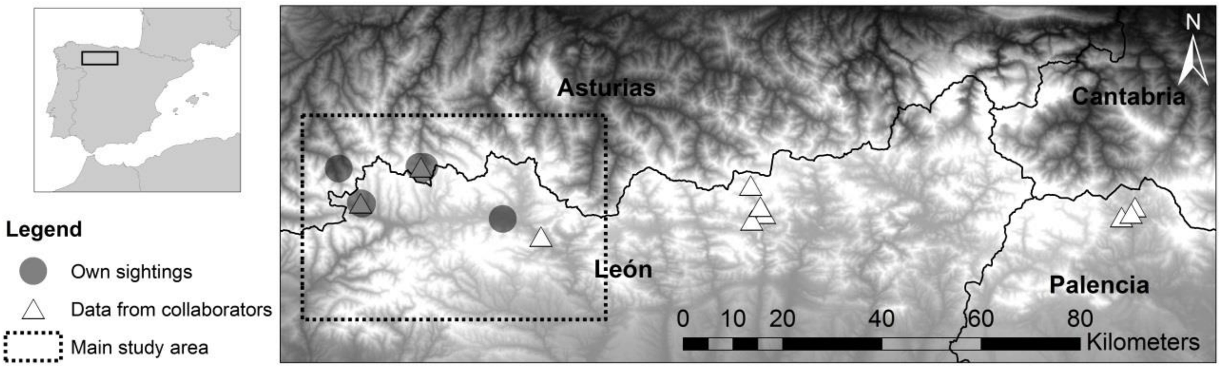


Figure 5.1. *Study area located in the Cantabrian Mountains (NW Spain). The dashed rectangle shows the main study area where we regularly did wildcat observations between 2012 and 2019. Grey circles represent observations resulting from such surveys (n=14) and white triangles represent observations collected from collaborators (n=11).*

Data collection

Between January 2012 and December 2019 we conducted a European wildcat monitoring study using a combination of two methods: opportunistic observations either along transects in car on main and secondary paved roads or from stationary points. We identified European wildcats based on the external morphological and pelage characteristics described by Ragni and Possenti (1996). They include some characters such as a blunt, thick and black-tipped tail with a few clear separated rings and a dorsal black line running from the shoulders to the beginning of the tail. Please see Ragni and Possenti (1996) for further details on European wildcat pelage characteristics. A recent study on wildcat-hybrid presence across Europe showed no presence of hybrids in our study area (Tiesmeyer et al., 2020) and the chances of misidentifying a wildcat and a hybrid in the Cantabrian Mountains seem to be low. However, as morphology solely does not fully allow wildcat differentiation from hybrids (Devillard et al., 2014) and we did not genetically analyse each observed individual wildcat, every time we use the term wildcat or European wildcat in the article we will be referring to phenotypic European wildcats. We used binoculars and a telescope (Swarovski Habitch 7x42 and Swarovski ATS 65 HD + Zoom 20X60, Swarovski Optik KG, Austria) to locate and observe wildcats, and when possible, recorded the individuals on video using a Canon Powershot SX60 HS (Canon Inc., Japan). As the use of spotlights during the night may influence wildlife behaviour (Wilson, 1999), we did all the observations between dawn and dusk, not having run observations during the night. We also compiled observations and videos from external collaborators with broad experience in wildlife monitoring.

Interaction analysis

We considered an encounter to occur when there were no visual obstacles and both species could directly see each other in the same grazing field or pastureland. The distance at which both species detected each other ranged from approximately 40 to 75 m. However, as terrain roughness and vegetation may have played a role in detection between species, we did not consider distance in the analysis. From the observations and the videos we determined: a. the species that initiated the interaction by approaching the opponent; b. the behaviour displayed by each species; and c. the species that remained in the area. We considered the initiator as the species that first observed and approached the opponent intentionally. When such behaviour was not clearly observed, we considered the initiator as unclear. We classified the behaviour displayed by each animal as follows (Supplemental File 5.1): 1. Offensive intimidation: The species approaches and displays direct persecution and/or physical contact with the rival. 2. Defensive intimidation: The species is approached by the rival and holds the position, crouches, side-walks, bristles or charges, straight looking at the rival and aimed at repelling its approximation. 3. Curiosity: The species slowly and curiously approaches the rival, sometimes in a playful way. 4. Ignore: There is no visible modification of the species behaviour after detecting the rival. 5. Flee: The species abandons the area as a clear consequence of the presence of the rival. We used Fisher´s exact test to assess for the significance of differences between frequency of occurrence of different wildcat and fox behaviours during encounters.

5.4 Results

Between January 2012 and December 2019 we observed wildcats in 597 occasions and obtained approx. 50 hours of video recording. We observed wildcat-fox interactions on 14 occasions, making the 2.34% of all the wildcat observations. We compiled other 11 observations from external collaborators.

Foxes initiated the interactions in approx. half of the cases (13 out of 25). The initiator was unclear in the remaining cases. Overall, both species behaved significantly different during encounters ($p = 0.0006$; Fig. 5.2). Foxes displayed significantly more “offensive intimidation” ($p = 0.014$), “curiosity” ($p = 0.014$) and “ignore” ($p = 0.023$) behaviours than wildcats. Wildcats displayed significantly more “defensive intimidation” behaviours than foxes ($p = 0.014$). We found no significant differences in fleeing responses between both species ($p > 0.1$). When crossing the behavioural responses of both species (Supplemental File 5.2), the most common interaction was that both species ignored each other (n=5), followed by wildcats fleeing when foxes displayed offensive intimidation (n=4); foxes fleeing when wildcats displayed defensive intimidation (n=4); and wildcats displaying defensive intimidation when foxed displayed curiosity (n=4). Both offensive intimidation displayed by foxes and defensive intimidation displayed by wildcats caused the opponent to flee the same number of times.

Wildcats were the only species remaining in the site after the encounters 20% of the times; whereas foxes were the only species remaining in the site after the encounters 28% of the times. Both species remained simultaneously in the field after the encounters 44% of the times and only twice both species left the area. Wildcats always left the site when foxes used offensive intimidation (n=4). On the other hand, wildcats stayed in the site 81.8% of the times they used defensive intimidation (n=11), as the foxes either fled, ignored or showed curious behaviours in such occasions.

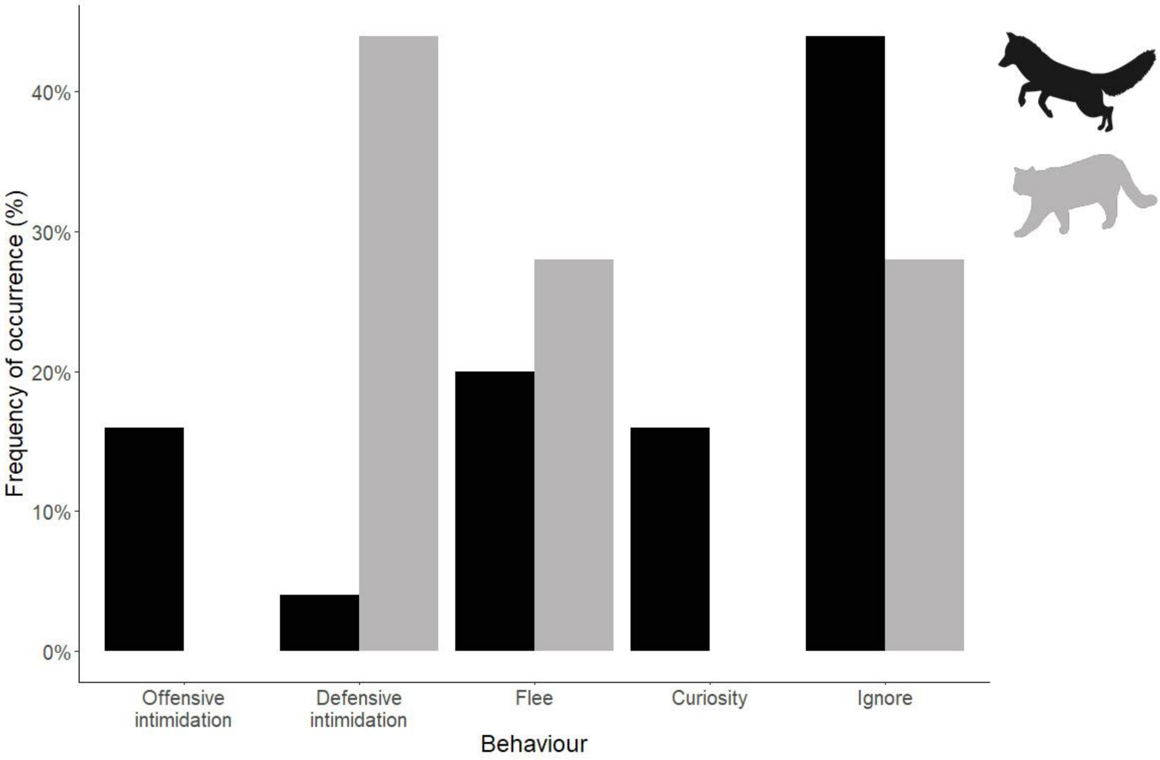


Figure 5.2. *Frequency of occurrence of the different behaviours displayed by foxes (black) and wildcats (grey) during wildcat-fox encounters (n=25).*

5.5 Discussion

Diurnal direct interactions between European wildcats and red foxes seem to be rare in the pastoral landscapes of the Cantabrian Mountains. This may be partly explained by the generally low population density typical for carnivores. Continual spatiotemporal avoidance among species is a common strategy between competitors to enable coexistence and reduce potential risks derived from agonistic encounters (Karanth et al. 2017), and could also explain the low rate of diurnal wildcat-fox encounters observed. Although wildcats and foxes seem to share habitat, at least partially and seasonally, as both species were shown to spatially overlap during camera trap surveys (Tsunoda et al., 2020), recent research showed that both species present micro-scale segregation in pasture fields (100 m resolution), with wildcats and foxes using areas closer and further from edges respectively (Rodríguez et al., 2020). Moreover, it has been shown that there is a spatial segregation between feral cats (*Felis catus*) and foxes in Australia (Molsher et al., 2017).

Small trophic differences can explain low degrees of agonistic interactions between species (Molsher et al., 2017) which occurs in our case, with foxes being a more generalist species than wildcats (Díaz-Ruiz et al., 2013)

Another possible explanation to the low encounter rate observed would be a wildcat-fox temporal segregation. Camera trap research in several areas of the Iberian Peninsula showed that both species are facultative nocturnal animals, although their activity patterns do not overlap completely (Monterroso et al., 2014). In the Cantabrian Mountains, both species are frequently observed during the day (Rodriguez et al. 2020) which allowed us to focus on diurnal interactions between both species. In order to discuss temporal segregation we should have included nocturnal observations, however, we did not, as the use of spotlights to study wildlife behaviour has been shown to potentially influence the behaviour of the study species (Wilson, 1999) and thus it may have affected the outcome of the interactions between wildcats and foxes. Moreover, the use of thermal viewers generally does not allow distinguishing between wildcats and domestic/feral cats so such approach would not have been reliable. As both species are described as facultative nocturnal in the Iberian Peninsula, it is possible that both species behave as such in our study area, and that interactions between foxes and wildcats could occur more frequently during the night than during the day.

Most likely, the low rate of diurnal encounters between wildcats and foxes could result from active avoidance between both species. Such dynamic strategy would allow the coexistence of two species in a given area sharing landscape and resources by actively avoiding the rival when being aware of its immediate presence and reducing potential agonistic encounters (Broekhuis et al. 2013; Karanth et al. 2017). Avoidance strategies are a recently documented behaviour among carnivores to minimize encounters with competitors (e.g. European lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) (López-Bao et al., 2016); tigers (*Panthera tigris*), leopards (*Panthera pardus*) and dholes (*Cuon alpinus*) (Karanth et al. 2017); cheetas (*Acinonyx jubatus*), lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) (Broekhuis et al., 2013)). It is thus possible that wildcats and foxes actively avoid each other when they are aware of their respective presence as it has been previously suggested (Monterroso et al., 2020; Ruiz-Villar et al., 2020). This would agree with Rodríguez et al. (2020), showing that wildcats remained closer to edges as they offer proximity to refuge against potential threats, in this case red foxes. Nonetheless, we do not know how this strategy exactly works between wildcats and foxes, as the mechanisms involved in their reciprocal detection (either visual or chemical) and the associated responses are difficult to observe in the wild.

Our results reflect that foxes displayed an offensive response when encountering wildcats by initiating the interactions half of the times and offensively intimidating/curiously approaching the wildcats. On the contrary, wildcats displayed behaviours based on defensively intimidating foxes while holding the position, crouching or charging the fox only after it approached. Foxes are larger than wildcats and several individuals can occasionally travel together. Our results agree with Palomares and Caro (1999), showing that larger and sociable species are more likely to initiate the interactions. It also agrees with Stankowich (2012) suggesting that features like sharp claws or compact morphologies are more suitable for defensive intimidation strategies, both characteristics of European wildcats. Thus, it is likely that the functional morphology and sociality of each species drives them to adopt certain strategies. Foxes ignored wildcats more frequently, maybe as foxes do not perceive wildcats as an immediate threat. Foxes occasionally predate upon feral cats (Kidawa and Kowalczyk, 2011), and although wildcats are generally larger than feral cats and we found no evidence of foxes predating wildcats, it is possible that red foxes initially perceive wildcats as potential prey.

Foxes would be more likely to win the encounters with wildcats as they are larger (Monterroso et al., 2020; Palomares and Caro, 1999) and several authors suggest that feral cats are subordinate to foxes (Marlow et al., 2015; Read and Bowen, 2001). However, subordination of wildcats to foxes may not be as clear as wildcat and fox sizes are more similar than feral cat and fox sizes. Our results showed that foxes and wildcats were equally successful at maintaining access to feeding sites throughout offensive and defensive intimidation respectively. Remaining in the area after the encounter could translate into higher access to rodents as a food resource. Biologically, this could have important consequences particularly for wildcats, as this species highly depends on rodents for its survival (Lozano et al., 2006). Some behaviours occurring out of the view (e.g. detection of the rival by chemical cues) may condition the behaviour of each species and the final outcome.

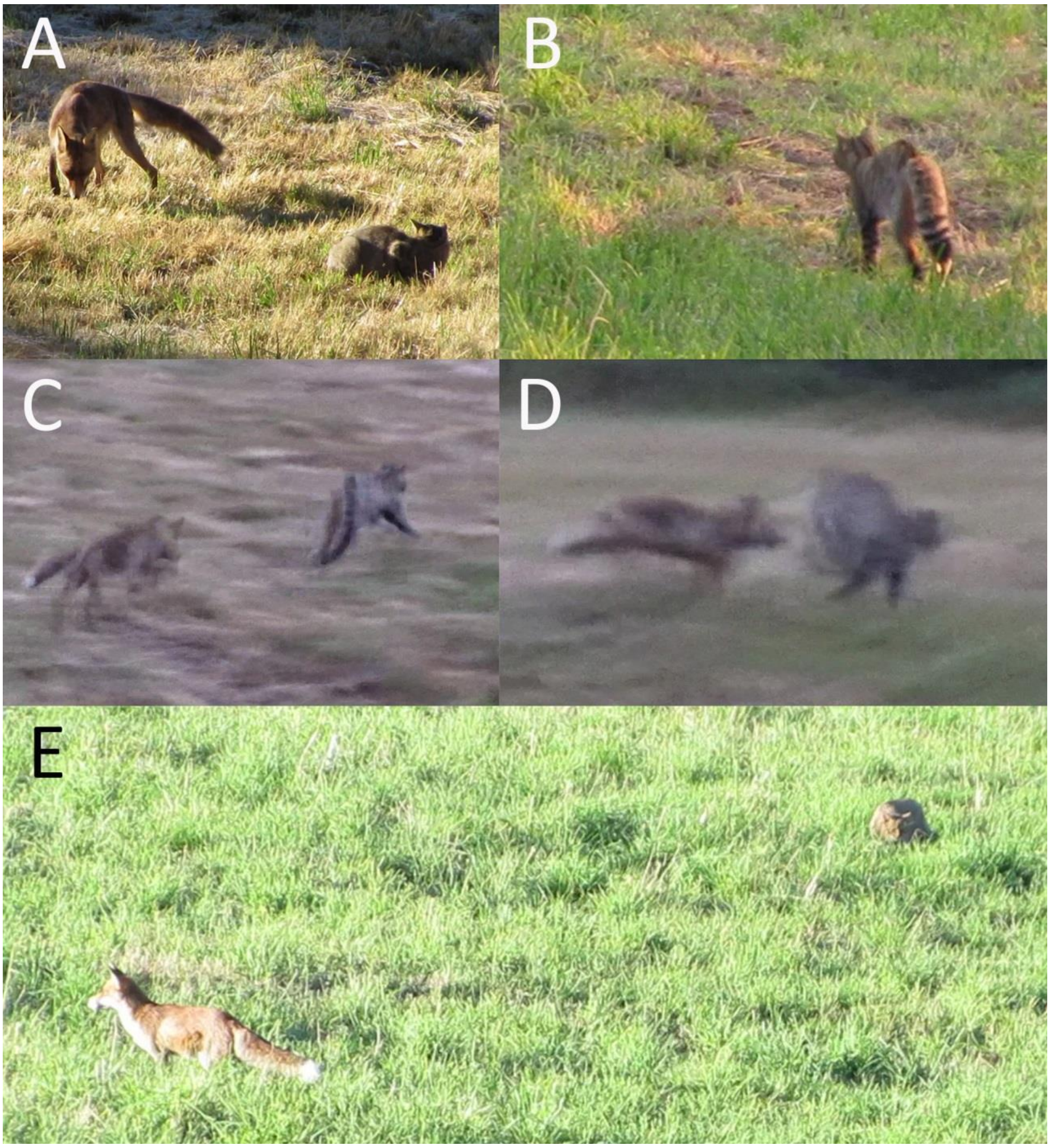
In conclusion, despite using simultaneously the same habitats for foraging, diurnal encounters between foxes and wildcats seem rare in the Cantabrian Mountains potentially as a result of active avoidance between the two species. Despite literature suggests that foxes would win the encounters with wildcats, our results show that both offensive and defensive intimidation are equally effective strategies when maintaining access to areas with presence of shared prey. We highly encourage the combination of technologies such as GPS monitoring or camera trapping with direct observation of the species to increase the quality and accuracy of the information on their interactions.

5.6 Acknowledgements

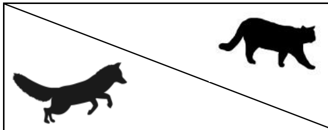
We thank M. Torres Diseños Industriales SAU and Land Rover Spain for their partial economic and logistic support. We thank Bernardino López, Rubén Barreda, Josechu Fdez., Ángel Rabanal, PV Albaladejo and Raúl López, for their collaboration when sharing their detailed observations of interactions with us. We thank two anonymous reviewers for their suggestions to improve the manuscript. HRV is beneficiary of a PhD scholarship "Severo Ochoa" from the Regional Government of Principality of Asturias. JVLB was supported by a Ramón y Cajal research contract (RYC-2015-18932) from the Spanish Ministry of Economy, Industry and Competitiveness.

5.7 Supplementary material

Supplemental file 5.1. *Video captures of different behaviours observed during wildcat-fox interactions.* ***A***. *A fox approaches a wildcat showing curiosity (head down inspecting the rival) while the latter displays a defensive intimidation strategy, in this case crouching down the ground.* ***B***. *A wildcat displays a defensive intimidation strategy known as side-walk in the presence of a fox. It bristles and walks showing the sides to the rival while arching the tail.* ***C*** *and* ***D***. *Sequence of a fox persecuting (offensive intimidation) a wildcat which flees from the rival.* ***E***. *A wildcat and a fox ignore each other while stalking rodents in a field. Image credit: A,B,E Héctor Ruiz; C,D Jacinto Román.*



Supplemental file 5.2. *Number of times each species (foxes in lines and wildcats in columns) displayed each behavioural response in relation to the behaviour of the opponent. OI: Offensive intimidation; DI: Defensive intimidation; FL: Flee; CUR: Curiosity; and IGN: Ignore.*

	OI	DI	FL	CUR	IGN
OI	0	0	4	0	0
DI	0	0	0	0	1
FL	0	4	1	0	0
CUR	0	4	0	0	0
IGN	0	2	2	0	5

CHAPTER 6

A small cat saving food for later: Caching behaviour in the European wildcat (*Felis silvestris silvestris*).

Publication: Ruiz-Villar, H., López-Bao, J.V. & Palomares, F. (2020). A small cat saving food for later: caching behavior in the European wildcat (*Felis silvestris silvestris*). ***European Journal of Wildlife Research***. 66, 1-5.

DOI: https://doi.org/10.1007/s10344-020-01413-x

6.1 Abstract

Caching behaviour consists on the relocation or storage of food to protect it from competitors, to delay food spoilage, or to exploit it during times of scarcity. While this behaviour has been widely described for some medium and large-sized felids, only a few cases documented caching behaviour in small felids. Here, we provide the first exhaustive description of a caching event on a European wildcat in the Cantabrian Mountains (NW Spain). The wildcat behaved like a lynx/puma, visiting a road-killed roe deer carcass at least 9 days along a 21 day period, consuming the main muscles and covering it with hair and vegetation.

6.2 Introduction

Caching behaviour consists on the relocation and/or storage of food to create a predictable food resource to exploit during times of scarcity (Vander Wall, 1990), protect it from competitors (Stein et al., 2015), and delay its spoilage (Bischoff-Mattson and Mattson, 2009). Caching is well studied for several taxa, such as seed-eating species like corvids or rodents (Vander Wall, 1990). Regarding mammalian carnivores, caching of prey has been documented, both when hunting prey and scavenging, for several families including felids (Bauer et al., 2005; Bischoff-Mattson and Mattson, 2009).

Felids display caching behaviour in multiple ways. Although leopards (*Panthera pardus*) can cache their prey into caves (Ruiter and Berger, 2001), they more commonly carry prey up to trees to reduce the risk of kleptoparasitism from not-climbing competitors (Balme et al., 2017). The same behaviour has occasionally been documented for European lynxes (*Lynx lynx*; Červený and Okarma, 2002) and caracals (*Caracal caracal*; Mills, 1997). Jaguars (*Panthera onca*) and tigers (*Panthera tigris*) drag their prey to areas under vegetation to periodically feed upon the remains (de Azevedo and Murray, 2007; Karanth and Sunquist, 2000). All lynx species (*L. lynx* (Podgórski et al., 2008)*; L. rufus* (Labisky and Boulay, 1998)*; L. canadiensis* (O'Donoghue et al., 1998)*, L. pardinus* (Delibes, 1980))*,* pumas (*Puma concolor*) (Bischoff-Mattson and Mattson, 2009), and rarely leopards (Karanth and Sunquist, 2000) cover their prey with a layer of soil, snow, plant litter or organic debris. Such strategy reduces prey visibility and odour dissemination (and thus, detection by kleptoparasites), and also slows down decomposition by microbes and arthropods (Bischoff-Mattson and Mattson, 2009). Predators can exhume, consume and inhume the carcass along several days (Bischoff-Mattson and Mattson, 2009).

Caching mainly occurs when prey are too large to be consumed in a single day (e.g. ungulates) (Bischoff-Mattson and Mattson, 2009); we thus expect medium and large-sized felids – being able to kill large prey – to display this behaviour more commonly. There are yet a limited number of records of caching behaviours in small felids. For instance, a sand cat (*Felis margarita*) killed and cached an Asian houbara (*Chlamydotis macqueenii*) in the deserts of Uzbekistan (Brighten and Burnside, 2019) and black-footed cats (*Felis nigripes*) captured and cached Southern black korhaans (*Afrotis afra*) in South Africa (Sliwa, 1994). Caching behaviour has also been observed in domestic cats (*Felis catus*) (Turner et al., 2000).

The European wildcat (*Felis silvestris silvestris*) is a small felid found across Europe that feeds mainly on rodents and other small animals (Lozano et al., 2006). Although scavenging (Moleón and Gil-Sánchez, 2006) and prey-covering caching behaviour has been documented for the wildcat (Hunter, 2015; Macdonald, D., & Loveridge, 2010), to our knowledge there is no previous detailed descriptions of a complete caching event on European wildcats. Here, we provide the first exhaustive description of the caching behaviour of a GPS-collared European wildcat upon a road-killed young roe deer (*Capreolus capreolus*) in the Cantabrian Mountains, NW Spain. We studied the wildcat feeding behaviour at the caching site, time and duration of the visits, and recorded other species consuming the carcass.

6.3 Methods

Study area

We located a roe deer carcass in the west of the Cantabrian Mountains (NW Spain; Fig 6.1.a) (42º 58' 32.65" N 6º 24' 3.90" W), an area with presence of large carnivores such as bears (*Ursus arctos*) and wolves (*Canis lupus*), and several scavenger species (e.g. griffon vultures (*Gyps fulvus*)). The weather during the study period was cold but sunny with two days of snow. Nevertheless, there was an important snowfall two months earlier that lasted until the week before we found the carcass.

Wildcat collaring

A male European wildcat was captured using a box-trap baited with sardines on 26th November 2019 (permit EP/P/128/2019) by workers of TRAGSATEC S.A., Spain. We anesthetized the wildcat using 0.35 cc of Ketamine (100 mg/ml) + 0.2 cc of Dexmedetomidine (1 mg/ml). We equipped the wildcat with a 80 g GPS-GSM Followit collar (Followit Sweden AB, Lindesberg, SE) programmed to get a GPS location every seven hours, except on the first Saturday of every month when it took one point every half an hour for a full 24-h period (intensive tracking).

Monitoring of the caching site

On Saturday 4th January of 2020 the intensive tracking showed a cluster of 11 locations next to a secondary road 10 m around the same spot. We visited the area the following morning and found a roe-deer carcass, presumably road-killed, on a slope with bushes scattered among natural pastureland at 1388 m.a.s.l. We deployed a camera-trap Browning Dark Ops HD Pro X (Browning International S.A., Herstal, BE) capturing video on the site 2 m away from the carcass. We visited the location every two to five days to replace the camera memory card and check the condition of the remaining flesh. We considered “feeding time” as the period any animal spent processing and consuming the carcass (i.e. plucking of hair and pulling, chewing and ingesting flesh). We compared time spent feeding by the wildcat between the first and the second week by using the nonparametric Mann–Whitney U test.

6.4 Results

The camera was active from 5th to 24th January (monitoring period), after when only bones and skin remained from the carcass. Over this period, the wildcat fed upon the carcass at least 8 times on 8 different days (Fig 6.2) (9 times if we include the GPS data): 2 times during daylight and 6 at night. Nevertheless, no data was collected between 9th and 12th January as the wildcat dragged the carcass out of the camera range.

When we found the carcass, it was partially covered by vegetation and hair that had been plucked from the roe-deer itself (Fig 6.1.b). Some flesh from the hindquarters was already missing. Between 5th and 18th January the wildcat was the only species feeding on the carcass, with the exception of a raven (*Corvus corax*) and a wood mouse (*Apodemus sylvaticus*) that fed briefly upon it (Fig 6.2). The wildcat consumed the hindquarters first (Fig 6.1.d) and then the groins, the snout and part of the chest. It also eviscerated the roe-deer. Although differences were marginal ($W = 1$, $p = 0.057$), the wildcat spent more time feeding on the carcass during the second week (Median = 92.5min/day; range = 76-127, n=4) than during the first one (Median = 44min/day; range=39-77, n=4). The wildcat plucked hair from the roe deer (Fig 6.1.c) to cover the carcass together with vegetation (Fig 6.1.b) on 5th, 6th and 14th January (37.5% of the monitored wildcat visits) (Online Resource 1).

The cat did not remain continuously in the proximity of the carcass during the monitoring period. Excluding the intensive tracking, only one out of 18 fixes was located at the carcass site. The average distance from the carcass was 1.220 m (SE=235.86, range= 1 – 2680, n= 18). Along days, we observed no trend on the wildcat distance from the carcass.

After two weeks, other species fed upon the carcass (Fig 6.2): wood mouse, common buzzard (*Buteo buteo*), raven, pine marten (*Martes martes*), magpie (*Pica pica*), wild boar (*Sus scrofa*), and red fox (*Vulpes vulpes*). The wildcat did not return to the carcass after the fox started visiting it.

Figure 6.1. *a) Location of the roe deer carcass cached by a European wildcat in the west of the Cantabrian Mountains, NW Spain. b) Roe deer carcass cached by a European wildcat partially covered by vegetation and roe deer hair. c) European wildcat plucking hair from the roe deer carcass. d) European wildcat feeding upon the hindquarters of the roe deer.*

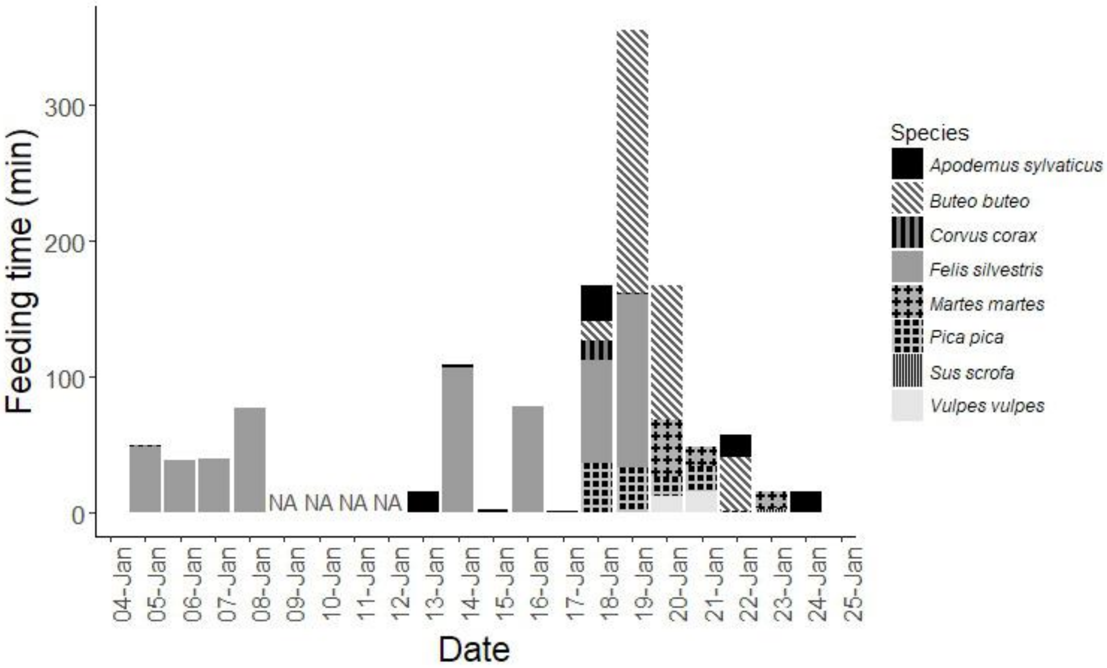


Figure 6.2 *Time each species spent feeding upon the roe deer carcass (Feeding time) between 5th and 24th January 2020. The carcass was out of the camera range (NA) between 09/01/2020 and 12/01/2020.*

6.5 Discussion

This is the first exhaustive description of a complete caching behaviour event in a European wildcat. Similarly to some medium and large-sized felids, for which caching behaviour is better described (particularly lynx and pumas; see Introduction section for references), the wildcat consumed the carcass along several days, and occasionally dragged it and covered it to protect it from other potential consumers. In the Eurasian lynx, covering the carcass was effective at reducing detection by avian scavengers (Krofel et al., 2019). Apparently, the mentioned strategy was effective for the wildcat during the first two weeks, as only a raven and mice fed briefly upon the carcass. The wildcat prey covering-behaviour was similar to that recorded for other small cat species (Brighten and Burnside, 2019; Sliwa, 1994), with the peculiarity that the referenced events were related to cases of predation, as it generally occurs with other felids that cache their prey (Bischoff-Mattson and Mattson, 2009). Nonetheless, the caching behaviour displayed by felids seems to be similar when scavenging prey found already dead (Bauer et al., 2005). Domestic cats have also been recorded covering the remains of their prey (Turner et al., 2000).

The large size of the carcass can also trigger caching behaviour in felids as a response to food abundance after satiation (Swanepoel, 2008). In our case, food scarcity during winter in an area where snow cover was important in previous months and rodents were probably inaccessible (Mermod and Liberek, 2002) may have contributed to trigger the caching behaviour reported for the wildcat. The consumption of a road-killed roe deer may show the importance of road-killed animals for an opportunistic scavenger (Schwartz et al., 2018). Nevertheless, considering that road kills are one of the main causes of wildcat mortality in Europe (Klar et al., 2009), the risks derived from frequenting road sides may be high. Encountering ungulate carcasses during winter seems to increase individual survival and improve body condition in other felids (Matlack and Evans, 1992) and thus could also be important for European wildcats inhabiting areas with harsh winters. The wildcat consumed the hindquarters first, which is an expected behaviour when felids feed on prey larger than themselves (Kitchener, 1991).

Recent research in the Cantabrian Mountains showed that wildcats and foxes may actively avoid each other in order to reduce the risk of agonistic encounters (Rodríguez et al., 2020; Ruiz-Villar et al., 2021). Our results support such idea as the wildcat did not return to the carcass after the fox started visiting it.

To conclude, the combination of finding a large prey that offered the wildcat an opportunity to feed upon a predictable food resource during a time of prey scarcity, together with potential detection of the carcass by competitors inhabiting the area, may explain the caching behaviour recorded for an individual wildcat in the Cantabrian Mountains. The behavioural pattern of the described caching event matches that broadly documented and described for other felids like pumas and lynxes.

6.6 Acknowledgements

We thank the Regional Government of Castilla y León for the permits to capture wildcats (EP/P/128/2019). We thank the Spanish Ministry of Science, Innovation and Universities as well as TRAGSATEC S.A. for their collaboration in the trapping of European wildcats. We thank Land Rover Spain for their economic and logistic support. We thank two anonymous reviewers for their suggestions to improve the manuscript. HRV is beneficiary of a PhD scholarship “Severo Ochoa” from the Regional Government of Principality of Asturias. JVLB was supported by a Ramón y Cajal research contract (RYC-2015-18932) from the Spanish Ministry of Economy, Industry and Competitiveness.

General discussion

Conservation faces multiple challenges in the current scenario of increasing human pressure occurring worldwide (Cumming et al., 2014; Khan et al., 2021; Milner and Boldsen, 2023). Many species have adapted their behaviour to coexist with humans and their activities, particularly in areas with high degrees of human occupancy like Europe (Tuomainen and Candolin, 2011). Among them, mammalian carnivores are particularly sensitive to human-related activities (Ripple et al., 2014; Sainsbury et al., 2019). Preserving healthy populations of large and medium carnivores in anthropogenic environments requires understanding the different effects that human activities may have on different ecological parameters, some of them encompassing basic and key ecological traits such as reproduction or interspecific interactions (Sévêque et al., 2020). In the present thesis, and through the use of long-term monitoring data gathered by both traditional and modern techniques, we successfully evaluated the effects of human activities such as agriculture, livestock rearing and human and traffic presence on European wildcat spatial use, prey consumption and hunting and vigilance behaviours. Additionally, we provided unique and novel information on wildcat breeding ecology and interspecific interactions in a human-modified context, as well as described the use of previously overlooked food resources.

The effects of human activities on wildlife can vary between species and ecosystems (Briner et al., 2005; Doherty et al., 2019). For instance, generalist carnivores may perceive increased foraging opportunities in human-dominated landscapes due to abundance of predictable food resources like garbage (Šálek et al., 2015). On the other hand, species with higher habitat and food requirements may be negatively affected by direct disturbance and impoverished habitat suitability in anthropogenic areas (Riley et al., 2003; Schüttler et al., 2017). Due to its particular characteristics regarding habitat selection (positively selecting for mosaic-structured landscapes (Lozano et al., 2003)) and prey preferences (rodent based diet (Lozano et al., 2006)), European wildcats inhabiting anthropogenic landscapes may perceive positive and negative effects depending on the intensity and degree of land occupancy of human activities. However, changes in landscape use, prey consumption, and time allocation to hunting or vigilance behaviours by wildcats can be difficult to translate into broader ecological effects at individual and population levels such as breeding success, population trends, and health status of populations (Beale and Monaghan, 2004; Gill et al., 2001). Hence, it is particularly challenging to evaluate the ecological trade-offs for wildcats inhabiting human-modified landscapes across Europe.

Human activities aiming at covering human food supply (i.e. agriculture and livestock rearing) contribute the most to habitat destruction and modification (Alkemade et al., 2013; Milner and Boldsen, 2023). Changes in habitat configuration alter location, availability and predictability of resources such as prey or refuge, which ultimately influence both spatial use and prey consumption by carnivores (Riley et al., 2003; Schüttler et al., 2017). In wildcats using human-modified landscapes across Europe, home range size increased when increasing the proportion and intensity of agriculture present inside the wildcat home ranges (Chapter 1). This may be a response of wildcats to decreased habitat suitability and distant resource availability for which they compensate by roaming across larger areas (Poessel et al., 2014; Riley et al., 2003; Schüttler et al., 2017). Such variation can ultimately increase energetic costs for wildcats as they move across further distances to obtain similar energetic intake than populations perceiving more suitable conditions. Hence, wildcats using landscapes with high presence of intensive agricultural fields would survive in worst conditions than those using better structured and connected habitats. This is particularly remarkable when intensive agricultural landscapes become homogeneous and do not provide refuge environments like forest patches (Jerosch et al., 2018). Surprisingly, large homogeneous forest patches seem also not optimal for wildcats as their home range increased in such environments. Nowadays, intensive agricultural practices requiring the modification of large surfaces continue to spread (Laurance et al., 2014), and consequently, survival of European wildcat populations in such environments could be compromised.

In this regard, and considering that human population continues to grow, two separate trends appear as proposed solutions for simultaneously preserving wildlife and exploit landscapes with food production objectives to satisfy the increasing human demands: i) land sharing, consisting on the creation of mosaic-structured landscapes that mix both agricultural and natural areas; and ii) land sparing, which suggest for agriculturally exploiting large landscape surfaces while simultaneously preserving large natural areas (Fischer et al., 2014). Although both approaches can potentially derive into tragic trade-offs both for humans and carnivores (Bruskotter et al., 2022), wildcats prefer for mosaic structured landscapes that provide both prey and shelter opportunities (Oliveira et al., 2018), so we may perceive land sharing as providing conditions that ensure their long-term survival, something also suggested for the effective conservation of certain large carnivores in a world with increasing levels of humanization (Johansson et al., 2016; López-Bao et al., 2017, 2015). However, when the agricultural portion of the landscape is exploited intensively, conditions may not be adequate for wildcats, probably due to decreased prey availability promoted by pest eradication programs and poor interconnection between refuge patches (Jerosch et al., 2018).

Furthermore, mosaic structured landscapes are not exclusively anthropogenic and also appear naturally. On the other hand, more sustainable practices like livestock rearing in pastoral fields seem to gather more suitable conditions for wildcats as they may create mosaic landscapes more similar to those occurring naturally and preferred by wildcats (Chapter 1) and may provide abundant and accessible prey in the pastoral fields where grass is harvested to feed the stock (Chapter 2). The combination of these two factors caused the home range size of wildcats to be smaller in this kind of landscapes. Hence, land sharing initially seems like a suitable option for preserving wildcat populations across Europe while simultaneously producing food for humans, although this will only be effective if agricultural and livestock practices are performed extensively and sustainably.

Nonetheless, considering that species-specific conservation strategies can be controversial and detrimental for other wildlife species with different ecological requirements (Seddon and Leech, 2008), the best option to simultaneously protect those species requiring high undisturbed habitats as well as species finding benefits in slightly disturbed landscapes would be to complement both strategies (land sparing and land sharing) (Tälle et al., 2023; Valente et al., 2022). In this hypothetic hybrid scenario already recommended for carnivore conservation in other anthropogenic landscapes (Mohammadi et al., 2021), large natural areas would appear mixed with some pastoral and agricultural areas located next to highly anthropogenic environments (roads, villages, etc.). Of course, to satisfy increasing human demands, other large areas (probably those already very modified such as the proximities of cities) should be dedicated to intensive agricultural practices. However, intensive practices should not necessarily occupy large surfaces, thanks to the evolution of land use optimization in agricultural techniques (Kaim et al., 2018). In this case, species with requirements for core natural habitats, mosaic structured landscapes and open areas could all survive in different interconnected locations.

The proposed scenario is similar to that already existing in some areas of the Cantabrian Mountains (Loidi, 2017), where we carried most monitoring of wildcats for the present dissertation. Nevertheless, the current landscape structure in these mountains is under change influenced by two opposite processes. On one hand, there locally exists a progressive intensification of extensive livestock rearing practices (Blanco-Fontao et al., 2011), which involves the removal of large shrub areas aiming at creating pasturelands, land consolidation destroying stripes of wooded vegetation between fields and increased livestock numbers that overpass the grazing load admitted by the environment. Shrub formations and linear structures of thick vegetation such as riparian vegetation and hedges are very important for wildcats which may use them with breeding, sheltering and feeding purposes (Chapter 1, 2 and 4). The removal of such landscape components may consequently threaten wildcat conservation in human-dominated landscapes (Jerosch et al., 2018; Lozano et al., 2003). In addition, wildcat main prey in pastoral fields (Chapter 2) is the montane water vole (*Arvicola monticola*), which could be negatively impacted by field overgrazing as they respond negatively to excessive cattle trampling (Morilhat et al., 2007).

On the other hand, abandonment of rural environments by people emigrating to cities promotes the disappearance of the activities that maintain pastoral fields, which consequently derives into the passive rewilding of such anthropogenic landscapes towards vegetation stages such as shrub and forest (Benayas et al., 2007; García et al., 2023). Rural abandonment, and the associated increase in forest surface, is handled as one of the principal reasons of European wildcat recovery across Europe

(Gerngross et al., 2022), and we have already mentioned the importance of shrub and forest patches for European wildcats, which means that this process should not remarkably threat European wildcats. However, it is possible that populations of montane water voles would decrease after the disappearance of pastoral fields, thus affecting European wildcat ecology and demography. As seen in Chapter 2, the pastoral field surface required for wildcats to mainly feed upon water voles is quite low (ca. 15%), which leaves considerable room for natural landscapes to persist. For this reason, we think that the maintenance of those relatively small and currently sustainably exploited pastoral fields (e.g. avoiding the use of machinery and chemicals and maintaining vegetation structures such as hedges) in those areas already altered by human activities (close to villages and roads) may benefit wild species like European wildcats while facilitating the preservation of large surfaces of natural habitats and allowing the persistence of social and economic activities (e.g. livestock rearing). The intermediate stages of passive rewilding in the abandoned areas (shrub and young forests) as well as the mature forests present in the surroundings of pastoral fields (García et al., 2023) would more likely be beneficial for wildcats, as they provide this species with the required shelter, refuge and alternative prey.

Wildcats seem to frequently use pastoral fields with feeding purposes as seen in Chapter 2, where the main prey item (*Arvicola monticola*) is a species mainly found in open anthropogenic areas like the pastoral fields of the Cantabrian Mountains. Wildcats seem to rely upon montane water vole availability for feeding, as when water vole populations declined wildcats responded one year later by switching to different prey items, but returned to montane water voles once their population numbers recovered (Chapter 2). In this regard, abundance of a considerable large prey item in these environments promoted by the pastoral practices carried in the majority of these fields inside the study area can provide positive effects to wildcat populations. For instance, increased food intake can decrease home range size, reducing energetic waste in territorial patrolling (Maher and Lott, 2000). It can also improve body condition of individuals which may increase individual survival and breeding success (Wilson et al., 2020). Indeed, female wildcats used the surrounding of pastoral fields with breeding purposes and were very successful at capturing prey to feed their kittens in such environments (Chapter 4). However, we lack the necessary information to know if breeding parameters actually differ from those of wildcats using other kind of environments (either more natural or more intensified) as information on wildcat breeding ecology is scarce and mostly based on captive-bred individuals (Ruiz-Olmo et al., 2018).

Pastoral fields are regularly used by humans with different purposes. Some are livestock-related such as grass harvesting and livestock grazing, and others are recreational, such as trekking, or wildlife photography. Moreover, pastoral fields are generally located in accessible areas in the flat valley bottoms, commonly next to villages and paved roads (Loidi, 2017). The mentioned activities can cause human disturbance in wildcats using pastoral fields (Piñeiro et al., 2012). While some can trigger antipredator responses as they are perceived as highly threatening like the actual presence of a human, other can derive into habituation after repetition of stimuli without negative consequences, for example, rolling traffic.

Wildcats responded differently to different sources of disturbance (Chapter 3). The most threatening ones triggered alert behaviours that deprived wildcats from foraging, which can negatively impact the individuals through reduced food intake. On the other hand, high traffic increased the time hunting in road proximities. Although not significantly, hunting success decreased more in females than in males with the presence of cars, which could be related with higher sensitivity to disturbance in female wildcats (Senzaki et al., 2016; Siemers and Schaub, 2011). In this regard, it is complicated to evaluate the balance between the increased foraging opportunities closer to roads and the disturbance affecting wildcat behaviour in such environments. Wildcats were seen using those fields during the last decades, and although they could perceive negative effects such as increased road mortality in those environments (Bastianelli et al., 2021) the benefits may be worth the risks. Otherwise, one would expect that wildcats would not use such environments so frequently, unless pastoral fields and their proximities are acting as ecological traps, causing detrimental effects on wildcat populations when they visit them after perceiving positive effects (Bastianelli et al., 2021). On the other hand, effects of encounters with humans are clearly negative, as there were not positive effects perceived. Whereas wildcats can deal with antipredator responses triggered by natural competitors such as foxes (Chapter 5), alert responses triggered by humans provide an extra load of antipredator behaviours that can potentially derive into negative consequences for the species after avoiding certain areas where disturbance by humans is higher.

Although we have studied the effects of several human-related activities on European wildcat ecology as well as some of their life history aspects, there is still much to explore in this direction. Particularly, it would be fundamental to know to which extent the effects perceived in our research translate into ecological and demographic effects in terms of fitness or health status. In addition, wildcats may interact with domestic cats in human-dominated landscapes, which may cause problems related to hybridization and disease transmission between both species (Leutenegger et al., 1999; Senn et al., 2019). Future research should specifically aim at knowing to which extent this is affecting wildcat populations in the Cantabrian Mountains. Moreover, other crucial demographic parameters such as dispersal of individuals could be affected by human activities in relation to human infrastructures and landscape connectivity (Bastianelli et al., 2021; Jerosch et al., 2018; Portanier et al., 2022). It is thus critical to determine the effects of human-related landscape fragmentation on wildcat dispersal. Finally, it would be essential to determine how the intersection between food abundance and human disturbance in anthropogenic landscapes influence the reproductive outcome of wildcats inhabiting such environments.

To sum up, the Cantabrian Mountains present a considerable surface of natural habitats mixed with a small proportion of pastoral fields in the valleys which provide suitable conditions for European wildcats in terms of prey, habitat and breeding opportunities. However, this involves interactions with humans and competitors that can cause negative effects on wildcats. Additionally, the current landscape structure of the Cantabrian Mountains is under change not only by the intensification of extensive agricultural practices involving habitat destruction and homogenization, but also by the abandonment of rural environments which promote the evolution of vegetation to mature stages. In this regard, long-term monitoring of the species like the one carried out for the present dissertation is essential to detect the effects of potential future changes in wildcat ecological parameters associated to landscape modification and variations in human presence. The Cantabrian Mountains currently provide suitable conditions for wildcats and could be used as a paradigm across their distribution range. For such reason we should protect the landscape structure of these mountains and prevent the evolution to intensive practices that may not only affect European wildcats but also other singular species inhabiting this mountain range.

Conclusions

1. Home range size of wildcats across Europe was larger in areas with higher land occupancy by intensive agricultural practices, which may be related with higher landscape fragmentation, and distant and low resource availability.

2. Wildcat home range size in Europe was larger in scenarios represented by large homogeneous forests, whereas it was smaller when increasing forest edge density, which confirms the suitability of mosaic structured landscapes for European wildcats and highlights the potential future risks for wildcats associated to the current scenario of expanding land intensification.

3. Wildcat prey consumption in the Cantabrian Mountains was affected by the presence of pastoral fields. Specifically, the montane water vole (*Arvicola monticola*; a large rodent species inhabiting pastoral fields) was the most consumed prey item as long as pastoral fields occupied more than 17% of the area daily used by wildcats and were closer than 700 m to scat locations.

4. Wildcat prey consumption varied between seasons, with *Arvicola* and *Apodemus* dominating the wildcat diet during summer and autumn, and during spring, respectively, which may be associated to varying habitat use and seasonal changes in prey accessibility. However, we found no relationship between inter-annual prey abundance and prey consumption.

5. Wildcats inhabiting human-modified landscapes of the Cantabrian Mountains allocated more time to alert and less time to hunting, feeding and moving behaviours in the presence of humans than in undisturbed scenarios.

6. Wildcats changed their time allocation to different behaviours in relation to vehicles and traffic. Specifically, wildcats allocated more time to hunting in scenarios with higher traffic levels, in the proximities of roads and further from villages. Similarly, they dedicated more time to vigilance behaviours while feeding in the presence of moving vehicles.

7. Wildcat litter size at weaning varied between one and three, with two being the most frequent size. Most observations occurred between July and September, although a late litter was observed in November.

8. Most wildcat auxiliary dens were located inside thick vegetation (shrub or riparian vegetation) close to pastoral fields, and wildcats occasionally used human constructions with breeding purposes. Breeding females moved dens frequently and showed high hunting success.

9. Diurnal encounters between wildcats and foxes seem to be rare, which could result from the two species displaying active avoidance. During encounters, foxes mainly showed offensive behaviours whereas wildcats showed a defensive intimidation strategy, probably in relation to their morphology. Both strategies were equally effective for maintaining the position in feeding grounds.

10. Wildcats can exploit ungulate carcasses, which were a previously overlooked food resource. The wildcat individual displayed caching behaviours similar to that observed in lynx or puma, and visited a road-killed roe deer carcass at least 9 days along a 21 day period, consuming the main muscles and covering it with hair and vegetation.

Agradecimientos

Al contrario que la mayoría de doctorados, limitados generalmente a cuatro o cinco años investigando un tema concreto, el germen de esta tesis doctoral se remonta unas pocas décadas en el tiempo (tampoco soy tan viejo).

Me considero afortunado de haber nacido y crecido en una de las regiones ibéricas con mejor estado de conservación y donde especies míticas como osos, lobos y urogallos resistían al creciente grado de antropización. Hablo del valle de Laciana, cuenca minera oculta cerca del extremo occidental de la Cordillera Cantábrica. Sin embargo, crecer en una zona con tantas posibilidades naturalistas no garantiza el respeto y la pasión por el medio natural y sus habitantes. Esa parte se la debo a mis padres, Tino y Loli, y también a mi hermano Víctor, los cuales me sacaron al campo desde bien pequeño empapando mis tiernas neuronas de inolvidables momentos en la naturaleza. Y es que la figura de Félix Rodríguez de la Fuente tiene un impacto transgeneracional y mi padre era un fehaciente seguidor del famoso divulgador. Además, durante su niñez, mi padre creció en una familia muy humilde en la que muchos hermanos se encargaban de cuidar el ganado en permanente contacto con el medio natural, algo habitual en zonas aisladas de montaña durante la mitad del pasado siglo. Esta fusión entre aprendizaje científico, experiencias personales y un gran conocimiento de la zona convirtieron a mi padre en un auténtico maestro con el que el descubrir todo aquello que nos rodeaba. Nunca olvidaré mis primeras jornadas de berrea con 6 años en los vecinos montes de Somiedo, cuándo el Parque era visitado por infinitamente menos personas que en la actualidad. Amaneceres de niebla y rocío tras noches en vela por la excitación ante la incipiente jornada campera, con los “fleitos” (helechos) engulléndome a cada paso y la ropa empapada hasta la cintura. Vivencias de las que crearon afición en aquellos años tempranos de la década de los 90, tales como la observación de las primeras huellas de oso en el barro o las subidas nocturnas a los bosques cimeros a escuchar el extraño y mitológico canto del urogallo, casi siempre en compañía de mis primos Ulpiano y Dani (padre e hijo), a los que agradezco y con los que atesoro tantos buenos recuerdos en la montaña.

A mi padre también le debo mi primer encuentro con un gato montés, especie a cuya observación y seguimiento he dedicado gran parte de mi vida. En los años 90, la seguridad vial era bastante más laxa que en la actualidad y era habitual que los niños pequeños fuesen de pie entre los asientos delanteros para no perderse nada de lo que sucedía en la carretera. Así me encontraba yo cuando mi padre frenó y con voz sosegada me dijo: “Mira hijo, un gato montés”. Y ahí estaba, a pocos metros del coche, un animal fuerte y compacto de mirada esmeralda y tupido pelaje clavaba sus afilados ojos en los míos mientras la cola de un desafortunado roedor asomaba de entre sus fauces.

Esa imagen causó tal impronta en mi retina que a partir de ese momento mi admiración e interés por la especie fue creciendo a medida que se iban acumulando los encuentros con la misma. Entonces, casi todo lo que leía acerca de estos félidos se reducía al gran desconocimiento que rodeaba a los mismos en la mayoría de sus aspectos vitales fundamentales. Quizá este aura misteriosa unida a la relativa facilidad con la que me encontraba con ellos hizo que mi fijación y obsesión por esta especie continuase creciendo, quizá entusiasmado por la idea (un tanto pretenciosa) de que yo tenía a mi alcance la llave para desentrañar muchos de sus secretos, cimentada fundamentalmente en la posibilidad de realizar observaciones directas de la especie. Ya entonces comencé a registrar mis observaciones de los gatos en cuadernos de campo junto a todos aquellos detalles que pudiesen resultar de alguna utilidad en el futuro. Alguien dijo que todo científico alberga un considerable componente obsesivo en su carácter, y creo que no le falta razón, ya que gran parte de lo que hacemos sería inviable sin ese nivel de pasión que nos empuja a obtener respuestas que a priori se plantean irresolubles.

Este caldo de cultivo contribuyó a que desde bien pequeño tuviese claro que quería dedicarme al estudio de la fauna silvestre. Mis padres no sólo me apoyaron si no que alimentaron mi interés. Mi padre siempre me ha acompañado al campo y hasta la actualidad ha ejercido como el mejor técnico de campo que uno puede imaginarse, participando de forma continua en los muestreos de excrementos, infinidad de esperas soportando las duras condiciones de la montaña cantábrica, o apoyándome logísticamente en el reparto de las observaciones para aumentar la cantidad de información recopilada. Por otro lado, mi madre siempre ha tolerado (y creo que en cierto modo disfrutado) de todas mis locuras camperas, como traerle todo tipo de restos biológicos de bichos a casa (desde excrementos a animales atropellados) o los desembolsos económicos en mis años mozos para costear el equipo de campo. Gracias a vosotros he llegado hasta aquí. Papá, Mamá, os quiero y muchas gracias por todo.

En base a mis intereses naturalistas, biología parecía la carrera más adecuada y León sonaba como un destino estupendo ya que un buen número de biólogos de fauna silvestre de los que había oído hablar habían estudiado allí. Además, este destino me permitía estar cerca de casa y no descuidar el seguimiento de los gatos, el cual proseguía perennemente. Por tanto, entre 2007 y 2012 estudié Biología en la Universidad de León, curiosamente el último año que se oferto la Licenciatura (luego llegó Bolonia con sus cambios y pasó a ser un Grado). Conocí a grandes personas durante mis años universitarios y aunque mi carácter introvertido me torna pésimo en lo que respecta a mantener y alimentar las amistades, a muchos de ellos todavía los considero buenos amigos: Humberto, Peña, Kike, Sevi, Getino, Villa…Con ellos compartí horas de clase, tardes de tapas y noches de fiesta por el Húmedo, y alguna que otra jornada de campo detrás de lepidópteros y herpetos. Gracias por todos esos momentos.

En mis años por León conocí a profesores cuyas vivencias y conocimientos admiraba, y que fueron referentes en aquellos momentos en los que uno mismo cuestiona sus propias decisiones. Fui alumno de Pancho Purroy, Vicente Ena, Benito Fuertes y Jorge Falagán, auténticos y bregados biólogos de campo de los de barro en la canilla y helada en la coronilla. También de profesores de disciplinas distintas a la zoología, pero que supieron transmitir pasión por aquello que enseñaban: Esperanza (Paleontología), Edén (Antropología), Reyes y Paco (Ecología) o Toño (Fisiología Vegetal). Conocí también a gente que en aquel momento hacía su tesis en la facultad: Manu y Bea “los del urogallo”, Carlos “el de los picos medianos”, Félix “el de las mariposas” o Nico “el de los pulgones”. Salta a la vista que el peso en la facultad de grandes figuras entomológicas como Nieto, Mier, Régil o Salgado sesgaban la mayoría del esfuerzo científico en el departamento de zoología hacia dichos taxones. Agradezco a todos ellos el conocimiento compartido y su siempre buena disponibilidad.

También en esos tiempos conocía a Ana, una de las personas más importantes en mi vida con la que llevo compartidas infinidad de experiencias dentro y fuera de España a lo largo de más de una década. Ella ha sido fundamental en mi crecimiento científico y personal y en el adecuado desarrollo de esta tesis doctoral, no sólo por sus inmensas aportaciones científicas si no por su apoyo moral en los momentos más difíciles. Te quiero y te debo mucho. Muchísimas gracias.

Al atisbar el fin de mi tiempo universitario, empezaba a tener claro que una tesis doctoral era la aproximación más adecuada para contribuir al conocimiento de los gatos monteses de la Cordillera Cantábrica y con el fin de convencer a científicos para que supervisasen mi trabajo, contacté a algunos expertos en el tema como Emilio Virgós, Jorge Lozano o José María Gil. No obstante la ausencia de financiación siempre se entrometía como el argumento limitante (algo, por otra parte, muy común en ciencia) y pese al buen recibimiento de mis ideas (lo cual agradezco enormemente), ningún proyecto terminó cuajando. No obstante, seguí empecinado con la idea de realizar una tesis con la especie, lo cual determinó la mayoría de decisiones a partir de ese momento.

Por ejemplo, en 2013 decidí cursar el Máster en Riesgos Naturales, también en León, para aumentar las opciones de ser admitido en algún programa de doctorado. Tuve entonces mi primera oportunidad de hacer ciencia de verdad con la información que había recogido hasta el momento sobre los gatos monteses, la cual cristalizó en mi trabajo fin de máster. Susana Suárez Seoane aceptó supervisar un proyecto en el que veríamos como diferentes variables climáticas ayudaban a predecir la distribución de los gatos monteses, algo que proporcionó resultados muy interesantes que adivinaban algunas de las tendencias descubiertas en la presente tesis y por lo que le estoy muy agradecido. Alrededor del mismo año, Jorge Falagán me convenció (gracias) para montar una especie de plataforma ciudadana en la que recopilábamos avistamientos y atropellos de gatos monteses en España. Conseguimos hacer acopio de una muy buena cantidad de datos gracias a la colaboración desinteresada de multitud de observadores. La lista es tan larga que es imposible mencionarlos a todos aquí, pero pueden leerse sus nombres en el blog creado para dicho fin (http://gatomontescantabrico.blogspot.com/). Además otras personas han contribuido generosamente con bastantes avistamientos de sus zonas habituales de campeo: Daniel Castañeda, Jonathan Rodríguez, Alberto Fernández Gil, Bernardino López, Iñigo Zuberogoitia, Ramón Pou, Jesús Sánchez, Javi Roces, Luis Fernández, José Díaz, Carlos Quirós o Luis Baragaño son algunos de ellos. Esta iniciativa ayudó a que la gente comenzase a vincular mi nombre a los gatos monteses. Muchas gracias a todos los que dedicaron tiempo en revisar cuadernos de campo, rellenar fichas y compartir la información. Parte ha sido utilizada para el desarrollo de esta tesis y alguna será utilizada en futuras investigaciones. Agradezco especialmente a aquellas personas que han contribuido con datos fundamentales para el estudio de la ecología reproductiva del gato montés, así como para el análisis de las interacciones entre zorros y gatos: Bernardino López, Rubén Barreda, Josechu Fernández, Ángel Rabanal, Pedro Víctor Albaladejo, Raúl López, Alberto Pola, Jonathan Rodríguez y Roberto Rodríguez.

Ante la imposibilidad a corto plazo de realizar la tesis doctoral, Ana y yo decidimos buscar oportunidades de trabajo en el extranjero y tras contactar a multitud de investigadores, nos ofrecieron la posibilidad de trabajar durante un año estudiando el comportamiento social en suricatas en la parte sudafricana del desierto del Kalahari. Trabajaríamos para el Kalahari Meerkat Project, un prestigioso proyecto de las Universidades de Cambridge y Zürich, dirigido por Tim Clutton-Brock y Marta Manser. Hicimos las maletas y en enero de 2015 aterrizamos en las finas arenas rojas del noroccidente sudafricano.

My time in South Africa allowed me to know from the inside how a prestigious and long-term scientific project works. However, the best memories are related with the daily field routines walking over the Kalahari dunes getting to see unique wildlife species, making such experiences one of the milestones of my life and my short scientific career. I got to know the hierarchy that rules scientific research, from field technicians like us, to PhD students, PostDocs, Project Managers and leader researchers. I also got familiar with the current scientific trend of “Publish or perish” in which the long-term persistence of a scientific project greatly depends on the amount and quality of scientific literature produced. Each of these information pills turned into thoughts on how to get funding to create a scientific project and do a PhD on the European wildcats of the Cantabrian Mountains. Thanks to the people that thought that we deserved to spend a year among meerkats, particularly to Constance Dubuc and Alecia Carter, which led the interview with us.

But if there is something fundamental from my Kalahari time is the quality of the people I met. Persons from very different countries and cultures, some of which I still consider very good friends: Miquel Torrents, Dave Seager, Nino Maag, Sam Lostrom, Elisa Sandoval, Young Ha Suh, Pauline Toni, Tim Vink, Louis Bliard, Gisela Sobral, Allison Brehm, Rita & Ryan, Rute Mendoça, Jack Thorley, Chris Duncan, Laura Meldrum, Julia Sutherland, Amy Cooke, Megan Soulsby, Jacob Brown, Sky Bischoff and a long list of people with who I shared great adventures. Once more, I am terrible at keeping up with all these relationships but thank you all guys for the many precious memories.

After a whole year volunteering for the University of Cambridge, the Zürich team studying dispersal in meerkats offered us the opportunity to stay another 9 months working as field managers of their project. Nino Maag, Gabriele Cozzi and Arpat Ozgul, thank you very much for trusting us and giving us the chance to keep learning. Furthermore, they offered the possibility to answer a scientific question on dispersing meerkats using the available information and try to publish a scientific paper on it. This was my first contact with scientific writing and I will always be grateful to Nino and Gabs for their incredible patience and persistence with my massive ignorance on how to write a paper at that time. This offer finally crystalized in one of our very first scientific publications. They also helped me to write a scientific proposal on a wildcat project, a document from which I used a considerable amount of information to later obtain the scholarship that allowed me to do the present thesis. Thank you guys, your help has been fundamental on my long path to do a PhD thesis on wildcats.

Tras casi dos años en Sudáfrica, la vuelta a España fue complicada pero pronto comencé a contactar con científicos que trabajaban en la Cordillera pensando en mantenerme en la rueda y seguir aprendiendo, y quien sabe, tal vez en algún momento conseguir hacer el doctorado. Isa Donoso, entonces estudiante de doctorado en Oviedo, me recomendó escribir a José Vicente López Bao, el cual trabajaba con carnívoros en paisajes humanizados, para ver si existía la posibilidad de que dirigiese mi doctorado. José Vicente me recibió encantado pero una vez más, la financiación brillaba por su ausencia. Justo en aquel momento (2017) salió la oferta de las Becas Severo Ochoa del Principado de Asturias, que precisamente en ese año ampliaba el plazo límite de tiempo transcurrido desde la finalización de la carrera, lo cual me permitía realizar la solicitud. Me puse entonces a redactar el proyecto de tesis, el cual trataría de responder cómo las actividades humanas afectan a los gatos monteses de la Cordillera Cantábrica, para lo cual utilizaría gran parte de los datos recogidos hasta ese momento. José Vicente me recomendó contactar e incluir a Paco Palomares en el proyecto como supervisor ya que él en ese momento estaba comenzando un proyecto a largo plazo de seguimiento de las poblaciones de gato montés en Montaña Palentina y contaba con mucha experiencia trabajando con felinos. Paco accedió encantado y realicé la solicitud de la beca. Muchísimas gracias a ambos por liaros la manta a la cabeza y apoyarme desde el principio, dándome total libertad para responder a mis preguntas y desarrollar mi propio proyecto. Gracias también por vuestros consejos en la escritura y redacción de los artículos y la tesis. No hay duda de que esta tesis no existiría sin vuestra determinación.

Mientras esperaba la resolución de la beca, contacté a otros investigadores para realizar colaboraciones, pero fueron María del Mar Delgado, Vincenzo Penteriani y Andrés Ordiz los que me incluyeron en el grupo de investigación del oso pardo cantábrico casi de inmediato y me hicieron por vez primera sentir parte de un proyecto científico en España. Muchísimas gracias por todo lo que me habéis enseñado y por contar conmigo para vuestras locuras oseras. Participé en el trabajo de campo y la redacción de artículos científicos estudiando las poblaciones de oso pardo cantábrico y esto me permitió adquirir más experiencia en el diseño experimental y la escritura de artículos científicos, además de poder hacer ciencia mientras disfrutaba de mis áreas de campeo habituales en compañía de Giulia, Alejandra y Enrique, doctorandos (hoy ya doctores) de Vincenzo.

En el transcurso de la espera surgió la oportunidad de realizar una estancia internacional en Escocia, estudiando las exiguas y malogradas poblaciones de gato montés que permanecen en el norte de las islas británicas. I then went to Scotland (once more accompanied by Ana) under the supervision of Kerry Kilshaw from the WildCRU (Oxford University) and Roo Campbell from what then was the Scottish Wildcat Action Program managed by the Scottish Natural Heritage (what is now called NatureScot). Thank you guys for hosting us and teaching us everything you knew from the difficult situation that Scottish wildcats are enduring, particularly regarding the role humans played in their functional extinction in the wild. Our work there consisted on: surveying previously unsurveyed areas potentially occupied by wildcats or hybrids using camera traps and collecting biological samples (hair and scats), participating in winter capture campaigns to GPS tag wildcat individuals, and basically understand the many factors that influence wildcat persistence in such environment (presence of domestic cats, human persecution, etc.). All those skills were incredibly useful during my posterior PhD research back in Spain. During this time we got to meet many friendly and dedicated people: Chris and Jenny (our landlords among the hay fields next to Bennachie in NE Scotland), Keri, Emma, and Alice (from the Scottish Wildcat Action) Jackie (from the Forestry Comission), Phil, Norman, Jill, Donna, and Dave (really motivated people working for the future of Scottish wildcats). Thank you very much for being so welcoming and patient with these couple of Spaniards.

Parte de mi tiempo en Escocia solapó con mis estudios de doctorado, ya que se resolvió la beca de forma favorable y me matriculé en el programa de doctorado en Biogeociencias de la Universidad de Oviedo. Tras volver a España, comenzó una campaña bastante intensa de trabajo de campo y bibliográfico: cientos de kilómetros recorridos recogiendo excrementos a lo largo de más de un año, decenas de horas de observaciones de gatos para aumentar el tamaño muestral de lo ya recogido acerca del efecto de las actividades humanas sobre el comportamiento de los gatos, y revisiones bibliográficas que permitiesen detectar tendencias a una escala mayor de los efectos de la agricultura sobre la ecología espacial de los gatos. Todo ello para responder las preguntas propuestas en cada uno de los capítulos.

For the analysis at European scale of variation in wildcat home-range size according to agricultural practices (Chapter 1) it was fundamental the role of the EUROWILDCAT working group. At the beginning I was trying to obtain the required information directly from the already published manuscripts, but José Vicente recommended contacting the researchers directly to have access to the raw spatial data and obtain more precise and realistic results. That is how I met Marco Heurich and Matteo Bastianelli, who quickly invited me to be a part of the EUROWILDCAT working group where most European experts on wildcats contribute either by providing data or publishing scientific papers. Thank you very much for including me in such a great collaborative project, the first chapter would have otherwise been impossible to obtain. Also thanks to all the authors that agreed on providing there data for my analysis. I had the chance to meet and change impressions with many European experts in the species (Pedro Monterroso, Stefano Anile, Miha Krofel, Saskia Jerosch, etc.), both virtually and in person through the annual meetings celebrated by the platform in different European countries.

En este capítulo también incluimos la información espacial correspondiente a un buen número de gatos monteses que pudimos capturar y equipar con collares GPS durante el transcurso de mi tesis. Paco y el resto del equipo vinculado a la Estación Biológica de Doñana (Eloy Revilla, Fernando Jubete, Fermín Urra, Jacinto Román, Juan Carlos Rivilla, Javier Calzada…) habían perfeccionado las técnicas de captura de individuos en la Montaña Palentina con bastante éxito. Aplicando dichas técnicas en el occidente cantábrico (gracias Paco por animarte a capturar individuos en este rincón agreste de la Cordillera) conseguimos capturar tres ejemplares en menos de un mes, dos hembras y un macho, todos en la misma trampa. Contamos además con la colaboración del personal del Ministerio para la Transición Ecológica y el

Reto Demográfico y TRAGSATEC S.A. que estaban en ese momento desarrollando campañas de captura de mesocarnívoros dentro del marco del proyecto de conservación del urogallo cantábrico. En el caso concreto de los gatos monteses, estaban interesados en marcar individuos y liberarlos en el lugar de captura. Gracias al esfuerzo de estas cuadrillas pudimos marcar con GPS a otros nueve ejemplares de gato montés. Quiero agradecer al personal que participó en esas campañas por haberme pegado un toque cada vez que un gato montés aparecía en sus trampas, posibilitando que equipásemos al individuo con una unidad GPS. En concreto Josep Piqué, Manuel Pina, Joselu y Adrián. Muchísimas gracias a Elena (Clínica Veterinaria Elena Alonso), la veterinaria encargada del manejo siempre cariñoso e impecable de los ejemplares para la obtención de muestras, toma de medidas e instalación del collar de seguimiento, casi siempre en domingo o festivos ya que daba la sensación de que los gatos preferían esas fechas para husmear las trampas. También agradezco a la Junta de Castilla y León y el Principado de Asturias la expedición de los permisos correspondientes para el manejo y captura de dichos ejemplares y al personal de Patrimonio Natural que nos informó de un ejemplar de gato capturado en sus trampas y que pasó a formar parte del grueso de individuos estudiados. Pese a nuestras enormes diferencias en lo que respecta a la utilidad de la captura de mesocarnívoros para mejorar el estado de conservación del urogallo, es indiscutible que sin su disponibilidad para colaborar con nosotros no habríamos conseguido un tamaño muestral tan representativo, algo por lo que les estoy muy agradecido.

Los datos de seguimiento GPS proporcionaron una imagen única del uso espacial que los gatos hacen de los paisajes ganaderos en la Cordillera Cantábrica. Poder asomarme a la aplicación cada mañana para ver las deambulaciones de los individuos es algo que había imaginado mucho tiempo, ya que los gatos se veían en los prados pero poco se sabía de qué zonas utilizaban fuera de los mismos. Aluciné con la capacidad de movimiento de estos bichos, haciendo excursiones considerables durante la época reproductora o utilizando hábitats relativamente degradados como cielos abiertos abandonados. Además, uno de los ejemplares marcados nos permitió asomarnos al comportamiento de “caching” descrito en el capítulo 6 y que no había sido descrito con anterioridad en la especie.

En cuanto al capítulo 2, centrado en analizar cómo la presencia de prados ganaderos influye en la dieta de los gatos monteses, el trabajo de campo implicó un pateo considerable de sendas y caminos repetidos estacionalmente apañando excrementos de la especie por algunos valles y crestas que ya conocía y otros que nunca había visitado. El sueño de cualquier biólogo de campo. Hay pocas sensaciones comparables al pico de dopamina liberado al hallar aquello que buscas, algo que sentía con cada excremento encontrado. Como siempre, mi padre y Ana estuvieron presentes en la mayoría de jornadas recorriendo trochas en busca de cagadas. Gracias al Principado de Asturias y a la Junta de Castilla y León por los permisos correspondientes para la recogida de estas muestras. Todos esos excrementos fueron almacenados, secados y posteriormente desmenuzados y analizados. Tarea en la que me ayudo Juan Carlos Rivilla, técnico de la EBD. Muchas gracias.

La intención era determinar el número de individuos de cada presa en cada excremento, algo que habría sido imposible sin las cualidades (casi sobrehumanas) de Jacinto Román en la identificación de las piezas dentales concretas, la especie a la que correspondían e incluso la edad del individuo mirando los dientes y huesos quebrados que aparecían en los excrementos. Si esta tarea ya es heroica en la egagrópila de una rapaz que traga enteras a sus presas haciendo que los restos aparezcan bastante enteros, imaginaos en el excremento de gato, los cuales mastican y machacan muy bien a sus presas antes de tragárselas. Muchas gracias Jacinto, por tu paciencia identificando y contando dientes y por compartir parte de tu conocimiento. Los datos recogidos por mí se combinaron con aquellos recogidos por las personas que habían creado el proyecto de seguimiento de gatos en Montaña Palentina: Paco, Fermín, Eloy, Javitxu, Jacinto, Fernando, Juan Carlos…y también con las estimas de abundancia de rata topera que el mismo equipo llevaba desarrollando desde hacía años, lo cual permitió realizar una aproximación de como el consumo de presas podía relacionarse con la abundancia de las mismas haciendo que el trabajo final englobase una escala mucho mayor y proporcionase resultados mucho más completos e interesantes. Gracias chicos por esas jornadas de campo en Montaña Palentina, facilitando cama, viandas y envidiables batallitas camperas en el porche de San Felices. Además, Juan Seijas estuvo dispuesto desde el principio a colaborar con los datos que lleva tantos años recogiendo acerca de la producción de montanera (bellota y hayuco) a lo largo y ancho de la Cordillera Cantábrica, lo cual fue fundamental para estimar fluctuaciones poblacionales en roedores forestales.

En cuanto al capítulo 3, centrado en los efectos de las actividades humanas sobre el comportamiento de los gatos monteses, he perdido la cuenta de las horas de campo invertidas para obtener un tamaño muestral representativo que permita obtener resultados con cierta robustez. Pero sarna con gusto no pica. En ese sentido el trabajo de observación fue muchas veces repartido con mi padre para aumentar la eficacia en la obtención de datos. Incluso el peso de dicho trabajo recayó de forma completa sobre mi padre mientras yo me encontraba en Sudáfrica y Escocia. Papá, es imposible agradecerte dicho esfuerzo lo suficiente. Ana también me acompañó en innumerables ocasiones pasando frío y calor hasta que los gatos decidían dar la cara. Estas valiosas observaciones de la especie recogidas durante años, permitieron conocer aspectos poco antes documentados de su vida como las interacciones con otros mesocarnívoros como los zorros, su éxito en la caza o parte de su ecología reproductiva, información que forma parte de varios capítulos de esta tesis. Además sirvieron para estudiar cambios en el tiempo dedicado a diferentes comportamientos en función de la presencia de algunas causas humanas de molestia, análisis que compone el grueso del capítulo 3. La acumulación de horas de observación te permite familiarizarte con los diferentes individuos, algunos de los cuales seguí durante muchos años hasta que dejaron de asomarse a mi telescopio. Gracias a ello llegué a apreciar las diferencias en su comportamiento y personalidad. Aunque soy bastante solitario en lo que respecta al campo, buenos amigos me acompañaron en algún momento durante dichos avistamientos: Dani y Ulpi, David Álvarez, Ángel Rabanal, Jon Morant, Luis Miguel Prieto o Ezequiel Martínez. A este último le quiero agradecer especialmente su insistencia en sacarme al campo en los momentos más complicados de la tesis, contagiando pasión y entusiasmo por cualquier forma de vida en estas húmedas montañas. Me has ayudado a mantenerme un poco más cuerdo.

Durante el desarrollo de la tesis también tuve la oportunidad de participar en el primer Sondeo Nacional de Gato Montés organizado por Emilio Virgós y José María Gil, muestreando una cuadrícula de 2000 hectáreas dentro de mi zona habitual de campeo y que me permitió obtener datos realistas sobre la abundancia de gatos monteses. Gracias por contar conmigo para dicho proyecto.

Multitud de personas no mencionadas hasta ahora han sido fundamentales en la finalización de la tesis, proporcionando compañía y estabilidad emocional. Gracias a mi hermano Víctor, mi cuñada Sandra y mis sobrinos

Álvaro y Laura, y en general a toda mi familia materna y paterna, y también a mi suegra Natuca por preocuparos por mí y preguntarme cómo llevaba la tesis. A mis buenos amigos David y Vero, gracias por las tardes de calecho "arreglando el mundo" y probando juegos de mesa. A científicos de otros ámbitos que han contado conmigo para trabajos de campo ajenos a los gatos que facilitaban la desconexión mental de un tema tan absorbente como es un doctorado. Entre otros, gracias a David César Manceñido y los muestreos de mariposas nocturnas, o Fernando Jubete (y el eBMS España) y los sondeos de mariposas diurnas. A mi psicóloga Judith que me enseñó a conocerme y a gestionar mejor la incertidumbre. A nuestros vecinos de Mataotero, por compartir vuestras vidas con nosotros durante estos últimos años y ayudarme a centrar mis pensamientos en algo que no fuese la tesis, aunque fuese brevemente. A todos los bicheros con los que en algún momento pude compartir avistamientos y que se me haya olvidado mencionar, espero que recordéis esos momentos. Gracias también a Luis Alberto Ramos Franco por la digitalización de las ilustraciones incluidas en esta tesis y la elaboración de la magnífica ilustración digital de la portada. Gracias también a los habitantes de las comarcas de Laciana y Alto Sil, Omaña, Babia y Luna en León y Degaña, Cangas del Narcea, Somiedo y Teverga en Asturias con los que haya coincidido durante el trabajo de campo y con los que he intercambiado interesantes conversaciones acerca de los gatos y otras fieras de estas montañas.

Por último y aunque no lo leerán, gracias a los gatos monteses, su presencia ha sido una constante en mi vida, tanto en los mejores como en los peores momentos. No obstante, han tenido la capacidad de que durante nuestros encuentros todo lo demás dejase de importar y mi energía se centrase en observarlos y aprender de ellos. Me han regalado momentos únicos, íntimos y rara vez documentados por los que me siento muy afortunado. Gatas alimentando a sus crías e interaccionando con ellas en los cubiles; encuentros con zorros, martas e incluso osos; infinitos lances a presas; encuentros durante el celo; distintos comportamientos de marcaje… He disfrutado mucho mientras os buscaba, observaba y aprendía de vosotros. Deseo enormemente que esta tesis contribuya, aunque sea mínimamente, a vuestro conocimiento y conservación.

Wildcat. Illustration by Samantha Lostrom.

References

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle, in: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akadémiai Kiadó, Budapest., pp. 268–281.

Alkemade, R., Reid, R.S., Van Den Berg, M., De Leeuw, J., Jeuken, M., 2013. Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. Proc. Natl. Acad. Sci. U. S. A. 110, 20900–20905. https://doi.org/10.1073/pnas.1011013108

Allan, J.R., Venter, O., Watson, J.E.M., 2017. Temporally inter-comparable maps of terrestrial wilderness and the Last of the Wild. Sci. Data 4, 1–8. https://doi.org/10.1038/sdata.2017.187

Almeida, D., Grossman, G.D., 2012. Utility of direct observational methods for assessing competitive interactions between non-native and native freshwater fishes. Fish. Manag. Ecol. 19, 157–166. https://doi.org/10.1111/j.1365-2400.2012.00847.x

Andersson, M., Erlinge, S., 1977. Influence of Predation on Rodent Populations. Oikos 29, 591. https://doi.org/10.2307/3543597

Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R., Segerström, P., 2006. Survival rates and causes of mortality in Eurasian lynx (Lynx lynx) in multi-use landscapes. Biol. Conserv. 131, 23–32. https://doi.org/10.1016/j.biocon.2006.01.025

Anile, S., Bizzarri, L., Lacrimini, M., Sforzi, A., Ragni, B., Devillard, S., 2017. Home-range size of the European wildcat (Felis silvestris silvestris): A report from two areas in Central Italy. Mammalia 82, 1–11. https://doi.org/10.1515/mammalia-2016-0045

Anile, S., Devillard, S., 2018. Camera-trapping provides insights into adult sex ratio variability in felids. Mamm. Rev. 48, 168–179. https://doi.org/10.1111/mam.12120

Anile, S., Devillard, S., Ragni, B., Rovero, F., Mattucci, F., Valvo, M. Lo, 2019. Habitat fragmentation and anthropogenic factors affect wildcat Felis silvestris silvestris occupancy and detectability on Mt Etna. Wildlife Biol. 2019, 1–13. https://doi.org/10.2981/wlb.00561

Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N(e). Biol. Conserv. 95, 303–315. https://doi.org/10.1016/S0006-3207(00)00037-9

Apostolico, F., Vercillo, F., La Porta, G., Ragni, B., 2016. Long-term changes in diet and trophic niche of the European wildcat (Felis silvestris silvestris) in Italy. Mammal Res. 61, 109–119. https://doi.org/10.1007/s13364-015-0255-8

Arenillas, M., Cobos, G., Navarro, J., 2008. Datos sobre la nieve y los glaciares en las cordilleras españolas. El programa ERHIN (1984–2008). Madrid.

Arlettaz, R., Nusslé, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P., Genoud, M., 2015. Disturbance of wildlife by outdoor winter recreation: Allostatic stress response and altered activity-energy budgets. Ecol. Appl. 25, 1197–1212. https://doi.org/10.1890/14-1141.1

Aronsson, M., Low, M., López-Bao, J. V., Persson, J., Odden, J., Linnell, J.D.C., Andrén, H., 2016. Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. Ecol. Evol. 6, 2957–2967. https://doi.org/10.1002/ece3.2032

Atkinson, A.C., 1994. Fast very robust methods for the detection of multiple outliers. J. Am. Stat. Assoc. 89, 1329–1339. https://doi.org/10.1080/01621459.1994.10476872

Balme, G.A., Miller, J.R.B., Pitman, R.T., Hunter, L.T.B., 2017. Caching reduces kleptoparasitism in a solitary, large felid. J. Anim. Ecol. 86, 634–644. https://doi.org/10.1111/1365-2656.12654

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2009.08.002

Barja, I., Silvan, G., Illera, J.C., 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats : Management implications for species conservation. Wildl. Res. 39, 532–539. https://doi.org/10.1071/WR10218

Barton, K., 2015. MuMIn: Multi-model inference. R Packag. version 1.15.1. 1.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Arild Høgda, K., Gaillard, J.-M., 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? Ecography (Cop.). 32, 683–691. https://doi.org/10.1111/j.1600-0587.2009.05712.x

Bastianelli, M.L., Premier, J., Herrmann, M., Anile, S., Monterroso, P., Kuemmerle, T., Dormann, C.F., Streif, S., Jerosch, S., Götz, M., Simon, O., Moleón, M., Gil-Sánchez, J.M., Biró, Z., Dekker, J., Severon, A., Krannich, A., Hupe, K., Germain, E., Pontier, D., Janssen, R., Ferreras, P., Díaz-Ruiz, F., López-Martín, J.M., Urra, F., Bizzarri, L., Bertos-Martín, E., Dietz, M., Trinzen, M., Ballesteros-Duperón, E., Barea-Azcón, J.M., Sforzi, A., Poulle, M.-L., Heurich, M., 2021. Survival and cause-specific mortality of European wildcat (Felis silvestris) across Europe. Biol. Conserv. 261, 109239. https://doi.org/10.1016/j.biocon.2021.109239

Bateman, P.W., Fleming, P.A., 2012. Big city life: carnivores in urban environments. J. Zool. 287, 1–23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. lme4: Linear mixed-effects models using Eigen and S4. J. Stat. Softw. 67, 1–48.

Bauer, J.W., Logan, K.A., Sweanor, L.L., Boyce, W.M., 2005. Scavenging Behavior in Puma. Southwest. Nat. 50, 466–471. https://doi.org/10.1894/0038-4909(2005)050[0466:sbip]2.0.co;2

Beale, C.M., Monaghan, P., 2004. Behavioural responses to human disturbance: A matter of choice? Anim. Behav. 68, 1065–1069. https://doi.org/10.1016/j.anbehav.2004.07.002

Beasley, J.C., Devault, T.L., Rhodes, O.E., 2007. Home-Range Attributes of Raccoons in a Fragmented Agricultural Region of Northern Indiana. J. Wildl. Manage. 71, 844–850. https://doi.org/10.2193/2006-022

Beaufoy, G., 1998. The EU habitats directive in Spain: Can it contribute effectively to the conservation of extensive agroecosystems? J. Appl. Ecol. 35, 974–978. https://doi.org/10.1111/j.1365-2664.1998.tb00017.x

Bednekoff, P.A., Lima, S.L., 1998. Randomness, chaos and confusion in the study of antipredator vigilance. Trends Ecol. Evol. 13, 284–287. https://doi.org/10.1016/S0169-5347(98)01327-5

Bellamy, P.E., Shore, R.F., Ardeshir, D., Treweek, J.R., Sparks, T.H., 2000. Road verges as habitat for small mammals in Britain. Mamm. Rev. 30, 131–139. https://doi.org/10.1046/j.1365-2907.2000.00061.x

Ben-David, M., Blundell, G.M., Kern, J.W., Maier, J.A.K., Brown, E.D., Jewett, S.C., 2005. Communication in river otters: creation of variable resource sheds for terrestrial communities. Ecology 86, 1331–1345. https://doi.org/10.1890/04-0783

Benayas, J.M.R., Martins, A., Nicolau, J.M., Schulz, J.J., 2007. Abandonment of agricultural land: An overview of drivers and consequences. CABI Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. https://doi.org/10.1079/PAVSNNR20072057

Benedek, A.M., Sîrbu, I., 2018. Responses of small mammal communities to environment and agriculture in a rural mosaic landscape. Mamm. Biol. 90, 55–65. https://doi.org/10.1016/j.mambio.2018.02.008

Benoist, S., Garel, M., Cugnasse, J.-M., Blanchard, P., 2013. Human Disturbances, Habitat Characteristics and Social Environment Generate Sex-Specific Responses in Vigilance of Mediterranean Mouflon. PLoS One 8, e82960. https://doi.org/10.1371/journal.pone.0082960

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P., Saltz, D., 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behav. Ecol. 22, 236–239. https://doi.org/10.1093/beheco/arq224

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biol. Lett. 3, 620–623. https://doi.org/10.1098/rsbl.2007.0415

Beugin, M.P., Leblanc, G., Queney, G., Natoli, E., Pontier, D., 2016. Female in the inside, male in the outside: insights into the spatial organization of a European wildcat population. Conserv. Genet. 17, 1405–1415. https://doi.org/10.1007/s10592-016-0871-0

Biró, Z., Szemethy, L., Heltai, M., 2004. Home range sizes of wildcats (Felis silvestris) and feral domestic cats (Felis silvestris f. catus) in a hilly region of Hungary. Mamm. Biol. 69, 302–310. https://doi.org/10.1078/1616-5047-00149

Bischoff-Mattson, Z., Mattson, D., 2009. Effects of Simulated Mountain Lion Caching on Decomposition of Ungulate Carcasses. West. North Am. Nat. 69, 343–350. https://doi.org/10.3398/064.069.0308

Bjørvik, L.M., Dale, S., Hermansen, G.H., Munishi, P.K.T., Moe, S.R., 2015. Bird flight initiation distances in relation to distance from human settlements in a Tanzanian floodplain habitat. J. Ornithol. 156, 239–246. https://doi.org/10.1007/s10336-014-1121-1

Blanco-Fontao, B., Quevedo, M., Obeso, J.R., 2011. Abandonment of traditional uses in mountain areas: Typological thinking versus hard data in the Cantabrian Mountains (NW Spain). Biodivers. Conserv. 20, 1133–1140. https://doi.org/10.1007/s10531-011-0016-1

Bland, L.M., Collen, B., Orme, C.D.L., Bielby, J., 2015. Predicting the conservation status of data-deficient species. Conserv. Biol. 29, 250–259. https://doi.org/10.1111/cobi.12372

Bonnot, N.C., Hewison, A.J.M., Morellet, N., Gaillard, J.M., Debeffe, L., Couriot, O., Cargnelutti, B., Chaval, Y., Lourtet, B., Kjellander, P., Vanpé, C., 2017. Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward. Anim. Behav. 124, 35–46. https://doi.org/10.1016/j.anbehav.2016.11.031

Börger, L., Dalziel, B.D., Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol. Lett. 11, 637–650. https://doi.org/10.1111/j.1461-0248.2008.01182.x

Boutros, D., Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Molinari-Jobin, A., Capt, S., Güntert, M., Breitenmoser, U., 2007. Characterisation of Eurasian lynx Lynx lynx den sites and kitten survival. Wildlife Biol. 13, 417–429. https://doi.org/10.2981/0909-6396(2007)13[417:COELLL]2.0.CO;2

Brieger, F., Kämmerle, J.L., Hagen, R., Suchant, R., 2022. Behavioural reactions to oncoming vehicles as a crucial aspect of wildlife-vehicle collision risk in three common wildlife species. Accid. Anal. Prev. 168, 106564. https://doi.org/10.1016/j.aap.2021.106564

Brighten, A.L., Burnside, R.J., 2019. Insights into the feeding ecology of and threats to sand cat Felis margarita Loche, 1858 /Mammalia: Carnivora: Felidae) in the Kyzylkum Desert , Uzbekistan. J. Threat. Taxa 11, 13492–13496. https://doi.org/10.11609/jott.4445.11.4.13492-13496

Briner, T., Nentwig, W., Airoldi, J.P., 2005. Habitat quality of wildflower strips for common voles (Microtus arvalis) and its relevance for agriculture. Agric. Ecosyst. Environ. 105, 173–179. https://doi.org/10.1016/j.agee.2004.04.007

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W., Macdonald, D.W., 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? J. Anim. Ecol. 82, 1098–1105. https://doi.org/10.1111/1365-2656.12077@10.1111/(ISSN)1365-2664.INTERNATIONAL

Broekhuis, F., Madsen, E.K., Klaassen, B., 2019. Predators and pastoralists: how anthropogenic pressures inside wildlife areas influence carnivore space use and movement behaviour. Anim. Conserv. 22, 404–416. https://doi.org/10.1111/acv.12483

Brooke, Z.M., Bielby, J., Nambiar, K., Carbone, C., 2014. Correlates of Research Effort in Carnivores: Body Size, Range Size and Diet Matter. PLoS One 9, e93195. https://doi.org/10.1371/journal.pone.0093195

Brooks, M., Kristensen, K., van Bentham, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. Package “glmmTMB,” The R Journal.

Bruskotter, J.T., Vucetich, J.A., Gilbert, S.L., Carter, N.H., George, K.A., 2022. Tragic trade-offs accompany carnivore coexistence in the modern world. Conserv. Lett. 15, e412841. https://doi.org/10.1111/conl.12841

Buschke, F.T., Coetzer, C., Pinceel, T., Mehlomakhulu, Z., Moreels, N., du Randt, L., Vanschoenwinkel, B., 2020. Mountains and rocky outcrops as ecological refuges in a high biodiversity working landscape. Biol. Conserv. 250, 108759. https://doi.org/10.1016/j.biocon.2020.108759

Butler, S.J., Gillings, S., 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. Ibis (Lond. 1859). 146, 123–130. https://doi.org/10.1111/j.1474-919X.2004.00352.x

Cappo, M., De'ath, G., Speare, P., 2007. Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. Mar. Ecol. Prog. Ser. 350, 209–221. https://doi.org/10.3354/meps07189

Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M. V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. Remote Sens. Ecol. Conserv. 3, 109–122. https://doi.org/10.1002/rse2.48

Caravaggi, A., Burton, A.C., Clark, D.A., Fisher, J.T., Grass, A., Green, S., Hobaiter, C., Hofmeester, T.R., Kalan, A.K., Rabaiotti, D., Rivet, D., 2020. A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. Conserv. Sci. Pract. 2, e239. https://doi.org/10.1111/csp2.239

Carrete, M., Tella, J.L., 2010. Individual consistency in flight initiation distances in burrowing owls: A new hypothesis on disturbanceinduced habitat sele. Biol. Lett. 6, 167–170. https://doi.org/10.1098/rsbl.2009.0739

Carter, S.P., Delahay, R.J., Smith, G.C., Macdonald, D.W., Riordan, P., Etherington, T.R., Pimley, E.R., Walker, N.J., Cheeseman, C.L., 2007. Culling-induced social perturbation in Eurasian badgers Meles meles and the management of TB in cattle: An analysis of a critical problem in applied ecology. Proc. R. Soc. B Biol. Sci. 274, 2769–2777. https://doi.org/10.1098/rspb.2007.0998

Cavia, R., Cueto, G.R., Suárez, O.V., 2009. Changes in rodent communities according to the landscape structure in an urban ecosystem. Landsc. Urban Plan. 90, 11–19. https://doi.org/10.1016/j.landurbplan.2008.10.017

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Sci. Adv. 1. https://doi.org/10.1126/sciadv.1400253

Červený, V., Okarma, H., 2002. Caching prey in trees by Eurasian lynx. Acta Theriol. (Warsz). 47, 505–508.

Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balečiauskas, L., Balys, V., Bedõ, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potoečnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science (80-.). 346, 1517–1519. https://doi.org/10.1126/science.1257553

Chase, A.F., Chase, D.Z., 2016. Urbanism and Anthropogenic Landscapes. Annu. Rev. Anthropol. 45, 361–376. https://doi.org/10.1146/annurev-anthro-102215-095852

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear. PLoS One 7. https://doi.org/10.1371/journal.pone.0050611

Coffin, A.W., 2007. From roadkill to road ecology: A review of the ecological effects of roads. J. Transp. Geogr. 15, 396–406. https://doi.org/10.1016/j.jtrangeo.2006.11.006

Cousineau, D., Chartier, S., 2010. Outliers detection and treatment: a review. Int. J. Psychol. Res. 3, 58–67. https://doi.org/10.21500/20112084.844

Cramer, M.J., Willig, M.R., 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sand-shinnery-oak landscape. J. Mammal. 83, 743–753. https://doi.org/10.1644/1545-1542(2002)083<0743:HHHAAR>2.0.CO;2

Creel, S., Creel, N.M., 1996. Limitation of African Wild Dogs by Competition with Larger Carnivores. Conserv. Biol. 10, 526–538. https://doi.org/10.1046/j.1523-1739.1996.10020526.x

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B Biol. Sci. 366, 2642–2651. https://doi.org/10.1098/rstb.2011.0120

Cui, Q., Ren, Y., Xu, H., 2021. The Escalating Effects of Wildlife Tourism on Human–Wildlife Conflict. Animals 11, 1378. https://doi.org/10.3390/ani11051378

Cumming, G.S., Buerkert, A., Hoffmann, E.M., Schlecht, E., Von Cramon-Taubadel, S., Tscharntke, T., 2014. Implications of agricultural transitions and urbanization for ecosystem services. Nature. https://doi.org/10.1038/nature13945

Daniels, M.J., Wright, T.C.M., Bland, K.P., Kitchener, A.C., 2002. Seasonality and reproduction in wild-living cats in Scotland. Acta Theriol. (Warsz). 47, 73–84. https://doi.org/10.1007/BF03193568

Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. Science (80-.). 349, 858–860. https://doi.org/10.1126/science.aac4249

Davies, T.W., Bennie, J., Inger, R., Ibarra, N.H., Gaston, K.J., 2013. Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? Glob. Chang. Biol. 19, 1417–1423. https://doi.org/10.1111/gcb.12166

De’ath, G., 2007. The mvpart package. http//cran. r-project. org/doc/packages/mvpart. pdf.

De’ath, G., 2002. Multivariate regression trees: A new technique for modeling species-environment relationships. Ecology 83, 1105–1117. https://doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2

De’ath, G., Fabricius, K.E., 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

de Azevedo, F.C.C., Murray, D.L., 2007. Spatial organization and food habits of jaguars (Panthera onca) in a floodplain forest. Biol. Conserv. 137, 391–402. https://doi.org/10.1016/j.biocon.2007.02.022

Delattre, P., Giraudoux, P., 2009. Le campagnol terrestre. Prévention et contrôle des populations. Éditions Quae, Versailles, Cedex, France.

Delibes, M., 1980. El lince ibérico. Ecología y comportamiento alimenticios en el Coto Doñana, Huelva. Doñana Acta Vertebr. 7–3, 1–128.

Devillard, S., Jombart, T., Léger, F., Pontier, D., Say, L., Ruette, S., 2014. How reliable are morphological and anatomical characters to distinguish European wildcats, domestic cats and their hybrids in France? J. Zool. Syst. Evol. Res. 52, 154–162. https://doi.org/10.1111/jzs.12049

Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, J.L., María López-Martín, J., Ferreira, C., Ferreras, P., 2013. Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. Mamm. Rev. 43, 59–70. https://doi.org/10.1111/j.1365-2907.2011.00206.x

DiGangi, B.A., Graves, J., Budke, C.M., Levy, J.K., Tucker, S., Isaza, N., 2020. Assessment of body weight for age determination in kittens. J. Feline Med. Surg. 22, 322–328. https://doi.org/10.1177/1098612X19844846

Do Linh San, E., Sato, J.J., Belant, J.L., Somers, M.J., 2022. The World's Small Carnivores: Definitions, Richness, Distribution, Conservation Status, Ecological Roles, and Research Efforts., in: Small Carnivores: Evolution, Ecology, Behaviour, and Conservation. Wiley, pp. 1–38. https://doi.org/10.1002/9781118943274.ch1

Dobrovolski, R., Diniz-Filho, J.A.F., Loyola, R.D., De Marco Júnior, P., 2011. Agricultural expansion and the fate of global conservation priorities. Biodivers. Conserv. 20, 2445–2459. https://doi.org/10.1007/s10531-011-9997-z

Doherty, T.S., Driscoll, D.A., 2018. Coupling movement and landscape ecology for animal conservation in production landscapes. Proc. R. Soc. B Biol. Sci. 285. https://doi.org/10.1098/rspb.2017.2272

Doherty, T.S., Fist, C.N., Driscoll, D.A., 2019. Animal movement varies with resource availability, landscape configuration and body size: a conceptual model and empirical example. Landsc. Ecol. 34, 603–614. https://doi.org/10.1007/s10980-019-00795-x

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Doxa, A., Bas, Y., Paracchini, M.L., Pointereau, P., Terres, J.-M., Jiguet, F., 2010. Low-intensity agriculture increases farmland bird abundances in France. J. Appl. Ecol. 47, 1348–1356. https://doi.org/10.1111/j.1365-2664.2010.01869.x

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:saaist]2.0.co;2

Duhamel, R., Quéré, J.P., Delattre, P., Giraudoux, P., 2000. Landscape effects on the population dynamics of the fossorial form of the water vole (Arvicola terrestris sherman). Landsc. Ecol. 15, 89–98. https://doi.org/10.1023/A:1008173508817

Edwards, M.A., Derocher, A.E., Nagy, J.A., 2013. Home Range Size Variation in Female Arctic

Grizzly Bears Relative to Reproductive Status and Resource Availability. PLoS One 8, 1–11. https://doi.org/10.1371/journal.pone.0068130

Edwards, M.S., Gaffney, M., Bray, R.E., 2001. Influence Of Fiber Source On Apparent Digestibility, Rate Of Passage And Fecal Consistency In Small Felids Fed A Beefbased Carnivore Diet. Proc. Am. Zoo Aquarium Assoc. Nutr. Advis. Group, Fourth Conf. Zoo Wildl. Nutr. 71–80.

Ekroos, J., Heliölä, J., Kuussaari, M., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. J. Appl. Ecol. 47, 459–467. https://doi.org/10.1111/j.1365-2664.2009.01767.x

Espinoza, M., Cappo, M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2014. Quantifying shark distribution patterns and species-habitat associations: Implications of Marine Park zoning. PLoS One 9, e106885. https://doi.org/10.1371/journal.pone.0106885

ESRI, 2012. ArcGIS® Software 10.1.

Estes, J.A., Tinker, M.T., Williams, T.M., Doak, D.F., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science (80-.). https://doi.org/10.1126/science.282.5388.473

Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., York, E.C., 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125, 258–270. https://doi.org/10.1007/s004420000448

Fernández, N., Palomares, F., 2000. The selection of breeding dens by the endangered Iberian lynx (Lynx pardinus): Implications for its conservation. Biol. Conserv. 94, 51–61. https://doi.org/10.1016/S0006-3207(99)00164-0

Fernández, N., Palomares, F., Delibes, M., 2002. The use of breeding dens and kitten development in the Iberian lynx (Lynx pardinus). J. Zool. 258, 1–5. https://doi.org/10.1017/S0952836902001140

Ferreira, A.S., Peres, C.A., Bogoni, J.A., Cassano, C.R., 2018. Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global-scale analysis. Mamm. Rev. 48, 312–327. https://doi.org/10.1111/mam.12137

Ferreras, P., Jiménez, J., Díaz-Ruiz, F., Tobajas, J., Alves, P.C., Monterroso, P., 2021. Integrating multiple datasets into spatially-explicit capture-recapture models to estimate the abundance of a locally scarce felid. Biodivers. Conserv. 30, 4317–4335. https://doi.org/10.1007/s10531-021-02309-1

Ferretti, F., Lazzeri, L., Sforzi, A., 2022. Spatio-temporal patterns of the European wildcat in a Mediterranean coastal area. Mamm. Biol. 1–9. https://doi.org/10.1007/s42991-022-00317-4

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., Wehrden, H., 2014. Land Sparing Versus Land Sharing: Moving Forward. Conserv. Lett. 7, 149–157. https://doi.org/10.1111/conl.12084

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16, 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Fleming, C.H., Calabrese, J.M., 2017. A new kernel density estimator for accurate home-range and species-range area estimation. Methods Ecol. Evol. 8, 571–579. https://doi.org/10.1111/2041-210X.12673

Fleming, C.H., Fagan, W.F., Mueller, T., Olson, K.A., Leimgruber, P., Calabrese, J.M., 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96, 1182–1188.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Liira, J., Morales, M.B., Oñate, J.J., Pärt, T., Wolfgang, W., Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M.B., Onate, J.J., Part, T., Weisser, W.W., Winqvist, C., Thies, C., Tscharntke, T., 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants , carabids , and birds Weisser , Camilla Winqvist , Carsten Thies and Teja Tscharntke Published by : Wiley on behalf of the Ecological Society of America St. Ecol. Appl. 21, 1772–1781.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Ecol. Soc. 6. https://doi.org/10.5751/es-00404-060111

García, D., Quevedo, M., Obeso, J.R., Abajo, A., 2005. Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). For. Ecol. Manage. 208, 29–43. https://doi.org/10.1016/j.foreco.2004.10.071

García, D., Suárez-Seoane, S., Jiménez-Alfaro, B., Álvarez, D., Álvarez-Álvarez, P., Álvarez-Martínez, J.M., Barquín, J., Calvo, L., Illera, J.C., Laiolo, P., Pérez-Silos, I., Quevedo, M., Roces-Díaz, J.V., Santín, C., 2023. Passive rewilding in the Cantabrian Mountain Range: scientific basis and challenges for socio-ecological sustainability. Ecosistemas 32. https://doi.org/10.7818/ECOS.2507

García, F.J., 2006. El gato montés Felis silvestris Schreber, 1775. Galemys 16, 1–14.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science (80-.). 360, 1232–1235. https://doi.org/10.1126/science.aar7121

Germain, E., Benhamou, S., Poulle, M.L., 2008. Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. J. Zool. 276, 195–203. https://doi.org/10.1111/j.1469-7998.2008.00479.x

Gerngross, P., Ambarli, H., Angelici, F.M., Anile, S., Campbell, R., Ferreras, P., Gil-Sanchez, J.M., Götz, M., Jerosch, S., Mengulluoglu, D., Monterroso, P., Zlatanova, D., 2022. Felis silvestris, The IUCN Red List of Threatened Species 2021.

Gil-Sánchez, J.M., Barea-Azcón, J.M., Jaramillo, J., Herrera-Sánchez, F.J., Jiménez, J., Virgós, E., 2020. Fragmentation and low density as major conservation challenges for the southernmost populations of the European wildcat. PLoS One 15, e0227708. https://doi.org/10.1371/journal.pone.0227708

Gil-Sánchez, J.M., Jaramillo, J., Barea-Azcón, J.M., 2015. Strong spatial segregation between wildcats and domestic cats may explain low hybridization rates on the Iberian Peninsula. Zoology 118, 377–385. https://doi.org/10.1016/j.zool.2015.08.001

Gil, M.A., Emberts, Z., Jones, H., St. Mary, C.M., 2017. Social information on fear and food drives animal grouping and fitness. Am. Nat. 189, 227–241. https://doi.org/10.1086/690055

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biol. Conserv. 97, 265–268. https://doi.org/10.1016/S0006-3207(00)00002-1

Giraudoux, P., Antonietti, J.-P., Beale, C., Pleydell, D., Treglia, M., 2018. “pgirmess”: Spatial analysis and data mining for field ecologists. R Packag. version 1.7.0 64.

Giraudoux, P., Delattre, P., Habert, M., Quéré, J.P., Deblay, S., Defaut, R., Duhamel, R., Moissenet, M.F., Salvi, D., Truchetet, D., 1997. Population dynamics of fossorial water vole (Arvicola terrestris scherman): A land use and landscape perspective. Agric. Ecosyst. Environ. 66, 47–60. https://doi.org/10.1016/S0167-8809(97)80706-2

Giraudoux, P., Pradier, B., Delattre, P., Deblay, S., Salvi, D., Defaut, R., 1995. Estimation of water vole abundance by using surface indices. Acta Theriol. (Warsz). 40, 77–96. https://doi.org/10.4098/AT.arch.95-9

Gittleman, J.L., 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. Am. Nat. 127, 744–771. https://doi.org/10.1086/284523

Goerlich, F.J., Cantarino, I., 2013. A population density grid for Spain. Int. J. Geogr. Inf. Sci. 27, 2247–2263. https://doi.org/10.1080/13658816.2013.799283

Gortázar, C., Travaini, A., Delibes, M., 2000. Habitat-related microgeographic body size variation in two Mediterranean populations of red fox (Vulpes vulpes). J. Zool. 250, 335–338. https://doi.org/10.1017/S0952836900003071

Gosselin, J., Zedrosser, A., Swenson, J.E., Pelletier, F., 2014. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. Proc. R. Soc. B Biol. Sci. 282. https://doi.org/10.1098/rspb.2014.1840

Grantham, H.S., Duncan, A., Evans, T.D., Jones, K.R., Beyer, H.L., Schuster, R., Walston, J., Ray, J.C., Robinson, J.G., Callow, M., Clements, T., Costa, H.M., DeGemmis, A., Elsen, P.R., Ervin, J., Franco, P., Goldman, E., Goetz, S., Hansen, A., Hofsvang, E., Jantz, P., Jupiter, S., Kang, A., Langhammer, P., Laurance, W.F., Lieberman, S., Linkie, M., Malhi, Y., Maxwell, S., Mendez, M., Mittermeier, R., Murray, N.J., Possingham, H., Radachowsky, J., Saatchi, S., Samper, C., Silverman, J., Shapiro, A., Strassburg, B., Stevens, T., Stokes, E., Taylor, R., Tear, T., Tizard, R., Venter, O., Visconti, P., Wang, S., Watson, J.E.M., 2020. Anthropogenic modification of forests means only 40% of remaining forests have high ecosystem integrity. Nat. Commun. 11, 1–10. https://doi.org/10.1038/s41467-020-19493-3

Grassni, P., 2013. Distinguishing between yield advances and yield plateaus in historical crop production trend. Nat. Commun. 4, 2918.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711. https://doi.org/10.1111/j.1420-9101.2010.02210.x

Hambäck, P.A., Oksanen, L., Ekerholm, P., Lindgren, Å., Oksanen, T., Schneider, M., 2004. Predators indirectly protect tundra plants by reducing herbivore abundance. Oikos 106, 85–92. https://doi.org/10.1111/j.0030-1299.2004.13029.x

Hartig, F., 2020. Package " DHARMa ". Version 0.3.0. R Packag.

Hawley, D.M., Altizer, S.M., 2011. Disease ecology meets ecological immunology: understanding the links between organismal immunity and infection dynamics in natural populations. Funct. Ecol. 25, 48–60. https://doi.org/10.1111/j.1365-2435.2010.01753.x

Healey, R.M., Atutubo, J.R., Kusrini, M.D., Howard, L., Page, F., Hallisey, N., Karraker, N.E., 2020. Road mortality threatens endemic species in a national park in Sulawesi, Indonesia. Glob. Ecol. Conserv. 24, e01281. https://doi.org/10.1016/j.gecco.2020.e01281

Helldin, J.O., Liberg, O., Glöersen, G., 2006. Lynx (Lynx lynx) killing red foxes (Vulpes vulpes) in boreal Sweden ? frequency and population effects. J. Zool. 270, 657–663. https://doi.org/10.1111/j.1469-7998.2006.00172.x

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A., Young, J., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe-A review. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2007.09.005

Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B., Andersen, R., 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J. Zool. 265, 63–71. https://doi.org/10.1017/S0952836904006053

Hervé, M., 2020. Package "RVAideMemoire." See https//CRAN. R-project. org/package= RVAideMemoire.

Hilborn, A., Pettorelli, N., Orme, C.D.L., Durant, S.M., 2012. Stalk and chase: How hunt stages affect hunting success in Serengeti cheetah. Anim. Behav. 84, 701–706. https://doi.org/10.1016/j.anbehav.2012.06.027

Hoffmann, J., Greef, J.M., 2003. Mosaic indicators - Theoretical approach for the development of indicators for species diversity in agricultural landscapes. Agric. Ecosyst. Environ. 98, 387–394. https://doi.org/10.1016/S0167-8809(03)00098-7

Holcomb, K., Young, J.K., Gerber, L.R., 2009. The influence of human disturbance on California sea lions during the breeding season. Anim. Conserv. 12, 592–598. https://doi.org/10.1111/j.1469-1795.2009.00290.x

Holderegger, R., Di Giulio, M., 2010. The genetic effects of roads: A review of empirical evidence. Basic Appl. Ecol. 11, 522–531. https://doi.org/10.1016/j.baae.2010.06.006

Humphreys, R.K., Ruxton, G.D., 2018. A review of thanatosis (death feigning) as an anti-predator behaviour. Behav. Ecol. Sociobiol. https://doi.org/10.1007/s00265-017-2436-8

Hunter, J.S., Durant, S.M., Caro, T.M., 2007. To flee or not to flee: Predator avoidance by cheetahs at kills. Behav. Ecol. Sociobiol. 61, 1033–1042. https://doi.org/10.1007/s00265-006-0336-4

Hunter, L.T.B., 2015. Wildcats of the world. Bloomsbury Publishing, London.

Ishii, Y., Shimada, M., 2010. The effect of learning and search images on predator-prey interactions. Popul. Ecol. https://doi.org/10.1007/s10144-009-0185-x

Ives, A.R., Dobson, A.P., 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. Am. Nat. 130, 431–447. https://doi.org/10.1086/284719

Jacob, J., Tkadlec, E., 2010. Rodent outbreaks in Europe: dynamics and damage, in: Singleton, G., Belmain, S., Brown, P., Hardy, B. (Eds.), Rodent Outbreaks: Ecology and Impacts. International Rice Research Institute, Los Baños, Philippines., pp. 207–223.

Jansen, B.D., Jenks, J.A., 2012. Birth Timing for Mountain Lions (Puma concolor); Testing the Prey Availability Hypothesis. PLoS One 7, e44625. https://doi.org/10.1371/journal.pone.0044625

Jarić, I., Courchamp, F., Gessner, J., Roberts, D.L., 2016. Potentially threatened: a Data Deficient flag for conservation management. Biodivers. Conserv. 25, 1995–2000. https://doi.org/10.1007/s10531-016-1164-0

Jenkins, A.R., Smallie, J.J., Diamond, M., 2010. Avian collisions with power lines: A global review of causes and mitigation with a South African perspective. Bird Conserv. Int. https://doi.org/10.1017/S0959270910000122

Jennings, A.P., Naim, M., Advento, A.D., Aryawan, A.A.K., Ps, S., Caliman, J.P., Verwilghen, A., Veron, G., 2015. Diversity and occupancy of small carnivores within oil palm plantations in central Sumatra, Indonesia. Mammal Res. 60, 181–188. https://doi.org/10.1007/s13364-015-0217-1

Jensen, A.L., 1987. Simple models for exploitative and interference competition. Ecol. Modell. 35, 113–121. https://doi.org/10.1016/0304-3800(87)90093-7

Jerosch, S., Götz, M., Roth, M., 2017. Spatial organisation of European wildcats (Felis silvestris silvestris) in an agriculturally dominated landscape in Central Europe. Mamm. Biol. 82, 8–16. https://doi.org/10.1016/j.mambio.2016.10.003

Jerosch, S., Kramer-Schadt, S., Götz, M., Roth, M., 2018. The importance of small-scale structures in an agriculturally dominated landscape for the European wildcat (Felis silvestris silvestris) in central Europe and implications for its conservation. J. Nat. Conserv. 41, 88–96. https://doi.org/10.1016/j.jnc.2017.11.008

Jiménez-Albarral, J.J., Urra, F., Jubete, F., Román, J., Revilla, E., Palomares, F., 2021. Abundance and use pattern of wildcats of ancient human-modified cattle pastures in northern Iberian Peninsula. Eur. J. Wildl. Res. 67. https://doi.org/10.1007/s10344-021-01533-y

Jiménez, J., Nuñez-Arjona, J.C., Mougeot, F., Ferreras, P., González, L.M., García-Domínguez, F., Muñoz-Igualada, J., Palacios, M.J., Pla, S., Rueda, C., Villaespesa, F., Nájera, F., Palomares, F., López-Bao, J.V., 2019. Restoring apex predators can reduce mesopredator abundances. Biol. Conserv. 238, 108234. https://doi.org/10.1016/j.biocon.2019.108234

Johansson, Ö., Rauset, G.R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L., Mishra, C., 2016. Land sharing is essential for snow leopard conservation. Biol. Conserv. 203, 1–7. https://doi.org/10.1016/j.biocon.2016.08.034

Jubete, F., Román, J., 2016. New large threatened populations of Phengaris nausithous discovered in the SW of Europe. J. Insect Conserv. 20, 155–158. https://doi.org/10.1007/s10841-016-9851-4

Kaim, A., Cord, A.F., Volk, M., 2018. A review of multi-criteria optimization techniques for agricultural land use allocation. Environ. Model. Softw. https://doi.org/10.1016/j.envsoft.2018.03.031

Karanth, K.U., Sunquist, M.E., 2000. Behavioural correlates of predation by tiger (Panthera tigris), leopard (Panthera pardus) and dhole (Cuon alpinus) in Nagarahole, India. J. Zool. 250, 255–265. https://doi.org/10.1017/S0952836900002119

Kays, R., Crofoot, M.C., Jetz, W., Wikelski, M., 2015. Terrestrial animal tracking as an eye on life and planet. Science (80-.). 348, aaa2478. https://doi.org/10.1126/science.aaa2478

Kays, R., McShea, W.J., Wikelski, M., 2020. Born-digital biodiversity data: Millions and billions. Divers. Distrib. 26, 644–648. https://doi.org/10.1111/ddi.12993

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, M.G., 2002. Effects of Roads and Human Disturbance on Amur Tigers. Conserv. Biol. 16, 97–108. https://doi.org/10.1046/j.1523-1739.2002.99290.x

Khan, I., Hou, F., Le, H.P., 2021. The impact of natural resources, energy consumption, and population growth on environmental quality: Fresh evidence from the United States of America. Sci. Total Environ. 754, 142222. https://doi.org/10.1016/j.scitotenv.2020.142222

Kidawa, D., Kowalczyk, R., 2011. The effects of sex, age, season and habitat on diet of the red fox Vulpes vulpes in northeastern Poland. Acta Theriol. (Warsz). 56, 209–218. https://doi.org/10.1007/s13364-011-0031-3

Kitchener, A., 1991. The natural history of the wild cats. Comstock Pub. Associates.

Kitchener, A.C., Van Valkenburgh, B., Yamaguchi, N., Macdonald, D., Loveridge, A., 2010. Felid form and function, in: Macdonald, D., Loveridge, A. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, Oxford, UK., pp. 83–106.

Klar, N., Herrmann, M., Kramer-Schadt, S., 2009. Effects and Mitigation of Road Impacts on Individual Movement Behavior of Wildcats. J. Wildl. Manage. 73, 631–638. https://doi.org/10.2193/2007-574

Klare, U., Kamler, J.F., MacDonald, D.W., 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. Mamm. Rev. 41, 294–312. https://doi.org/10.1111/j.1365-2907.2011.00183.x

Koenig, W., Mumme, R., Carmen, W., Mark, T., 1994. Acorn Production by Oaks in Central Coastal California : Variation within and among years. Ecology 75, 99–109.

Kortello, A.D., Hurd, T.E., Murray, D.L., 2007. Interactions between cougars (Puma concolor) and gray wolves (Canis lupus) in Banff National Park, Alberta. Ecoscience 14, 214–222. https://doi.org/10.2980/1195-6860(2007)14[214:ibcpca]2.0.co;2

Krauß, W., Olwig, K.R., 2018. Special issue on pastoral landscapes caught between abandonment, rewilding and agro-environmental management. Is there an alternative future? Landsc. Res. https://doi.org/10.1080/01426397.2018.1503844

Krebs, J.R., Stephens, D.W., Sutherland, W.J., Myers, J.P., 2010. Perspectives in optimal foraging, in: Perspectives in Ornithology. Cambridge University Press, pp. 165–222. https://doi.org/10.1017/cbo9780511759994.008

Krofel, M., Južnič, D., Allen, M.L., 2021. Scavenging and carcass caching behavior by European wildcat (<scp> *Felis silvestris* </scp>). Ecol. Res. 1440–1703.12211. https://doi.org/10.1111/1440-1703.12211

Krofel, M., Skrbinsec, T., Mohorovic, M., 2019. Using video surveillance to monitor feeding behaviour and kleptoparasitism at Eurasian lynx kill sites. Folia Zool. 68, 274–284.

Krüger, O., 2005. Age at first breeding and fitness in goshawk Accipiter gentilis. J. Anim. Ecol. 74, 266–273. https://doi.org/10.1111/j.1365-2656.2005.00920.x

Kuefler, D., Hudgens, B., Haddad, N.M., Morris, W.F., Thurgate, N., 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91, 944–950.

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., Cromsigt, J.P.G.M., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.1625

Labisky, R.F., Boulay, M.C., 1998. Behaviors of Bobcats Preying on White-tailed Deer in the Everglades. Am. Midl. Nat. 139, 275–281. https://doi.org/10.1674/0003-0031(1998)139[0275:bobpow]2.0.co;2

Larsen, D.R., Speckman, P.L., 2004. Multivariate Regression Trees for Analysis of Abundance Data. Biometrics 60, 543–549. https://doi.org/10.1111/j.0006-341X.2004.00202.x

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2013.12.001

Lemel, J., Truvé, J., Söderberg, B., 2003. Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. Wildlife Biol. 9, 29–36. https://doi.org/10.2981/wlb.2003.061

Lemons, P.R., Sedinger, J.S., Herzog, M.P., Gipson, P.S., Gilliland, R.L., 2010. Landscape effects on diets of two canids in Northwestern Texas: A multinomial modeling approach. J. Mammal. 91, 66–78. https://doi.org/10.1644/07-MAMM-A-291R1.1

Leroux, S.J., Schmitz, O.J., 2015. Predator-driven elemental cycling: the impact of predation and risk effects on ecosystem stoichiometry. Ecol. Evol. 5, 4976–4988. https://doi.org/10.1002/ece3.1760

Leutenegger, C.M., Hofmann-Lehmann, R., Riols, C., Liberek, M., Worel, G., Lups, P., Fehr, D., Hartmann, M., Weilenmann, P., Lutz, H., 1999. Viral infections in free-living populations of the European wildcat. J. Wildl. Dis. 35, 678–686. https://doi.org/10.7589/0090-3558-35.4.678

Levi, T., Kilpatrick, A.M., Mangel, M., Wilmers, C.C., 2012. Deer, predators, and the emergence of Lyme disease. Proc. Natl. Acad. Sci. U. S. A. 109, 10942–10947. https://doi.org/10.1073/pnas.1204536109

Li, C., Monclús, R., Maul, T.L., Jiang, Z., Blumstein, D.T., 2011. Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. Appl. Anim. Behav. Sci. 129, 146–152. https://doi.org/10.1016/j.applanim.2010.11.013

Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48, 25–34. https://doi.org/10.2307/1313225

Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: The predation risk allocation hypothesis. Am. Nat. 153, 649–659. https://doi.org/10.1086/303202

Lima, S.L., Blackwell, B.F., DeVault, T.L., Fernández-Juricic, E., 2015. Animal reactions to oncoming vehicles: a conceptual review. Biol. Rev. 90, 60–76. https://doi.org/10.1111/brv.12093

Loidi, J., 2017. The vegetation of the Iberian Peninsula. Springer Nature, Cham, Switzerland.

López-Bao, J.V., Aronsson, M., Linnell, J.D.C., Odden, J., Persson, J., Andrén, H., 2019. Eurasian lynx fitness shows little variation across Scandinavian human-dominated landscapes. Sci. Rep. 9, 8903. https://doi.org/10.1038/s41598-019-45569-2

López-Bao, J.V., Bruskotter, J., Chapron, G., 2017. Finding space for large carnivores. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-017-0140

López-Bao, J.V., Kaczensky, P., Linnell, J.D.C., Boitani, L., Chapron, G., 2015. Carnivore coexistence: Wilderness not required. Science (80-.). https://doi.org/10.1126/science.348.6237.871-b

López-Bao, J.V., Mattisson, J., Persson, J., Aronsson, M., Andrén, H., 2016. Tracking neighbours promotes the coexistence of large carnivores. Sci. Rep. 6, 1–9. https://doi.org/10.1038/srep23198

López-Bao, J. V., Palomares, F., Rodríguez, A., Delibes, M., 2010. Effects of food supplementation on home-range size, reproductive success, productivity and recruitment in a small population of Iberian lynx. Anim. Conserv. 13, 35–42. https://doi.org/10.1111/j.1469-1795.2009.00300.x

López, M.M., 2002. Landscapes of northern Spain and pastoral systems, in: Pasture Landscapes and Nature Conservation. Springer Berlin Heidelberg, pp. 67–86. https://doi.org/10.1007/978-3-642-55953-2_5

Loureiro, B.A., Sakomura, N.K., Vasconcellos, R.S., Sembenelli, G., Gomes, M.O.S., Monti, M., Malheiros, E.B., Kawauchi, I.M., Carciofi, A.C., 2017. Insoluble fibres, satiety and food intake in cats fed kibble diets. J. Anim. Physiol. Anim. Nutr. (Berl). 101, 824–834. https://doi.org/10.1111/jpn.12468

Lovell, C., Li, S., Turner, J., Carbone, C., 2022. The effect of habitat and human disturbance on the spatiotemporal activity of two urban carnivores: The results of an intensive camera trap study. Ecol. Evol. 12, e8746. https://doi.org/10.1002/ece3.8746

Loveridge, A.J., Valeix, M., Davidson, Z., Murindagomo, F., Fritz, H., MacDonald, D.W., 2009. Changes in home range size of African lions in relation to pride size and prey biomass in a semi-arid savanna. Ecography (Cop.). 32, 953–962. https://doi.org/10.1111/j.1600-0587.2009.05745.x

Lozano, J., 2010. Habitat use by European wildcats (Felis silvestris) in central Spain: what is the relative importance of forest variables? Anim. Biodivers. Conserv. 33, 2–5.

Lozano, J., Moleon, M., Virgos, E., 2006. Biogeographical patterns in the diet of the wildcat, Felis silvestris Schreber, in Eurasia: factors affecting the trophic diversity. J. Biogeogr. 33, 1076–1085. https://doi.org/10.1111/j.1365-2699.2006.01474.x

Lozano, J., Virgós, E., Malo, A.F., Huertas, D.L., Casanovas, J.G., 2003. Importance of scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (Felis silvestris). Biodivers. Conserv. 12, 921–935. https://doi.org/10.1023/A:1022821708594

Macdonald, D., & Loveridge, A., 2010. The biology and conservation of wild felids ., Second edi. ed. Oxford University Press., Oxford, UK.

MacDonald, D.W., 1983. The ecology of carnivore social behaviour. Nature. https://doi.org/10.1038/301379a0

Maher, C.R., Lott, D.F., 2000. A Review of Ecological Determinants of Territoriality within Vertebrate Species. Am. Midl. Nat. 143, 1–29. https://doi.org/10.1674/0003-0031(2000)143[0001:AROEDO]2.0.CO;2

Malo, A.F., Lozano, J., Huertas, D.L., Virgós, E., 2004. A change of diet from rodents to rabbits (Oryctolagus cuniculus). Is the wildcat (Felis silvestris) a specialist predator? J. Zool. 263, 401–407. https://doi.org/10.1017/S0952836904005448

Mammola, S., Riccardi, N., Prié, V., Correia, R., Cardoso, P., Lopes-Lima, M., Sousa, R., 2020. Towards a taxonomically unbiased European Union biodiversity strategy for 2030: Popularity drives EU conservation. Proc. R. Soc. B Biol. Sci. 287. https://doi.org/10.1098/rspb.2020.2166

Mander, Ü., Mikk, M., Külvik, M., 1999. Ecological and low intensity agriculture as contributors to landscape and biological diversity. Landsc. Urban Plan. 46, 169–177. https://doi.org/10.1016/S0169-2046(99)00042-0

Marino, A., Johnson, A., 2012. Behavioural response of free-ranging guanacos (Lama guanicoe) to land-use change: habituation to motorised vehicles in a recently created reserve. Wildl. Res. 39, 503. https://doi.org/10.1071/WR11174

Marlow, N.J., Thomas, N.D., Williams, A.A.E., Macmahon, B., Lawson, J., Hitchen, Y., Angus, J., Berry, O., 2015. Cats (Felis catus) are more abundant and are the dominant predator of woylies (Bettongia penicillata) after sustained fox (Vulpes vulpes) control. Aust. J. Zool. 63, 18. https://doi.org/10.1071/ZO14024

Marneweck, C., Butler, A.R., Gigliotti, L.C., Harris, S.N., Jensen, A.J., Muthersbaugh, M., Newman, B.A., Saldo, E.A., Shute, K., Titus, K.L., Yu, S.W., Jachowski, D.S., 2021. Shining the spotlight on small mammalian carnivores: Global status and threats. Biol. Conserv. https://doi.org/10.1016/j.biocon.2021.109005

Maron, J.L., Estes, J.A., Croll, D.A., Danner, E.M., Elmendorf, S.C., Buckelew, S.L., 2006. An introduced predator alters aleutian island plant communities by thwarting nutrient subsidies. Ecol. Monogr. 76, 3–24. https://doi.org/10.1890/05-0496

Martin, J., Basille, M., van Moorter, B., Kindberg, J., Allainé, D., Swenson, J.E., 2010. Coping with human disturbance: Spatial and temporal tactics of the brown bear (Ursus arctos). Can. J. Zool. 88, 875–883. https://doi.org/10.1139/Z10-053

Martínez, S., Arregui, J., 1999. Bioclimatology of the Iberian Peninsula. Itinera Geobot. 13, 41–47.

Matlack, C.R., Evans, A.J., 1992. Diet and condition of bobcats, Lynx rufus, in Nova Scotia during autumn and winter. Can. J. Zool. 70, 1114–1119. https://doi.org/10.1139/z92-156

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R., Pedersen, H.C., 2013. Home range size variation in a recovering wolf population: Evaluating the effect of environmental, demographic, and social factors. Oecologia 173, 813–825. https://doi.org/10.1007/s00442-013-2668-x

McDonald, T., Regerh, E., Manly, B., Bromaghin, J., 2018. Package “mra.”

McHuron, E.A., Costa, D.P., Schwarz, L., Mangel, M., 2017. State-dependent behavioural theory for assessing the fitness consequences of anthropogenic disturbance on capital and income breeders. Methods Ecol. Evol. 8, 552–560. https://doi.org/10.1111/2041-210X.12701

Meijaard, E., Sheil, D., Marshall, A.J., Nasi, R., 2007. Phylogenetic Age is Positively Correlated with Sensitivity to Timber Harvest in Bornean Mammals. Biotropica 0, 070924063552006–??? https://doi.org/10.1111/j.1744-7429.2007.00340.x

Mermod, C.P., Liberek, M., 2002. The role of snowcover for European wildcat in Switzerland. Z. Jagdwiss 48, 17–24.

Migli, D., Astaras, C., Boutsis, G., Diakou, A., Karantanis, N.-E., Youlatos, D., 2021a. Spatial Ecology and Diel Activity of European Wildcat (Felis silvestris) in a Protected Lowland Area in Northern Greece. Animals 11, 3030. https://doi.org/10.3390/ani11113030

Migli, D., Astaras, C., Boutsis, G., Diakou, A., Karantanis, N.-E., Youlatos, D., 2021b. Spatial Ecology and Diel Activity of European Wildcat (Felis silvestris) in a Protected Lowland Area in Northern Greece. Animals 11, 3030. https://doi.org/10.3390/ani11113030

Millon, A., Bretagnolle, V., 2008. Predator population dynamics under a cyclic prey regime: numerical responses, demographic parameters and growth rates. Oikos 117, 1500–1510. https://doi.org/10.1111/j.0030-1299.2008.16458.x

Mills, G., 1997. The complete book of southern African mammals. Struik Publishers.

Milner, G.R., Boldsen, J.L., 2023. Population trends and the transition to agriculture: Global processes as seen from North America. Proc. Natl. Acad. Sci. U. S. A. 120, e2209478119. https://doi.org/10.1073/pnas.2209478119

Miñarro, M., Montiel, C., Dapena, E., 2012. Vole pests in apple orchards: Use of presence signs to estimate the abundance of Arvicola terrestris cantabriae and Microtus lusitanicus. J. Pest Sci. (2004). 85, 477–488. https://doi.org/10.1007/s10340-012-0438-x

Mitchell, M.S., Powell, R.A., 2007. Optimal use of resources structures home ranges and spatial distribution of black bears. Anim. Behav. 74, 219–230. https://doi.org/10.1016/j.anbehav.2006.11.017

Moen, G.K., Ordiz, A., Kindberg, J., Swenson, J.E., Sundell, J., Støen, O.G., 2019. Behavioral Reactions of Brown Bears to Approaching Humans in Fennoscandia. Ecoscience 26, 23–33. https://doi.org/10.1080/11956860.2018.1513387

Mohammadi, A., Lunnon, C., Moll, R.J., Tan, C.K.W., Hobeali, K., Behnoud, P., Moghadas, P., Macdonald, D.W., Farhadinia, M.S., 2021. Contrasting responses of large carnivores to land use management across an Asian montane landscape in Iran. Biodivers. Conserv. 30, 4023–4037. https://doi.org/10.1007/s10531-021-02290-9

Moleón, M., Gil-Sánchez, J.M., 2006. Food habits of the wildcat (Felis silvestris) in a peculiar habitat: the Mediterranean high mountain. J. Zool. 260, 17–22. https://doi.org/10.1017/S0952836902003370

Moller, H., MacLeod, C.J., Haggerty, J., Rosin, C., Blackwell, G., Perley, C., Meadows, S., Weller, F., Gradwohl, M., 2008. Intensification of New Zealand agriculture: Implications for biodiversity. New Zeal. J. Agric. Res. 51, 253–263. https://doi.org/10.1080/00288230809510453

Molsher, R., Newsome, A., Dickman, C., 1999. Feeding ecology and population dynamics of the fetal cat (Felis catus) in relation to the availability of prey in central-eastern New South Wales. Wildl. Res. 26, 593–607. https://doi.org/10.1071/WR98058

Molsher, R., Newsome, A.E., Newsome, T.M., Dickman, C.R., 2017. Mesopredator management: Effects of red fox control on the abundance, diet and use of space by feral cats. PLoS One 12. https://doi.org/10.1371/journal.pone.0168460

Monterroso, P., Alves, P.C., Ferreras, P., 2014. Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: Implications for species coexistence. Behav. Ecol. Sociobiol. 68, 1403–1417. https://doi.org/10.1007/s00265-014-1748-1

Monterroso, P., Alves, P.C., Ferreras, P., 2013a. Catch me if you can: Diel activity patterns of mammalian prey and predators. Ethology 119, 1044–1056. https://doi.org/10.1111/eth.12156

Monterroso, P., Brito, J.C., Ferreras, P., Alves, P.C., 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: Dealing with small radio-tracking datasets in species conservation. J. Zool. 279, 27–35. https://doi.org/10.1111/j.1469-7998.2009.00585.x

Monterroso, P., Castro, D., Silva, T.L., Ferreras, P., Godinho, R., Alves, P.C., 2013. Factors affecting the (in)accuracy of mammalian mesocarnivore scat identification in South-western Europe. J. Zool. 289, 243–250. https://doi.org/10.1111/jzo.12000

Monterroso, P., Díaz-Ruíz, F., Lukacs, P.M., Alves, P.C., Ferreras, P., 2020. Ecological traits and the spatial structure of competitive coexistence among carnivores. Ecology ecy.3059. https://doi.org/10.1002/ecy.3059

Monterroso, P., Sillero, N., Rosalino, L.M., Loureiro, F., Alves, P.C., 2013b. Estimating home-range size: when to include a third dimension? Ecol. Evol. 3, 2285–2295. https://doi.org/10.1002/ece3.590

Moore, C.H., Harvey, E.S., Van Niel, K., 2010. The application of predicted habitat models to investigate the spatial ecology of demersal fish assemblages. Mar. Biol. 157, 2717–2729. https://doi.org/10.1007/s00227-010-1531-4

Morales-González, A., Ruiz-Villar, H., Ordiz, A., Penteriani, V., 2020. Large carnivores living alongside humans: Brown bears in human-modified landscapes. Glob. Ecol. Conserv. https://doi.org/10.1016/j.gecco.2020.e00937

Morales-González, A., Fernández-Gil, A., Quevedo, M., Revilla, E., 2022. Patterns and determinants of dispersal in grey wolves (*Canis lupus*). Biol. Rev. 97, 466–480. https://doi.org/10.1111/brv.12807

Moreira-Arce, D., Vergara, P.M., Boutin, S., Simonetti, J.A., Briceño, C., Acosta-Jamett, G., 2015. Native forest replacement by exotic plantations triggers changes in prey selection of mesocarnivores. Biol. Conserv. 192, 258–267. https://doi.org/10.1016/j.biocon.2015.09.015

Morelli, F., Mróz, E., Pruscini, F., Santolini, R., Goławski, A., Tryjanowski, P., 2016. Habitat structure, breeding stage and sex affect hunting success of breeding Red-backed Shrike (Lanius collurio). Ethol. Ecol. Evol. 28, 136–147. https://doi.org/10.1080/03949370.2015.1022907

Moreno, R.S., Kays, R.W., Samudio, R., 2006. Competitive release in diets of ocelot (Leopardus pardalis) and puma (Puma concolor) after jaguar (Panthera onca) decline. J. Mammal. 87, 808–816. https://doi.org/10.1644/05-MAMM-A-360R2.1

Morilhat, C., Bernard, N., Bournais, C., Meyer, C., Lamboley, C., Giraudoux, P., 2007. Responses of Arvicola terrestris scherman populations to agricultural practices, and to Talpa europaea abundance in eastern France. Agric. Ecosyst. Environ. 122, 392–398. https://doi.org/10.1016/J.AGEE.2007.02.005

Morin, D.J., Higdon, S.D., Lonsinger, R.C., Gosselin, E.N., Kelly, M.J., Waits, L.P., 2019. Comparing methods of estimating carnivore diets with uncertainty and imperfect detection. Wildl. Soc. Bull. 43, 651–660. https://doi.org/10.1002/wsb.1021

Mueller, S.A., Reiners, T.E., Steyer, K., von Thaden, A., Tiesmeyer, A., Nowak, C., 2020. Revealing the origin of wildcat reappearance after presumed long-term absence. Eur. J. Wildl. Res. 66, 1–8. https://doi.org/10.1007/s10344-020-01433-7

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. U. S. A. 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Natural Research Council, 2006. Nutrient Requirements of Dogs and Cats. National Academies Press, Washington DC, USA.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J., Dickman, C.R., 2015. The ecological effects of providing resource subsidies to predators. Glob. Ecol. Biogeogr. 24, 1–11. https://doi.org/10.1111/geb.12236

Nisi, A.C., Suraci, J.P., Ranc, N., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., Wilmers, C.C., 2022. Temporal scale of habitat selection for large carnivores: Balancing energetics, risk and finding prey. J. Anim. Ecol. 91, 182–195. https://doi.org/10.1111/1365-2656.13613

Northrup, J.M., Pitt, J., Muhly, T.B., Stenhouse, G.B., Musiani, M., Boyce, M.S., 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. J. Appl. Ecol. 49, 1159–1167. https://doi.org/10.1111/j.1365-2664.2012.02180.x

Nour, N., Currie, D., Matthysen, E., Van Damme, R., Dhondt, A.A., 1998. Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit). Oecologia 114, 522–530. https://doi.org/10.1007/s004420050476

O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., Hofer, E.J., 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology 79, 1193–1208. https://doi.org/10.1890/0012-9658(1998)079[1193:FROCAL]2.0.CO;2

Oberosler, V., Groff, C., Iemma, A., Pedrini, P., Rovero, F., 2017. The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. Mamm. Biol. 87, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2013. Package "vegan." Community Ecol. Packag. 2, 1–295.

Oliveira, T., Urra, F., López-Martín, J.M., Ballesteros-Duperón, E., Barea-Azcón, J.M., Moléon, M., Gil-Sánchez, J.M., Alves, P.C., Díaz-Ruíz, F., Ferreras, P., Monterroso, P., 2018. Females know better: Sex-biased habitat selection by the European wildcat. Ecol. Evol. 8, 9464–9477. https://doi.org/10.1002/ece3.4442

Ordiz, A., Moen, G.K., Sæbø, S., Stenset, N., Swenson, J.E., Støen, O.G., 2019. Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. Biol. Conserv. 232, 228–237. https://doi.org/10.1016/j.biocon.2019.01.016

Ordiz, A., Støen, O.-G., Saebø, S., Sahlén, V., Pedersen, B.E., Kindberg, J., Swenson, J.E., 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. J. Appl. Ecol. 50, 306–314. https://doi.org/10.1111/1365-2664.12047

Ostfeld, R.S., Holt, R.D., 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Front. Ecol. Environ. https://doi.org/10.1890/1540-9295(2004)002[0013:APGFYH]2.0.CO;2

Ouellette, M.H., Legendre, P., 2013. Package "MVPARTwrap." URL http//cran. r-project. org/web/packages/MVPARTwrap/MVPARTwrap. pdf.

Palomares, F., Caro, T.M., 1999. Interspecific Killing among Mammalian Carnivores. Am. Nat. 153, 492–508.

Palomares, F., Lucena-Pérez, M., López-Bao, J.V., Godoy, J.A., 2017. Territoriality ensures paternity in a solitary carnivore mammal. Sci. Rep. 7, 1–6. https://doi.org/10.1038/s41598-017-04820-4

Palomo, L.J., Gisbert, J., Blanco, J.C., 2007. Atlas y Libro Rojo de los Mamíferos Terrestres de España. DirecciónGeneral para la Biodiversidad-SECEM-SECEM, Madrid.

Pangle, W.M., Holekamp, K.E., 2010. Lethal and nonlethal anthropogenic effects on spotted hyenas in the masai mara national reserve. J. Mammal. 91, 154–164. https://doi.org/10.1644/08-MAMM-A-359R.1.

Papanastasis, V.P., Kyriakakis, S., Kazakis, G., 2002. Plant diversity in relation to overgrazing and burning in mountain Mediterranean ecosystems. J. Mediterr. Ecol. 3, 53–64.

Piñeiro, A., Barja, I., 2011. Trophic strategy of the wildcat Felis silvestris in relation to seasonal variation in the availability and vulnerability to capture of Apodemus mice. Mamm. Biol. 76, 302–307. https://doi.org/10.1016/j.mambio.2011.01.008

Piñeiro, A., Barja, I., Silván, G., Illera, J.C., 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildl. Res. 39, 532–539. https://doi.org/10.1071/WR10218

Pirotta, E., Brookes, K.L., Graham, I.M., Thompson, P.M., 2014. Variation in harbour porpoise activity in response to seismic survey noise. Biol. Lett. 10.

https://doi.org/10.1098/rsbl.2013.1090

Podgórski, T., Schmidt, K., Kowalczyk, R., Gulczyńska, A., 2008. Microhabitat selection by Eurasian lynx and its implications for species conservation. Acta Theriol. (Warsz). 53, 97–110. https://doi.org/10.1007/BF03194243

Poessel, S.A., Burdett, C.L., Boydston, E.E., Lyren, L.M., Alonso, R.S., Fisher, R.N., Crooks, K.R., 2014. Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biol. Conserv. 180, 224–232. https://doi.org/10.1016/j.biocon.2014.10.010

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297–330.

Portanier, E., Léger, F., Henry, L., Gayet, T., Queney, G., Ruette, S., Devillard, S., 2022. Landscape genetic connectivity in European wildcat (Felis silvestris silvestris): a matter of food, shelters and demographic status of populations. Conserv. Genet. 23, 653–668. https://doi.org/10.1007/s10592-022-01443-9

Powell, R.A., Mitchell, M.S., 2012. What is a home range? J. Mammal. 93, 948–958. https://doi.org/10.1644/11-MAMM-S-177.1

Prokopenko, C.M., Boyce, M.S., Avgar, T., 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. J. Appl. Ecol. 54, 470–479. https://doi.org/10.1111/1365-2664.12768

Pucek, Z., Jedrzejewski, W., Jedrzejewska, B., Pucek, M., 1993. Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. Acta Theriol. (Warsz). 38, 199–232. https://doi.org/10.4098/AT.arch.93-18

Pudyatmoko, S., 2017. Free-ranging livestock influence species richness, occupancy, and daily behaviour of wild mammalian species in Baluran National Park, Indonesia. Mamm. Biol. 86, 33–41. https://doi.org/10.1016/j.mambio.2017.04.001

Quenette, P.Y., 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologica 11, 801–818.

Rabbinge, R., Van Diepen, C.A., 2000. Changes in agriculture and land use in Europe, in: European Journal of Agronomy. Elsevier, pp. 85–99. https://doi.org/10.1016/S1161-0301(00)00067-8

R Core Team, 2021. R: A language and environment for statistical computing.

Ragni, B., 1981. Gatto selvatico Felis silvestris Schreber, 1777., in: Distribuzione E Biologia Di 22 Specie Di Mamiferi in Italia. Consiglio nazionale delle Ricerche, Roma, pp. 105–113.

Ragni, B., Possenti, M., 1996. Variability of coat-colour and markings system in felis silvestris. Ital. J. Zool. 63, 285–292. https://doi.org/10.1080/11250009609356146

Read, J., Bowen, Z., 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. Wildl. Res. 28, 195–203. https://doi.org/10.1071/WR99065

Reilly, M.L., Tobler, M.W., Sonderegger, D.L., Beier, P., 2017. Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. Biol. Conserv. 207, 117–126. https://doi.org/10.1016/j.biocon.2016.11.003

Richards, S.A., 2007. Dealing with overdispersed count data in applied ecology. J. Appl. Ecol. 45, 218–227. https://doi.org/10.1111/j.1365-2664.2007.01377.x

Richards, S.A., Whittingham, M.J., Stephens, P.A., 2011. Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. Behav. Ecol. Sociobiol. 65, 77–89. https://doi.org/10.1007/s00265-010-1035-8

Riley, S., DeGloria, S., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. J. Soil Sci. 5.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conserv. Biol. 17, 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science (80-.). https://doi.org/10.1126/science.1241484

Rivas-Martínez, S., Penas, Á., Díaz González, T.E., Cantó, P., del Río, S., Costa, J.C., Herrero, L., Molero, J., 2017. Biogeographic Units of the Iberian Peninsula and Baelaric Islands to District Level. A Concise Synopsis, in: The Vegetation of the Iberian Peninsula. Springer, Cham, pp. 131–188. https://doi.org/10.1007/978-3-319-54784-8_5

Roberts, D.L., Taylor, L., Joppa, L.N., 2016. Threatened or Data Deficient: assessing the conservation status of poorly known species. Divers. Distrib. 22, 558–565. https://doi.org/10.1111/ddi.12418

Rodriguez, A., Crema, G., Delibes, M., 1997. Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway. Ecography (Cop.). 20, 287–294.

Rodríguez, A., Urra, F., Jubete, F., Román, J., Revilla, E., Palomares, F., 2020. Spatial Segregation between Red Foxes (Vulpes vulpes), European Wildcats (Felis silvestris) and Domestic Cats (Felis catus) in Pastures in a Livestock Area of Northern Spain. Diversity 12. https://doi.org/10.3390/d12070268

Roemer, G.W., Gompper, M.E., Valkenburgh, B. Van, 2009. The ecological role of the mammalian mesocarnivore. Bioscience 59, 165–173. https://doi.org/10.1525/bio.2009.59.2.9

Román, J., 2019. Manual para la identificación de los cráneos de los roedores de la península ibérica, islas baleares y canarias. Colección Manuales de Mastozoología., Málaga.

Ruiter, D., Berger, L., 2001. Leopard (Panthera pardus Linneaus) cave caching related to anti-theft behaviour in the John Nash Nature Reserve, South Africa. Afr. J. Ecol. 39, 396–398. https://doi.org/10.1046/j.1365-2028.2000.00205.x

Ruiz-Olmo, J., Pinyol, C., Sánchez, D., Such-Sánz, Á., 2018. Breeding pattern of wildcat Felis silvestris (Schreber, 1777) studied in captivity in the iberian peninsula. Hystrix, Ital. J. Mammal. 29, 202–210. https://doi.org/10.4404/hystrix

Ruiz-Villar, H., Bastianelli, M.L., Heurich, M., Anile, S., Díaz-Ruiz, F., Ferreras, P., Götz, M., Herrmann, M., Jerosch, S., Jubete, F., López-Martín, J.M., Monterroso, P., Simon, O., Streif, S., Trinzen, M., Urra, F., López-Bao, J.V., Palomares, F., 2023. Agriculture intensity and landscape configuration influence the spatial use of wildcats across Europe. Biol. Conserv. 277, 109854. https://doi.org/10.1016/j.biocon.2022.109854

Ruiz-Villar, H., Jubete, F., Revilla, E., Román, J., Urra, F., López-Bao, J.V., Palomares, F., 2021. Like cat and fox: diurnal interactions between two sympatric carnivores in pastoral landscapes of NW Spain. Eur. J. Wildl. Res. 67, 1–6. https://doi.org/10.1007/s10344-021-01469-3

Ruiz-Villar, H., López-Bao, J.V., Palomares, F., 2020. A small cat saving food for later: caching behavior in the European wildcat (Felis silvestris silvestris). Eur. J. Wildl. Res. 66. https://doi.org/10.1007/s10344-020-01413-x

Ruiz-Villar, H., Morales-González, A., López-Bao, J. V., Palomares, F., n.d. Humans and traffic influence European wildcat behaviour in pastoral landscapes. Under Rev.

Ruiz-Villar, H., Urra, F., Jubete, F., Morales-González, A., Adrados, B., Revilla, E., Rivilla, J.C., Román, J., Seijas, J., López-Bao, J. V., Palomares, F., 2022. Presence of pastoral fields in mountain landscapes influences prey consumption by European wildcats. J. Zool. 319, 63–75. https://doi.org/10.1111/jzo.13027

Russo, L.F., Barrientos, R., Fabrizio, M., Di Febbraro, M., Loy, A., 2020. Prioritizing road-kill mitigation areas: A spatially explicit national-scale model for an elusive carnivore. Divers. Distrib. 26, 1093–1103. https://doi.org/10.1111/ddi.13064

Russo, S.E., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. Ecology 87, 3160–3174. https://doi.org/10.1890/0012-9658(2006)87[3160:IABISD]2.0.CO;2

Sainsbury, K.A., Shore, R.F., Schofield, H., Croose, E., Campbell, R.D., Mcdonald, R.A., 2019. Recent history, current status, conservation and management of native mammalian carnivore species in Great Britain. Mamm. Rev. 49, 171–188. https://doi.org/10.1111/mam.12150

Šálek, M., Drahníková, L., Tkadlec, E., 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mamm. Rev. 45, 1–14. https://doi.org/10.1111/mam.12027

Šálek, M., Kreisinger, J., Sedláček, F., Albrecht, T., 2010. Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? Landsc. Urban Plan. 98, 86–91. https://doi.org/10.1016/j.landurbplan.2010.07.013

Sandell, M., 1989. The Mating Tactics and Spacing Patterns of Solitary Carnivores, in: Carnivore Behavior, Ecology, and Evolution. Springer US, pp. 164–182. https://doi.org/10.1007/978-1-4757-4716-4_7

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand, H., Unger, D., Wabakken, P., López-Bao, J.V., 2016. The role of human-related risk in breeding site selection by wolves. Biol. Conserv. https://doi.org/10.1016/j.biocon.2016.06.022

Schoener, T.W., 1987. A Brief History of Optimal Foraging Ecology, in: Foraging Behavior. Springer US, pp. 5–67. https://doi.org/10.1007/978-1-4613-1839-2_1

Schoener, T.W., 1976. Alternatives to Lotka-Volterra competition: Models of intermediate complexity. Theor. Popul. Biol. 10, 309–333. https://doi.org/10.1016/0040-5809(76)90022-8

Schüttler, E., Klenke, R., Galuppo, S., Castro, R.A., Bonacic, C., Laker, J., Henle, K., 2017. Habitat use and sensitivity to fragmentation in America's smallest wildcat. Mamm. Biol. 86, 1–8. https://doi.org/10.1016/j.mambio.2016.11.013

Schwartz, A.L.W., Williams, H.F., Chadwick, E., Thomas, R.J., Perkins, S.E., 2018. Roadkill scavenging behaviour in an urban environment. J. Urban Ecol. 4, 1–7. https://doi.org/10.1093/jue/juy006

Seddon, P.J., Leech, T., 2008. Conservation short cut, or long and winding road? A critique of umbrella species criteria. ORYX. https://doi.org/10.1017/S003060530806119X

Senn, H. V., Ghazali, M., Kaden, J., Barclay, D., Harrower, B., Campbell, R.D., Macdonald, D.W., Kitchener, A.C., 2019. Distinguishing the victim from the threat: SNP-based methods reveal the extent of introgressive hybridization between wildcats and domestic cats in Scotland and inform future in situ and ex situ management options for species restoration. Evol. Appl. 12, 399–414. https://doi.org/10.1111/eva.12720

Senzaki, M., Yamaura, Y., Francis, C.D., Nakamura, F., 2016. Traffic noise reduces foraging efficiency in wild owls. Sci. Rep. 6, 1–7. https://doi.org/10.1038/srep30602

Sévêque, A., Gentle, L.K., López-Bao, J. V., Yarnell, R.W., Uzal, A., 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biol. Rev. 95, 1689–1705. https://doi.org/10.1111/brv.12635

Sévêque, A., Gentle, L.K., Yarnell, R.W., 2021. Impact of human disturbance on temporal partitioning within carnivore communities. Mammal Rev. Mammal Rev. https://doi.org/10.1111/mam.12265

Shamoon, H., Shapira, I., 2019. Limiting factors of Striped Hyaena, Hyaena hyaena, distribution and densities across climatic and geographical gradients (Mammalia: Carnivora). Zool. Middle East 65, 189–200. https://doi.org/10.1080/09397140.2019.1596589

Shannon, G., Angeloni, L.M., Wittemyer, G., Fristrup, K.M., Crooks, K.R., 2014. Road traffic noise modifies behaviour of a keystone species. Anim. Behav. 94, 135–141. https://doi.org/10.1016/j.anbehav.2014.06.004

Sherley, R., Underhill, L., Barham, B., Barham, P., Coetzee, J., Crawford, R., Dyer, B., Leshoro, T., Upfold, L., 2013. Influence of local and regional prey availability on breeding performance of African penguins Spheniscus demersus. Mar. Ecol. Prog. Ser. 473, 291–301. https://doi.org/10.3354/meps10070

Siemers, B.M., Schaub, A., 2011. Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators. Proc. R. Soc. B Biol. Sci. 278, 1646–1652. https://doi.org/10.1098/rspb.2010.2262

Signer, J., Fieberg, J., Avgar, T., 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol. Evol. 9, 880–890. https://doi.org/10.1002/ece3.4823

Sikes, R.S., Ylönen, H., Ylonen, H., 1998. Considerations of Optimal Litter Size in Mammals. Oikos 83, 452. https://doi.org/10.2307/3546673

Sládek, J., 1973. Jahreszeitliche und jahresbedingte Verän- derungen der Nahrung der Wildkatze (Felis silvestris, Schreber 1777) in den Westkarpaten. Zool. List. 22, 127–144.

Sliwa, A., 1994. Diet and feeding behaviour of the black-footed cat (Felis nigripes Burchell, 1824) in the Kimberley region, South Africa. Der Zool. Garten 64, 83–96.

Smith, J.A., Gaynor, K.M., Suraci, J.P., 2021. Mismatch Between Risk and Response May Amplify Lethal and Non-lethal Effects of Humans on Wild Animal Populations. Front. Ecol. Evol. 9, 140. https://doi.org/10.3389/fevo.2021.604973

Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human “super predator” reduces feeding time in large carnivores. Proc. R. Soc. B Biol. Sci. 284. https://doi.org/10.1098/rspb.2017.0433

Smith, J.A., Wang, Y., Wilmers, C.C., 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. Proc. R. Soc. B Biol. Sci. 282. https://doi.org/10.1098/rspb.2014.2711

Smith, J.E., Lehmann, K.D.S., Montgomery, T.M., Strauss, E.D., Holekamp, K.E., 2017. Insights from long-term field studies of mammalian carnivores. J. Mammal. 98, 631–641. https://doi.org/10.1093/jmammal/gyw194

Spellerberg, I.F., 1998. Ecological effects of roads and traffic: A literature review. Glob. Ecol. Biogeogr. Lett. 7, 317–333. https://doi.org/10.1046/j.1466-822X.1998.00308.x

Stahl, P., Leger, F., Société française pour l’étude et la protection des mammifères., 1992. Le Chat sauvage (Felis silvestris Schreber, 1777). Société française pour l’étude et la protection des mammifères.

Stankowich, T., 2012. Armed and dangerous: predicting the presence and function of defensive weaponry in mammals. Adapt. Behav. 20, 32–43. https://doi.org/10.1177/1059712311426798

Stankowich, T., Blumstein, D.T., 2005. Fear in animals: A meta-analysis and review of risk assessment. Proc. R. Soc. B Biol. Sci. https://doi.org/10.1098/rspb.2005.3251

Stanton, L.A., Sullivan, M.S., Fazio, J.M., 2015. A standardized ethogram for the felidae: A tool for behavioral researchers. Appl. Anim. Behav. Sci. 173, 3–16. https://doi.org/10.1016/j.applanim.2015.04.001

Steidl, R.J., Anthony, R.G., 2000. Experimental effects of human activity on breeding bald eagles. Ecol. Appl. 10, 258–268. https://doi.org/10.1890/1051-0761(2000)010[0258:eeohab]2.0.co;2

Stein, A.B., Bourquin, S.L., McNutt, J.W., 2015. Avoiding Intraguild Competition: Leopard Feeding Ecology and Prey Caching in Northern Botswana. African J. Wildl. Res. 45, 247–257. https://doi.org/10.3957/056.045.0247

Stevens, R.D., Tello, J.S., 2009. Micro- and macrohabitat associations in mojave desert rodent communities. J. Mammal. 90, 388–403. https://doi.org/10.1644/08-MAMM-A-141.1

Sumasgutner, P., Terraube, J., Coulon, A., Villers, A., Chakarov, N., Kruckenhauser, L., Korpimäki, E., 2019. Landscape homogenization due to agricultural intensification disrupts the relationship between reproductive success and main prey abundance in an avian predator. Front. Zool. 16, 1–14. https://doi.org/10.1186/s12983-019-0331-z

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D., Zanette, L.Y., 2016. Fear of large carnivores causes a trophic cascade. Nat. Commun. 7, 1–7. https://doi.org/10.1038/ncomms10698

Suraci, J.P., Clinchy, M., Zanette, L.Y., Wilmers, C.C., 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol. Lett. 22, 1578–1586. https://doi.org/10.1111/ele.13344

Swanepoel, L.H., 2008. Ecology and conservation of leopards, Panthera pardus, on selected game ranches in the Waterberg region, Limpopo, South Africa. University of Pretoria.

Swenson, J.E., 1999. Does hunting affect the behavior of brown bears in Eurasia? Ursus 11, 157–162.

Symons, J., Pirotta, E., Lusseau, D., 2014. Sex differences in risk perception in deep-diving bottlenose dolphins leads to decreased foraging efficiency when exposed to human disturbance. J. Appl. Ecol. 51, 1584–1592. https://doi.org/10.1111/1365-2664.12337

Tälle, M., Öckinger, E., Löfroth, T., Pettersson, L.B., Smith, H.G., Stjernman, M., Ranius, T., 2023. Land sharing complements land sparing in the conservation of disturbance-dependent species. Ambio. https://doi.org/10.1007/s13280-022-01820-1

Terborgh, J., Lopez, L., Nuñez, P. V., Rao, M., Shahabuddin, G., Orihuela, G., Riveros, M., Ascanio, R., Adler, G.H., Lambert, T.D., Balbas, L., 2001. Ecological meltdown in predator-free forest fragments. Science (80-.). 294, 1923–1926. https://doi.org/10.1126/science.1064397

Theuerkauf, J., 2009. What Drives Wolves: Fear or Hunger? Humans, Diet, Climate and Wolf Activity Patterns. Ethology 115, 649–657. https://doi.org/10.1111/j.1439-0310.2009.01653.x

Thiel, R.P., Merrill, S., Mech, D.L., 1998. Tolerance by denning wolves, Canis lupus, to human disturbance. Can. Field-Naturalist 122, 340–342.

Thrall, P.H., Oakeshott, J.G., Fitt, G., Southerton, S., Burdon, J.J., Sheppard, A., Russell, R.J., Zalucki, M., Heino, M., Ford Denison, R., 2011. Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. Evol. Appl. 4, 200–215. https://doi.org/10.1111/j.1752-4571.2010.00179.x

Thurfjell, H., Ciuti, S., Boyce, M.S., 2017. Learning from the mistakes of others: How female elk (Cervus elaphus) adjust behaviour with age to avoid hunters. PLoS One 12, e0178082. https://doi.org/10.1371/journal.pone.0178082

Tiesmeyer, A., Ramos, L., Manuel Lucas, J., Steyer, K., Alves, P.C., Astaras, C., Brix, M., Cragnolini, M., Domokos, C., Hegyeli, Z., Janssen, R., Kitchener, A.C., Lambinet, C., Mestdagh, X., Migli, D., Monterroso, P., Mulder, J.L., Schockert, V., Youlatos, D., Pfenninger, M., Nowak, C., 2020. Range-wide patterns of human-mediated hybridisation in European wildcats. Conserv. Genet. 21, 247–260. https://doi.org/10.1007/s10592-019-01247-4

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U. S. A. 108, 20260–20264.

https://doi.org/10.1073/pnas.1116437108

Tilman, D., Fargione, J., Wolff, B., D’Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science (80-.). 292, 281–284. https://doi.org/10.1126/science.1057544

Torres-Romero, E.J., Giordano, A.J., 2022. Impact of the Anthropocene on the status of the world’s small carnivores: A global macroecological perspective. J. Biogeogr. 49, 916–929. https://doi.org/10.1111/jbi.14357

Tsunoda, H., Newman, C., Peeva, S., Raichev, E., Buesching, C.D., Kaneko, Y., 2020. Spatio-temporal partitioning facilitates mesocarnivore sympatry in the Stara Planina Mountains, Bulgaria. Zoology 141, 125801. https://doi.org/10.1016/j.zool.2020.125801

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., Van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., De Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., De MirandaMourão, G., Morato, R.G., Morellet, N., Morrison, T.A., Díaz-Muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O’Hara, R.B., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., De Paula, R.C., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zięba, F., Zwijacz-Kozica, T., Mueller, T., 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science (80-.). 359, 466–469. https://doi.org/10.1126/science.aam9712

Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x

Turner, D., Bateson, P., Bateson, P., 2000. The domestic cat: the biology of its behaviour. Cambridge University Press., Cambridge.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. Trends Ecol. Evol. https://doi.org/10.1016/S0169-5347(03)00070-3

Ullas Karanth, K., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., Samba Kumar, N., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proc. R. Soc. B Biol. Sci. 284. https://doi.org/10.1098/rspb.2016.1860

Ullmann, W., Fischer, C., Pirhofer-Walzl, K., Kramer-Schadt, S., Blaum, N., 2018. Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes. Landsc. Ecol. 33, 1505–1517.

https://doi.org/10.1007/s10980-018-0676-2

Urra, F., 2003. El gato montés en Navarra: distribución, ecología y conservación.

Valente, J.J., Bennett, R.E., Gómez, C., Bayly, N.J., Rice, R.A., Marra, P.P., Ryder, T.B., Sillett, T.S., 2022. Land-sparing and land-sharing provide complementary benefits for conserving avian biodiversity in coffee-growing landscapes. Biol. Conserv. 270, 109568. https://doi.org/10.1016/j.biocon.2022.109568

van der Meer, E., Moyo, M., Rasmussen, G.S.A., Fritz, H., 2011. An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (Lycaon pictus) inside and outside a protected area. Behav. Ecol. 22, 985–992. https://doi.org/10.1093/beheco/arr079

Van Der Ree, R., Jaeger, J.A.G., Van Der Grift, E.A., Clevenger, A.P., Van Der Ree, R., Jaeger, J.A.G., 2011. Effects of Roads and Traffic on Wildlife Populations and Landscape Function. Ecol. Soc. 16, 48. https://doi.org/10.5751/ES-03982-160148

Vander Wall, S.B., 1990. Food hoarding in animals. University of Chicago Press, Chicago, IL, USA.

Verbeek, N.A.M., 2010. Behavioural Interactions between Avian Predators and their Avian Prey: Play Behaviour or Mobbing? Z. Tierpsychol. 67, 204–214. https://doi.org/10.1111/j.1439-0310.1985.tb01389.x

Vinter, T., Dinnétz, P., Danzer, U., Lehtilä, K., 2016. The relationship between landscape configuration and plant species richness in forests is dependent on habitat preferences of species. Eur. J. For. Res. 135, 1071–1082. https://doi.org/10.1007/s10342-016-0994-3

von Thaden, A., Cocchiararo, B., Mueller, S.A., Reiners, T.E., Reinert, K., Tuchscherer, I., Janke, A., Nowak, C., 2021. Informing conservation strategies with museum genomics: Long-term effects of past anthropogenic persecution on the elusive European wildcat. Ecol. Evol. 11, 17932–17951. https://doi.org/10.1002/ece3.8385

Wachter, B., Blanc, A.S., Melzheimer, J., Höner, O.P., Jago, M., Hofer, H., 2012. An advanced method to assess the diet of free-ranging large carnivores based on scats. PLoS One 7. https://doi.org/10.1371/journal.pone.0038066

Wam, H.K., Eldegard, K., Hjeljord, O., 2014. Minor habituation to repeated experimental approaches in Scandinavian wolves. Eur. J. Wildl. Res. 60, 839–842. https://doi.org/10.1007/s10344-014-0841-0

Wang, Z., Li, Z., Beauchamp, G., Jiang, Z., 2011. Flock size and human disturbance affect vigilance of endangered red-crowned cranes (Grus japonensis). Biol. Conserv. 144, 101–105. https://doi.org/10.1016/j.biocon.2010.06.025

Watson, J.E.M., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., Mackey, B., Venter, O., 2016. Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. Curr. Biol. 26, 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049

Weber, J., Aubry, S., 1993. Predation by foxes, Vulpes vulpes, on the fossorial form of the water vole, Arvicola terrestris scherman, in western Switzerland. J. Zool. 229, 553–559.

Westekemper, K., Tiesmeyer, A., Steyer, K., Nowak, C., Signer, J., Balkenhol, N., 2021. Do all roads lead to resistance? State road density is the main impediment to gene flow in a flagship species inhabiting a severely fragmented anthropogenic landscape. Ecol. Evol. 11, 8528–8541. https://doi.org/10.1002/ece3.7635

Wevers, J., Fattebert, J., Casaer, J., Artois, T., Beenaerts, N., 2020. Trading fear for food in the Anthropocene: How ungulates cope with human disturbance in a multi-use, suburban ecosystem. Sci. Total Environ. 741, 140369. https://doi.org/10.1016/j.scitotenv.2020.140369

Wezel, A., Casagrande, M., Celette, F., Vian, J.F., Ferrer, A., Peigné, J., 2014. Agroecological practices for sustainable agriculture. A review. Agron. Sustain. Dev. https://doi.org/10.1007/s13593-013-0180-7

White, S., Briers, R.A., Bouyer, Y., Odden, J., Linnell, J.D.C., 2015. Eurasian lynx natal den site and maternal home-range selection in multi-use landscapes of Norway. J. Zool. 297, 87–98. https://doi.org/10.1111/jzo.12260

Wikenros, C., Gicquel, M., Zimmermann, B., Flagstad, Ø., Åkesson, M., 2021. Age at first reproduction in wolves: Different patterns of density dependence for females and males. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2021.0207

Wikenros, C., Liberg, O., Sand, H., Andrén, H., 2010. Competition between recolonizing wolves and resident lynx in Sweden. Can. J. Zool. 88, 271–279. https://doi.org/10.1139/Z09-143

Williams, R., Lusseau, D., Hammond, P.S., 2006. Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). Biol. Conserv. 133, 301–311. https://doi.org/10.1016/j.biocon.2006.06.010

Williams, S.T., Maree, N., Taylor, P., Belmain, S.R., Keith, M., Swanepoel, L.H., 2018. Predation by small mammalian carnivores in rural agro-ecosystems: An undervalued ecosystem service? Ecosyst. Serv. 30, 362–371. https://doi.org/10.1016/j.ecoser.2017.12.006

Wilson, M.W., Ridlon, A.D., Gaynor, K.M., Gaines, S.D., Stier, A.C., Halpern, B.S., 2020. Ecological impacts of human-induced animal behaviour change. Ecol. Lett. 23, 1522–1536. https://doi.org/10.1111/ele.13571

Wilson, R., 1999. Possums in the spotlight. Nat. Aust. 26, 34–41.

Wolff, A., Paul, J.-P., Martin, J.-L., Bretagnolle, V., 2001. The benefits of extensive agriculture to birds: the case of the little bustard. J. Appl. Ecol. 38, 963–975. https://doi.org/10.1046/j.1365-2664.2001.00651.x

Wood, S., 2015. Package “mgcv.” R Packag. version 29, 729.

Wright, H.L., Lake, I.R., Dolman, P.M., 2012. Agriculture-a key element for conservation in the developing world. Conserv. Lett. 5, 11–19. https://doi.org/10.1111/j.1755-263X.2011.00208.x

Zemanova, M.A., Perotto-Baldivieso, H.L., Dickins, E.L., Gill, A.B., Leonard, J.P., Wester, D.B., 2017. Impact of deforestation on habitat connectivity thresholds for large carnivores in tropical forests. Ecol. Process. 6, 1–11. https://doi.org/10.1186/s13717-017-0089-1

Zuberogoitia, I., Zabala, J., Martínez, J.A., Martínez, J.E., Azkona, A., 2008. Effect of human activities on Egyptian vulture breeding success. Anim. Conserv. 11, 313–320. https://doi.org/10.1111/j.1469-1795.2008.00184.x

Zurcher, A.A., Sparks, D.W., Bennett, V.J., 2010. Why the bat did not cross the road? Acta Chiropterologica 12, 337–340. https://doi.org/10.3161/150811010X537918

Resumen

Introducción

La población humana ha crecido de forma exponencial en las últimas décadas, causando una modificación del 77% de los hábitats naturales con el principal objetivo de satisfacer las necesidades humanas, principalmente de alimentación (agricultura y ganadería).

Los cambios en el paisaje pueden generar efectos letales y no letales en la fauna que los habita. Mientras que los primeros derivan en la muerte de los ejemplares por atropellos, persecución directa o colisión con infraestructuras energéticas, los segundos generan cambios comportamentales. Dichos cambios responden a respuestas antipredatorias en la fauna, enfocadas a reducir el contacto con los humanos mediante, por ejemplo, variaciones temporales y espaciales en el uso del paisaje o en el tiempo invertido en diferentes comportamientos. Además, la fragmentación del paisaje por actividades humanas puede variar la distribución de los recursos o dificultar los movimientos de los individuos. Finalmente, estas variaciones comportamentales pueden generar efectos ecológicos en cascada que afecten al funcionamiento de los ecosistemas.

Los depredadores son especialmente sensibles a dichos cambios dadas sus peculiaridades ecológicas, lo cual es clave considerando el papel fundamental que cumplen en los ecosistemas. En concreto, los mesocarnívoros regulan las poblaciones de roedores y consecuentemente limitan sus efectos sobre la producción primaria, el ciclo de los nutrientes o la transmisión de enfermedades. La persecución histórica de estas especies por los humanos ha hecho que estas especies sean discretas y nocturnas, lo cual dificulta su estudio y seguimiento, particularmente a través de observaciones directas del comportamiento. Además, el 50% de los mesocarnívoros presentan tendencias poblacionales decrecientes, relacionadas eminentemente con actividades humanas como el furtivismo o la destrucción de los hábitats.

La importancia de los mesocarnívoros en los ecosistemas justifica la necesidad urgente de investigar cómo estas especies se ven afectadas por las actividades humanas con el objetivo de diseñar y aplicar estrategias de conservación efectivas que promuevan su mantenimiento y funcionalidad en los ecosistemas. Para ello, los científicos han de utilizar factores comportamentales que puedan ser usados como indicadores de cambios ecológicos, por ejemplo en relación a la alimentación, reproducción y movimiento; y discutir las consecuencias potenciales de dichos cambios. Esta información ha de ser recogida mediante el monitoreo tradicional a largo plazo de aspectos observables en campo o mediante la recogida de muestras biológicas; y mediante el uso de nuevas tecnologías (GPS) que permitan la obtención de información espacial de alta resolución. Comparando la información recogida en zonas con diferente grado de presencia humana, podremos estudiar los impactos y discutir las consecuencias de dichas actividades en los mesocarnívoros.

Nuestra especie de estudio es el gato montés europeo (*Felis silvestris*), un pequeño felino que ocupa paisajes en mosaico (naturales o antropogénicos) de forma fragmentada a lo largo de Europa. Dichos paisajes proporcionan de forma simultánea refugio, en forma de parches densos de vegetación, y alimento, el cual consiste principalmente en roedores. Por tanto, los gatos monteses pueden utilizar de forma habitual paisajes humanizados que alternan zonas refugio y áreas con abundancia de presas. Dados los hábitos nocturnos y discretos de esta especie, muchos aspectos ecológicos básicos de los gatos monteses siguen siendo desconocidos.

A pesar de una recuperación generalizada de sus poblaciones, la especie sigue en claro declive en algunas zonas y son múltiples las causas humanas que siguen afectando a la especie. Entre ellas destacan la intensificación de los usos, los atropellos y la hibridación con gatos domésticos en las zonas donde la especie es más escasa.

Objetivos y estructura de la tesis

El principal objetivo de esta tesis es detectar cambios comportamentales causados por las actividades humanas en los gatos monteses que habitan paisajes humanizados. Además, pretende discutir los efectos ecológicos de dichos cambios y proponer medidas de conservación que promuevan la coexistencia entre humanos y gatos monteses.

La tesis se divide en 2 secciones y 6 capítulos. En la primera sección utilizamos datos a largo plazo de indicadores comportamentales para estudiar los efectos de las actividades humanas sobre los gatos monteses. En concreto, analizamos la influencia de: la intensidad de la agricultura y la configuración del paisaje en el tamaño de territorio de los gatos monteses a escala europea (Capítulo 1); la presencia de los prados ganaderos en la dieta de los gatos monteses en la Cordillera Cantábrica (Capítulo 2); la presencia de humanos y tráfico en el tiempo dedicado por los gatos monteses a diferentes comportamientos en la Cordillera Cantábrica Occidental (Capítulo 3). En la segunda sección, describimos parámetros ecológicos fundamentales y poco conocidos de los gatos monteses. En particular, describimos: la ecología reproductiva de los gatos monteses en condiciones silvestres (Capítulo 4); las interacciones interespecíficas entre gatos monteses y zorros

(*Vulpes vulpes*; Capítulo 5); y el comportamiento de los gatos monteses al explotar un recurso trófico poco conocido (Capítulo 6). Los principales objetivos de la tesis son:

Capítulo 1. Este capítulo pretende desarrollar una evaluación a gran escala de los efectos de la proporción e intensidad de la agricultura (intensiva vs. extensiva) así como su distribución en el paisaje (configuración del paisaje) en el tamaño de las áreas de campeo de los gatos monteses a lo largo de su rango de distribución. Para ello, analizamos la variación en las áreas de campeo de los gatos obtenidas del marcaje de ejemplares con collares VHF y GPS, obtenida en 4 países Europeos durante los últimos 20 años, en relación al uso y estructura del paisaje.

Capítulo 2. Este capítulo analiza los efectos de la presencia y proporción de los prados ganaderos sobre el consumo de diferentes presas por los gatos en la Cordillera Cantábrica, además de su variación estacional. Además explora la relación entre la abundancia y el consumo de presas. Para ello, determinamos el consumo de presas mediante la recogida y análisis macroscópico de excrementos de gato montés obtenidos en diferentes estaciones y obtuvimos estimas de la densidad de presas mediante aproximaciones directas e indirectas.

Capítulo 3. Este capítulo evalúa los impactos de las molestias humanas y el tráfico en el tiempo dedicado por los gatos monteses a diferentes comportamientos y en el éxito en la caza en la Cordillera Cantábrica occidental. En concreto, investiga el tiempo dedicado a la caza o la vigilancia bajo diferentes fuentes de molestia; estudia los efectos del tráfico sobre el tiempo cazando y el tiempo vigilando mientras se alimentaban y analiza los efectos del tráfico sobre el éxito en la caza. Para ello combinamos información comportamental obtenida mediante la observación de gatos monteses con datos de tráfico y distancia a infraestructuras humanas.

Capítulo 4. Este capítulo describe los parámetros reproductivos de los gatos monteses que utilizan prados ganaderos de la Cordillera Cantábrica. En concreto analizamos el tamaño de camada, estacionalidad y localización, así como la reutilización de cubiles y el comportamiento de ceba por parte de las hembras durante la cría. Para ello realizamos observaciones de hembras de gato montés durante el período reproductivo.

Capítulo 5. Este capítulo investiga las interacciones interespecíficas entre dos carnívoros simpátricos y de tamaños similares: el gato montés y el zorro. En particular, analizamos las respuestas comportamentales de ambas especies durante los encuentros y discutimos las posibles consecuencias. Para ello realizamos observaciones directas de las interacciones entre gatos y zorros y categorizamos las respuestas de ambas especies.

Capítulo 6. Este capítulo describe de forma exhaustiva y pionera el comportamiento de almacenamiento de comida por parte de un gato montés consumiendo una carroña de corzo. Este análisis deriva de la detección oportunista y observación de este comportamiento en un gato marcado con GPS en la Cordillera Cantábrica.

Resultados

Capítulo 1. Los resultados de este capítulo muestran que las áreas de campeo de los gatos monteses en Europa aumentaron al aumentar la proporción en las mismas de terreno dedicado a agricultura intensiva. De forma similar, las áreas de campeo también aumentaron al aumentar la integridad de los bosques, lo cual se corresponde con bosque extensos y homogéneos. De forma contraria, las áreas de campeo disminuyeron al aumentar la densidad del borde de bosque, lo cual se corresponde con paisajes en mosaico en los que se intercalan zonas forestales y zonas abiertas. De hecho, el borde de bosque es capaz de contrarrestar los efectos perjudiciales sobre los gatos monteses ocasionados por la agricultura intensiva. Por tanto, los gatos monteses encuentran buenas condiciones en escenarios donde la agricultura extensiva se intercala con parches de bosque y peores condiciones en escenarios homogéneos asociados a destrucción de hábitat por agricultura intensiva o a bosques muy extensos, lo cual apoya la tendencia reciente de considerar a los gatos monteses como especializados en paisajes en mosaico. Por tanto, para promover la conservación a largo plazo de los gatos monteses en Europa, es fundamental proteger los paisajes en mosaico, tanto los naturales como los asociados a actividades antrópicas sostenibles, y evitar su transformación a paisajes agrícolas intensivos y homogéneos.

Capítulo 2. Los resultados de este capítulo muestran que la presencia de prados ganaderos influyó en el consumo de presas por parte del gato montés. En concreto, el consumo de presas en áreas con presencia de prados (incluso en proporciones relativamente bajas) estuvo dominado por la rata topera (*Arvicola monticola),* un roedor pratense de gran tamaño y rentable energéticamente para los gatos. El consumo de *Arvicola* no estuvo correlacionado con su abundancia y fue mayor durante el verano y el otoño. Los ratones del género *Apodemus,* dominaron la dieta del gato en zonas con mayor presencia de bosque y alejadas de los prados, particularmente durante la primavera. Estos resultados sugieren que las variaciones en el uso de hábitat y cambios estacionales en el acceso a las presas pueden determinar el consume de presas por parte de los gatos en paisajes ganaderos.

Capítulo 3. Los resultados de este capítulo muestran que los gatos monteses dedicaron más tiempo a comportamientos de alerta y menos tiempo a cazar, alimentarse y moverse en la presencia de humanos que en escenarios sin molestias antrópicas. Además, los gatos dedicaron más tiempo a cazar en escenarios con mayores niveles de tráfico, más cerca de las carreteras y más lejos de los poblados. De forma similar, los gatos monteses dedicaron más tiempo a comportamientos de vigilancia mientras se alimentaban de presas en la presencia de vehículos. Por último, el éxito en la caza de los gatos monteses disminuyó en la presencia de vehículos pero fue mayor a menor distancia de las carreteras. Por tanto, los humanos y el tráfico influyeron en el comportamiento de los gatos monteses que habitan paisajes ganaderos, aunque es difícil determinar hasta qué punto dichos cambios se traducen en efectos demográficos.

Capítulo 4. En este capítulo proporcionamos la primera información científica sobre la ecología reproductiva del gato montés en libertad y los primeros datos sobre el éxito en la caza y la tasa de aporte de presas a los cachorros por parte de las hembras reproductoras. En concreto, el tamaño medio de camada durante el destete fue de dos individuos, con la mayoría de observaciones ocurriendo entre Julio y Septiembre. Las cubiles secundarias estaban localizadas en su mayoría en el interior de vegetación espesa (matorral y vegetación de ribera) en las proximidades de los prados ganaderos, aunque en algunas ocasiones los gatos utilizaron construcciones antrópicas con fines reproductivos. Además registramos dos casos de hembras de gato montés criando a sus respectivas camadas a menos de 500 m de distancia. Por último, el éxito en la caza de las hembras reproductoras fue mayor que el de hembras no reproductoras y el de machos, y las hembras reproductoras cebaron un 80% de las presas capturadas.

Capítulo 5. Los resultados de este capítulo muestran que las interacciones diurnas entre gatos monteses y zorros en prados ganaderos son raras. Durante los encuentros, los zorros mostraron comportamientos ofensivos mientras que los gatos utilizaron la intimidación defensiva como estrategia, probablemente en relación a sus respectivas morfologías. Ambas estrategias fueron igualmente efectivas para mantener el uso de las zonas de alimentación.

Capítulo 6. Los resultados de este capítulo muestran la primera descripción exhaustiva del comportamiento de “caching” o almacenamiento de alimento en un gato montés, el cual fue registrado en la Cordillera Cantábrica. Dicho comportamiento consiste en la relocalización o almacenamiento de alimento para protegerlo de competidores, retrasar la putrefacción del alimento o explotarlo durante épocas de escasez. En nuestro caso el gato montés se comportó como un lince/puma, visitando la carroña de un corzo atropellado al menos 9 días durante un período de 21 días, consumiendo los principales músculos y cubriendo los restos con pelo y vegetación.

Discusión

Los efectos de las actividades humanas sobre la fauna pueden variar entre especies y ecosistemas. Por ejemplo, los carnívoros generalistas pueden ver aumentado su acceso al alimento en paisajes humanizados, por ejemplo por el aumento de fuentes como la basura. Por otra parte, especies con mayores requerimientos de hábitat pueden verse perjudicadas por las molestias y el empobrecimiento del hábitat en áreas antrópicas. Dadas sus peculiaridades en cuanto a selección de hábitat (prefiriendo paisajes en mosaico) y selección de presas (con dietas basadas en el consumo de roedores), los gatos monteses utilizando paisajes antrópicos pueden percibir tanto efectos positivos como negativos dependiendo de la intensidad y el grado de ocupación humano. Sin embargo, los cambios en el uso del paisaje, el consumo de presas o el tiempo dedicado a la caza y la vigilancia pueden ser difíciles de traducir en consecuencias ecológicas a nivel individual y poblacional como el éxito reproductivo, las tendencias poblacionales o el estado sanitario de las poblaciones.

En gatos monteses utilizando paisajes humanizados, las áreas de campeo aumentaron al aumentar la proporción e intensidad de la agricultura, lo cual puede ser una respuesta de los gatos a una disminución en la idoneidad de hábitat y a la disponibilidad distante de los recursos, lo cual obliga a los individuos a utilizar áreas mayores. Estos cambios pueden aumentar los costes energéticos para los gatos. Por tanto, los gatos usando paisajes intensivos sobreviven en peores condiciones que aquellos habitando paisajes más sostenibles y mejor estructurados, principalmente si en el primer caso se priva a los gatos monteses del acceso al refugio, por ejemplo en parches forestales.

Los gatos monteses que habitan paisajes ganaderos en la Cordillera Cantábrica aprovecharon los prados ganaderos para acceder a una presa de gran tamaño y rentable energéticamente, la rata topera. Las poblaciones de este roedor se ven beneficiadas por las prácticas tradicionales consistentes en el uso de fertilizantes orgánicos o un uso limitado de maquinaria, y los gatos monteses perciben por tanto un aumento en la disponibilidad de presas en dichos ambientes. Esto puede tener consecuencias ecológicas como por ejemplo una disminución en el tamaño de las áreas de campeo, lo cual reduce el gasto energético en patrullar el territorio. También podría mejorar la condición corporal de los individuos aumentando la supervivencia y el éxito reproductivo. De hecho, las hembras de gato montés utilizaron los prados ganaderos con fines reproductivos y fueron muy exitosas en la captura de presas en dichos ambientes.

La intensificación del paisaje sigue aumentado, lo cual compromete la supervivencia de los gatos monteses en ambientes humanizados. Dos tendencias pretenden solucionar el problema del mantenimiento simultaneo de la producción alimenticia y la conservación de la fauna: 1) land sharing (compartir el paisaje), que consiste en la creación de paisajes en mosaico que mezclen zonas agrícolas y naturales y 2) land sparing (dividir del paisaje) que sugiere la dedicación de largas superficies separadas tanto a la agricultura como a la conservación. Como hemos visto, los paisajes en mosaico proporcionan refugio y presas, por lo que la primera opción podría parecer la más adecuada para el éxito de los gatos monteses. Sin embargo, la parte agrícola de dichos paisajes ha de ser sostenible para evitar la simplificación de los paisajes y proporcionar los elementos que pueden beneficiar a los gatos monteses.

Sin embargo, las medidas de conservación han de ser lo más integrativas posibles y beneficiar al mayor número de taxones. Por ello, la mejor opción sería utilizar ambas estrategias (land sharing y sparing) de forma complementaria para proteger de forma simultánea aquellas especies que requieren de hábitats íntegros y las que pueden beneficiarse de ciertas actividades humanas. Este escenario estaría compuesto por grandes áreas naturales mezcladas con algunas zonas ganaderas y agrícolas en el entorno de los poblados y en otras zonas, quizá las más humanizadas, grandes superficies dedicadas a la producción intensiva de alimentos. Este escenario es similar a lo ya existente en la Cordillera Cantábrica, zona en la que desarrollamos la mayoría de nuestro trabajo. Sin embargo, estos paisajes están cambiando debido a dos componentes principales. Primero la intensificación de las prácticas ganaderas que desarrollan labores de eliminación de matorral, concentración parcelaria y sobrepastoreo de pastizales subalpinos, lo cual se traduce en una simplificación y sobreexplotación de estos paisajes. Esto perjudicaría a los gatos monteses ya que necesitan de formaciones de matorral para refugiarse y reproducirse y un uso sostenible de los prados para que su presa principal siga presente.

Segundo, el abandono rural que dificulta el mantenimiento de los prados ganaderos y favorece la evolución natural de la vegetación hacia etapas más maduras. El abandono rural y consecuente aumento de la superficie forestal es considerado uno de los componentes favorecedores de la recuperación de las poblaciones de gato montés en las décadas recientes, por lo que dicho proceso no parece preocupante para el mantenimiento de las poblaciones de la especie. Sin embargo, es posible que la desaparición de los prados reduzca las poblaciones de rata topera, lo cual podría afectar a la ecología y demografía de los gatos monteses usando estas zonas. El capítulo 2 muestra que la superficie de prados necesaria para que los gatos seleccionen las ratas toperas como presa principal es relativamente baja (ca. 15%), dejando una superficie considerable disponible para la conservación de los hábitats naturales no modificados. Por este motivo, creemos que el mantenimiento de superficies relativamente pequeñas de prados manejados de forma tradicional próximos a las zonas ya alteradas por las actividades humanas, pueden beneficiar a los gatos monteses sin perjudicar en exceso aquellos entornos más naturales.

Por otra parte los prados se encuentran en zonas frecuentadas por humanos (cerca de poblados y carreteras), lo cual puede ocasionar molestias humanas a los gatos monteses que utilizan estos lugares. De hecho, los gatos cambiaron su comportamiento en dichos ambientes, con respuestas variando en intensidad en función de la amenaza (por ejemplo, alta para la presencia de humanos y baja para la presencia de tráfico, al cual pueden habituarse hasta cierto punto como consecuencia de repetición de un estímulo no dañino). Estos cambios afectaron al tiempo cazando y vigilando, , lo cual podría asociarse con molestias acústicas por parte del tráfico. Sin embargo, es complicado determinar el balance energético que esto supone para los gatos. Los gatos llevan décadas utilizando estos ambientes, y aunque puedan percibir efectos negativos como un aumento de la mortalidad por atropello, los beneficios puede que superen los perjuicios. De otra forma uno esperaría que los gatos no utilizasen dichos ambientes de forma tan frecuente, a no ser que dichos ambientes actúen como trampas ecológicas.

Resumiendo, la Cordillera Cantábrica presenta una superficie considerable de hábitats naturales mezclados con paisajes ganaderos en los fondos de valle, lo cual proporciona condiciones aptas para los gatos monteses en relación a las presas, el hábitat y las opciones de reproducirse. Sin embargo esto implica interaccionar con humanos y competidores, lo cual puede causar efectos negativos en la especie. Además el paisaje actual está cambiando por la intensificación de prácticas ganaderas y agrícolas y por el abandono rural, para lo cual el monitoreo a largo plazo de las especies es esencial para detectar los efectos de dichos cambios sobre los parámetros ecológicos de las especies. La cordillera cantábrica actualmente proporciona condiciones adecuadas para los gatos monteses por lo que su estructura de paisaje ha de ser conservada evitando su intensificación, la cual podría amenazar no solo al gato montés si no a muchas otras especies.

Conclusiones

1. El tamaño de las áreas de campeo de los gatos monteses en Europa aumentó en zonas con mayor ocupación del paisaje por prácticas agrícolas intensivas, lo cual puede relacionarse con una mayor fragmentación del paisaje en dichos escenarios y una disponibilidad más distante de los recursos.
2. El tamaño de las áreas de campeo de los gatos monteses en Europa aumentó en escenarios caracterizados por bosques homogéneos y extensos, mientras que disminuyó al aumentar la densidad del borde de bosque, lo cual confirma la idoneidad de los hábitats en mosaico para los gatos monteses y destaca los potenciales riesgos futuros asociados a la creciente intensificación de los usos.
3. El consumo de presas por los gatos monteses en la Cordillera Cantábrica se vio afectado por la presencia de prados ganaderos. En concreto, la rata topera (un roedor pratense de tamaño considerable) fue la presa más consumida siempre y cuando los prados ocupasen más del 17% de las zonas usadas diariamente por los gatos y estuviesen más cerca de 700 m del lugar de defecación.
4. El consumo de presas varió entre estaciones, con *Arvicola* y *Apodemus* dominando la dieta del gato en verano y otoño, y en primavera, respectivamente, lo cual puede asociarse con variaciones en el uso de hábitat y cambios estacionales en la accesibilidad de las presas. Sin embargo, no encontramos relación entre la abundancia y el consumo de presas.
5. Los gatos monteses que habitan paisajes humanizados de la Cordillera Cantábrica dedicaron más tiempo a comportamientos de alerta y menos tiempo a cazar, alimentarse y moverse en presencia de humanos que en escenarios sin molestias.

6. Los gatos monteses cambiaron su comportamiento en relación al tráfico y la presencia de vehículos. En concreto, los gatos dedicaron más tiempo a cazar en escenarios con más tráfico, más cerca de carreteras y más lejos de poblados. Del mismo modo, dedicaron más tiempo a comportamientos de vigilancia durante eventos de alimentación en presencia de vehículos en movimiento.
7. El tamaño de camada de los gatos monteses durante el destete varió entre uno y tres, siendo dos el tamaño más frecuente. La mayoría de observaciones ocurrieron entre Julio y Septiembre, aunque una camada tardía fue observada en Noviembre.
8. La mayoría de cubiles secundarios fueron localizados en vegetación densa (matorral o vegetación riparia) cerca de prados ganaderos, aunque ocasionalmente los gatos utilizaron construcciones humanas con fines reproductivos. Las hembras reproductoras movieron a las crías de forma frecuente y mostraron un elevado éxito en la caza.
9. Los encuentros diurnos entre gatos monteses y zorros parecen raros, lo cual puede relacionarse con una evitación activa por parte de ambas especies. Durante los encuentros, los zorros mostraron principalmente comportamientos ofensivos, mientras que los gatos adoptaron estrategias de intimidación defensiva, probablemente en relación a su morfología. Ambas estrategias fueron igualmente efectivas para mantener el acceso a los prados de alimentación.
10. Los gatos monteses pueden explotar carroñas de ungulados, una fuente alimenticia poco documentada con anterioridad. El gato montés monitoreado utilizó comportamientos de “caching” o almacenamiento de comida similar al observado en linces o pumas, y visitó una carroña de corzo atropellado durante al menos 9 días en un

período de monitoreo de 21 días, consumiendo los principales músculos y cubriendo los restos con pelo y vegetación.