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DOCTORAL THESIS

Methods and models to analyse the abundance and spatiotemporal relationships of mesocarnivore communities from camera-trapping data

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Abstract/Resumen

Antecedentes

Durante las últimas décadas, la destrucción del hábitat y diversos factores antropogénicos han provocado modificaciones en la estructura de los ecosistemas. Entre las especies que se han visto más perjudicadas estarían los carnívoros, los cuales han sufrido amenazas constantes como la persecución directa hasta la disminución de sus poblaciones debido a la desaparición de sus presas o la fragmentación del hábitat. La desaparición de los grandes carnívoros ha permitido que especies de carnívoros más pequeñas, mesocarnívoros, ocupen nichos ecológicos antes ocupados por estos grandes depredadores. Sin embargo, esta transición también ha expuesto a los mesocarnívoros a nuevas amenazas, como la caza no selectiva y la pérdida de hábitat debido a la actividad humana. Esto ha generado la necesidad de implementar programas de monitoreo para comprender sus dinámicas de abundancia, funciones e interacciones con otras especies y su impacto en los ecosistemas.

El estudio de la abundancia de las especies se ha abordado desde numerosas perspectivas, como puede ser a través de los modelos de idoneidad de hábitat derivados de los modelos de nicho ecológico (ENM). Sin embargo, si bien se espera una relación positiva entre la idoneidad del hábitat y la abundancia, esta relación puede ser más compleja de lo esperado debido a la información que nos aportan los datos de presencia, o bien a la implicación de factores bióticos, limitaciones de dispersión y otras interacciones de coexistencia. Los avances tecnológicos y estadísticos han mejorado la precisión en la estimación de la abundancia de las especies. Entre ellos, el conteo físico de individuos, el uso de índices relativos de abundancia basados en heces o capturas de cámara trampa o la identificación individual mediante la extracción de ADN de heces son usadas para evaluar la abundancia. Sin embargo, es necesario evaluar las diferencias y las limitaciones del uso de cada método. El uso de un método u otro puede verse limitado por el número de sitios de muestreo, el número de capturas de cada individuo, la posibilidad de identificación individual de la especie, y la probabilidad de detección entre otras. Conocer la relación entre diferentes métodos que estiman abundancia puede ayudar a identificar que método se puede usar bajo diferentes escenarios. Así, la obtención de los datos de abundancia se realizará de una forma más eficiente y se podrá estudiar su efecto en diversos estudios que impliquen interacciones bióticas.

Estudios recientes señalan la necesidad de incorporar variables bióticas, como la abundancia de presas y otras especies intervinientes, para comprender mejor la ocupación de especies en un hábitat. La abundancia de presas desempeña un papel crucial en la ocupación de depredadores, y la competencia por este recurso puede influir en la coexistencia de especies. La partición de recursos y la segregación espacial y temporal son mecanismos clave para minimizar la competencia y facilitar la coexistencia. Existe una compleja interacción entre características del hábitat, abundancia de presas, competencia interespecífica y patrones de actividad y ocupación en la coexistencia de especies de carnívoros terrestres. Estos factores son fundamentales para comprender la ecología de las comunidades de carnívoros y pueden tener implicaciones importantes para la conservación de la biodiversidad.

El zorro (*Vulpes vulpes*) y la garduña (*Martes foina*) comprenden dos de los mesocarnívoros intragremiales más abundantes de la Comunidad de Madrid. Ambas especies presentan un marcado comportamiento nocturno, comparten hábitat y tienen un elevado solapamiento trófico siendo sus presas principales los roedores (*Apodemus sylvatucus, Mus spp*.**)** y el conejo **(***Oryctolagus cuniculus*). Sin embargo, algunos estudios han descrito depredación del zorro sobre la garduña mostrando cierta dominancia del zorro sobre esta. Así, el estudio de la coexistencia entre ambas especies y los factores que la regulan es de sumo interés en áreas donde los grandes depredadores están ausentes.

Objetivos

Dada la urgencia de comprender el estado de una amplia gama de especies y sus roles ecológicos, el objetivo principal de esta tesis es estudiar la relación entre metodologías de muestreo en la estimación de la abundancia de especies. Se evalúa las ventajas, limitaciones, costes y esfuerzos de muestreo para estimar la abundancia de una forma eficiente. Además, la incorporación de datos de abundancia de las especies, junto con los factores abióticos puede ser crucial para comprender las relaciones de coexistencia entre especies que comparten el mismo nicho ecológico. Para abordar este objetivo esta tesis se centra en dos de los mesocarnívoros más abundantes en la Comunidad de Madrid: el zorro rojo y la garduña. En el capítulo 1 comparamos índices relativos de abundancia obtenidos mediante metodologías de fototrampeo y conteo de excremento. Además se compararon los modelos de abundancia obtenidos con los índices con aquellos que usan conteos controlando la detección incompleta. En el capítulo 2 se estudia el número mínimo de individuos obtenidos por la metodología de fototrampeo y genotipado de ADN extraído de excrementos. Además se evalúa el número mínimo de individuos como un índice de abundancia mediante su comparación con estimaciones de la abundancia. En ambos capítulo se utiliza el zorro como especie modelo. En el capítulo 3 y 4 se aborda la implicación de la abundancia de las especies intragremiales (zorro y garduña) y presas (roedores y conejo) en la ocupación y en las relaciones de coexistencia. Específicamente en el capítulo 3 se evalúa si la ocupación entre zorros y garduñas están reguladas por la selección de hábitat, la abundancia de presas y la dominancia de los zorros sobre las garduñas. En el capítulo 4 se examina el solapamiento espacial y de los patrones de actividad entre zorros, garduñas y sus principales presas (roedores y conejos) en diferentes hábitats. Además, se evalúa la implicación de la abundancia relativa de ambos mesocarnívoros y presas en la superposición espacio-temporal entre los dos mesocarnívoros.

Metodología

Se eligieron 18 localidades independientes dentro de la Comunidad de Madrid, algunas de las cuales fueron muestreadas en diferentes estaciones y años, generando un total de 24 áreas de muestreo. Estas se organizaron en tres áreas geográficas: Norte, Sureste y Suroeste, cada una con condiciones climáticas y vegetación distintas. El área de muestreo se delimitó mediante la disposición de cámaras trampa. En cada área se colocaron entre 8 y 10 cámaras separadas entre 450-600 metros durante 20 a 36 días. Se asumió que el área total muestreada comprendía el mínimo polígono convexo (MCP) que abarcaba el perímetro trazado por las ubicaciones de las cámaras más un buffer de 500 metros alrededor del MCP. Las cámaras operaron las 24 horas del día, tomando tres fotografías secuenciales a cinco segundos de diferencia, y registrando la fecha y hora de captura. Se colocaron dos cebos frente a la cámara (aproximadamente 2 metros), sardinas y un atrayente comercial. Se revisaron las cámaras cada cuatro a siete días.

Específicamente, en el capítulo 1 y 2 se tomaron muestras de heces de diferentes senderos de un kilómetro de longitud. Cada sendero se subdividió en segmentos de 100 metros y se recogieron y cuantificaron el número de heces en el sendero y el número de segmentos marcados con heces.

En el capítulo 1 usando al zorro como especie modelo se seleccionaron 12 áreas de muestreo y 24 transectos para censo de excrementos. Estudiamos la relación entre diferentes índices de abundancia relativa: RAI (número de capturas/ocasiones totales); NI (número de individuos identificados por fotografía) generados por la metodología de fototrampeo y NSE (número de segmentos con heces) obtenido mediante el método de muestreo de censo de heces. Además, modelamos la abundancia relativa del zorro en relación a un conjunto de predictores de hábitat para cada uno de los tres índices de abundancia relativa estimados. Finalmente, comparamos los modelos de abundancia relativa explicados para cada índice con modelos *N-Mixture* que estiman la abundancia controlada para la variación en la detección.

En el capítulo 2 usando de nuevo el zorro rojo como especie modelo y usando los datos de siete localidades comparamos el mínimo número de individuos detectados. Para ello, analizamos las características morfológicas de los diferentes individuos que aparecían en las fotografías y genotipamos ADN fecal mediante un conjunto de 16 microsatélites. Además usamos los modelos *N-Mixture* para estimar la abundancia y estudiar su relación con el número mínimo de individuos detectados.

En el capítulo 3 se estudió como la abundancia relativa de las presas puede influir en la ocupación de los depredadores en un hábitat. Para esto se usó el zorro y la garduña como mesocarnívoros modelo y a los roedores y conejo como sus presas principales. Utilizamos los datos de fototrampeo de las 24 áreas de muestreo y realizamos modelos de ocupación individual para conocer la presencia de estas especies. Examinamos variables vegetales y la abundancia relativa de presas como un factor involucrado en la presencia del zorro rojo y la garduña.

El capítulo 4 se centró en la coexistencia entre el zorro, garduña, roedores y conejo. Para ello se estudió la presencia y los patrones de actividad de las cuatro especies usando los datos de fototrampeo de las 24 áreas de muestreo durante dos períodos estacionales (estación cálida y fría). Aplicamos modelos de ocupación de múltiples especies para estudiar la presencia e interacción entre zorros y garduñas y si está se veía influida por la abundancia relativa de las especies estudiadas. Además se estimó coeficientes de superposición de los patrones de actividad entre las cuatro especies utilizando el paquete *R overlap* para estudiar la coexistencia temporal entre las especies.

Resultados

Capítulo 1: No se observó una relación positiva entre todos los índices relativos de abundancia. Mientras que los índices derivados de fototrampeo (RAI y NI) tuvieron una correlación positiva entre ellos (|r| = 0.77), ambos índices mostraron una relación negativa con el índice derivado del censo de excremento (NSE) (RAI-NSE: |r| = − 0.44; NI-NSE: |r| = − 0.33). Los modelos de abundancia relativa y los modelos de *N-Mixture* mostraron una selección diferente de predictores para explicar las tendencias de abundancia. De hecho, los índices NSE y RAI seleccionaron predictores de abundancia (estación y caza) los cuales en los modelos *N-Mixture* explicaban variabilidad en la detección de zorros. Sin embargo, el índice NI y los modelos de *N-Mixture* seleccionaron los mismos predictores para explicar la abundancia de zorros (distancia a núcleos urbanos y matorral)

Capítulo 2: El número mínimo de individuos (NI) identificados mediante fototrampeo fue ligeramente mayor que el obtenido mediante el genotipado de heces de ADN, con 23.66 y 19 individuos, respectivamente. Además, la abundancia estimada mediante los modelos *N-Mixture* y el NI detectados mediante la captura con cámaras mostraron una relación positiva ($|r| = 0.68$; p-). Sin embargo, hubo una relación negativa no significativa entre los NI detectados por ambas metodologías ($|r| = -0.07$) y por NI del ADN fecal y las estimaciones de abundancia ($|r|= -0.32$).

Capítulo 3: El zorro y la garduña seleccionaron características de hábitat similares que sus presas en función del área de estudio. En el norte y sureste de la Comunidad de Madrid los mesocarnívoros seleccionaron hábitat ocupados por roedores (bosque de pino; bosques de *Quercus ilex* y áreas urbanizadas) mientras que en suroeste eligieron zonas ocupadas por conejo (zonas con mayor abundancia de conejo y matorral). El zorro seleccionó sitios con una mayor abundancia de roedores en el norte y sureste mientras que en el suroeste selecciono sitios con mayor abundancia de conejos. Sin embargo, la garduña no siguió este patrón en el norte y sureste y seleccionó los mismos hábitats que los roedores pero sin seleccionar sitios con mayor abundancia de esta presa.

Capítulo 4: Se observó una relación espacial positiva entre ambos mesocarnívoros. Así la ocupación de la garduña era mayor en áreas donde el zorro estaba presente. Los resultados mostraron una interacción espacial positiva: la ocupación de las garduñas aumentó en áreas donde estaban presentes los zorros. Así la probabilidad condicionada de la garduña en presencia de zorro fue de 0.488, mientras que en ausencia de zorro fue de 0.283. Además, la ocupación del mismo sitio aumentó cuando ambas especies eran más abundantes ($p = 0.325$). El zorro y la garduña tuvieron un patrón de actividad nocturno. Sin embargo, ambos mesocarnívoros mostraron una baja superposición temporal independientemente de la estación y del área de muestreo. Sus patrones de actividad fueron más dispares cuando la abundancia relativa de ambos mesocarnívoros era mayor. El solapamiento temporal entre zorros y roedores siguió un patrón estacional siendo mayor en los meses de invierno. El solapamiento temporal entre roedores y garduña fue mayor cuando el solapamiento temporal entre zorros y roedores era menor.

Conclusiones

Esta tesis destaca la necesidad de seleccionar métodos de muestreo adecuados para estudiar la abundancia. Diferentes métodos pueden proporcionar resultados dispares debido a sus requerimientos y limitaciones inherentes. Por lo tanto, es muy importante seleccionar cuidadosamente la técnica usada dependiendo de objetivos específicos de investigación y la especie en estudio. Independientemente del método usado es imprescindible controlar la variabilidad de detección para una modelización precisa de la abundancia. De hecho, cuando métodos de muestreos de abundancia más sofisticados no pueden ser implementados, el índice no invasivo mínimo número de individuos (NI) puede ser una alternativa fiable para estudiar la variación de abundancia de las especies foto-identificadas. Este índice muestra una correlación positiva con la abundancia real y no se ve influenciado por el sesgo de detección. Sin embargo, si se elige métodos basados en capturas por ocasión, se sugiere un procesamiento de datos que implique un control de la variación en la detección. El uso de las heces para el estudio de la abundancia puede verse influido por el diseño de muestreo. Los diseños de muestreo que se centran en transectos en lugar de senderos existentes, probablemente aumentaría la variabilidad de heces encontradas al reducir el sesgo causado por individuos que marcan con más intensidad a lo largo de los senderos. Del mismo modo, es necesario realizar más investigaciones para comparar la relación costo-eficacia de los nuevos métodos genéticos con la metodología de foto-trampeo con el fin de establecer los pros y contras de cada uno. Una estimación eficiente de la abundancia ayudaría a incorporar estos datos en estudios relacionados con las interacciones y coexistencia entre especies. La adaptabilidad ecológica de los mesocarnívoros hace que estudiar su coexistencia y los factores biológicos que la impulsan sea de interés para comprender su papel dentro de diferentes ecosistemas. Dentro de los mecanismos de coexistencia, la ocupación de las especies dominantes puede seguir un patrón dirigido principalmente por la abundancia de alimentos, mientras que las especies subordinadas tendrían patrones más complejos dependientes de la interacción con competidores dominantes. Cuando las especies tienen un solapamiento de hábitat y trófico significativo, la segregación temporal puede ser el mecanismo que permite la coexistencia entre competidores. Las especies dominantes pueden ajustar sus patrones de actividad con los patrones de actividad de sus presas, teniendo una mayor disponibilidad de alimento. Sin embargo, las especies subordinadas adaptan sus patrones para priorizar hábitats de bajo riesgo de interacciones con sus competidores a pesar de tener una menor disponibilidad de recursos alimenticios. En las zonas de la Comunidad de Madrid estudiadas bajo la

ausencia de carnívoros superiores, el zorro puede estar ejerciendo un papel de carnívoro dominante e influir significativamente en las relaciones de coexistencia con la garduña.

Abstract

Background

Over the past few decades, habitat destruction and anthropogenic factors have modified the structure of ecosystems. Among the species most affected are carnivores, which have faced constant threats from population declines due to the disappearance of their prey or habitat fragmentation. The disappearance of large carnivores has allowed smaller carnivores, or mesocarnivores, to occupy ecological niches abandoned by these large predators. However, this transition has exposed mesocarnivores to new threats, such as non-selective hunting and habitat loss due to human activity. This has generated the need to implement monitoring programs to understand their dynamics of abundance, functions, interactions with other species, and impact on ecosystems.

The study of species abundance has been approached from numerous perspectives, such as through habitat suitability models derived from ecological niche models (ENM). While a positive relationship between habitat suitability and abundance is expected, this relationship can be more complex. The information provided by presence/absent data the involvement of biotic factors, dispersal limitations, and other coexistence interactions can affect this positive relationship. Technological and statistical advances have improved the precision in estimating species abundance. Among these, physical counts of individuals, as well as the use of relative abundance indices based on scat or camera trap captures, or individual identification through DNA extraction from scat, which are used to evaluate abundance. However, it is necessary to assess the differences and limitations of each method. The use of one method or another may be limited by the number of sampling sites, the number of captures of each individual, the possibility of individual identification of the species, or the detection probability, among others. Understanding the relationship between the different methods that estimate abundance can identify which method can be used under different scenarios. As a result, obtaining abundance data will be more efficient, and it’s effect can be seen in various studies related to biotic interactions.

Recent studies show the need to incorporate biotic variables, such as the abundance of prey and other coexisted species, to better understand species occupation in a habitat. The abundance of prey plays a crucial role in predator occupation, and competition for this resource can influence species coexistence. Resource partitioning and spatial and temporal segregation are mechanisms to minimize competition and facilitate coexistence. There is a complex interaction between habitat characteristics, prey abundance, interspecific competition, and patterns of activity and occupation in the coexistence of terrestrial carnivore species. These factors are fundamental to

understanding the ecology of carnivore communities and can have important implications for biodiversity conservation.

The red fox and the stone marten (*Martes foina*) are two of the most abundant intraguild mesocarnivores in the Community of Madrid. Both species have nocturnal behaviour, share habitats, and have a high trophic overlap, with their main prey being rodents (*Apodemus sylvaticus, Mus spp*.) and rabbits (*Oryctolagus cuniculus*). However, some studies have described predation of the stone marten by the red fox, indicating a certain dominance of the fox over the marten. Thus, the study of the coexistence between these two species and the factors driving it is of great interest in areas where large predators are absent.

Objectives

Given the urgency of understanding the status of a wide range of species and their ecological roles, the main objective of this thesis is to study the relationship between sampling methodologies to estimate species abundance. The advantages, limitations, costs, and sampling efforts for efficiently estimating abundance are evaluated. Additionally, incorporating species abundance data along with abiotic factors can be crucial for understanding the coexistence relationships between species that share the same ecological niche. To address this objective, this thesis focuses on two mesocarnivores: the red fox and the stone marten. In Chapter 1, we compare relative abundance indices obtained through camera-trapping and scat counts methods. Additionally, we compare abundance models obtained with these indices to those using counts that control imperfect detection. In Chapter 2, the minimum number of individuals obtained through camera-trapping and DNA genotyping from scat is studied. Moreover, the minimum number of individuals is evaluated as an abundance index by comparing it with abundance estimates. In both chapters, the red fox is used as a model species. Chapters 3 and 4 address the implications of the abundance of intraguild species (fox and marten) and prey (rodents and rabbits) on occupancy and coexistence relationships. Specifically, in Chapter 3, we evaluate whether the occupancy of foxes and martens is regulated by habitat selection, prey abundance, and fox dominance over martens. In Chapter 4, we examine the spatial overlap and activity patterns between foxes, martens, and their main prey (rodents and rabbits) in different habitats. Finally, we assess the implications of the relative abundance of both mesocarnivores and prey in the spatiotemporal overlap between the two mesocarnivores.

Methodology

Eighteen independent locations within the Community of Madrid were selected, some of which were sampled in different seasons and years, including a total of 24 sampling areas. These were encompassed into three geographic areas: north, southeast, and southwest, each with different climatic and vegetation characteristics. The sampling area was delimited by the arrangement of camera traps. In each area, between 8 and 10 cameras were placed 450-600 metres apart for 20 to 36 days. It was assumed that the total sampled area comprised the minimum convex polygon (MCP) encompassing the perimeter outlined by the camera locations plus a 500-metre buffer around the MCP. The cameras operated 24 hours a day, taking three sequential photographs at five-second intervals, and recording the date and time of capture. Two baits were placed in front of the camera (approximately 2 metres away), sardines and a commercial attractant. The cameras were checked every four to seven days. Specifically, as discussed in chapters 1 and 2, faecal samples were taken from different trails one kilometre in length. Each trail was subdivided into 100-metre segments, and the number of scats on the trail and the number of segments marked with scats were collected and quantified.

In Chapter 1, using the fox as a model species, 12 sampling areas and 24 transects for scat census were selected. We studied the relationship between different relative abundance indices: RAI (number of captures/total occasions); NI (number of individuals identified by photograph) generated by the camera-trapping methodology and NSE (number of segments with scats) obtained through the scat census sampling method. Additionally, we modelled the relative abundance of the fox in relation to a set of habitat predictors for each of the three estimated relative abundance indices. Finally, we compared the relative abundance models explained for each index with *N-Mixture* models that estimate abundance controlled for variation in detection.

In Chapter 2, again using the red fox as a model species and using data from seven locations, we compared the minimum number of individuals detected. For this, we analysed the morphological characteristics of the different individuals captured in the photographs and genotyped faecal DNA using a set of 16 microsatellites. We also used *N-Mixture* models to estimate abundance and study its relationship with the minimum number of individuals detected.

In Chapter 3, we studied how the relative abundance of prey can influence the occupancy of predators in a habitat. For this, the fox and stone marten were used as

model mesocarnivores and rodents and rabbits as their main prey. We used camera-trapping data from the 24 sampling areas and conducted individual occupancy models to determine the presence of these species. We examined vegetation variables and the relative abundance of prey as a factor involved in the presence of the red fox and stone marten.

Chapter 4 focused on the coexistence between the fox, stone marten, rodents, and rabbits. We studied the presence and activity patterns of the four species using camera-trapping data from the 24 sampling areas during two seasonal periods (warm and cold seasons). We applied multi-species occupancy models to study the presence and interaction between foxes and martens. We evaluated whether the relative abundance of both mesocarnivores influence in their interactions. Additionally, we estimated the coefficients of overlap of the activity patterns among the four species using the R package *overlap* to study the temporal coexistence between the species.

Results

Chapter 1: No positive relationship was observed among all the relative abundance indices. While the indices derived from camera-trapping (RAI and NI) were positively correlated with each other (|r| = 0.77), both indices showed a negative relationship with the index derived from scat census (NSE) (RAI-NSE: |r| = −0.44; NI-NSE: |r| = −0.33). The relative abundance models and the *N-Mixture* models showed different selections of predictors to explain abundance pattern. In fact, the NSE and RAI indices selected predictors of abundance (season and hunting), which in the *N-Mixture* models explained variability in fox detection. However, the NI index and the *N-Mixture* models selected the same predictors to explain fox abundance (distance to urban centres and scrubland).

Chapter 2: The minimum number of individuals (NI) identified by camera-trapping was slightly higher than that obtained through faecal DNA genotyping, with 23.66 and 19 individuals, respectively. Additionally, the abundance estimated by the *N-Mixture* models and the NI detected by camera-trapping showed a positive relationship (|r| = 0.68). However, there was a non-significant negative relationship between the NI detected by both methodologies (|r| = -0.07) and between the NI from faecal DNA and the abundance estimates (|r| = -0.32).

Chapter 3: Foxes and stone martens selected habitat characteristics similar to their prey depending on the study area. In the north and southeast of the Community of Madrid, the mesocarnivores selected habitats occupied by rodents (pine forest;

Quercus ilex forests and urban areas), while in the southwest, they chose areas occupied by rabbits (areas with higher rabbit abundance and scrubland). Foxes selected sites with a higher abundance of rodents in the north and southeast, while they selected sites with higher rabbit abundance in the southwest. However, stone martens did not follow this pattern in the north and southeast, selecting the same habitats as rodents but not selecting sites with higher rodent abundance.

Chapter 4: A positive spatial relationship was observed between both mesocarnivores. Thus, the occupancy of stone martens was higher in areas where foxes were present. The results showed a positive spatial interaction: the occupancy of stone martens increased in areas where foxes were present. The conditional probability of stone marten occupancy in the presence of foxes was 0.488, while in the absence of foxes, it was 0.283. Additionally, co-occupancy increased when both species were more abundant ($p = 0.325$). Both foxes and stone martens had a nocturnal activity pattern. However, both mesocarnivores showed low temporal overlap regardless of season and sampling area. Their activity patterns were more disparate when the relative abundance of both mesocarnivores was higher. The temporal overlap between foxes and rodents followed a seasonal pattern, being greater in the winter months. The temporal overlap between rodents and stone martens was higher when the temporal overlap between foxes and rodents was lower.

Conclusions

This thesis highlights the need to select appropriate sampling methods to study abundance. Different methods can provide disparate results due to their inherent requirements and limitations. Therefore, it is very important to carefully select the technique used depending on the specific research objectives and the species under study. Regardless of the method used, it is essential to control for detection variability for accurate abundance modelling. In fact, when more sophisticated abundance sampling methods cannot be implemented, the non-invasive minimum number of individuals index (NI) can be a reliable alternative for studying the variation in abundance of photo-identified species. This index shows a positive correlation with actual abundance and is not influenced by detection bias. However, if methods based on captures per occasion are chosen, data processing that involves controlling for detection variation is suggested. The use of scats to study abundance can be influenced by sampling design. Sampling designs that focus on transects rather than existing trails are likely to increase the variability of scats found by reducing the bias caused by individuals marking more intensively along trails. Similarly, further research is needed to compare the cost-effectiveness of new genetic methods with camera-trapping methodology to establish the pros and cons of each. Efficient abundance estimation would help incorporate this data into studies related to species interactions and coexistence. The ecological adaptability of mesocarnivores makes studying their coexistence and the biological factors driving it of interest to understand their role within different ecosystems. Among coexistence mechanisms, the occupancy of dominant species may follow a pattern mainly driven by food abundance, while the subordinate species may have more complex patterns dependent on interaction with dominant competitors. When species have significant habitat and trophic overlap, temporal segregation may be the mechanism allowing coexistence among competitors. Dominant species may adjust their activity patterns to match those of their prey, having greater food availability. However, subordinate species adapt their patterns to prioritise low-risk habitats of interaction with competitors despite having lower food resource availability. In the areas of the Community of Madrid studied, in the absence of higher carnivores, the fox may be playing the role of a dominant carnivore, significantly influencing a coexistence relationship with the stone marten.

General Introduction

Background

Loss of carnivore biodiversity

During the last decades, anthropogenic-driven agents of environmental change such as global warming, habitat destruction, invasive species, pollution and the overexploitation of resources have all seen a substantial rise causing the loss of biodiversity (Habibullah et al. 2022). In the Mediterranean regions, the impact of these global threats has particularly caused significant modifications in the structure and organisation of terrestrial ecosystems (Peñuelas et al. 2017), with the loss of habitat for many wildlife species (Bermúdez 2001; Valladares 2007; Pörtner et al. 2022).

Other human-driven impacts, stemming from competition with wildlife species for shared resources, also frequently cause conservation conflicts with detrimental effects for wildlife species. This is particularly evident with mammalian carnivores that, due to their predatory behaviour, target game and domestic species (Lozano et al. 2019). Consequently, 60% of carnivore species are classified as vulnerable, endangered, or critically endangered on the IUCN Red List, and 70% have experienced population declines (Ripple 2014; Trouwborst 2015).

Despite persecution and negative perceptions, carnivore species play a vital role in ecosystems (Terborgh et al. 1999; Ray et al. 2013). By regulating prey populations they trigger cascade effects throughout food chains (Beschta and Ripple 2009; Estes et al. 2011). This important function has received increased attention on the conservation of carnivores and their habitats (LCIE.org 2013; Ripple et al. 2014; Papp et al. 2020). Protecting carnivore areas benefits other coexisting species through a process known as the 'umbrella effect' (Noss et al. 1996).

Among carnivore species, the population of large carnivores have suffered significant declines worldwide (Ripple et al. 2014) due to habitat loss, human persecution, removal of prey presence or reductions of prey abundance (Gittleman et al. 2001; Wolf and Ripple et al. 2016; Wolf and Ripple et al. 2017). A consequence of the decline of large carnivores is a phenomenon called 'meso-predator release' (Ritchie and Johnson 2009; Brashares et al. 2010; Prugh et al. 2009). With less predation pressure from apex carnivores, the populations of smaller carnivore species can surge, which alters the entire trophic community (Prugh et al. 2009). .

Mesocarnivores, defined as carnivore species weighing less than 15 kg, are characterized by a remarkable diversity, richness, and greater behavioural and ecological versatility compared to larger carnivores (Roemer et al. 2009). Mesocarnivores play crucial roles in various ecosystem functions. Notably, they can influence soil nutrient availability by altering plant composition and nutrient cycling (Roemer et al. 2009). Additionally, they may facilitate seed dispersal over longer distances, either directly or by preying on seed dispersing animals (Herrera 1989; Silverstein 2005; Jordano et al. 2007). However, mesocarnivores can also have negative impacts in the abundance and distribution of prey, and even lead to the extinction of native species when introduced as exotic predators (Johnson 2006; Letnic and Dickman 2010). Due to this potential duality, the role of mesocarnivores remains a topic of ongoing debate. Further research is required to fully understand their abundance dynamics, functions, and interactions with other species.

In the Iberian Peninsula, large carnivores like the wolf (*Canis lupus*) and the Iberian lynx (*Lynx pardinus*) (Blanco et al. 1992; Delibes et al. 2000; Molsher et al. 2017) were extirpated from many areas. Consequently, this loss of apex predators allowed mesocarnivores to fill the vacant ecological niches. The emergence of mesocarnivores led to new interactions and ecological roles among predators, impacting local ecosystem functions and dynamics (Monterroso et al. 2020).

The Iberian Peninsula is home to two relevant and abundant mesocarnivores: the red fox (*Vulpes vulpes*) and the stone marten (*Martes foina*). The stone marten, a member of the Mustelidae family, is a generalist that thrives in a wide range of habitats across its distribution range (Virgós and García 2002; Santos and Santos-Reis 2010). It weights between 1.100-2.500 g for males and 900-1.400 g for females. With a remarkable diet adaptability, the primary prey of the stone marten are micromammals such as *Apodemus* and *Microtus*, but its diet also includes small and medium-sized birds and reptiles, and fruits, with seasonal variations (Genovesi et al. 1996; Bakaloudis et al. 2012).

The red fox, on the other hand is a member of the family Canidae and the sole representative of the genus *Vulpes* in the Iberian Peninsula. Males typically weigh around 8.6 Kg and females are slightly smaller at 7.8 Kg (Gortázar 2007). The fox is broadly distributed throughout the Iberian Peninsula and selects heterogeneous habitats (Virgós et al. 2002; Pita et al. 2009; Pereira et al. 2012). Well known for its opportunistic foraging behaviour, the red fox selects prey according to the relative abundance of available food sources (Díaz-Ruiz et al. 2013). Rabbits (*Oryctolagus cuniculus*), micromammals, fruits, and invertebrates, are all part of the fox diet in the Iberian Peninsula (Padial et al. 2002; Delibes-Mateos et al. 2008; Díaz-Ruiz et al.

2013). Additionally, this dietary flexibility extends to scavenging carrion and consuming anthropogenic waste in human-dominated environments (Lucherini and Lovari 1995; Jankowiak et al. 2016).

While mesocarnivores may benefit from the loss or decline of large carnivores through the 'meso-predator release' effect (Prugh and Sivy 2020), they also face threats from humans. The use of non-selective hunting techniques such as snares traps or poisons significantly reduce their populations (Virgós and Travaini 2005). Habitat fragmentation caused by human fragmentation also restricts their movements and resources (Virgós et al. 2002). Additionally, intra and inter specific (within and between species, respectively) competition and interactions can further exacerbate population decline (Remonti et al. 2022). Therefore, monitoring programs of mesocarnivore populations is crucial for understanding the patterns and factors influencing their abundance and the potential consequences for ecosystem function. In this vein, sampling methods have been developed over the last decades to estimate species abundance (MacKenzie et al. 2002; Royle and Nichols 2003; Efford et al. 2004; O'Brien 2011; Jiménez et al. 2019). However, there is still a need for comparative studies to evaluate the most cost-effective and reliable methods for conducting abundance estimates. Accurate estimates of mesocarnivore species abundance are essential for understanding how they respond to their environment and to inform effective management and conservation programs.

Abundance data are often used to identify the population status of a species and its interactions with the physical environment. These data are also valuable for determining the nature and strength of relationships between species, including their ability to coexist (Chase et al. 2002). Processes such as competition, coexistence, and predation between species sharing the same habitat can be substantially affected by the abundance of resources and the species involved in these ecological interactions (Amarasekare 2008; Kendall et al. 2012; Barrull et al. 2014). Moreover, these relationships often show variation depending on specific locations, habitat type, productivity, and other contextual factors (Virgós et al. 2002; Pita et al. 2009; Carbone et al. 2011; Ripple et al. 2013). Understanding these relationships between species is vital for delineating species’ ecological niche (Elton 1957; Hutchinson 1957; Soberón 2010), including competitive interactions, coexistence mechanisms, and predator-prey dynamics within a shared habitat (i.e. the physical environment that allows organisms to survive and reproduce). Moreover, comprehending the biotic and abiotic factors influencing these relationships is essential for accurately interpreting each species' role in the ecosystem. This knowledge is fundamental for developing specific conservation and management strategies that ensure a healthy and balanced ecosystem.

Ecological niche models (ENMs) *and abundance*

Hutchinson (1957) built upon the concept of the ecological niche as an n-dimensional hyper volume. Each dimension represents an environmental factor crucial for a species' survival and reproduction. He further distinguished two types of niche:

1. The fundamental niche (NF), building on Grinnell's (1917) niche concept, encompasses the abiotic variables (environmental conditions) and scenopoietic variables (factors unrelated to species interactions) that define the theoretical conditions where a species could exist and thrive in the absence of competition or other interactions with other species.
2. The realized niche (NR), building upon Elton's (1927) niche concept, reflects a species' actual ecological niche. Unlike the fundamental niche, the realized niche incorporates biotic interactions (bionomic variables) alongside abiotic conditions. These biotic factors encompass competition, predation, mutualism, and diseases (Vandermeer 1972).

The ecological niche concept links a set of environmental variables to a species’ ability to survive and reproduce, also known as fitness (Hizel and Lay 2008). Ecological niche models (ENMs) take observations of a species occurrence and absence and relate them to its environment. This approach allows estimating aspects of the species’ niche across space and time (Brown and Griscom 2022). The main goal of ENM is to create a map showing the probability of a species' presence at each geographic location. This map is built based on the abiotic variables that define the species’ ecological niche (Wiens et al. 2010; Becerra-López et al. 2017). Multiple available modelling approaches use either species’ presence-only or both presence and absence data to project the potential distribution of suitable habitat for the species across the geographic landscape (Ríos-Muñoz et al. 2021).

Several limitations need to be considered when using ENMs for niche modelling (Sillero et al. 2021). Most models rely solely on abiotic variables, which define the fundamental niche. However, the biotic relationships between the species and accessibility of areas are also crucial factors to model the realized niche where a species actually thrives (Soberón and Peterson 2005; Peterson et al. 2011). This limitation stems from the challenges of measuring biotic variables, their geographical accessibility, and the lack of knowledge for some species (Soberón and Peterson

2005; Soberón 2007). Consequently, models using only abiotic variables may have limited explanatory and predictive accuracy in explaining species distributions (Ríos-Muñoz et al. 2021). Furthermore, presence data in ENMs might not always represent optimal environmental conditions for a species' ecological niche. For instance, presence data can come from sink populations, which exist in very low-quality habitats that would not typically support a population. In such cases, the presence data would reflect areas accessible to the species but with suboptimal variables for its ecological niche (Pulliam 1988; Clark et al. 1993).

Ecological niche models are widely used to model and map species distributions, but the link between these models and the species' remains a topic of investigation (Weber et al. 2017). Habitat suitability models derived from ENM offer an approach to identify the spatial variation of a species abundance within a population (VanDerWal et al. 2009; Weber and Grelle 2012; Pérez-Irineo et al. 2019; Fuente et al. 2021). In fact, both abundance and distribution are ultimately limited by the combination of physical and biotic environmental factors defining a species' niche (Brown 1984; Fuente et al. 2021). Weber et al. (2017) found a positive relationship between abundance and environmental suitability. Brown (1984) further proposed that the specific spatial distribution of abundance depends on the number and nature of environmental factors shaping the niche, as well as the spatial variations of these factors. Distance-abundance niche theory (Maguire 1973) suggests that abundance at a particular site should be related to its environmental position within the niche space. Sites with environments closest to the centre of the fundamental niche, where species fitness is expected to be highest, would then harbour the highest population densities (Martínez-Meyer et al. 2013; Osorio-Olvera et al. 2019). However, this theory is controversial and has been contested by other studies (Sagarin and Gaines 2002; Dallas et al. 2017; Dallas and Hastings 2018; Santini et al. 2018).

Gathering data on how a species' abundance varies across its geographic range can be a significant challenge due to the high costs and logistic efforts involved (Soberón and Peterson 2004). This challenge leads to a critical question: can habitat suitability models, built using presence-only data, provide insights into local abundance patterns? (Jiménez-Valverde 2011). Intuitively, this might seem unlikely in many cases. Sites with higher environmental suitability likely represent the best environmental conditions for a species, leading to larger populations. Conversely, areas with lower environmental suitability are expected to support smaller populations (VanDerWal et al. 2009; Weber et al. 2017). This suggests a positive relationship with abundance, which could be linear (Pearce and Ferrier 2001; Nielsen et al. 2005; Jiménez-Valverde et al. 2009) or more moderate (Seoane et al. 2005; Tellería et al. 2012). Some studies have even suggested that high species abundance may be associated with low habitat suitability values, suggesting a more complex interplay between niche suitability, abundance, and species fitness (Morris 1989; Gergs et al. 2014; Aliperti et al. 2022). Certain abiotic factors, biotic interactions, or limitations on dispersal can potentially restrict the abundance in otherwise suitable areas (Soberón and Peterson 2005; VanDerWal et al. 2009; Torres et al. 2012; Osorio-Olvera et al. 2016; Dallas and Hastings 2017). In fact, the predicted environmental suitability often reflects the upper limit of abundance for a species in a given location rather than the mean abundance (VanDerWal et al. 2009; Acevedo et al. 2017).

Abundance estimation

Ecologists have developed various methods to directly assess species abundance. These methods can involve physically counting individuals or using relative abundance indices based on indicators such as scat counts or camera trap captures (Karanth and Nichols 1998; Cavallini 1994; Virgós et al. 2000; Palmer et al. 2018). Recent technological and statistical advancements have revolutionized the study of species abundance, particularly through individual identification of animals. These methods include camera-trapping, which allows researchers to identify animals based on unique physical characteristics like body size, age, markings, tail features, or any other trait. Another widely used non-invasive technique involves extracting DNA from scats for individual identification (Karanth and Nichols 1998; Jackson et al. 2006; Mondol et al. 2009; Galaverni et al. 2012). Data on identified individuals from these methods are then incorporated into capture-recapture models to estimate species abundance or other population parameter of interest like birth and mortality rates, as well as immigration and emigration rates.

Recent advancements in capture-recapture methods, particularly those incorporating spatially capture-recapture (SCR) techniques, have significantly improved our ability to assess species abundance. These techniques account for the variations in detection probability across an area, providing more accurate and comprehensive abundance estimates (O'Brien et al. 2011; Morin et al. 2016; Burgar et al. 2018; Davis et al. 2022).

Also, SCR methods address spatial limitations of conventional capture-recapture techniques (Borchers and Efford 2008; Royle et al. 2014). Traditional capture-recapture methods often neglect the spatial distribution and structure of the data. Additionally, traditional methods fail to link between abundance and sampling area. This can lead to arbitrary estimates. Furthermore, abundance estimates in standard capture-recapture methods depend on the size of the capture grid. Thus, traditional methods require a grid size at least four times larger than an individual's home range to avoid biases in density estimation (Sollmann et al. 2012; Royle et al. 2014; Roffler et al. 2019). However, SCR methods also come with certain assumptions that can be challenging. Maintain key assumptions, such as demographic and geographic closure, random distribution of activity centres, and a decrease in detection probability with distance, can be difficult through a study (Royle and Andrew 2013). SCR methods also require substantial sampling effort, with typically a minimum of 20-25 recaptures, including spatial recaptures, to accurately model movement patterns (Efford et al. 2004; Efford et al. 2009). Alternatively, movement data from telemetry tags can be incorporated to enhance abundance estimates (Jiménez et al. 2019a).

If individual identification or species' range is unknown, employing traditional capture-recapture methods or spatially explicit capture-recapture (SCR) methods becomes impractical. In such cases, techniques such as *N-Mixture* models offer a valuable alternative. *N-Mixture* models use data from spatially-replicated count surveys to estimate population size while accounting for the detection process (Royle 2004; Ficetola et al. 2018; Kidwai et al. 2019; Costa et al. 2020). However, these methods have limitations. To account for imperfect detection, a substantial number of spatially replicated surveys are typically required, often exceeding 20 sites (Kéry and Schaub 2012). Additionally, a high probability of detection is necessary for reliable abundance estimates (Royle 2004; Veech et al. 2016).

When implementing more robust methods for studying species abundance are impractical, indices of relative abundance can be a practical and valuable alternative, especially for species that are difficult to monitor or capture (Williams et al. 2002; O'Brien 2011). Common alternatives are faecal counts along transects and capture rates in camera traps (Barea-Azcón et al. 2007; Palmer et al. 2018). These indices often correlate positively with population size (Caughley and Sinclair 1994), meaning changes in index values typically reflect changes in true abundance (Romesburg 1981; Anderson 2003). However, this relationship is not always constant or positive across species or over time (O'Brien 2011). Moreover, different indices can respond differently to the same habitat characteristics, requiring careful selection of habitat predictors to explain abundance patterns specific to the chosen index (Martin-Garcia et al. 2022). A major limitation of these indices is their tendency to underestimate population size when detection probability is less than 1 or varies over time (O'Brien 2011). Detection variability is influenced by factors influencing count variations, not just changes in species abundance (Pollock et al. 2002; Gu and Swihart 2004; Royle et al. 2005).

Furthermore, the effectiveness of these sampling techniques can be constrained under certain conditions, impacting the reliability of abundance estimates. For instance, low humidity and temperature can lead to poor quality of DNA in faecal samples (Murphy et al. 2007). Individual variation in faecal deposition or habitat preferences can also affect accuracy (Vila et al. 1994; Webbon et al. 2004; Barja and List 2014). Similarly, temperature fluctuations can reduce animal detection and introduce detection biases in camera-trapping with infrared camera traps (Meek et al. 2015).

The role of spatial and temporal overlap in species coexistence: Utilizing occupancy models

Habitat characteristics have long been linked to species presence and their habitat preferences (Virgós et al. 2003; McDonald et al. 2008; Santos and Santos-Reis 2010; Soto and Palomares 2015). Niche models have traditionally relied on these habitat characteristics and abiotic factors to investigate species coexistence (Fedriani et al. 1999; Zielinski et al. 2017; Hemami et al. 2018). However, recent research suggest that beyond abiotic factors, other biotic elements such as prey abundance and the abundance of interacting species can significantly influence a species' occupancy within a habitat and its ability to coexist with others (Soto and Palomares 2015; Karanth et al. 2017; Pokheral and Wegge 2018; Monterroso et al. 2020; Strampelli et al. 2023). Therefore, incorporating spatial interactions that facilitate species coexistence into niche modelling becomes a crucial research area.

Occupancy models have significantly revolutionized the study of habitat selection to explain species occupancy within a habitat (MacKenzie et al. 2002; Bailey and Adams 2005). Similar to ecological niche models, occupancy models use presence and absence data to determine a species' presence in a specific location. However, occupancy models can incorporate spatial-temporal or biotic variables (Bailey et al. 2014) while accounting for imperfect detection. This means the model can account for situations where a species might be present but go undetected (Royle 2006). Iidentifying factors that influence a species' detectability across different habitats is crucial for constructing robust occupancy models. Failing to consider these variations, assuming perfect or constant detection, can lead to biased estimates of occupancy, especially when detectability varies between habitat types (Guand Swihart 2004; MacKenzie and Royle 2005). By addressing these issues, occupancy models have enabled a more precise understanding of factors influencing species occupancy within a habitat. Furthermore, occupancy models can potentially identify those variables that remain consistent across diverse habitats, influencing the selection of other habitat variables. Distinguishing between invariant variables and those exhibiting spatial and contextual variations is critical to better understand species occurrence across different habitats. This knowledge is particularly valuable for assessing occupancy patterns and coexistence mechanism, especially for wide-ranging mesocarnivores (Cavallini and Lovari 1991; Virgós et al. 2002; Pereira et al. 2012).

Biotic variables such as prey abundance play an important role in shaping the occupancy patterns of predator species. Predators tend to prefer areas with high prey abundance (Robison et al. 2014; Rabelo et al. 2019). Thus, food becomes a critical resource, and its partitioning among sympatric species (i.e. species occupying the same geographic area) is essential for their coexistence (Jedrzejewski et al. 1989; Carvalho and Gomes 2004). Mesocarnivores can achieve trophic segregation through various mechanisms, including differences in body size, seasonal variations in prey abundance, or their level of dietary specialization (Carvalho and Gomes 2004; Santos et al. 2019). Prey abundance significantly influences the competitive dynamics between species that share these resources. For example, low prey abundance can lead to the exclusion of dominant species, while high abundance may facilitate the displacement of subordinate species. Intermediate prey levels, however, can promote coexistence by reducing agonistic encounters (direct confrontations) between dominant and subordinate species (Holt and Polis 1997; Robison et al. 2014). Additionally, other variables such as the density of dominant species can further regulate the intensity of competition (Creel and Creel 1996; St-Pierre et al. 2006). Creel and Creel 1996 observed a negative correlation between the densities of African wild dogs (*Lycaon pictus*) spotted hyenas (*Crocuta Crocuta*), and lions (*Panthera leo*). Similarly, St-Pierre et al. 2006 studied the intraguild competition between two mustelid species. They found that the smaller species, the least weasel (*Mustela erminea*) responded to increased abundance of the larger species, the long-tailed weasel (*Mustela frenata*), by reducing its use of preferred habitats already occupied by the latter.

For terrestrial carnivores, resource partitioning (i.e. dividing resources like food or shelter) or spatial and temporal segregation (i.e. separating activity times or locations) are key mechanisms that minimize competition and facilitate coexistence (Ramesh et al. 2012; Torreta et al. 2016; Monterroso et al. 2020). However, maintaining these strategies can be particularly challenging for species like the red fox and the marten, which exhibit significant overlap in their diets and habitat use (Padial et al. 2002; Papakosta et al. 2010; Pereira et al. 2012). In competitive interactions, body size ratio plays a crucial role in determining the intensity and direction of the interaction (Palomares and Caro 1999, Donadio and Buskirk 2006). The larger red fox, in some areas no longer subject to control by even larger carnivores, can be considered the dominant species in this relationship with the marten. Dominant individuals can influence the population size, distribution, and behaviour of subordinate species (Vanak et al. 2013; Fedriani et al. 2000; Monterroso et al. 2020). One potential consequence of this competition is intraguild predation, where one species prey on the other, as both the fox and the marten share prey resources (Polis et al. 1989; Rosenheim et al. 1995).

For species sharing spatial and trophic resources (habitat and food), segregation of activity patterns can emerge as a key regulatory mechanism for species coexistence (Monterroso et al. 2014). Daily activity patterns are influenced by internal factors like genetics (Buhr and Takahashi 2013) and endogenous rhythms (Kronfeld-Schor and Dayan 2003). However, external factors play a crucial role in shaping and modifying these patters, including abiotic and biotic factors that ultimately shape and modulate activity patterns (Monterroso et al. 2013; Torretta et al. 2016). Studying activity patterns can therefore provide valuable insights into the ecological and behavioural strategies that enable species to coexist.

As previously mentioned, predators often select areas with an abundant prey but may adjust their activity patterns to match those of their prey, maximizing access to food resources (Linkie and Ridout 2011; Foster et al. 2013). They may even exploit the same prey species but at different times of the day (Garneau et al. 2007). However, dominant species can significantly influence the activity patterns of subordinate competitors, impacting their access to food (Hayward and Slotow 2009; Monterroso et al. 2014; Elbroch and Kusler 2018). Dominant species may disrupt the synchronization between subordinate species and their shared prey, leading to reduced food availability for the subordinates (Kronfeld-Schor and Dayan 2003). Consequently, subordinate species must weigh the risk of encountering dominant competitors against the potential benefits of increased prey availability (Fedriani et al. 2000). In addition to prey abundance, the abundance of dominant species, climate conditions, and habitat composition are additional factors that can influence the activity patterns of mesocarnivores (Rosalino et al. 2005; Suraci et al. 2016; Monterroso et al. 2013).

Objectives

This doctoral thesis steams from the key methodological issues raised in the introduction. While recent decades have seen significant progress in developing more sophisticated and reliable techniques for studying species abundance, these methods often involve and require increased sampling effort and financial investment. However, the pressing need to understand the status of a wider range of species and their ecological roles requires the development of faster, less expensive, and reliable methods for population size estimations. With this aim, this thesis studies two of the most abundant mesocarnivores in the Community of Madrid: the red fox and the stone marten. The general aim is to gain a deeper understanding of how the different abundance estimators correlate and their advantages and limitations under varying environmental conditions. Furthermore, incorporating biotic data, such as species population size, can be crucial in understanding the relationships (predation-prey, coexistence) between species sharing the same ecological niche. Therefore, assessing species abundance alongside abiotic factors will provide valuable insights into the mechanisms of coexistence between species. To achieve this overarching goal, the following four specific objectives are addressed in four dedicated chapters:

Chapter 1.- Comparing abundance indices: This chapter compares relative abundance indices obtained by camera-trapping and scat counting methodologies. Additionally, the abundance models generated by each index are compared with models that account for imperfect species detection.

Chapter 2.- Minimum Number of Individuals as an Abundance Index: the red fox as a model species within the same spatiotemporal environment, this chapter compares the effectiveness of camera-trapping and DNA genotyping from scats in detecting the minimum number of individuals. Furthermore, it evaluates the minimum number of individuals as an abundance index by comparing it with estimates of fox abundance derived using other methods.

Chapter 3.- Occupancy Patterns and Coexistence of Foxes and Martens: This chapter investigates the factors that consistently influence the occupancy patterns of foxes and martens across different habitats and their implications for coexistence. Specifically, it assesses whether the spatial overlap between foxes and martens is regulated by habitat selection, prey abundance, and the dominance of foxes over martens.

Chapter 4.- Activity Patterns and Overlap Between Mesocarnivores and Prey: This chapter examines the overlap in activity patterns between foxes, martens, and their main prey (rodents and rabbits) across different habitats. Additionally, it evaluates whether the relative abundance of both mesocarnivores and prey determines the spatiotemporal overlap between the two mesocarnivores.

General material and methods

General material and methods

Study area

We chose 18 independent locations within the Community of Madrid. Five of these locations were surveyed in different years and seasons, resulting in data from a total of 24 locations (Figure 1). These locations were grouped into three geographical areas: North, Southeast and Southwest. Each area encompassed unique climatic conditions, land uses, and predominant plant communities, spanning both supramediterranean and mesomediterranean bioclimatic environments (Ministerio de Medio Ambiente y Ordenación del Territorio, 2001) (Table 1).

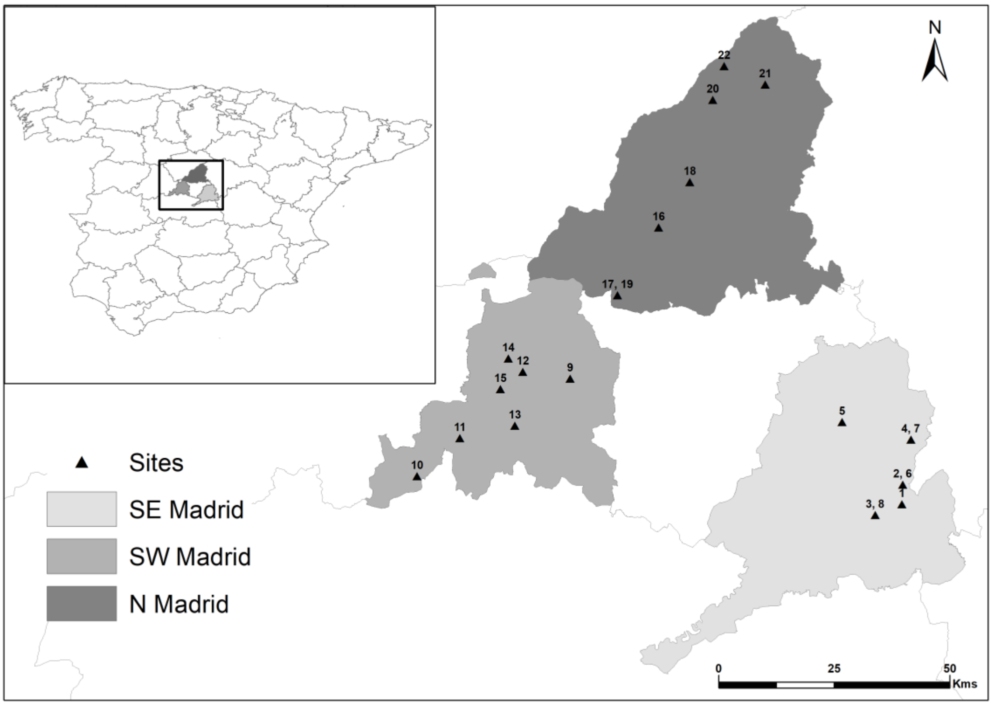

Figure 1. Location of the 24 sampling sites in three areas of central Iberian Peninsula (Autonomous Community of Madrid): north (N), noutheast (SE) and southwest (SW).

The specific locations and sampling years employed varied depending on the research objective of each chapter (Table 2). Chapter 1 utilized data from 12 locations, Chapter 2 from 7 locations and for chapter 3 and 4 leveraged data from all 24 locations. Details regarding the specific locations chosen for each chapter can be found in the respective material and methods sections.

Table 1. Plant composition; Climate; Temperature (T (ºC)); Precipitations (PP (mm)) and Land uses of the three areas studied in the Autonomous Community of Madrid

Area	Plant composition	Climate	T (ºC)	PP(mm)	Land uses
North	Holm oak (*Quercus ilex*) accompanied by *Juniperus oxycedrus*, *Fraxinus angustifolia* and *Cistus ladanifer*. Melojar oak woodlands (*Q. pirenaica*) with *C. laurifolius, Genista florida, J.communi* and some grassland areas. Areas of Scots pine (*Pinus sylvestris*). Rockrose broom (*Cistus spp*) and thyme (*Thymus vulgaris*) form thickets with the presence of pine forests over 1400 meters above sea level.	Meso and supra-mediterranean	Average minimum temperature of -1.5 and a maximum of 28ºC	Annual precipitation around 561 mm	Pasture, livestock and recreational areas
Southeast	Different vegetation mosaics with a predominance of olive groves (*Olea europaea*); holm oak groves (*Q. ilex*) accompanied by *Q. coccifera* and *C. clusii*; thyme groves (*Thymus vulgaris*), atochares (*Stipa tenacissima*), *Genista scorpius* and *Rosmarinus officinalis*.	Meso-mediterranean	Average minimum temperature of -0.4 and a maximum of 33.2ºC	Annual precipitation around 267.5 mm	Predominantly agricultural and game hunting uses
Southwest	Mostly coniferous forest, particularly stone pines (*Pinus pinea*) and *Pinus pinaster*. On the slopes, holm oaks (*Quercus ilex*), cork oaks (*Quercus suber*), junipers (*Juniperus oxycedrus*) and chestnuts trees (*Catanea sativa*) occur.	Meso-mediterranean	Average minimum temperature of 2 and a maximum of 33ºC	Annual precipitation around 382 mm	Predominantly agricultural, pasture uses, with some game hunting areas.

Table 2. Sampling of 18 locations within the study areas. Data show the year and season of scats and camera-trapping sampling. Faecal DNA was extracted from 7 study areas. Camera-trapping (days) show the number of nights cameras-traps were operating depending on the year. Number of camera traps shows the number of cameras placed for each year. The number between brackets together to each location corresponds to the numbered locations represented on the map in Figure 1.

Location	Area	Year	Season	Scats sampling	Faecal DNA	Camera-trapping (days)	Number of camera traps
Manzanares del Real (16)	North	2013	Spring	2013	-	Yes (20)	10
La Berzosa (17/19)	North	2013/2017	Spring/Autumn	2013	2017	Yes (20/35)	9/9
Miraflores de la Sierra (18)	North	2013	Spring	2013	-	Yes (19)	8
Carabaña (2/6)	Southeast	2014/2017	Autumn/Summer	2014	2017	Yes (36/35)	8/10
Ambite (4/7)	Southeast	2014/2019	Winter/Summer	2014	-	Yes (23/35)	9/8
Villarejo de Salvanés (3/8)	Southeast	2014/2018	Winter/Spring	2014	2018	Yes (35/35)	10/8
Valdaracete (1)	Southeast	2014	Autumn	2014	-	Yes (36)	8

Torres de la Alameda (5)	Southeast	2014	Spring	2014	-	Yes (21)	8
San Mames (20)	North	2017	Summer	2017	2017	Yes (35)	8
Robledo (14)	Southwest	2017	Autumn	2017	2017	Yes (35)	10
Pelayos de la Presa (11)	Southwest	2018	Summer	2018	2018	Yes (35)	8
Quijorna (9/23)	Southwest	2018/2019	Spring/Summer	2018	2018	Yes (35/35)	8/8
Madarcos (21)	North	2019	Winter	-	-	Yes (35)	8
Cenicientos (10/24)	Southwest	2016/2019	Autumn /Spring	-	-	Yes (23/35)	8/8
Chapineria (13)	Southwest	2019	Autumn	-	-	Yes (35)	8
Fresnedillas de la Oliva (12)	Southwest	2019	Autumn	-	-	Yes (35)	8
Braojos (22)	North	2020	Winter	-	-	Yes (35)	8
Navas del Rey (15)	Southwest	2016	Winter	-	-	Yes (28)	8

General material and methods

Sampling area and camera-trapping arrangement (Chapters 1, 2, 3, 4)

The arrangement of camera traps defined the sampling area. We placed 8-10 camera traps at each of the study location for 20-36 days, resulting in 751 sampling nights and 6336 capture occasions (number of nights × number of cameras) (Table 2). We spaced the cameras approximately 450-600 m apart. This arrangement maximized the number of individuals photographed while minimizing potential "shadows" resulting from unsampled foxes (similar to Sarmento et al. 2009). ArcGis 10.2 ESRI Inc., Redlands, California, USA) was used to generate the minimum convex polygon (MCP) based on camera locations. The resulting polygon was buffered by 500 m (Figure 2). This buffer area extended approximately half the length of the fox home range (~600 m; Cruz and Sarmento, 1998). According to the methodology applied by Sarmento et al. (2009), we assumed the total sampled area was the MCP encompassing the outermost camera locations, plus the buffer area. The total area covered differed across regions: 2595 ha in the north, 3607 ha in the southeast and 3541 ha in southwest. The mean area of sampled locations within each study area mirrored this variation, with 370 ha in the north, 450 ha in the southeast and 395 ha in the southwest. These values are comparable to the average home-range area reported for red foxes in the mountains of Central Spain (López-Martín 2010).

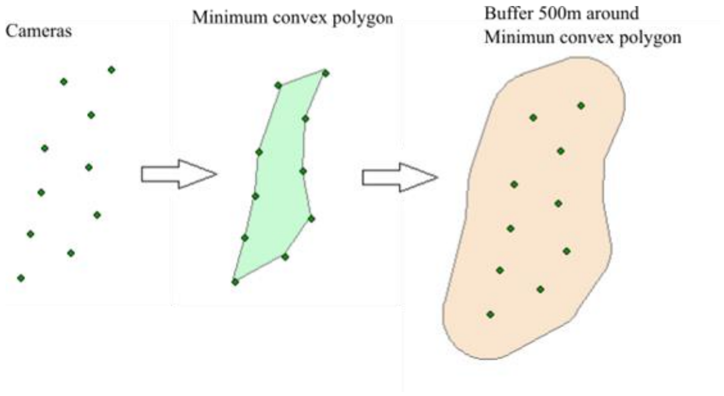

Figure 2. Representation of sampled area.

Eight camera models were deployed for this study: Wildview Xtreme2, Bushnell Trophy, DLC Covert II, Acorn LTL, Cuddle Back Ambrush, HCO Scoutguard SG565, Scout Guard SG560K, and Scout Guard SG562. These cameras operated continuously (24 hours a day) and captured three sequential photographs at five-seconds intervals, with each image recording the date and time for each photo. To maximize the probability of detection, we placed two baits approximately 2 meters in front of each camera: sardines (Heinlein et al. 2020; Sebastián-González et al. 2020) and a commercial lure (HAGOPUR® Premium Attractant Fox) (Monterroso et al. 2013; Gil-Sánchez et al. 2021). The baits were tethered to prevent any species from consuming them. This ensured that the baits did not influence the behaviour of the target species or their activity levels (Gerber et al. 2012; Braczkowski et al. 2016). We checked the cameras every four to seven days to replenish baits and batteries, and download captured photographs.

Photo-identification of red foxes (Chapter 1 and 2)

Fox individuals were identified in camera trap photographs (Chapter 1 and 2) based on a combination of physical characteristics, including body size, age class, tail appearance, specific spotting patterns, and other distinctive features. We adopted the criteria outlined by Sarmento et al. (2009) and Dorning and Harri (2019) to select these diagnostic traits that aided individual identification (Figure 3). Seasonal variations in fur coloration were not considered in this analysis. The sampling period was not extensive enough to capture these seasonal changes, and the same area was not sampled over different seasons.

To minimize potential bias in photo-identification and reduce the risk of overestimation (Foster and Harmsen 2012; Ferreras et al. 2017; Johansson et al. 2020), a second observed reviewed all captures photographs. In cases where the first and second observers disagreed on the number of foxes identified, a third observer reanalysed the photographs to reach a consensus. We considered the minimum number of individuals as the mean of the number of individuals identified by each observer (Chapter 2) or the number of individuals on which both observers agreed (Chapter 1).

Figure 3. Examples of identification of individual foxes by camera trap A) Individual with two spots at the base of the snout and tail with thick fur. b) Individual with thin tail and, distinct fur pattern on the base of the tail and snout.

Sampling of scats (Chapter 1 and 2)

Faecal samples were collected along designated trails measuring one-kilometre in length (Chapter 2). We further divided each trail into 100-meter segments. We then quantified the total number of scats encountered along the entire trail, as well as the number of segments marked containing scats (Chapter 1) (Figure 4A).Carreras-Duro et al. (2015) identified 1.5 km transects as the most efficient sampling effort, minimizing the discrepancy between trail length and red fox detection probability (72.9% detection rate). To maximize the probability of detecting the same individuals using both camera traps and faecal sampling, trails were selected in close proximity to camera locations (Figure 4B). On the day camera deployment commenced, nearby sampling trails were cleared of any existing scats. Trails within the same location were always inspected on the same day. The sampling regime varied between a single sampling in the middle of the study (Chapter 1), or three sampling events distributed throughout the entire study (Chapter 2). For scats DNA extraction (Chapter 2), scats were soaked in 96% alcohol for 12 hours after collection and then stored on silica gels at 2-4°C until further processing (Nsubuga et al. 2004). Sample collection was conducted by trained personnel with expertise in carnivore sign identification, achieving a high accuracy rate of 90% (Martin-Garcia et al. 2023). The detailed procedures for DNA extraction, microsatellite genotyping, and the specific genotype identification software employed are addressed in Chapter 2.

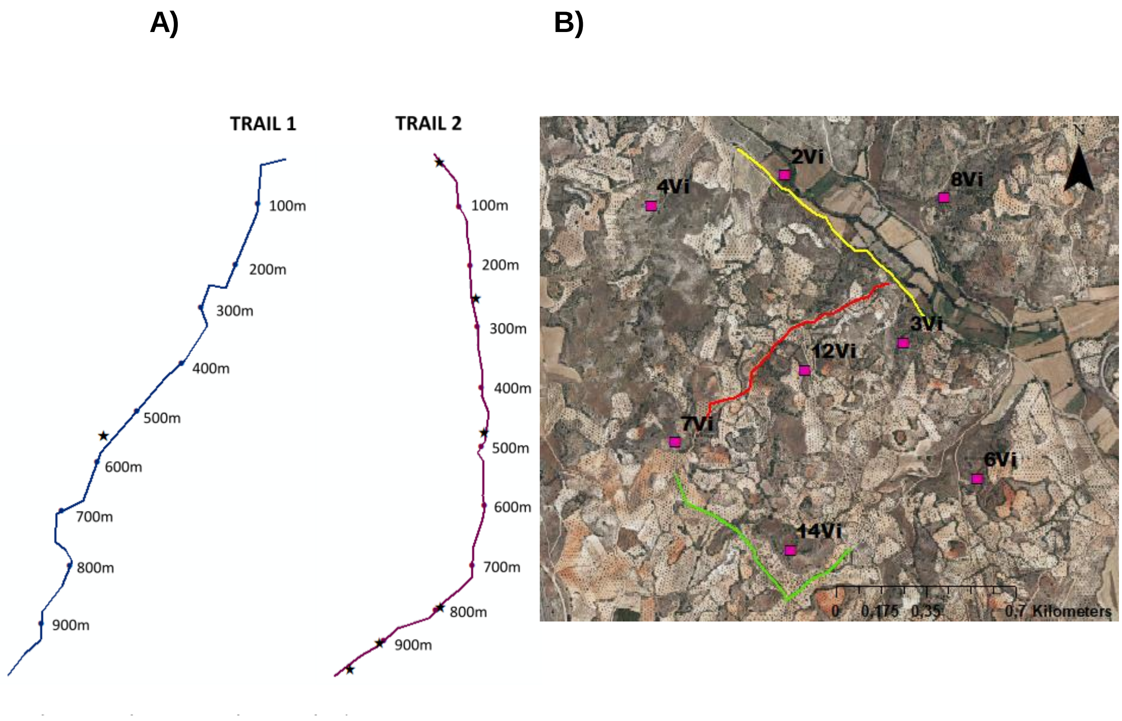

Figure 4. Faecal sampling protocol. A) Illustrates the division of each trail into segments for estimation purposes. Stars represent the locations of faecal samples, while dots represent the starting points of each trail segment. B) Example of trail and camera location sampling. Green, yellow and read lines represent trails, and pink squares represent cameras traps

N-Mixture models for the study of abundance and the correlations between indices of abundance and relative abundance (Chapters 1 and 2).

We employed *N-Mixture* models to estimate fox abundance while accounting for potential detection biases. The 'Unmarked' package (Fiske and Chandler, 2011) within R software was used to parameterize these models through the *pcount* function. This package utilizes a hierarchical modelling approach to estimate abundance based on repeated count data and the maximum likelihood to fit the models. The count data were organized into a matrix containing the number of captures per occasion and site (Fiske and Chandler, 2011). We counted each independent fox trapping event per camera-trap and occasion (24 h). We defined an occasion with multiple fox captures as an instance where several foxes were detected together during the same independent capture event.

N-Mixture models estimate true abundance by considering the local variation in abundance (λ) across sites i over multiple j temporal counts, while simultaneously incorporating the influence of detection probability. There are two linked processes involved in the abundance estimation (Kéry and Schaub 2012):

a) Abundance process (λ): This process is modelled using a Poisson distribution with a mean of (λ) and the variation of local abundance at a given site i

$$(\lambda) \sim Poisson\,(\lambda)$$

b) Observation process(p): This process is modelled using a binomial distribution. It estimates the probability of detection (p) based on observed counts (yi, j) of individuals at each site (i) and for each temporal replicate (j).

$$yi, j\,|\lambda \sim Binomial\,(\lambda, p)$$

To investigate both abundance and detection probability across sampling areas (Chapter 2), we compared three competing models using Akaike's Information Criterion corrected for small sample size (AICc) (Akaike 1974) ranked three models to study (Burnham and Anderson 2002). The models were:

(1) Constant detection probability: This model assumes a consistent detection probability across all areas, with variation in abundance estimates between areas (i.e. $p\,(.) \sim \lambda\,(site)$).
(2) Variation in detection probability and abundance estimates: This model allows for both detection probability and abundance estimates to vary across areas (i.e. $p\,(site) \sim \lambda\,(site)$).
(3) Variation in detection probability with constant abundance: This model assumes variation in detection probability across areas, but with constant abundance estimates across all areas (i.e.$p\,(site) \sim \lambda\,(.)$).

For each model, we compared the performance of three candidate distributions: Poisson, zero-inflated Poisson, and negative binomial. Following selection using AICc, we employed the 'Unmarked' package to estimate the posterior distribution of both detection and abundance (λ) using empirical Bayes random effects (ranef) methods.

To assess model fit, we implemented a parametric bootstrap approach involving 5000 simulated bootstrap samples for each fit. This procedure allowed us to obtain the mean abundance for each area, along with its corresponding standard error and confidence interval.

In Chapter 1, we added predictor variables into abundance models to explore how they influenced both abundance and observation/detection processes. Due to limitations imposed by our relatively small sample size, we restricted each model to a maximum of two predictors for abundance. Additionally, we excluded models containing highly correlated predictors ($|r|>0.61$). We employed AIC to identify the most plausible predictors of fox abundance under the assumption of constant detection probability. Following this initial analysis, we selected abundance models with constant detection exhibiting a $\Delta AIC \leq 2$ (Burnham & Anderson, 2002). Subsequently, we added detection predictors into these models to assess how detectability affects the modelling of fox abundance. Finally, we ranked all resulting models, encompassing both constant detection model and those incorporating detection predictors to select the most plausible top-ranked models based on $\Delta AIC \leq 2$ threshold (Burnham and Anderson, 2002).

In Chapter 1, we compared abundance models derived from *N-Mixture* models with those generated by applying General Linear Models (GLMs) to relative abundance indices. In addition, we quantified the correlation between these relative abundance indices using a Spearman rank correlation test. We proposed three relative abundance indexes:

1) *NSE*: Number of segments with fox scat presence (scat sampling).
2) *RAI*: Ratio of total fox captures (photographs) to the number of sampling occasions (camera-trapping).
3) *NI*: Number of identified foxes (camera-trapping).

In Chapter 2, we also investigated the correlation between the relative abundance index *NI* obtained by camera-trapping and faecal DNA genotyping. Furthermore, we compared its relationship with the abundance obtained using *N-Mixture* models.

Occupancy and temporal models (Chapter 3 & 4) of foxes, martens, rodents and rabbits.

In Chapter 3, we utilized the ‘Unmarked’ package (Fiske and Chandler 2011) in R software to parameterize single season occupancy models using the *occu* function.

This function fits occupancy models based on zero inflated binomial models (MacKenzie et al. 2006). The model incorporates two processes:

1) The occupancy state process (zi) modelled as a Bernoulli distribution. Represents the probability of species occupancy at a given site (*i*).

$$z_i \sim Bernoulli(\psi_i)$$

2) The observation process models the probability of detecting a species at site (*i*) on a particular survey occasion (*j*), given the site's occupancy state:

$$yij\ |zi\ \sim\ Bernoulli(zipij)$$

Data for each species were organized into matrices where rows represent sites and columns represent surveys (i.e. sampling occasion, i.e. each day a camera was operational). Each entry into the matrix indicated whether the species was observed (value 1) at the site i and survey j or not (value 0). Additionally, "NA" indicated a site i was not sampled on a particular survey j. In our study, i is each camera site and j is the sampling occasion (i.e. each day of camera operation).

We evaluated the influence of various predictor variables on both occupancy (Ψ) and detection probability (p), considering models with and without covariates. This involved running a global model that included all predictors and comparing it to the null model assuming constant occupancy and detection probability (i.e. $\Psi\,(.), p\,(.)$). We used AICc to rank candidate models and calculate their Akaike weights (Burhman and Anderson 2002). For top-ranked models with ∆AICc <2, we employed a model averaging technique to estimate occupancy and the relative importance of predictor variables across these multiple models. We used the 'MuMIn'package to select the model and calculating the relative importance of the model parameters (Barton 2022).

In Chapter 4, we employed multispecies occupancy models (Rota et al. 2016) to study the occurrence and potential interactions between red fox and stone marten. This analysis was conducted using the *occuMulti* function within the 'Unmarked' package of R software (Fiske and Chandler 2011). Multispecies occupancy models follow single season occupancy models of Mackenzie et al. 2009 to model occupancy and detection processes. Nevertheless, multispecies models assume a latent occupancy state vector Zi of length s for a set of s potentially interacting species at site i. The latent state is modelled as a multivariate Bernoulli random variable, denoted as:

$$Zi \sim MVB\ (\psi i)$$

where ψi represents a vector of length $2^{s,}$ where "s" is the number of potentially interacting species at a site i. Each element in this vector corresponds to the probability of a specific combination of species occupancy states (0 = absent, 1 = present). The sum of all elements in ψi equals 1.

Observations yij at site i on occasion j are also vectors of length s. The observation process allows for independent detection probabilities (p) for each species s. This is modelled by:

$$yij|Zi \sim Bernoulli\ (Zi * psij)$$

In addition, multispecies occupancy models incorporate three natural parameters:

1) Occupancy of dominant specie fA: This parameter is estimated by

   $$fA\ = log(/\psi 00),$$

   representing the difference in occupancy probability between a site with only the dominant species present $(\psi 10)$ and a site with neither species present $(\psi 00)$.

2) occupancy of subordinate specie fB: This is estimated by

   $$fB\ = log(\psi 01/\psi 00),$$

   representing the difference in occupancy probability between a site with only the subordinate species present $(\psi 01)$ and a site with neither species present $(\psi 00)$.

3) Occupancy/interaction between species (fA/fB): This parameter is estimated by

   $$fA/fB\ = log((\psi 11 * \psi 00)/(\psi 10 * \psi 01)),$$

reflecting the interaction effect of occupancy.

The summary of the possible states comprises [11], [10], [01], or [00], corresponding to both species present, only species 1 present, only species 2 present, or both species absent, respectively.

Our analysis focused on occupancy probability (psi) and strength of interaction between species (fA/fB). We investigated the influence of relative abundance of mesocarnivores and prey on this interaction parameter. Models were constructed by incorporating various combinations of variables within fA/fB, including the relative abundance of mesocarnivores and prey using RAI. We employed AIC (Burnham and Anderson 2012) to select models with ΔAIC < 2. The *optimizePenalty* function with K-fold cross-validation was used to determine the optimal penalty term value for model re-fitting (Clipp et al. 2021). We predicted the occupancy probability for all four possible states, including the marginal occupancy of both mesocarnivores and the conditional occupancy.

In Chapter 4, we estimated the overlap coefficients between fox, stone marten rodents and rabbits by assessing the activity patterns of target species. For this goal, we used the overlap package (Ridout and Linkie 2009) within R 3.4.4 software (R Development Core Team 2017). Photographic captures were first organized by location, camera, species, and time (UTC). For each camera, independent detections were defined as photographs of the same species separated by at least one hour (Silveira et al. 2003; Linkie and Ridout 2009). Captures of multiple individuals were considered multiple detections (Ridout and Linkie 2009). We analysed the activity pattern of each target species based on their independent detections. Overlap coefficients i (Δ) were then estimated for all pairwise comparisons between the combined target species. An overlap coefficient closer to 1 indicates a higher degree of overlap in activity patterns. We categorized the overall pairwise comparisons made across the three study areas into three levels of activity overlap (see Monterroso et al. 2014 for a similar approach): 1) low overlap (below the 50th), 2) Moderate overlap (between the 50th and 75th percentiles) and 3) high overlap (above the 75th percentile).

Finally, we calculated in the R package 'CircStats' (Agostinelli and Lund 2018) a Watson's two-sample test for homogeneity of activity patterns between species (Jammalamadaka and Sengupta 2001). This test assessed statistically significant differences in the activity patterns between species pairs ($p < 0.05$).

CHAPTER 1

Comparing relative abundance models from different indices, a study case on the red fox

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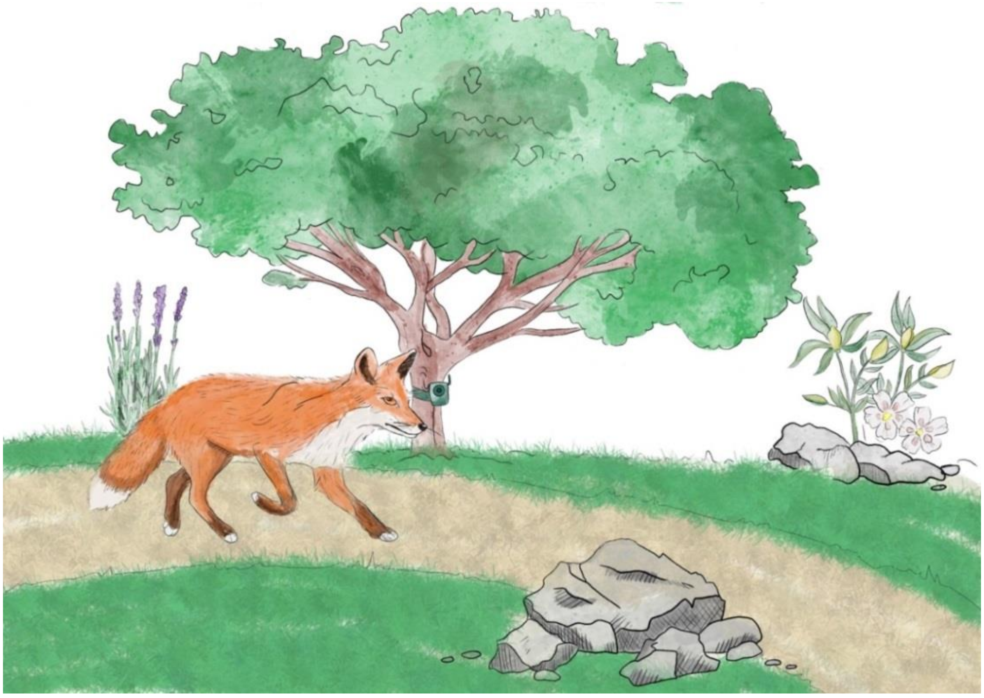
Keywords: Camera-trap survey; scat-track survey; abundance modelling; abundance estimator; relative abundance; detection variability.



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Abstract

The correct interpretation of relative abundance indices provided by different sampling methods is essential to correctly estimate population size. Although multiple indices and models have been proposed, their ability to estimate relative abundances and their performance in models explaining abundance trends remains unclear. We used the red fox (*Vulpes vulpes*) as a model species to compare the relationship and derived models of relative abundance between three indices of relative abundance: *RAI* (number of captures/total occasions); *NI* (number of photo-identified individuals) obtained by camera-trapping, and *NSE* (number of segments with scats) obtained by the scat census sampling method. In addition, we modelled the relationship between a set of habitat predictors and fox relative abundance for each of the three estimated relative abundance indices. We compared the relative abundance models explained for each index against *N-Mixture* models that estimate abundance controlled for variation in detection. Results showed a positive correlation between the *RAI* and *NI* indices, while both indices showed a negative relationship with the *NSE* index. Relative abundance models and *N-Mixture* models showed a different selection of predictors to explain abundance trends. *NSE* and *RAI* indices selected predictors that could explain variability in fox detection rather than fox abundance. In contrast, the *NI* index and *N-Mixture* models selected the same predictors to explain fox abundance. Our results suggest the use of the *NI* index for abundance models without the need to control for variation in detection. Relative abundance indices based on scats and captures per occasion are suboptimal indices for species abundance studies due to possible bias caused by animal behaviour. If count-based methods on captures per occasion (*RAI*) are selected, we suggest using session-based data processing to incorporate detectability variation in *N-Mixture* models.

Introduction

In the current scenario of increasing biodiversity loss, understanding the factors that influence the abundance of wildlife species is paramount for appropriate conservation and management actions. Relative abundance indices are widely used to quantify, model, and predict a proxy of the actual abundance of wildlife species across their habitat under the assumption that their persistence depends on specific environmental conditions (Kinnaird and O'Brien 2012; Güthlin et al. 2013; Ramesh and Downs 2015; Weber et al. 2017). However, the relationship between the relative abundance of species and their habitat may be highly dependent on the sampling method and the index of relative abundance used. Despite the large number of methods and indices available for estimating relative abundance, their ability to effectively estimate species abundance as well as their performance in models used to explain abundance patterns still need to be assessed.

A relative abundance index is a count of animal's signals (e.g. nests, scats, etc.) that is assumed to correlate with the population size of the species (Caughley and Sinclair 1994); thus, changes in index values reflect changes in population numbers (Romesburg 1981; Anderson 2003). A classic method for collecting data based on animal signals is the count of scats along transects or paths (Cavallini 1994; Virgós et al. 2000; Virgós 2001a; Webbon et al. 2004, Barea-Azcón et al. 2007). This sampling method has been widely used to calculate RAI and subsequent models (Mangas and Rodríguez-Estival 2010; Güthlin et al. 2013), although it is often limited by the difficulty of accurately assigning signals to a species (Kohn and Wayne 1997; Hansen and Jacobsen 1999; Davidson et al. 2001) and the lack of validation of the index with actual abundance data (Anderson 2003). Alternatively, recent methods based on camera-trapping (Bengsen et al. 2011; Karanth and Nichols 2011; Palmer et al. 2018) are used to estimate the actual abundance or population density of a species when individual body characteristics or artificial markings (e.g. radio collars, tags) of photographed animals can be used. A relative abundance index is then calculated by considering the frequency of capture as the number of captures (photographs) per the total number of capture occasions (Carbone et al. 2001; O'Brien 2011, Palmer et al. 2018). This is a common and widely used index in relative abundance models (O'Brien et al. 2003; Kinnaird and O'Brien 2012; Gil-Sánchez et al. 2021).

The use of relative abundance indices provides an approximation of species abundance while reducing sampling effort, which is especially important for species that are difficult to monitor or capture (O'Brien 2011). Although any relative abundance index is assumed to require a monotonic relationship with actual abundance, this may not necessarily be a constant and positive relationship across habitats and time. In fact, an index may fail to provide accurate estimates when the species' population size is large (O'Brien 2011). In addition, different indices may show different sensitivity to the same habitat characteristics and therefore, conclusions on the environmental drivers of species abundance may depend on the index. Another major problem with the use of indices is that the counts underestimate the population size when the probability of detection is <1 and is not constant between periods (O'Brien 2011). Moreover, the non-detection of a species may be the consequence of a true absence or a failed detection attempt (type I error, also known as imperfect detection) (MacKenzie et al. 2002; Royle et al. 2005). Factors influencing variability in detection are associated with differences in counts that cannot be attributed solely to variations in the species abundance (Pollock et al. 2002; Gu and Swihart 2004; Royle et al. 2005). Therefore, to address this variability in detection, *N-Mixture* models incorporating detection probability have been used to improve the less accurate inferences of species abundance produced by classical relative abundance indices (Royle, 2004). *N-Mixture* models were proposed to estimate species abundance using count data without identifying animals at the individual level while controlling for detection biases (Royle 2004; Kéry et al. 2005). In particular, this method takes into account imperfect detection per sampling unit by integrating a state process (animal abundance) and an observation process (detectability).

Numerous studies have focused on the comparison of *N-Mixture* models with capture-recapture methods (e.g. mark-recapture-recapture models, removal sampling) to quantify abundance (Schmidt et al. 2015; Keever et al. 2017; Ficetola et al. 2018; Link et al. 2018; Costa et al. 2020, Della Rocca et al. 2020). However, the comparison of *N-Mixture* models with relative abundance indices in the production of abundance models to identify which predictors explain species abundance has not been studied. Understanding the performance and sensitivity of different indices of relative abundance and methods for determining the relationship between the relative abundance of a species and the environment is critical for a suitable management of wildlife populations.

Here, we compared indices of relative abundance and relative abundance models obtained from widely used sampling methods such as camera-trapping and scat sampling. We considered three relative abundance indices: 1) the number of total captures (i.e. photographs) of animals per number of occasions (*RAI*), 2) the number of animals identified (*NI*), and 3) the number of segments marked with scats (*NSE*). Next, we compared the relative abundance models generated by each index with the results obtained by applying *N-Mixture* models. In total, we specifically tested the following questions: 1) Are RAI, NSE and NI indices correlated? 2) Do *RAI*, *NSE* and *NI* indices tend to identify the same predictors when used in relative abundance models? and 3) Do *RAI*, *NSE* and *NI* models provide relative abundance models similar to *N-Mixture* models in explaining the abundance of a wildlife species?. We tested these questions using the red fox (*Vulpes vulpes*) as a model species. This is one of the most abundant species of meso-carnivores in Europe and particularly in the Iberian Peninsula (Lloyd 1980), which added to a curious and territorial behaviour makes it suitable to sampling using non-invasive methods based on camera-trapping and scat sampling (Sadlier et al. 2004; Mackay et al. 2008; Lyra-Jorge et al. 2008).

Material and Methods

Study area

We selected 12 independent study areas in the central Iberian Peninsula (**Figure 1**). We sampled fox populations in the selected study sites in the years 2013, 2014, 2017 and 2018. This period spanned different seasons to account for variability in detectability and marking behaviour of foxes (Travaini et al. 1993; Ralls et al. 2010). The selected areas encompassed a wide variety of climatic conditions and plant communities in typical supra and meso-mediterranean environments (Ministry of Environment and Spatial Planning, 2001).

The daily average temperature ranged between 14º C and 29 ºC during the hottest season and 3ºC to 15ºC during the cool season. Annual precipitations were over 400 mm with a pronounced minimum in summer (particularly in July and August), which is the characteristic trend of Mediterranean climates. Vegetation included typical Mediterranean forest of holm oaks (*Quercus ilex*), junipers (*Juniperus oxycedrus*), holly oak (*Quercus ilex*), kermes oak (*Quecus coccifera*) and Pyrenean oak (*Quercus pyrenaica*). Coniferous forest was represented by Scots pine (*Pinus sylvestris*), Stone pine (*Pinus pinea*) and Aleppo pine (*Pinus halepensis*). Scrubland of gum rockrose (*Cistus ladanifer*), and thyme (*Thymus vulgaris*) were also typical. Irrigated and non-irrigated crops, pasture grass vegetation, and gypsophilous were the most common agricultural land use. Other land uses included livestock and recreational areas and game hunting. In these areas, the red fox is common and is considered a species to control due to its predation pressure on game species (Beja et al. 2009). However, the effectiveness of predator control strategies to reduce the abundance of this specie in game areas is controversial, as the lack of a selective fox control programme could negatively affect or harm other endangered species (Virgós and Travaini 2005). Therefore, an accurate assessment of fox abundance can provide more precise assessments of the need and intensity of control campaigns in these areas.

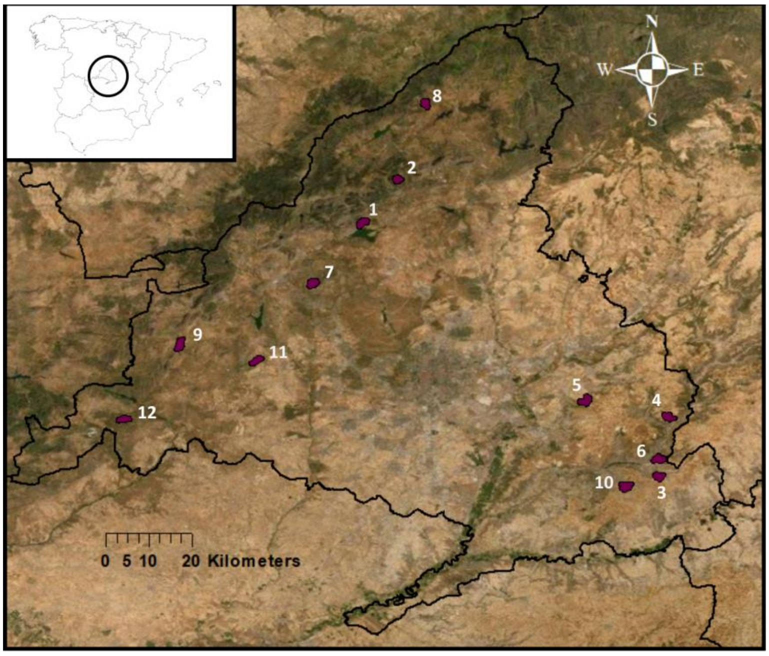


Figure 1. Location of the 12 sampling areas.

Cameras - sampling

For *RAI* (number of total captures (i.e. photographs) of animals per number of occasions) and *NI* (number of animals identified), we placed 8–10 camera traps in each of the 12 study areas during 20–36 days, resulting in 365 sampling nights and 3158 captures (Supplementary Table 1). Each camera was separated from each other by approximately 450–600 m, which we considered a sufficiently large area to maximize the number of individuals photographed while reducing possible 'shadows' from unsampled foxes (similar to Sarmento et al. 2009). We used ArcGis 10.2 (ESRI Inc., Redlands, California, USA) to generate a minimum convex polygon (MCP) using the camera locations, and buffered the resulting polygon by 500 m. This buffer area was approximately half the length of fox's average home range (~600 m; Cruz and Sarmento 1998). According to the method implemented by Sarmento et al. (2009), we assumed that the total sampled area comprised the MCP encompassing the perimeter drawn by the outermost camera locations plus the buffer area. In total, this area covered the average home-range area of the red fox reported in the mountains of Central Spain (412 ha; López-Martín 2010).

We used eight models of cameras, Wildview Xtreme2, Bushnell Trophy, DLC Covert II, Acorn LTL, Cuddle Back Ambrush, HCO Scoutguard SG565, Scout Guard SG560K, and Scout Guard SG562. We configured the cameras to with a five second delay. Each photograph recorded the date and time. For camera placement, we selected sites of relatively dense wild woodland vegetation near trails or tracks typically used by carnivores (Macdonald 1980; Barja et al. 2004), and tie the cameras to the trunk of trees or shrubs about 20 cm above the ground. We placed two types of bait in front of each camera (~1 m), sardines (Heilein et al. 2020; Sebastián-González et al. 2020) and a commercial lure (HAGOPUR® Premium Attractant Fox) to maximize the probability of detecting foxes. We checked the cameras every four to seven days to download photographs, replenish baits and change batteries when necessary.

Scat - sampling

We sampled 24 trails (two per study area) of one kilometre and subdivided each trail into 100-metre segments to meet with *NSE* index calculations (i.e. number of segments marked with scats). Carreras-Duro et al. (2015) showed that the most efficient sampling effort minimizing the difference between the transect length and red fox detection was 1.5 km (72.9% detection rate). We selected trails close to camera sites to increase the probability of detecting the same individuals by both sampling methods. On the same day that we set up a camera, we also cleared of scats the nearby two trails to be sampled. We then surveyed these two trails per study site in the middle of the camera deployment period; both trails were surveyed on the same day. We counted the number of fox scats along the trail and the segments where they were deposited. Sampling was carried out by operators skilled in carnivore sign identification with a ~ 90% accuracy in identifying scats (Martin-Garcia et al. 2023).

Index description

We calculated the relative abundance index *NSE* from the scat sampling. This index takes into account the total number of segments with fox scat present (Supplementary Material 1). We discarded the count of the total number of scats to control for any individual fox marking the same segment and thus avoid overestimating abundance. From the camera-trapping data, we quantified the total number of fox captures (photographs) by the number of occasions (*RAI*) (Supplementary Material 1) and the number of foxes identified (*NI*). We used occasions (i.e. the total number of cameras times total number of camera placement nights) rather than nights (i.e. total number of cameras placement nights) to control for bias due to differences in the number of nights and cameras between the study areas

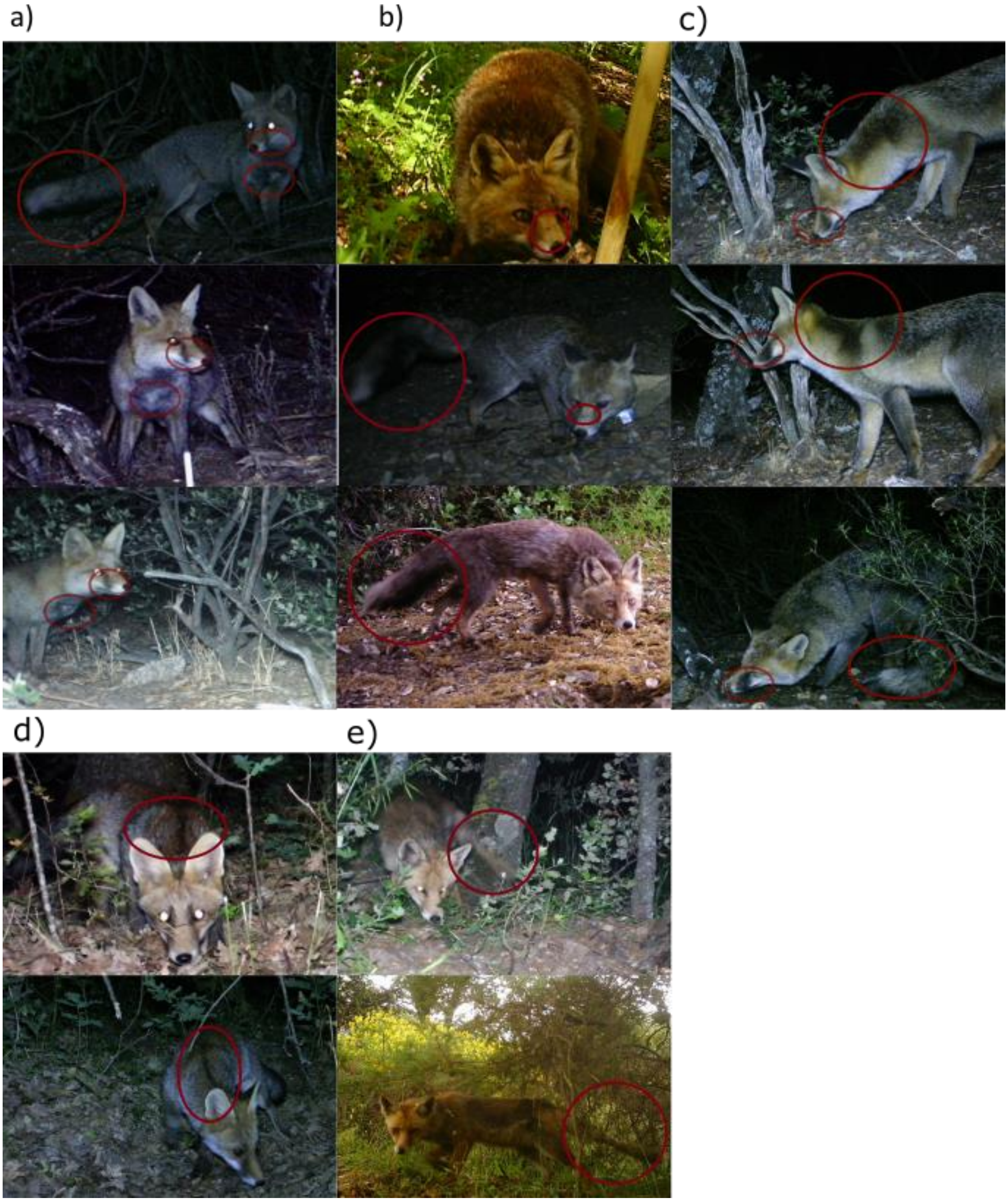


Figure 2. Examples of camera-trap identification of fox individuals from different sampling areas. a) Individual from area number seven with narrow lateral fur pattern on the muzzle and well-defined white circular feature on the chest. b) Individual from area number 11 with two dots at the base of the muzzle and tail with thick fur. c) Individual from area number seven with a distinct coat pattern on the shoulder, base of the tail, leg and under the neck. d) Individual from area number five with a distinct black line on the neck e) individual from area number 11 with a fine hairless tail.

We identified foxes at the individual level based on unique characteristics of body size, age range (cub, juvenile, and adult), tail appearance, fur patches, and any other particular characteristics that might aid identification (Sarmento et al. 2009; Dorning and Harris 2019) (Figure 2). To reduce identification bias, each photograph was revised by a second observer (Ferreras et al. 2017; Johansson et al. 2020). When agreement could not be reached, a third observer reviewed the photograph to obtain a third opinion, so that the same two opinions of all three determined the identification.

Predictor's selection

We modelled the relationship between a set of habitat predictors and fox relative abundance for each of the three estimated relative abundance indices. For this, we selected relevant habitat predictors identified as relevant for red foxes identified in previous studies in Mediterranean ecosystems (Cavallini and Lovari 1994; Lucherini et al. 1995; Virgós 2001b; Pereira et al. 2012). These predictors included vegetation cover and human activities (Virgós and Travaini 2005; Diaz-Ruíz et al. 2015; Recio et al. 2015). We also included season of the year, because it is considered to influence fox activity (Andelt and Andelt 1984; Vine et al. 2009). We extracted predictors of vegetation cover from digital vegetation maps produced by the Autonomous Community of Madrid using ArcGis 10.2. The extracted vegetation classes were grouped into lush forest, crops, pastures, urbanized land, and shrubs. Lush forests comprised conifers (e.g. *Pinus pinea* and *Pinus silvestris*), oak trees (e.g. *Quercus ilex*, *Q. Pyrenaica*, *Q. coccifera*) and other hardwoods (e.g. *Fraxinus sp*). Crops category included irrigated and rained crops, vineyards and olive trees. Shrubs included different species of shrubs (e. g. *Rosaceae sp*, *Cistus sp*, legume, and bushy riparian vegetation), *Lavandula stoechas*, *Thymus vulgaris* and *Retama sphaerocarpa* species. The pastures included high mountain pasture and meadows. We calculated the area of each patch within the sampled area (i.e. the buffered MCP).

Additionally, we also measured the distance from the boundary of each study area to the nearest urban area. We added the categorical predictor period, which included the categories spring, summer and autumn–winter. These categories represented a balanced duration of the sampling periods, for which we also accounted for differences in fox behaviour. The birth and lactation stages occur in spring (Lopéz-Martín 2010), cubs continue to accompany the mother in summer, and the autumn–winter category includes the dispersal of juveniles and the mating period (Andelt and Andelt 1984; Travaini et al. 1993; Phillips and Catling 1991; Vine et al. 2009; Ralls et al. 2010). Lastly, we included a binomial predictor on the presence/absence of small game hunting activities in the area. The red fox is considered a predatory species to control due to its predation habits on game populations. Virgós and Travaini (2005) showed a similar presence of red fox in places with/without predator control while Barrull et al. (2014) identified an increasing presence of the specie in areas with predator control. Also, Beja et al. (2009) found the fox was more abundant in hunting reserves than in areas without hunting management.

Relationship between indices and relative abundance modelling

As a measure of proportionality and similarity between the relative abundance values of the different indices, we quantified the correlation between *RAI*, *NI*, and *NSE* using a Spearman rank correlation test. We considered a moderate correlation (|r|) between 0.41 and 0.60, a strong correlation between 0.61 and 0.80, and a very strong correlation between 0.81 and 1 (Prion and Haerling 2014).

Relative abundance models

To model the relationship between red fox abundance and habitat using the different indices, we performed a General Lineal Model (GLM) analysis with a Poisson, Binomial and Gaussian distribution for the *NI*, *NSE* and *RAI* indices, respectively. For each model procedure, we performed a stepwise forward model selection based on the Akaike's Information Criterion (AIC) as the selection parameter (Burnham and Anderson, 2002) using the step function of the stats package of the R software (version 2.14.2; R Core Team 2012). We calculated the deviance explained by the selected model and the likelihood ratio test (LRT) (which follows a chi-squared distribution) to assess the goodness of fit of the selected model. Significant p-values (<0.05) indicated that the final selected model was accurate (i.e. better than the null model, that is, the model with no variables depending on the selected predictors).

N-Mixture Models from count data

We performed N-Mixture models of fox abundance taking into account the influence of detection. N-Mixture models were parameterized in the unmarked package (Fiske and Chandler, 2011) in R software using the pcount function. This package estimates abundance following a hierarchical model approach of repeated count data using the maximum likelihood to fit models. Count data are organized into a matrix containing the number of captures per occasion and site (Fiske and Chandler 2011). The effect of predictors is determined by the logit-link part (i.e. the detection component of the model (p)) and the log-link function (i.e. the abundance component (ni)) (Royle, 2004). We proposed the following predictors in the abundance component of the model: lush forest, crops, pasture, urbanized land, shrubs, small game, distance to urban areas, and period. Small game and period were also chosen for the detection component of the model. We selected the predictors of detection in line with previous research that showed that small game and predator control had a more significant influence on fox activity patterns than on variations in fox abundance (Harding et al. 2001; Virgós and Travaini 2005; Díaz-Ruíz et al. 2016). Moreover, seasonality could influence the movement of foxes and thus the variation in detection (Cavallini and Lovari 1994; Vine et al. 2009). We identified the correlation between predictors using Spearman's correlation test to avoid multicollinearity (Graham 2003). Given our small sample size, we used the "one-in-ten rule" that considers only one predictor can be used per ten samples (n = 10) (Harrell et al. 1996). Thus, we combined up to two predictors of abundance in each model. We removed models that included highly correlated predictors ($|r| > 0.61$). We ranked our models using the Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to identify the most plausible predictors of fox abundance when the uniform detection process is maintained. We then selected abundance models with a uniform detection process that obtained a $\Delta AIC \leq 2$. We added detection predictors to these models to study the influence of detectability on the modelling of fox abundance. Finally, all resulting models (i.e. the model with uniform detection and the models with predictors in the detection process) were ranked to select the most plausible top-ranked models with $\Delta AIC \leq 2$ (Burnham and Anderson 2002).

Results

Correlation between relative abundance indices

From camera-trapping, we obtained 390 fox captures among a total of 3158 occasions (18% of occasions), which represented a mean of 32.46 ± 24.91 SE (standard error) of fox captures per site. In total, we identified 30 fox individuals (2.5 ± 1.38 SE per site). From the scat surveys, we found fox scats on 24.58% of the trails and a mean of 4.92 ± 2.9 SE of segments with scats per site (Supplementary Table 2). The *RAI* index was strongly correlated with NI (n = 12; $|r| = 0.77$; pvalue = 0.003). Conversely, the *NSE* index showed a negative, although not significant, correlation with the *RAI* and *NI* indices ($|r| = -0.44$; p-value = 0.13 and $|r| = -0.33$; p-value = 0.3 respectively). This result indicates that a higher number of captures per occasion or a higher number of individuals implies a lower number of segments with scats present.

Relative abundance models

Stepwise selection-based modelling analyses resulted in a model indicating that the RAI index on fox relative abundance was explained by the presence of small game and shrubs (AIC = − 20.62). Both predictors showed a negative relationship with relative fox abundance, but this relationship was only significant with the predictor presence of small game (i.e. confidence intervals (CI) not contained zero) (Table 1). For the categorical predictor small game activities, the absence of small game hunting had a positive relationship with the relative abundance of foxes ($\beta_{absence}$ = 0.11). This model explained 39% of the total deviance and the goodness-of-fit test indicated a good model fit (χ^2 = 5.98; p-value = 0.05). Modelling procedures associated with the *NI* index resulted in a final model that included the distance to urban areas and shrubs to explain relative abundance (AIC = 41.38).

Table 1 Results of step-wise regression model for each relative abundance index (*RAI*, *NI*, and *NSE*). Predictor's selection is represented for each relative abundance model. The following statistics are shown: Regression coefficient (Estimate); standard error (S.E); lower and upper interval coefficient (CI [2.5, 97.5%]).

	Estimate	**S.E**	**CI [2.5, 97.5%]**
RAI index model			
Intercept	0.208	0.043	[0.122, 0.294]
Small game (presence)	-0.11	0.05	[-0.206, -0.011]
Shrubs	-0.0004	0.0003	[-0.0009, 0.0001]
NI index model			
Intercept	1.541	0.282	[0.950, 2.062]
Distance urban areas	-0.001	0.0007	[-0.003, 0.0001]
Shrubs	-0.003	0.002	[-0.008, 0.0005]
NSE index model			
Intercept	-1.293	0.313	[-1.940, -0.703]
Small game (presence)	1.031	0.328	[0.408, 1.711]
Period(Spring)	-0.458	0.343	[-1.167, 0.182]
Period(Summer)	-1.011	0.458	[-1.962, -0.146]

Model coefficients showed a negative relationship between fox relative abundance, with the distance to urban areas, and with cover of shrubs. However, only distance to urban areas showed a significant relationship (Table 1). This model explained 60% of the total deviance and the goodness-of-fit test indicated that the model fitted well (χ^2 = 6.47; p-value = 0.03). Finally, period and presence of small game were the predictors included in the model that best explained relative abundance using the *NSE* index (AIC

= 55.49). We considered absence and autumn–winter as the reference level for the predictors of small game and period, respectively. Results showed that areas with presence of small game have a positive and significant relationship with fox relative abundance (Table 1). In contrast, the absence of small game showed a negative relationship with relative abundance ($\beta = -1.031$). Moreover, the number of segments with scats had a negative and significant relationship with the summer period and negative but non-significant with the spring period (i.e. confidence intervals (CI) contained zero) (Table 1). Therefore, autumn–winter period also showed a negative relation ($\beta_{\text{autumn-winter}} = -0.263$) (i.e. β (intercept) – β (absence) = β (autumn–winter)) with red fox relative abundance, but less intense. This model explained 59% of the total deviance and the goodness-of-fit test indicated that the model fit well ($\chi^2 = 17.667$; p-value < 0.01)

N-Mixture models from count data

Spearman's correlation test showed a high correlation between the predictors crops and small game (n = 12; |r| = 0.80; p-value = 0.015). We also found a moderate correlation between crops and the distance to urban areas (n = 12; |r| = 0.60; p-value = 0.04). We used a total of 35 models with uniform detection that combined a maximum of two explanatory variables in the abundance process. We discarded the model that included crops and small game due to a high correlation (|r| = 0.80; p-value = 0.015). According to the ΔAIC, model selection revealed two top-ranked models with ΔAIC < 2 that explained abundance when detection was uniform. The first-ranked model contained the predictors distance to urban areas and period (AIC = 358.19). The second-ranked model included shrubs and distance to urban areas (AIC = 359.98) (Table 2).

Then, the small game and period, and the combination of both predictors were included in the process of detecting the best models with uniform detection to the influence of observer detection. A total of 41 models were ranked (35 models with uniform detection and six with variable detection). The final model selection analysis favoured one model with ΔAIC < 2 (Table 2). Distance to urban areas and shrubs showed a negative and significant relationship with fox abundance. Fox detection had a negative and significant relationship with the presence of small game but a positive and significant relationship with period spring and summer. The intercept of detection process indicated that the reference level absence of small game had a positive influence on fox detection ($\beta_{\text{absence}} = 0.932$) but the reference level autumn–winter period ($\beta_{\text{autumn-winter}} = -2.019$) has a high negative relationship with fox detection (Table 3).

Table 2 Model selection ranking on fox abundance from *N-Mixture* model considering abundance and detection predictors. ni is the abundance component and p is the detection component. (.) indicates only the intercepts. Model selection based on Akaike's Information Criterion (AIC), number of estimated parameters in the model (nPars), AIC difference of best fit models (ΔAIC < 2), model weights (wAIC).

Model	nPars	AIC	ΔAIC	wAIC
With Uniform detection				
p(.)~ ni (Period + Distance to urban area)	5	358.19	0	0.53
p(.)~ ni (Shrubs + Distance to urban area)	4	359.98	1.8	0.21
p(.)~ ni (Small game + Distance to urban areas)	4	361.2	3.21	0.12
With Detection predictor				
p(Period + Small Game) ~ ni (Shrubs + Distance to urban areas)	10	340.48	0	0.99
p(Period + Small Game) ~ ni (Period + Distance to urban areas)	8	350.71	10.23	0.006

Table 3 Predictor selection in the abundance model using *N-Mixture* models. The abundance component is defined by predictors that explain variations in fox abundance. The detection component is defined by the predictors that explain variations in fox detection. The regression coefficients (Estimate) are shown, and also the standard error (S.E) and the lower and upper interval coefficient (CI [2.5, 97.5%]).

	Estimate	S.E	CI [2.5, 97.5%]
Abundance component			
Intercept	3.794	0.15	[3.499,4.089]
Distance urban areas	-0.002	0.0003	[-0.0025, -0.0013]
Shrubs	-0.003	0.001	[-0.005,-0.001]
Detection component			
Intercept	-1.089	0.215	[-1.509, -0.668]
Small game (presence)	-0.932	0.236	[-1.393, -0.469]
Period(Spring)	1.025	0.267	[0.502, 1.548]
Period(Summer)	0.693	0.252	[0.199, 1.187]

Discussion

By using non-invasive sampling methods such as camera-trapping and scat sampling, we evaluated and compared the performance of different indices of relative abundance of the red fox, as study case, and whether they provide similar results on abundance-habitat relationships. Using camera-trapping method, we found that the indices on the number of animals identified (*NI*) and the number of total captures per number of occasions (*RAI*, i.e. photographs of foxes per number of occasions) explained the same patterns of variation in fox relative abundance. In contrast, the scat census method showed that locations with a higher number of segments with scats (*NSE*) showed low values of the *RAI* and *NI* indices. The observed differences in predictors associated with fox abundance suggested that management or conservation guidelines based on abundance indices are not comparable. Furthermore, we observed that *NI* and the *N-Mixture* models selected the same predictors to explain variations in fox abundance. In contrast, *RAI* and *NSE* indices selected predictors to explain fox abundance that were selected to *N-Mixture* models to explain variations in fox detection rather than fox abundance. Thus, our results reveal that the relative abundance indices *NSE* and *RAI* might be sensitive to detection variability. In this case, they might not correctly explain abundance variations. Therefore, using these indices would provide unreliable estimates and models of fox abundance.

Despite differences in the interpretations of index-based abundance models, *RAI* and *NI* showed similar trends in variations in fox abundance. Therefore, areas with more foxes identified were those that yielded more captures per occasion in a camera-trap survey. In this vein, previous research focusing on the relationship between indices of relative abundance and tiger population size showed that the number of camera days/tiger photographs (*RAI* index) correlated with independent estimates of tiger density (Carbone et al. 2001). Similarly, evaluation of relative abundance indices of African herbivore species showed a strong correlation of the *RAI* index with independent abundance estimates from aerial surveys (Palmer et al. 2018). The number of identified individuals has been widely used to estimate abundance in species populations using capture-recapture methods (Karanth 1995; Silver et al. 2004; Jackson et al. 2006; Sarmento et al. 2010). However, the use of this information as a proper index of relative abundance and its implementation in abundance models has not been proposed previously. Unexpectedly, the scat index was not related to the remaining indices, so despite our lack of actual abundance estimates we can conclude that some of these indices could not be related to actual abundance. In fact, methods based on scat sampling have been questioned for estimating abundance because scats are primarily used for communication and marking function by carnivore species (Gorman and Trowbridge 1989; Gese 2004) therefore, the *NSE* index may be closer to explaining marking behaviour at each site than fox abundance in this area. Defecation rates often change during the mating and dispersal periods (Barja et al. 2008) and depend on season and diet (Andelt and Andelt 1984; Goszczynski 1990). Changes in marking frequency due to the location of tracks within foraging areas have been extensively studied (Vila et al. 1994; Barja and List 2014; Zaman et al. 2019). We chose well-demarcated and random paths that covered the areas selected for camera deployment; however, the site selected for fox depositions might have followed a non-random distribution (Kruuk et al. 1986; Macdonald 1980; Gorman 1990; Soler et al. 2009). Scats tend to occur at the boundary of territories or are used to mark key resources for individuals (see Macdonald 1985; Barja et al. 2001; Monclús et al. 2009, Burgos et al. 2019 for other carnivores species). In addition, not all individuals mark the territory in the same way, so information on some individuals is lost and biased results on abundance are obtained (Gorman and Trowbridge 1989; Webbon et al. 2004). Consequently, to reduce the influence of the scat marking function, other scat sampling methods (e.g. random transect) should be considered to cover different areas and not only well-defined trails (Güthlin et al. 2012).

Differences in interpretations of abundance models and relative abundance values derived by an index cannot be unambiguously attributed to actual differences in abundance, but may have arisen from differences in detection (Pollock et al. 2002; Archaux et al. 2012). Gu and Swihart (2004) studied non-random detectability in relation to habitat characteristic using occupancy models. Their simulations showed that models derived from non-random detectability tend to increase the importance of habitat variables that are positively related to detection probability as factors influencing occupancy. Their results on occupancy models showed an analogy with our abundance models. The sensitivity of certain indices to detection variations was observed in the interpretation of abundance models based on each index when compared to *N-Mixture* abundance models controlling for detection variation. Results showed that predictors of high importance in relative abundance models might be mainly involved in the detection variability rather than abundance variation. We observed that the *RAI* abundance model and *N-Mixture* model selected shrub predictor to explain fox abundance. However, the small game predictor explained fox abundance in the *RAI* model but fox detection in *N-Mixture* models. The resulting negative selection of small game hunting areas in the models explaining relative abundance by *RAI* could be a consequence of variation in detection due to behavioural patterns. Fox activity seems to be affected by human presence in areas of high human disturbance, thus decreasing diurnal activity (Díaz-Ruíz et al. 2015). Areas with small game are considered landscape of fear, which could affect the behavioural patterns of foxes. Some individuals might be more shy and fearful, avoiding interactions with cameras, which could introduce variations in the number of fox captures on cameras. Thus, the number of captures on camera could be explaining whether some foxes are more subject to small games than others. Sensitivity to detection variations was most strongly observed in the abundance models produced with the *NSE* index. These models selected the same predictors to explain fox abundance as the *N-Mixture* models did to explain fox detection, which were small game and period. The positive selection of the small game predictor in the *NSE* model suggests that the *NSE* index could explain variation in fox detection in relation to marking behaviour rather than variation in abundance. Hunting areas often have suitable vegetation for rabbits (Fa et al. 1999), the main prey of the red fox (Villafuerte et al. 1998; Díaz-Ruíz and Ferreras 2013; Fernandez-de-Simon et al. 2015). Therefore, more resources, including prey, are available and more marking behaviour could occur (Burgos et al. 2019). Also in hunted areas, fox restocking may be higher, so foxes may mark their territories more frequently than in non-game areas (Murdoch et al. 2016). In addition, scat detection might be higher in hunting areas where trails are cleaner due to human transit and more exposed areas are available facilitating their detection (Cortázar-Chinarro et al. 2019). The influence of seasonality on faecal detection has occurred in other fox species. Consistent with our results, Schauster et al. (2002) and Dempsey et al. (2014) found that scat detection was highest during the breeding period (winter) and lowest during pup-rearing period (summer).

In contrast to the *RAI* and *NSE* indices, the *NI* and *N-Mixture* models selected the same predictors to explain abundance. This result suggests that the *NI* index might be less biased by detection variability, so it could be used directly to easily explain abundance patterns in red foxes when the capture-recapture method is not possible (e.g. a minimum number of identified individuals in the population and a minimum number of captures of these identified individuals for reliable estimates (Otis et al. 1978). Both models selected distance to urban areas and shrubs as predictors of abundance. This result aligned with the positive selection of areas closer to urban areas in central Spain (Recio et al. 2015), where generalist carnivores such as red foxes were more abundant in urban and ex-urban areas. Proximity to urban areas could provide human associated resources (e.g. rubbish, rodent prey, or shelters in abandoned buildings) (Fraterrigo and Wiens 2005; Sorace and Gustin 2009; Bateman et al. 2012) capable of supporting higher number of foxes. Regarding shrubs, Pita et al. (2009), showed the importance of forest cover and mosaic landscape (i.e. open, woody habitat patches) favouring carnivore diversity, and not only the prevalence of semi-natural habitats (i.e. the proportion of area with cork oak, scrubland, marshes and coastal dunes), which provide safe refuges and positively affect fox abundance. Similarly, Mangas et al. (2008) showed the importance of tree cover and tree height in carnivore richness in Mediterranean scrubland. In terms to variations in detection provided by *N-Mixture* models, red fox activity appeared to be determined by increased human disturbance (Díaz-Ruíz et al. 2015). In this vein, persecution might affect fox behaviour, with more wary and cautious individuals resulting in a lower probability of detection. During spring (birth/ lactation) and summer (mother accompanied by cubs), the probability of detection was higher, which may be explained by the behavioural changes that occur during these periods. During the denning period, female foxes were more active on a daily basis (Phillips and Catling 1991). In addition, during summer and spring, foxes have larger activity ranges (Martin-Garcia et al. unpublished) with greater movements within the sampled areas and thus increasing the probability of detection. The presence of cubs and juveniles during these seasons could also increase detection due to their curious and exploratory behaviour.

Overall, our research supports the importance of controlling for detection variability for a proper study of abundance modelling. Relative abundance indices are widely used to explain changes in abundance. For this reason, knowledge of their sensitivity to the influence of detection is essential for a correct interpretation of abundances trends. Our results suggest concordance between *N-Mixture* and *NI* models, supporting the use of *NI* index for abundance models without the need to control for detection variation. Therefore, the *NI* index could easily be used as an index of abundance when there are limitations to implement capture-recapture methods. If methods based on a capture-per-occasion count (*RAI*) are selected, we suggest using session-based data processing to incorporate variation in detectability into *N-Mixture* models (Royle 2004). Other methods of scat sampling could be tested, such as the use of transects that do not follow existing trails. This method would cover landscapes that are varied in both composition and configuration (Güthlin et al. 2012) and could reduce the bias caused by some individuals marking more intensively by depositing scats along trails. It could also reduce the influence of detection on the *NSE* index and improve the precision of relative abundance estimation. Other indices of abundance, such as the minimum number of individuals identified from faecal DNA genotyping, could also be tested. The influence of detection on relative abundance models derived from DNA genotyping could be compared with those using an *NI* index.

Supporting information chapter 1

Supplementary Table 1 Sampling design of sampled areas. Presence of small game (Yes) and absence of small game (No); Period: birth and lactation stage (B/L), dispersal and mating stage (D/H), period when cubs are with mother (M/C); Season during sampling (Season); Ha: size of area sampled (Ha); Number of night during cameras placement (No. of nights); Number of cameras used (No. of cameras); No. occasions (No. of nights per No. of cameras

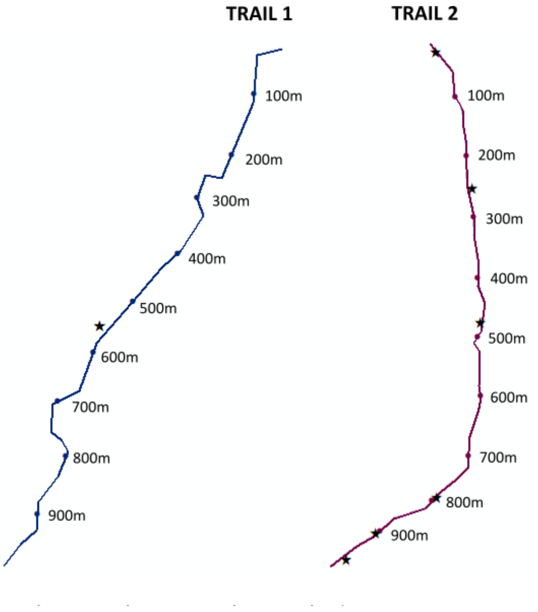
Area	Hunting	Period	Season	Ha	No. of night	No. of cameras	No. occasions
1	No	B/L	Spring	413	20	10	200
2	No	B/L	Spring	311	20	8	160
3	Yes	D/H	Autumn	390	36	8	288
4	Yes	D/H	Winter	417	23	9	207
5	Yes	B/L	Spring	507	21	8	168
6	Yes	M/C	Summer	479	35	10	350
7	No	M/C	Summer	422	35	9	315
8	No	D/H	Autumn	364	35	8	280
9	No	D/H	Winter	466	35	10	350
10	Yes	B/L	Spring	438	35	8	280
11	Yes	B/L	Spring	377	35	8	280
12	No	M/C	Summer	369	35	8	280

).

Supplementary Table 2 Results of total of number of captures (photographs) of foxes (No. of total capture of foxes); RAI (total number of captures/number of occasions); NSE (number of segments with scats); NI (number of identified foxes) using camera-trap and scats census methods.

Area	No. of captures	*RAI*	*NSE*	*NI*
1	16	0.08	1	2
2	47	0.293	6	3
3	5	0.016	9	1
4	12	0.06	10	2
5	0	0.00	6	0
6	24	0.068	4	3
7	88	0.28	1	3
8	62	0.221	1	5
9	29	0.082	6	2
10	29	0.103	5	2
11	56	0.2	7	5
12	22	0.078	3	2
Total	390		59	30

a)



b)

Trail	Segment	Number of scats	Number of segments with scats	Number of segments without scats
1	0-100	0	1	9
1	100-200	0		
1	200-300	0		
1	300-400	0		
1	400-500	0		
1	500-600	1		
1	600-700	0		
1	700-800	0		
1	800-900	0		
1	900-1000	0		
2	0-100	1	5	5
2	100-200	0		
2	200-300	1		
2	300-400	0		
2	400-500	1		
2	500-600	0		
2	600-700	0		
2	700-800	1		
2	800-900	0		
2	900-1000	2		
Total				
2	20	7	6	14

$$\boldsymbol{SE - k) - (} \qquad \boldsymbol{\imath - k}$$

n= number of segments

k= total number of segments with scats

p= probability of segment with scats

$p - 1$= probability of segments without scats c)

Area	Number of cameras	Number of nights	Number of captures	*RAI* index
1	10	20	16	0.08
2	8	20	47	0.293
3	8	36	5	0.016
4	9	23	12	0.06
5	8	21	0	0.00
6	10	35	24	0.068
7	9	35	88	0.28
8	8	35	62	0.221
9	10	35	29	0.082
10	8	35	29	0.103
11	8	35	56	0.2
12	8	35	22	0.078

$$\boldsymbol{RAI\ index} = {}^{\boldsymbol{Number\ of\ captures}}\Big/_{\underbrace{\boldsymbol{number\ of\ cameras} * \boldsymbol{number\ of\ nights}}_{\boldsymbol{Number\ of\ occasions}}}$$

Supplementary Material 1. Estimation of NSE and RAI relative abundance indices. a) Example of the division of each trail into segments and estimation of the NSE index. The stars represent the scats' location, and the dots represent the beginning of the trail segments. b) The table shows the information on the organization of the scat data: name of the trail (Trail); segments of trails (Segment); the number of scats in each segment (Number of scats); the number of segments that included scats in each trail (Number of segments with scats); the number of segments without scats in each trail (Number of segments without scats). The formula shows the estimation of the NSE index: n (number of segments); k (total number of segments with scats); p (probability of having a segment with scats); $p-1$ (probability of having a segment without scats). c) Example of RAI index estimation. The table contains information on camera-trapping sampling: the number of cameras used in each area (Number of cameras); the number of camera nights (Number of nights); the number of photographs of foxes (Number of captures). The formula shows the estimation of RAI index. The numbers of occasions are defined as the number of cameras per nights.

CHAPTER 2

Comparing minimum number of individuals and abundance from non-invasive DNA sampling and camera-trapping in the red fox (Vulpes vulpes)

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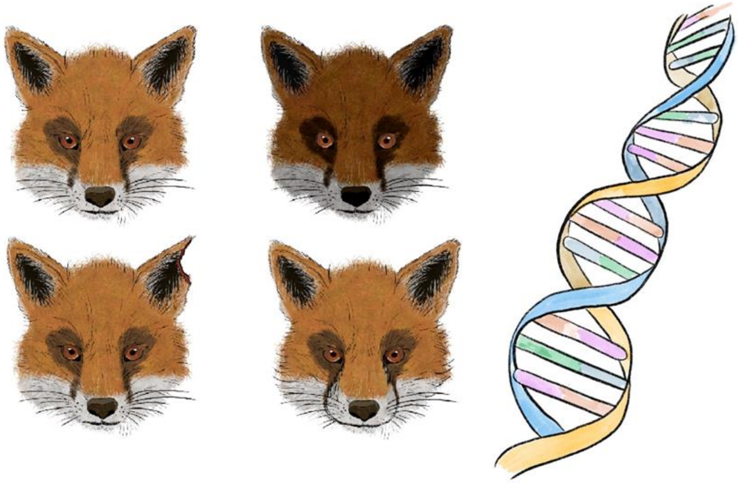

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Abstract

Applying the most appropriate sampling method is essential for estimating population size. Sampling methods and techniques to estimate abundance may be limited by environmental characteristics, species traits, and specific requirements of the techniques, or the economic resources to carry out the sampling. Thus, evaluating multiple sampling methods in monitoring populations is essential for establishing effective conservation strategies. In this study, we compare two of the most commonly used sampling methods with the red fox (*Vulpes vulpes*) as the type species. On the one hand, we compared the minimum number of individuals (*NI*) detected by camera-trapping, identifying individuals by morphological characteristics with the minimum number of individuals detected by DNA scats and a set of 16 microsatellites. On the other hand, we estimated abundance by performing an *N-Mixture* model using information from camera-traps to study the relationship between abundance and the minimum number of individuals detected. Results showed that the minimum *NI* provided by camera-trapping was slightly higher than that of DNA faecal genotyping, with 23.66 and 19 individuals, respectively. In addition, abundance and *NI* detected by camera-trapping showed a positive relationship. In contrast, there was a non-significant negative relationship between *NI* detected by faecal DNA and abundance estimates. Our results suggest using the minimum number of photo-identified individuals as a reliable index to study variation in red fox abundance when other advanced methods cannot be implemented in the study of population size. However, it is necessary to improve the methods of faecal sampling to study the relationship with camera-trap data.

Introduction

The recent acceleration of biodiversity loss urgently requires the development of monitoring programmes to understand trends and spatial patterns of the abundance of wildlife species. Among these, the order Carnivora is among the most threatened groups worldwide (Gittleman et al. 2001). Carnivores are emblematic species with an important ecological role; however, they also cause conservation conflicts with human and their activities (Linnell and Strand 2000; Prugh et al. 2009; Ritchie et al. 2012). Many carnivore species are elusive and solitary mesocarnivores (hereafter mesocarnivores), with nocturnal habits, large territories and low population densities. These characteristics make non-invasive survey methods highly suitable for studying and monitoring these species. Camera-trapping and DNA-genotyping are currently the most relevant non-invasive sampling methods applied to monitor mesocarnivores and analyse their abundance assisted by different analytical techniques (Srbek-Araujo and Chiarello 2005; Trolle et al. 2007; O'Connell et al. 2011; Sollmann et al. 2013; Rodgers et al. 2014). However, these methods are unreliable in all scenarios because environmental characteristics and species traits may limit them, as well as the specific requirements of the techniques to estimate species abundance or the economic resources available to carry out the sampling. Therefore, because different sampling methods and techniques can be applied to estimate mesocarnivore abundance in different regions or seasons, it is necessary to assess the relationship between these methods and how they can be selected in terms of their sampling effort, economic costs, precision and accuracy of abundance estimates (Silveira et al. 2003; Gaidet-Drapier et al. 2006; Gompper et al. 2006; Balme et al. 2009).

Abundance can be assessed using population size estimates or indices of relative abundance. Among the former, capture-recapture methods are widely used by biologists to estimate parameters of wildlife population (Pollock 1976) using the capture histories of identified individuals to draw the detection probability. Camera-trapping and non-invasive DNA samplings are among the most widespread techniques used to identify individuals (Karanth and Nichols 1998; Jackson et al. 2006; Mondol et al. 2009; Galaverni et al. 2012). However, other techniques such as *N-Mixture* methods can be used when individuals cannot be individually identified. *N-Mixture* models use data from spatially replicated count surveys to effectively estimate population sizes while accounting for the detection process (Royle 2004; Ficetola et al. 2018; Kidwai et al. 2019; Costa et al. 2020). However, these methods imply a great effort and resources as they require a high number of spatial replicates to account for imperfect detection (instance >20 sites; Kéry and Schaub 2012) and a high probability of detection (Royle

2004; Veech et al. 2016) to obtain reliable abundance estimates. Under these limitations for estimating abundance, relative abundance indices are helpful and convenient for studying population size. Indices of relative abundance are positively correlated with the population size of the species (Caughley and Sinclair 1994), so changes in index values reflect a change in actual abundance (Romesburg 1981; Anderson 2003). Among relative abundance indices scats counts along transects and capture rates by camera-traps are the most important. However, using relative abundance indices should be taken with caution because the monotonic relationship with true abundance may not be constant and positive over time and across habitats. In addition, different indices may show different sensitivities to the same habitat characteristics; therefore, relative abundance estimates will depend on the index used. In addition, the indices do not control the probability of detection of a species as do the technique mentioned above (CR and *N-Mixture* methods), which may influence abundance estimates. Moreover, we should consider that the efficient use of camera-trapping and DNA scats sampling might be limited under some circumstances that could affect abundance estimation. For example, environments with high humidity and temperature poorly preserve DNA in scats (Murphy et al. 2007). Temperature differences can also lead to reduced detection of animals and undesirable detection biases in camera-traps triggered by 'heat-in-motion' (Meek et al. 2015).

Identifying relative abundance indices that follow a constant relationship with abundance without depending on the sampling method used, habitat characteristics or probability of detection is of great interest when other advanced methods cannot be implemented in the study of population size. Here, we compare the relationship between camera-trapping and DNA faecal sampling to study population size during the same spatio-temporal settings. We compared the minimum number of individuals (NI) identified by each sampling method in several areas covering different habitat characteristics. We propose the minimum NI as a relative index of abundance and study the relationship of this index with abundance estimation. In particular, we used *N-Mixture* models (Royle 2004) to estimate abundance using camera traps. Previous studies focused on carnivore species with spotted fur or animals marked to facilitate the identification of individuals using camera-traps (Karanth and Nichols 1998; Silveira et al. 2003; Soisalo and Cavalcanti 2006; Mosquera et al. 2016). We used one of the most abundant mesocarnivore species in Europe and particularly in the Iberian Peninsula (Lloyd 1980), the red fox (*Vulpes vulpes*). Although the red fox lacks a distinct fur pattern, all individuals show distinctive characteristics (i.e. body and tail coat; muzzle, head and ears shape; leg and paw marking; injuries) that allow individual for identification (Sarmento et al. 2009; Dorning and Harris 2019). Furthermore, territory marking by foxes' character facilitates scats sampling (Goszczyński 1990). These characteristics make the fox a model species to test non-invasive sampling techniques in carnivores. The abundance of red foxes is not well-documented in all areas of the Iberian Peninsula. However, some studies have tested different non-invasive sampling techniques to determine its abundance (Jiménez et al. 2017; Jiménez et al. 2019a; Jiménez et al. 2019b). The red fox has a critical ecological role in seed dispersal (Campos and Ojeda 1997; Juan et al. 2006), the transmission of rabies disease (Chautan et al. 2000), and its impact on game species (Beja et al. 2009). In Spain, the red fox is a game species with annual hunting quotas. However, the quota implementation follows non-scientific criteria based on abundance estimations. Also, the lack of selective techniques for fox control may harm other endangered carnivores without an effective control of fox abundance (Virgós and Travaini 2005), which highlights the importance of the species for the carnivore guild and associated conservation conflicts.

Using red fox as model species, we tested the following questions: (1) are both methods correlated in detecting the same minimum NI? (2) is the minimum NI index correlated with red fox abundance estimates by both methods? (3) which method is the most economical for estimating red fox abundance in the same spatial and temporal environment? Our applied aim is to provide methodological information to assist decision-making in research requiring estimates of the relative abundance of mesocarnivores.

Material and Methods

Study area

The red fox is continuously distributed in the Autonomous Community of Madrid (Spain). Thus, we selected seven areas in this region for our study: Carabaña (C) and Villarejo de Salvanés (V) in the southeast, La Berzosa (B) and San Mames (SM) in the north and Robledo (R), Quijorna (Q) and Pelayos de la Presa (P) in the southwest (Figure 1).

The southeast part of the mesomediterranean floor has a temperature range of 5.7–7.5 °C in winter and 20.7–25.2ºC in summer and annual precipitation of around 390 mm per year. Here, rained crops, irrigated, and pasture predominate. Oak (*Quercus ilex rothundifolia* and *Quercus coccifera*) forests on calcareous soils result in a fragmented landscape characterized by a mixture of open spaces, low vegetation (https://www.comunidad.madrid/servicios/urbanismo-medio-ambiente/parque-regional-sureste), also with a strong human influence (Pascual et al. 2010).

The northern part of our study area lay between the meso- and supramediterranean floors characterized by milder summers and colder winters than the southeaster area; precipitations are also more abundant in this area. The landscape consists of Sclerophyllous vegetation (vegetation with hard leaves, short internodes and leaf orientation parallel or oblique to direct sunlight), oaks with gum rockrose (*Cistus spp*) and abundant granite boulders. Likewise, scrublands of broom (*Cistus spp*) and thyme (*Thymus vulgaris*) with pine woods are present from an altitude of 1400 m a.s.l.

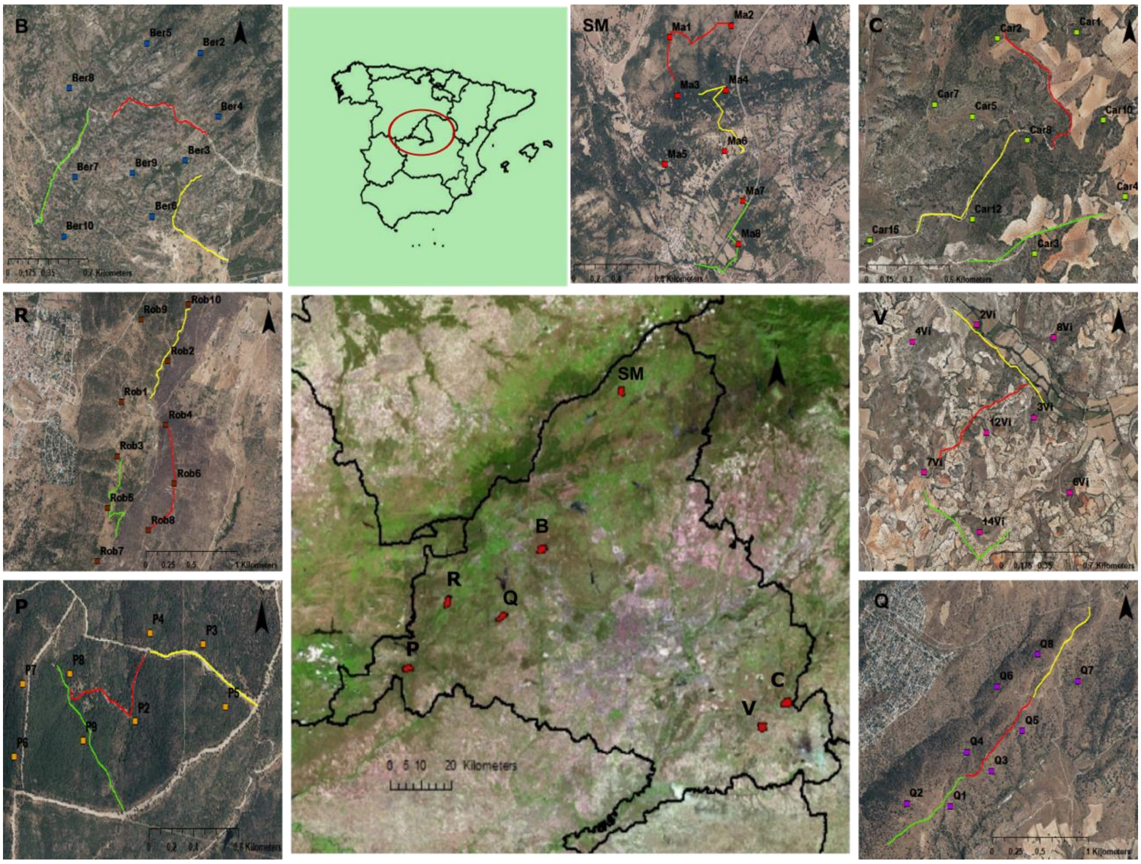

Figure 1. Sampling areas, cameras, and trail distribution in the study areas. Carabaña (C), Villarejo de Salvanés (V), La Berzosa (B), San Mames (SM), Robledo (R), Quijorna (Q) and Pelayos de la presa (P). The dots show the camera locations, and the lines show the faecal trails (red is trail 1; yellow is trail 2, and green is trail 3).

The southwest region of Madrid is characterized by a great variety of landscapes, reliefs and plant species, with predominant coniferous forests, especially stone pine (*Pinus pinea*). On the slopes, there are holm oaks (*Quercus ilex*), cork oaks (*Quercus suber*), other oaks (*Quercus spp*), and junipers (*Juniperus communis*), which are typical species of Mediterranean forests. Rainfall is abundant throughout the year except in summer, and winters are cold with occasional frosts and snowfalls.

The sampling period took place in 2017 (B, C, SM and R) and 2018 (V, Q and P) to cover different seasons: B, C and P in summer, V and Q in spring, SM in autumn, and R in winter. In this way, differences in detectability and marking that depend on seasonality were avoided (Ralls et al. 2010).

Camera-trapping sampling and scats collection sampling

At each site, we placed eight to ten cameras (Scoutguard SG562C LED White model), spaced approximately 450–600 m apart, covering as large an area as possible to maximize the number of individuals photographed and reduce the likelihood of unsampled foxes (similar to Sarmento et al. 2009). We used ArcGIS 10.2 (ESRI Inc., Redlands, California, USA) to create a minimum convex polygon (MCP) using the camera locations. We placed sardines and a commercial lure (HAGOPUR® Premium Attractant Fox) at the camera-trap sites to increase the probability of detection of foxes (Heinlein et al. 2020; Sebastián-González et al. 2020). The cameras operated for 35 days and were checked every seven days to replenish baits, collect the photographs and check the battery (see Martin-Garcia et al. 2022 for additional information on the photographic sampling design).

We collected scats in 21 trails of 1 km distributed in seven areas (i.e. three trails per area) (Supplementary Table 1). We cleaned each trail on the first day of camera placement to ensure an exclusive collection of scats deposited within the sampling period. After that, each trail was sampled every two weeks three times during camera placement to increase the probability of detecting scats from all individuals in the population. Trails were also inspected the day after the cameras were checked. We chose trails based on proximity to the camera placement areas to increase the probability of detecting the same individuals by both methods (Figure 1). Fresh scats that could potentially belong to foxes due to morphology and odour were collected by the same operators. All the operators had broad experience in recognizing carnivore scats. We placed scats in 96% alcohol for the first 12 h and then stored them on silica gels at 2–4ºC until they were processed (Nsubuga et al. 2004).

DNA extraction and amplification

We extracted DNA from the scats using a QIAamp DNA Stool Kit (Qiagen) following the manufacturer´s protocol. DNA purity and quantification were determined with a NanoDrop® 2000 spectrophotometer and Qubit® 3.0 fluorometer Quantitation Kit

(Invitrogen™). For species verification, we amplified a short region (120 bp) of the mitochondrial (mt) DNA “ND1” gene. Samples were BLAST using the BLASTx option at the NCBI platform to identify foxes. PCR reactions were performed in a total volume of 20 µL (the protocol for species verification is explained in detail in Supplementary material S1). All amplifications were carried out using filter tips in separate rooms (pre- and post- PCR), and negative controls/blanks were included in all amplifications to avoid contamination. PCR products were run and visualized on a 1.5% agarose gel using gel green (BIOTIUM). PCR products were sequenced at Macrogen (Netherlands).

We used 16 autosomal microsatellites loci of different canid species (*Canis familiaris*, *Canis lupus* and *Vulpes vulpes*) to genotype the individuals. The 16 autosomal microsatellites markers were: DB1, DB3 (Holmes et al. 1993); CXX173 (u173), CXX225 (u225), CXX 109 (u109) (Ostrander et al. 1993); c2168. CPH9, CPH1 (Fredholm and Wintero 1995); FH2054 (CXX/c2054), FH2001 (CXX/c2001), c2168, c2140, c2004 (Francisco et al. 1996); REN105L 03, INU030 (Sacks et al. 2011) and PEZ03 (Perkin-Elmer, Zoogen). Another set of ten microsatellite loci was unsuccessfully tested (Supplementary Table 2). Microsatellites were multiplexed in combinations with similar melting temperatures. We included from two to seven microsatellites in each multiplexed combination (Mplex). For PCR amplification, we followed the two-step multiplexing touch-down approach modified from Arandjelovic et al. 2009 (Supplementary Tables S3 and S4). For the Mplex, microsatellites were amplified by combinations, all in the same PCR reaction (Supplementary Table 3). The amplification was performed in a volume of 20 µL using DreamTaq polymerase (Thermo Scientific). The Mplex was diluted to 1:100 for the second PCR reaction. For the second PCR amplification, the Singleplex (Splex), we used 1 µL of 1:100 diluted multiplex (Mplex) and each microsatellite was amplified independently (see Supplementary Table 4). Splex PCR amplification was performed in a final volume of 10 µL. PCR conditions for the Mplex and the Splex are summarized in Supplementary Tables S3 and S4. The PCR products from the Splex were then diluted in water (1:10), mixed 1 µL with 9.8 µL EDTA (0.1 M) and 0.2 µL of size standard (GeneScanTM, 600 LIZ®, Thermo Scientific) and run on 3730xl DNA Analyzer (Applied Biosystems ™). Samples were genotyped using GeneMapper® Software 5 (Applied Biosystems ™).

Photo-identification and microsatellite genotyping

Individuals were identified based on traits such as body size, age range and, the appearance of the tail, spotting at specific points and other diagnostic features. We followed Sarmento et al. (2009) and Dorning and Harri (2019) to select traits to assist identification (Table 1; see also Figure 2 for examples of individual identification). We did not account for seasonal changes in coat for each individual. The sampling time was not long enough to appreciate these seasonal differences, and we did not repeat sampling in the same area during different seasons. Cubs were not individually identifiable due to their juvenile fur lacking sufficient distinctive features. However, juveniles tend to move together, so we decided to consider the maximum number of juveniles appearing together in the same photo as the minimum number of juveniles in the population and include it in the study.

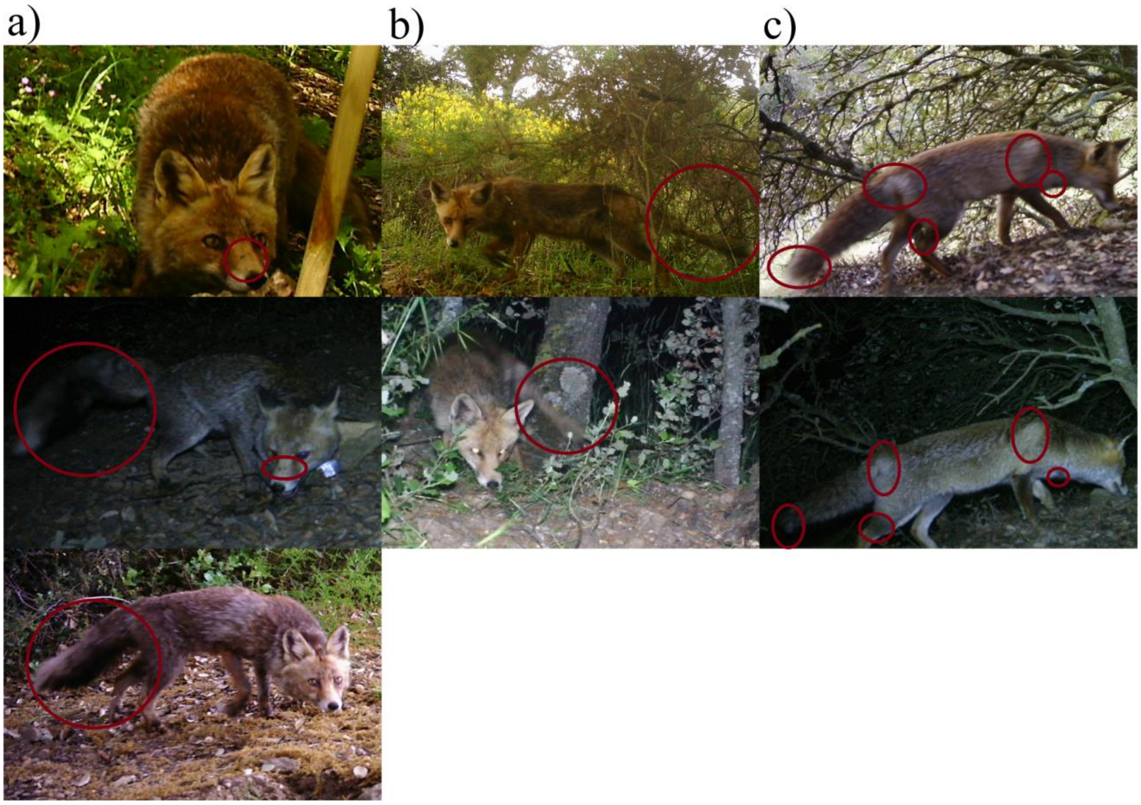

Figure 2. Examples of identification of individual foxes by camera trap a) Individual with two spots at the base of the snout and tail with thick fur. b) Individual with thin tail and no fur. c) Individual with a distinct fur pattern on the shoulder, base of the tail, paw and under the neck.

We reviewed photos by a second observer to control for photo-identification bias and reduce overestimation (Foster and Harmsen 2012; Ferreras et al. 2017; Johansson et al. 2020). A third observer re-analysed fox photographs when the first and second observers disagreed on the number of foxes identified. We considered the minimum number of individuals as the mean of the number of individuals identified by each observer. We also estimated the standard error and confidence intervals of the number of individuals photo-identified.

Table 1 Features selected for fox identification

Feature	Source of variation
Body coat	Condition and colour of coat on body, belly and chest (black or white patches or stripes).
Head/face/muzzle shape	Size of the head; length of the muzzle; the fullness of cheeks; marks on top of nose; colour and shape of fur markings on each side of the muzzle.
Ears	Length; shape (rounded or pointed); colour and texture of the coat on the inside of the ears; mottling on the back of the ears; wounds on the rims of ears
Leg and paw	Height and shape of black socks on the legs; black or white coat on the front of the thighs; coat colour on the inside of the legs; mottling of the coat and presence of white markings.
Tail coat	Coat condition; colour and pattern; shape and size of the dark patch around the supracaudal gland.
Tail shape	Length; thickness; straightness; tip shape (pointed, rounded, tapered, tufted, curly or flattened)
Injuries	Sarcoptic mange infection; bites; scars and deformities.

In microsatellite genotyping, allele sizes were manually scored relative to an internal size standard (GeneScan GS600LIZ) in GeneMapper version 5 (Applied Biosystems ™). Each locus was amplified three times to minimise genotyping errors. Genotypes were accepted as reliable if: (1) a heterozygote was observed at least twice in two independent reactions, and/ or (2) a homozygote was observed at least twice independently and failed amplification of the third replicate (Taberlet et al. 1996; Frantz et al. 2003; Flagstad et al. 2004). We defined ambiguous genotypes as (1) genotypes with only one amplified replicate, (2) genotypes that failed all replicates, (3) genotypes that generated different alleles in each replicate, or (4) genotypes with two identical homozygous replicates and a different third. These genotypes were annotated as missing alleles (000000) for the corresponding marker.

We used FreeNA program to test the null allele frequency (Chapuis and Estoup 2009). Gimlet 3.4 (Valière 2003) was used to evaluate heterogeneity observed (Ho) and expected (He); Hardy-Weinberg equilibrium (H-W equilibrium) and probability of identity (P_{ID}) to evaluate the reliability of the microsatellites used. The P_{ID} among genotypes (Kalinowski et al. 2007) is the most widely used statistical method to quantify the power or ability of molecular markers to distinguish between two individuals. We tested P_{ID}, $P_{ID\ (sib)}$, multilocus P_{ID} and Multi-locus $P_{ID\ (sib)}$. The P_{ID} is the probability that a single unrelated individual has this genotype (individuals are randomly mated); $P_{ID\ (sib)}$ is the probability that a single full sibling has this genotype (sister-sibling only population), and the multi-locus P_{ID} is the P_{ID} calculated over several loci by sequentially multiplying the P_{ID} value over the loci (considering that the loci are independent) (Scandura et al. 2001). The multi-locus $P_{ID\ (sib)}$ is the $P_{ID\ (sib)}$ calculated over several loci. We considered that a multi-locus $P_{ID\ (sib)}$ less than 0.01 (Mills et al. 2000) or a multi-locus P_{ID} between 0.001 and 0.0001 was sufficiently sensitive for identification and avoided underestimation (Waits et al. 2001). The presence of null alleles was checked with the FreeNa program. We also tested the effect of removing markers with a null allele frequency above 0.30 (Dakin and Avise 2004; Huang et al. 2016).

We used Cervus 3.0.7 (Kalinowski et al. 2007) and Gimlet 3.4 to create genotype profiles for all the samples and test the consensus in the number of individuals provided by both programs. Cervus 3.0.7 identifies samples with identical genotypes for the specified number of loci. From our set of 16 microsatellites, we scored individuals as the same if they had identical genotypes for at least eight or more common loci. This grouping method with matching samples ensures a conservative number of identified individuals by minimizing individuals created through erroneous, multi-locus genotypes (Mondol et al. 2009). Also, we allowed a maximum of two mismatching loci to control genotyping errors and increase success in genotype assignment (Kalinowski et al. 2007). We used Gimlet 3.4 to reconstruct the consensus genotypes. Finally, we tested the genotype reassortment function with the assumption that missing alleles are considered distinctive alleles.

Model selection: abundance estimation

We ran *N-Mixture* models to estimate fox abundance from camera-trapping without individual identification and accounting for the influence of imperfect detection. We used unmarked package (Fiske and Chandler 2011) in R software (R Core Team 2022) using the pcount function. This function estimates abundance in a hierarchical model. The actual abundance is estimated from the local variation of abundance (λ) at i sites using j temporal counts controlling for detection probability. There are two linked processes for estimating abundance (Kéry and Schaub 2012):

a) Abundance process (λ): Fitted by a Poisson distribution with mean λ and the variation of local abundance at site i

$$\lambda \sim Poisson\,(\lambda)$$

b) Observation process (p): Fitted by a binomial distribution of the observed counts (yi, j) of individuals at each site (i) in each temporal replicate (j) with a probability of detection.

$$yi, j\,|\lambda \sim Binomial\,(\lambda, p)$$

We counted each independent fox trapping event in each camera-trap per occasion (24 h). We considered more than one fox capture per occasion when we detected several foxes together in the same independent fox capture event. We first ranked three models to study abundance and detection probability among sampling areas: (1) constant detection probability among areas with a variation of abundance estimates among areas (i.e. $p\,(.) \sim \lambda\,(site)$), (2) variation in detection probability and variation of abundance estimates among areas (i.e. $p\,(site) \sim \lambda\,(site)$), and (3) variation in detection probability among areas with constant abundance estimates among areas (i.e. $p\,(site) \sim \lambda\,(.)$). We compared the performance of the Poisson, zero-inflated Poisson, and negative binomial distributions for each model. For model selection, we used Akaike's Information Criterion (AIC) (Akaike 1974) corrected for small sample size (AICc) (Burnham and Anderson 2002). We run a chi-square test in *Nmix.gof.test* function of package AICcmodavg (Mazerolle and Mazerolle 2017) to assess the goodness-of-fit and overdispersion of the selected model. We then estimated the posterior distribution of detection and abundance (λ) using empirical Bayes random effects (*ranef*) methods from the unmarked package. We used a parametric bootstrap approach with a simulation of 5000 bootstrap samples for each fit assessment. We obtained the mean abundance of each area, the standard error and the confidence interval.

Pearson correlation

We used a Pearson's correlation test to quantify the proportionality and similarity between (a) minimum photo-identified and genotyped *NI*, (b) minimum photo-identified *NI* and abundance estimates, (c) minimum genotyped *NI* and abundance estimates. We performed a logarithmic transformation when data were not normally distributed. We followed Prion's classification to establish correlation ranges (Prion and Haerling 2014).

Results

Individual identification: photo-identification and microsatellite genotyping

We obtained 309 photos of foxes. We identified a total of 23.66 individuals with a mean of 3.38 individuals per area (Table 2). Identified foxes per each observer were described in Supplementary Table 5.

We collected 77 scats along the trails (Table 2). According to the molecular species identification, mtDNA sequence ("ND1" gene) identified 69 samples of *Vulpes vulpes*. Based on GIMLET analyses, six samples (three from C and three from Q) could not be assigned to a specific genotype and were eliminated from the analyses, resulting in 63 faecal genotypes.

Table 2 Identified individuals and the number of photos and scats using both methods. Total photos (total number of fox photos per area); Foxes (*NI* identified); Total scats (number of fox scats collected per area). The following statistics are shown: standard error of *NI* photo-identified (S.E); lower and upper interval coefficient of error of *NI* photo-identified (CI [2.5, 97.5%]).

			CAMERA-TRAPPING		**DNA SCATS SAMPLING**	
	Total photos	**Foxes**	**S.E**	**CI [2.5, 97.5%]**	**Total scats**	**Foxes**
La Berzosa (B)	81	3.33	1.15	[2.08; 4.64]	6	1
Carabaña (C)	26	3	0	[3.00; 3.00]	19	3
Villarejo de Salvanés (V)	32	2	0	[2.00;2.00]	12	4
Quijorna (Q)	56	5	0	[5.00; 5.00]	16	4
Pelayos de la Presa (P)	22	2.66	0.57	[2.01; 3.32]	5	2
San Mames (SM)	54	5	1	[3.86; 6.13]	2	2
Robledo de Chavela (R)	31	2.66	0.57	[2.01; 3.32]	9	3

Consensus genotypes of sample types with 16 microsatellite loci (N=63) revealed the presence of 19 individuals (Table 2). All loci included in the study were polymorphic. We found 3–12 alleles per locus and an average of 7.06 annotated alleles per locus.

The mean allelic dropout rate was 24% (loci=16; SD=0.149) among loci and 35% (samples=69; SD=0.235) among samples. The single locus probabilities were combined to obtain the total probability over the 16 loci, assuming the independence of different loci. Results of Ho, He and H-W equilibrium of 16 microsatellites are shown in Supplementary Table 6. The different identity probabilities for the 16 microsatellites loci were multi-locus P_{ID} =1.98×10–14 and multi-locus $P_{ID\ (sib)}$ = 3.43×10−06. Based on the identified probability, the 16 loci considered were sufficient to distinguish with 99% certainty between sibling red foxes (Supplementary Table 6). We obtained null allele values of less than 0.30 in almost all loci, except for INU030, which had a null allele frequency of 0.33 (Supplementary Table 6). We repeated the analyses after removing INU030 and obtained the same results regarding the same number of individuals and sample genotypes. However, the multi-locus P_{ID} increased slightly to 1.16×10–13. Therefore, we decided to retain this microsatellite in subsequent analyses (Huang et al. 2016). The number of individuals identified was consistent between the two software tools used (Cervus 3.0 and Gimlet 3.4), with a single exception in the P location population, where we detected two individuals by Gimlet 3.4 but could not obtain results with Cervus 3.4. The number of assigned scats to each individual is described in Supplementary Table 5.

Model selection: abundance estimation

Model selection resulted in two top-ranked models (lowest AICc). The model with lower AICc indicated a constant detection probability and variation in abundance estimation between areas. The second model maintained a constant abundance estimate and a variable detection probability between areas (Table 3). In both models, the Poisson distribution was more supported than the zero-inflated Poisson and negative binomial. Although the two top-ranked models were close (i.e. ∆AICc < 2) we decided to select the first top-ranked model because it explained our predictions for estimating abundance in each area (Table 3) to study the relationship between abundance estimates and the minimum NI between areas. This model yielded a detection probability of 0.03 (S.E=0.01; intercept = -3.36; CI [-4.017, -2.694]). The *Nmix.gof.test* with 100 bootstrapped samples indicated that the selected model fit well (χ2=2167.27; p-value=0.37) with no evidence of overdispersion (c-hat=1.01) (i.e. observed test statistic divided by the mean of the simulated test statistics).

Table 3. Model selection to determine detection probability and abundance between areas. Model selection results to compare Poisson [P], zero-inflated Poisson [ZIP], and negative binomial [NB] distributions. Model selection was based on Akaike's information criterion (AIC), the number of degrees of freedom (df), the difference AICc from the best-fit models (∆AICc<2), and the model weights (AICwt). λ defines the abundance process, and p is the detection process. p(.) and λ(.) indicates constant detection probability and abundance between areas, respectively, and p(site) and λ(site) indicates the variation in detection probability or abundance between areas.

Model	df	AICc	∆AICc	AICcwt
p (.) ~ λ (site) [P]	8	1695.359	0.000	0.342
p (site) ~ λ (.) [P]	8	1695.476	0.117	0.323
p (.) ~ λ (site) [ZIP]	9	1698.135	2.776	0.085
p (.) ~ λ (site) [NB]	9	1698.135	2.776	0.085
p (site) ~ λ (.) [ZIP]	9	1698.253	2.894	0.080
p (site) ~ λ (.) [NB]	9	1698.258	2.899	0.080
p (site) ~ λ (site) [P]	14	1705.847	10.488	0.001
p (site) ~ λ (site) [ZIP]	15	1709.422	14.063	0.0003
p (site) ~ λ (site) [NB]	15	1709.425	14.066	0.0003

Pearson correlation

Genotypes for fox *NI*, photo-identified data of fox *NI* and abundance data showed a normal distribution (Table 4). We found no significant correlation between the minimum *NI* derived from photo-identification and faecal genotyping (n= 7; |r| = -0.07; p-value= 0.87), while photo-identified minimum *NI* showed a strong positive (Prion and Haerling

2014) but non-significant correlation with abundance estimates (n= 7; |r| = 0.68; p-value= 0.08). In contrast, minimum *NI* from faecal genotyping and abundance estimates were weakly (Prion and Haerling 2014) and non-significantly correlated (n= 7; |r|= -0.32; p-value= 0.48).

Table 4. Comparison between the minimum number of individual photo-identified (NI photo-identified), the minimum number of individual faecal genotyping (NI faecal genotyping) and the abundance**.** Estimation of fox abundance in each area was conducted using Poisson models. The following statistics are shown: mean abundance (abundance mean); standard error of abundance (abundance S.E); lower and upper interval coefficient of abundance (abundance CI [2.5, 97.5%]).

Area	NI photo-identified	NI faecal genotyping	Abundance mean	Abundance S.E	Abundance CI [2.5, 97.5%]
La Berzosa (B)	3.33	1	6.8	0.6	[5.78;8.0]
San Mames (SM)	5	2	5.5	0.5	[4.5;6.6]
Carabaña (C)	3	3	2.4	0.3	[1.8;3.1]
Pelayos de la Presa (P)	2.66	2	1.8	0.3	[1.2;2.5]
Quijorna (Q)	5	4	5.7	0.6	[4.6;6.9]
Robledo de Chavela (R)	2	3	2.6	0.3	[2.0;3.3]
Villarejo de Salvanés (V)	2.66	4	3.0	0.4	[2.2;3.9]

Discussion

Evaluating multiple sampling methods in monitoring carnivore populations is essential for establishing effective conservation strategies (Caughley and Sinclair 1994; Sadlier et al. 2004; Barea-Azcón et al. 2007). We used camera-trapping and DNA faecal genotyping to estimate the minimum number of foxes. We estimated fox abundance by implementing *N-Mixture* models to assess and compare the relationship between abundance and minimum *NI* provided by camera-trapping and DNA faecal sampling. First, we found that the estimation of minimum *NI* provided by camera-trapping was slightly higher than that of DNA faecal genotyping. Second, there are indications that areas with more *NI* identified were those with higher fox abundance, following a positive relationship between abundance and *NI* detected by camera-trapping. However, we also found a non-significant negative relationship between *NI* detected by faecal DNA and abundance estimates.

The comparison of camera-trapping and DNA faecal sampling methods showed a slight variation in the number of the identified foxes. We identified three more individuals with camera-traps than DNA faecal sampling (minimum *NI* was identical in Carabaña and Pelayos). However, despite this slight variation, we found no significant correlation between the minimum *NI* calculated from photo-identified and faecal genotyped. Comparisons between both non-invasive sampling methods to estimate the population abundance of carnivore species are relatively common in the literature (Mondol et al. 2009 (*Panthera tigris*); Janečka et al. 2011 (*Panthera uncia*); Galaverni et al. 2012 (*Canis lupus*); Velli et al. 2015 (*Felis silvestris*)). Galaverni et al. (2012) found concordance between the two sampling methods in the number of identified wolves, which supported their complementarity. However, the minimum number of wolves identified was slightly higher with the use of DNA than with the cameras. In particular, Mondol et al. (2009) found non-significant differences between sampling methods in tigers, although they detected three more individuals using camera-traps than DNA methods.

We identified fewer individuals using DNA faecal sampling than camera-trapping (especially in San Mamés and La Berzosa). This difference could be explained by limitations in the scats sampling design due to the use of scats for communication between foxes. Carnivores mark their home ranges and territories with scats deposited in a non-random distribution (Kruuk 1978; Macdonald 1980; Gorman 1990; Soler et al. 2009). Accounting for this behaviour, we chose random but well-delimited paths (trails and roads) that covered the entire area sampled by cameras. Fox scats often mark the boundary of territories or sites with critical resources (Macdonald 1985; Barja et al. 2001). Because resource and territory marking occurs unevenly between individuals, marks of specific individuals in a given area may be over-represented (Gorman and Trowbridge 1989). Moreover, defecation rates differ between individuals (Cavallini 1994), particularly between males and females, adults, and juveniles (Goszczyński 1990; Peterson et al. 2002; Ralls et al. 2010; Fawcett et al. 2012), which can influence the number of individuals detected. Defecation rate also vary according to season and diet (Andelt and Andelt 1984; Goszczyński 1990). Other effects, such as changes in marking behaviour caused by the spatial distribution of roads (Vilà et al. 1994; Barja and List 2014; Zaman et al. 2019) may also lead to increased non-uniform distribution of scats. In our study area of Villarejo, in contrast to other locations, the number of individuals identified by DNA in scats was higher than using cameras. These differences suggest some limitations of the camera-trapping method. Although 32 photos were obtained for identifying individuals, we obtained 15 unidentified photos of either new or previously detected individuals. Camera traps could alter red fox behaviour, especially in females due to the sounds and flashes they make (Meek et al. 2014). Predation risk or anthropogenic disturbance (Lucherini et al. 1995) might also increase trap avoidance, thus influencing individual detection. These potential behavioural changes might impact the more elusive individuals more effusively, with the consequent bias in their detection.

Although we found a non-significant correlation between the genotyped and photo-identified minimum NI, the minimum photo-identified *NI* and the abundance estimation showed a positive relationship. This result suggests the possibility of using *NI* as a straightforward index to explain variations in species abundance. We validated individual red fox photoidentification according to previous studies (Sarmento et al. 2009; Dorning and Harris 2019but see, Güthlin et al. 2014) to obtain a minimum *NI*. However, we recommend at least three observers to reduce the bias in over- or under-estimating the number of individuals (Foster and Harmsen 2012; Ferreras et al. 2017; Johansson et al. 2020). Photo identification also has limitations for juveniles or cubs. Identifying juveniles becomes difficult when individuals are alone. Therefore, we consider the minimum number of juveniles as the total number of juveniles together in the same photo. However, we acknowledge this approach might be susceptible to underestimating juvenile populations because we considered only the minimum number of juveniles. Nevertheless, we assume that adding juveniles to the study generated less bias when comparing the minimum *NI* identified and the abundance estimated by both sampling methods. The identification of individuals has become a standard method for the abundance estimation of animal populations, such as using the Spatial Capture-Recapture (SCR) method (Efford 2014; Royle et al. 2014; Rodgers et al. 2014; Wegge et al. 2019). However, CR methods for abundance estimates require a sufficient number of recaptures to obtain accurate estimates (Otis et al. 1978). SCR approaches need at least 20–25 recaptures, including spatial recaptures to correctly describe the movement (Efford et al. 2004), or alternatively using movement data from telemetry tagged individuals (Jimenez et al. 2019) to improve the estimate. Due to the data limitations, we used *N-Mixture* models to estimate fox abundance.

The *N-Mixture* model estimates abundance using count data without needing individual identification or reference to the effective trapping area. Other studies focused on the reliability of the *N-Mixture* models to estimate abundance. Basile et al. (2016) found that *N-Mixture* models and SCR methods yielded a similar estimation of the abundance of the short-toed tree creeper (*Certhia brachydactyla*). Ficetola et al. (2018) obtained limited differences between *N-Mixture* models and capture-mark-recapture to estimate the abundance of small vertebrates. Also, to avoid violating assumptions of *N-Mixture* caused by double counting of a single sampling occasion (Link et al. 2018), we only considered more than one fox capture per occasion (24 h) when we detected several foxes together in the same capture event. Our results between photo-identified *NI* and abundance showed that *NI* results are helpful when the minimum number of identified individuals in the population is not sufficient, or the number of captures of identified individuals is not enough to produce reliable abundance estimates (Otis et al. 1978). *NI* may also be recommended when sufficient temporal and spatial replicates are unavailable or the assumptions of *N-Mixture* models are not met (e.g. independence in the case of gregarious animals). Thus, Martin-Garcia et al. (2022) found that the minimum photo-identified *NI* might not be biased by detection probability, thus obtaining the same predictors as the *N-Mixture* models to explain abundance patterns.

We found no significant correlation between minimum *NI* genotyped and abundance. Including more scats could help identify a potential relationship between the minimum number of individuals identified by DNA scats sampling, *NI* photo-identified, and abundance (Wegge et al. 2019; Lindsø et al. 2022). Future research should include random transects out of existing trails to increase the number of scats and detections of individuals. Implementing a random transect design that covers many landscapes with different compositions and configurations (Güthlin et al. 2012) could reduce the bias caused by some individuals marking more intensively along the trails. In this vein, we could better refine and compare the relationship between estimated abundances of faecal DNA and camera-trapping sampling methods (Rodgers et al. 2014) and between *NI* genotypes and abundance. In addition, new state-of-the-art genomic approaches based on SNPs approach (e.g. RAD-seq) may increase the accuracy of DNA amplification decreasing the loss of samples and consequently improving abundance estimates (Andrews et al. 2016; De Barba et al. 2017; Erwin et al. 2021). Another timely method is the SNP genotyping method based on high-throughput real-time PCR technique known as Dynamic Array™ by Fluidigm® that is mainly used for degraded samples such as scats and ancient DNA studies samples (Kraus et al. 2015).

In our experience, using camera-trapping was cheaper than DNA sampling methods to study red foxes. Our budget for the camera-trapping method was 2756 euros (including cameras, baits and placement in the study areas) compared to 7500 euros for the faecal DNA method (including fieldwork, sample shipment and protocol optimization). Several aspects should be considered in terms of budget. Firstly, a small pilot optimization study beforehand could help to reduce costs in future analyses. The optimization process with fewer samples is helpful to check the protocol used and obtain preliminary results avoiding using all the valuable samples. Secondly, using other less costly genetic techniques. Single nucleotide polymorphism (SNPs) is frequently used as a new genotyping method for individual and sex identification (Parker et al. 2021; Buchalski et al. 2022; Lopez-Bao et al. 2020). To date, developing a SNP panel for individual identification is considered an efficient and cost-effective method to simultaneously genotype hundreds of individuals (Carroll et al. 2018). Lastly, researchers should consider an extra budget for the replacement of the cameras in case of loss or failure during the study. Consequently, the budget for camera-trapping may increase depending on the number of cameras needed for our research.

Our research highlights the importance of correctly selecting sampling methods for abundance studies. Researchers can adjust the broad choices in sampling methods to their available funds and logistics. Different methods can perform differently and provide different results; thus, it is required to identify first the costs and limitations of the potential techniques for our specific research objectives and the species to study. Our results suggest the minimum photo-identified *NI* is a reliable index for studying abundance variation when other methods are unavailable. In contrast, it is necessary to improve the methods of scats sampling to estimate population size and to explore its relationship with camera trap data. Sampling designs with transects away from existing trails will increase the probability of finding more scats. We should mention that both methods were compared to study abundance over a short period. On the other hand, DNA sampling in scats could be useful to identify individuals over a longer period, over years and seasons when this would be very difficult with photos (Bellemain et al. 2005). In addition, assessments of genetic diversity, population substructure, gene flow, paternity, and heritability are easy to evaluate with DNA stool genotyping (Pilot et al. 2014; Zanin et al. 2016). However, this was not the main objective of this study. Regarding our model species, the red fox, and camera-trapping methods can be a reference for future red fox management actions. In our study, the validity of using the camera-trapping method to estimate fox population abundance is also motivated by its lower cost when compared to the faecal DNA genotyped method. However, further research on the cost-effectiveness of new genetic methods is encouraged.

Supporting information Chapter 2

Supplementary material 1 DNA extraction and amplification protocol for species identification

For species verification, we amplified of a short region (120 bp) of the mitochondrial (mt) DNA "ND1" gene. The primers F1 (5-CGAAACCAGACGAGCTACC-3) and F2 (3-AACCAGCTATCACCAGGCTC-5) were primarily designed based on mammal mitochondrial sequences (unpublished data). PCR reactions were conducted in a total volume of 20µl containing 1 µl of genomic DNA, 2µl of 10X Dream taq buffer (Thermo Scientific Lab), 0.4µl of 2mM of each dNTP, 0.5µl of each 10µM primer (F1 and F2, respectively), 1.5 µl of Bovine serum albumine (BSA; 5mg/ml) and 0.25µl of Dream taq DNA polymerase (5U/µl, Thermo scientific lab) in deionized water. Thermocycling was performed on the ABI 2720 (Applied Biosystems®). An initial denaturation step of 3min at 95°C was followed by 35 cycles consisting of 30s at 95°C, annealing for 30s at temperatures decreasing from 61 to 56°C during ending with an extension step at 72°C for 1min. PCR products were stored at 4°C.

Supplementary Table 1 Number of scats collected per area, trail, date, session and scats location (UTM coordinates) on each trail.

ID	Area	Session	Date	Trail	Typo	X	Y
1	Carabaña	1	11/06/17	C1	30T	481523	4455741
2	Carabaña	1	11/06/17	C1	30T	481697	4455980
3	Carabaña	1	11/06/17	C1	30T	481718	4456000
4	Carabaña	1	11/06/17	C2	30T	481847	4456694
5	Carabaña	1	11/06/17	C3	30T	481814	4455446
6	Carabaña	2	25/06/17	C1	30T	481111	4455578
7	Carabaña	2	25/06/17	C1	30T	481421	4455688
8	Carabaña	2	25/06/17	C1	30T	481467	4455671
9	Carabaña	2	25/06/17	C1	30T	481525	4455760
10	Carabaña	2	25/06/17	C1	30T	481546	4455805
11	Carabaña	2	25/06/17	C1	30T	481674	4455957
12	Carabaña	2	25/06/17	C2	30T	481838	4456256
13	Carabaña	2	25/06/17	C2	30T	481514	4456297
14	Carabaña	2	25/06/17	C2	30T	481234	4456331
15	Carabaña	3	09/07/17	C1	30T	481516	4455710
16	Carabaña	3	09/07/17	C1	30T	481655	4455930
17	Carabaña	3	09/07/17	C1	30T	481781	4456055
18	Carabaña	3	09/07/17	C1	30T	481629	4456287
19	Carabaña	3	09/07/17	C2	30T	482223	4456169
20	San Mames	1	08/08/17	SM2	30T	440803	4539135
21	San Mames	2	21/08/17	SM2	30T	440528	4539712
22	La Berzosa	1	03/10/17	B2	30T	421056	4497618
23	La Berzosa	2	17/10/17	B1	30T	420378	4496924
24	La Berzosa	2	17/10/17	B1	30T	420314	4497151

25	La Berzosa	2	17/10/17	B3	30T	419662	4497208
26	La Berzosa	2	17/10/17	B3	30T	420242	4498052
27	La Berzosa	3	31/10/17	B1	30T	420472	4496832
28	La Berzosa	3	31/10/17	B1	30T	420472	4496832
29	La Berzosa	3	31/10/17	B3	30T	419727	4497355
30	Robledo de Chavela	2	19/12/17	R2	30T	396820	4482983
31	Robledo de Chavela	2	19/12/17	R2	30T	396531	4482506
32	Robledo de Chavela	3	26/12/17	R1	30T	396697	4484071
33	Robledo de Chavela	3	26/12/17	R2	30T	396733	4483443
34	Robledo de Chavela	3	26/12/17	R2	30T	396799	4483197
35	Robledo de Chavela	3	26/12/17	R2	30T	396815	4482955
36	Robledo de Chavela	3	26/12/17	R2	30T	396735	4482638
37	Robledo de Chavela	3	26/12/17	R2	30T	396626	4482574
38	Robledo de Chavela	3	26/12/17	R2	30T	396528	4482507
39	Robledo de Chavela	3	26/12/17	R3	30T	396188	4482531
40	Robledo de Chavela	3	26/12/17	R3	30T	396154	4482428
41	Villarejo de Salvanes	1	20/03/18	V2	30T	475520	4449597
42	Villarejo de Salvanes	2	10/04/18	V1	30T	475725	4450090
43	Villarejo de Salvanes	2	10/04/18	V2	30T	475836	4449772
44	Villarejo de Salvanes	2	10/04/18	V2	30T	475734	4449715
45	Villarejo de Salvanes	2	10/04/18	V2	30T	475730	4449712
46	Villarejo de Salvanes	2	10/04/18	V2	30T	475656	4449637
47	Villarejo de Salvanes	2	10/04/18	V2	30T	475640	4449686
48	Villarejo de Salvanes	2	10/04/18	V3	30T	475178	4448965
49	Villarejo de Salvanes	2	10/04/18	V3	30T	475344	4448856
50	Villarejo de Salvanes	2	10/04/18	V3	30T	475377	4448867
51	Villarejo de Salvanes	3	17/04/18	V2	30T	475731	4449715
52	Villarejo de Salvanes	3	17/04/18	V3	30T	475894	444878
53	Quijorna	1	22/05/18	Q1	30T	410498	4479832
54	Quijorna	1	22/05/18	Q1	30T	410448	4479739
55	Quijorna	1	22/05/18	Q1	30T	410434	4479703
56	Quijorna	1	22/05/18	Q2	30T	410301	4479537
57	Quijorna	1	22/05/18	Q2	30T	410115	4479366
58	Quijorna	1	22/05/18	Q2	30T	410231	4479437
59	Quijorna	1	22/05/18	Q2	30T	410260	4479509
60	Quijorna	1	22/05/18	Q2	30T	409941	4479197
61	Quijorna	1	22/05/18	Q2	30T	410204	4479468
62	Quijorna	1	22/05/18	Q3	30T	409661	4479027
63	Quijorna	1	22/05/18	Q3	30T	409649	4478968
64	Quijorna	1	22/05/18	Q3	30T	409477	4478784
65	Quijorna	1	22/05/18	Q3	30T	409485	4478786
66	Quijorna	1	22/05/18	Q3	30T	409622	4478955
67	Quijorna	3	05/06/18	Q1	30T	410547	4479893
68	Quijorna	3	05/06/18	Q2	30T	410278	4479565
69	Quijorna	3	05/06/18	Q2	30T	410366	4479663
70	Pelayos de la presa	1	19/06/18	P1	30T	387436	4466086
71	Pelayos de la presa	1	19/06/18	P2	30T	386670	4466324
72	Pelayos de la presa	1	19/06/18	P2	30T	386307	4466033
73	Pelayos de la presa	2	26/06/18	P2	30T	386349	4466027
74	Pelayos de la presa	2	26/06/18	P2	30T	386024	4466153
75	Pelayos de la presa	2	26/06/18	P3	30T	386180	4465578
76	Pelayos de la presa	3	17/07/18	P2	30T	385685	4466497
77	Pelayos de la presa	3	17/07/18	P2	30T	385685	4466497

Supplementary Table 2 Microsatellites characteristics. Microsatellite name (Microsatellite); Type of nucleotide (Type), DNA Motif (Motif); Species isolated (Species); Sequence of forward and reverse primers in 5'-3' direction (Sequence 5'-3'); citation; original PCR product size in base-pair (bp) (original PCR product (bp); and PCR product size in base-pair (bp) of the current study (PCR product (bp)).

Microsatellite	Type	Motif	Species	Sequence 5-3	Paper source	Original PCR product (bp)	PCR product (bp)
REN105L 03	Dinucleotide	(CA)21	Redfox	F-GGTGCCTGACAAGATGGAA R-CATTGAAAGGGAATGCTGGT	Sacks et al. 2011	161-167	150-170
PEZ03	Dinucleotide	?	Wolf/Dog	F-CACTTCTCATACCCAGACTC R-CAATATGTCAACTATACTTC	Perkin-Elmer, Zoogen	95-154	102-138
INU030	Dinucleotide	(CA)10	Redfox	F-GGCTCTGTGCTCAAGTCTGT R-CATTGAAAGGGAATGCTGGT	Sacks et al. 2011	127-133	128-136
FH2054 (CXX/c2054)	Tetranucleotide	(GATA)16	Wolf/Dog	F-GCCTTATTCATTGCAGTTAG R-ATGCTGAGTTTTGAACTTTCCC	Francisco et al. 1996	151	139-195
FH2001(CXX/c2001)	Tetranucleotide	(GATA)8	Wolf/Dog	F-TCCTCCTCTTCTTTCCATTG R-TGAACAGAGTTAAGGATAGACACG	Francisco et al. 1996	131	116-194
CXX173 (u173)	Dinucleotide	(TG)17	Wolf/Dog	F-ATCCAGGTCTGGAATACCCC R-TCCTTTGAATTAGCACTTGGC	Ostrander et al. 1993	unknown	122-132
CPH5	Dinucleotide	(TG)17	Wolf/Dog	F-TCCATAACAAGACCCCAAAC R-GGAGGTAGGGGTCAAAAGTT	Fredholm and Wintero 1995	unknown	106-128
c2168	Tetranucleotide	(GAAA)2	Red fox	F-GCAAATTACTTACTTCACTATGC R-TTGCAAGACTTCAACATGGC	Francisco et al. 1996	213	210-248

CXX225 (u225)	Dinucleotide	(GT13)	Wolf/Dog	F-AGCGACTATTATATGCCAGCG R-CTCATTGGTGTAAAGTGGCG	Ostrander et al. 1993	unknown	160-172
DB3	Dinucleotide	(CA)20	Red fox	F-ACAATGCCTCCAGKTAAGG R-GATCACGTGCITATGTGCTG	Holmes et al. 1993	128-138	118-124
DB1	Dinucleotide	(CA)22	Red fox	F-CCCAATACAGCAAGACCTCT R-ACCTACTCTGCACAGAGAAG	Holmes et al. 1993	141-159	131-149
CPH9	Dinucleotide	(GT)18	Wolf/Dog	F-CAGAGACTGCCACTTTAAACACAC R-AAAGTTCTCAAATACCATTGTGTTACA	Fredholm and Wintero 1995	unknown	140-152
CPH1	Trinucleotide	(TGG)3 TAG(TGG)11	Red fox	F-GCCTAGCCCAGTGAAAGTTAAC R-TTCCAATGCCTGATAACTGAGA	Fredholm and Wintero 1995	125-144	124-130
c2140	Tetranucleotide	(GAAA)18	Red fox	F-GGGGAAGCCATTTTTAAA R-TGACCCTCTGGCATCTAGGA	Francisco et al. 1996	228	94-102
c2004	Tetranucleotide	(GAAA) 13	Red fox	F-CTAAGTGGGGAGCCTCCT R-ACTGTGACCTACTGAGGTTGCA	Francisco et al. 1996	237	210-218
CXX 109 (u109)	Dinucleotide	(AC)15	Wolf/Dog	F-AACTTTAAGCCACACTTCTGCA R-ACTTGCCTCTGGCTTTTAAGC	Ostrander et al. 1993	unknown	137-159

Markers did not work

PEZ05	?	?	Wolf	F-GCTATCTTGTTTCCCACAGC R-TCACTGTATACAACATTGTC	Perkin-Elmer, Zoogen	97-121	
PEZ06	?	?	Wolf	F-ATGAGCACTGGGTGTTATAC R-ATGAGCACTGGGTGTTATAC	Perkin-Elmer, Zoogen	164-214	
PEZ12	?	?	Wolf	F-GTAGATTAGATCTCAGGCAG R-TAGGTCCTGGTAGGGTGTGG	Perkin-Elmer, Zoogen	250-320	

PEZ01	?	?	Wolf	F-GGCTGTCACTTTTCCCTTTC R-CACCACAATCTCTCTATAAATAC	Perkin-Elmer, Zoogen	92-136
CPH11	Dinucleotide	(TA)26(CA) 15	Red fox	F-TTAATGTTTCTCCGATGTTTACAT R-GAAAGCCAAGCATGACTAGG	Fredholm and Wintero 1995	120-178
CPH6	Dinucleotide	(CA)I9	Red fox	F-CATTGGCTGTTTGACTCTAGG R-ACTGATGTGGGTGTCTCTGC	Fredholm and Wintero 1995	107-136
CPH3	Dinucleotide	(GA)2TA(GA) 17	Red fox	F-CAGGTTCAAATGATGTTTTCAG R-TTGACTGAAGGAGATGTGGTAA	Fredholm and Wintero 1995	154-182
DB4	Dinucleotide	(GT)23	Red fox	F-CTTCCATCCCTTGTCTGT R-CATTTTCTCTCTGTCCACTT	Holmes et al. (1993)	114-144
DB6	?	(CA)16	Red fox	F-ACTTTCATATTACTGTACTG R-AACACGTCACTTGCTGTCCA	Holmes et al. (1993)	104-110

Supplementary Table 3 Microsatellites grouped in combos according to Multiplex-PCR temperature conditions and PCR mix volumes for Mplex PCR 20µL: Combo; type of marker (Type); Sequences of primer in direction (5'-3') (Sequences(5'-3')); Temperature of Melting (Tª Melting (Cº); Polymerase type; $MgCl_2$ (25mM); double-distilled water (ddH_20); Bovine serum albumin (BSA (20mg/ml)); Buffer Taq (10xPCR); Super Taq DNA Polymera enzyme (SuperTaq); Primer Forward and Reverse (Primer (10µM)); Deoxynucleotide Triphosphates (DNTPs).

						PCR Mix volumes for Mplex PCR (20µL)									
Combo	**Marker**	**Type**	**Sequences(5'-3')**	**Tª melting (Cº)**	**Polymerase type**	**$MgCl_2$ (25mM)**	**ddH_20**	**BSA (20mg/ml)**	**Buffer (10xPCR)**	**SuperTaq**	**Primer (10µM)**	**DNTPs (2.5mM)**	**Genomic DNA**	**Cycles**	**Touch-down**
1	CXX109(u109)	Microsatellite	AACTTTAAGCCACACTTCTGCA	57	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			ACTTGCCTCTGGCTTTTAAGC	58											
1	CXX225(u225)	Microsatellite	AGCGACTATTATATGCCAGCG	58	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			CTCATTGGTGTAAAGTGGCG	57											
1	CXX173 (u173)	Microsatellite	ATCCAGGTCTGGAATACCCC	58	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			TCCTTTGAATTAGCACTTGGC	57											
1	CPH9	Microsatellite	CAGAGACTGCCACTTTAAACACAC	58	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			AAAGTTCTCAAATACCATTGTGTTACA	58											
1	DB1	Microsatellite	CCCAATACAGCAAGACCTCT	55	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			ACCTACTCTGCACAGAGAAG	50											
1	c2140	Microsatellite	GGGGAAGCCATTTTTAAA	53	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			TGACCCTCTGGCATCTAGGA	59											
1	CPH1	Microsatellite	GCCTAGCCCAGTGAAAGTTAAC	58	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
1			TTCCAATGCCTGATAACTGAGA	58											

2	DB3	Microsatellite	ACAATGCCTCCAGKTAAGG	51	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	55-48
2			GATCACGTGCITATGTGCTG	54											
2	c2168	Microsatellite	GCAAATTACTTACTTCACTATGC	51	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	55-48
2			TTGCAAGACTTCAACATGGC	58											
3	PEZ03	Microsatellite	CACTTCTCATACCCAGACTC	50	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	55-48
3			CAATATGTCAACTATACTTC	40											
3	CPH5	Microsatellite	TCCATAACAAGACCCCAAAC	55	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	55-48
3			GGAGGTAGGGGTCAAAAGTT	55											
4	FH2001	Microsatellite	TCCTCCTCTTCTTTCCATTG	57	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
4			TGAACAGAGTTAAGGATAGACACG	56											
4	FH2054	Microsatellite	GCCTTATTCATTGCAGTTAG	54	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	57-52
4			ATGCTGAGTTTTGAACTTTCCC	59											
5	c2004	Microsatellite	CTAAGTGGGGAGCCTCCT	63	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	62-55
5			ACTGTGACCTACTGAGGTTGCA	63											
5	INU030	Microsatellite	GGCTCTGTGCTCAAGTCTGT	63	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	62-55
5			CATTGAAAGGGAATGCTGGT	59											
5	REN105L03	Microsatellite	GGTGCCTGACAAGATGGAAT	61	Dream taq (5Units/µL)	1,4	9,1	0,8	2	0,1	0,3	1	5	35	62-55
5			GAGATTGCTGCCCTTTTTACT	58											

Supplementary Table 4 Singleplex-PCR temperature conditions and PCR mix volumes for Splex PCR 10µL for each Microsatellite: type of marker (Type); Sequences of primer in direction (5'-3') (Sequences(5'-3')); Temperature of Melting (Cº) (Tª Melting (Cº)); Polymerase type; $MgCl_2$ (25mM); double-distilled water (ddH_20); Bovine serum albumin (BSA (20mg/ml)); Buffer Taq (10xPCR); Super Taq DNA Polymera enzyme (SuperTaq); Primer Forward and Reverse (Primer (10µM)); Deoxynucleotide Triphosphates (DNTPs)

								PCR Mix volumes for Splex PCR (10µL)						
Marker	**Type**	**Sequences(5'-3')**	**Tª melting (Cº)**	**Polymerase type**	**$MgCl_2$ (25mM)**	**ddH_20**	**BSA (20mg/ml)**	**Buffer (10xPCR)**	**SuperTaq**	**Primer (10µM)**	**DNTPs (2.5mM)**	**Genomic DNA**	**Cycles**	**Touch-down**
CXX109(u 109)	Microsatellite	AACTTTAAGCCACACTTCTGCA	57	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	62-57
		ACTTGCCTCTGGCTTTTAAGC	58											
CXX225(u 225)	Microsatellite	AGCGACTATTATATGCCAGCG	58	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	62-57
		CTCATTGGTGTAAAGTGGCG	57											
CXX173 (u173)	Microsatellite	ATCCAGGTCTGGAATACCCC	58	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	62-57
		TCCTTTGAATTAGCACTTGGC	57											
CPH9	Microsatellite	CAGAGACTGCCACTTTAAACACAC	58	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	57-52
		AAAGTTCTCAAATACCATTGTGTTACA	58											
DB1	Microsatellite	CCCAATACAGCAAGACCTCT	55	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	57-52
		ACCTACTCTGCACAGAGAAG	50											
c2140	Microsatellite	GGGGAAGCCATTTTTAAA	53	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	57-52
		TGACCCTCTGGCATCTAGGA	59											
CPH1	Microsatellite	GCCTAGCCCAGTGAAAGTTAAC	58	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	57-52
		TTCCAATGCCTGATAACTGAGA	58											

DB3	Microsatellite	ACAATGCCTCCAGKTAAGG	51	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	53-48
		GATCACGTGCITATGTGCTG	54											
c2168	Microsatellite	GCAAATTACTTACTTCACTATGC	51	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	55-50
		TTGCAAGACTTCAACATGGC	58											
PEZ03	Microsatellite	CACTTCTCATACCCAGACTC	50	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	48-43
		CAATATGTCAACTATACTTC	40											
CPH5	Microsatellite	TCCATAACAAGACCCCAAAC	55	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	55-50
		GGAGGTAGGGGTCAAAAGTT	55											
FH2001	Microsatellite	TCCTCCTCTTCTTTCCATTG	57	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	57-53
		TGAACAGAGTTAAGGATAGACACG	56											
FH2054	Microsatellite	GCCTTATTCATTGCAGTTAG	54	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	56-51
		ATGCTGAGTTTTGAACTTTCCC	59											
c2004	Microsatellite	CTAAGTGGGGAGCCTCCT	63	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	62-57
		ACTGTGACCTACTGAGGTTGCA	63											
INU030	Microsatellite	GGCTCTGTGCTCAAGTCTGT	63	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	62-57
		CATTGAAAGGGAATGCTGGT	59											
REN105L03	Microsatellite	GGTGCCTGACAAGATGGAAT	61	Dream taq (5Units/ µL)	0,45	6,3	0,3	1	0,05	0,2	0,5	1	35	60-55
		CATTGAAAGGGAATGCTGGT	58											

Supplementary Table 5 Identification of foxes, number of assigned photos per observer and number of assigned scats for each fox. Foxes (list of identified foxes); Observer1, Observer2, Observer3 (number of assigned photos of each fox by each observer); Assigned scats (number of genotyped scats assigned for each individual).

		CAMERA-TRAPPING			**DNA SCATS SAMPLING**	
Area	**Foxes**	**Observer1**	**Observer2**	**Observer3**	**Foxes**	**Assigned scats**
Berzosa	BER.A	64	32	19		
	BER.B	7	19	15	BER.1	6
	BER.C		4	2		
	BER.D(2)*		3			
	BER.D(3)*			20		
Carabaña	CAR.A	5	5		CARA.1	2
	CAR.B	4	9		CARA.2	4
	CAR.C	4	6		CARA.3	10
Villarejo					VILLA.1	2
	VILLA.A	22	16		VILLA.2	3
	VILLA.B	2	2		VILLA.3	3
					VILLA.4	4
Quijorna	QUI.A	28	22		QUI.1	5
	QUI.B	3	2		QUI.2	4
	QUI.C**	1	1		QUI.3	2
	QUI.D**	1	1		QUI.4	2
	QUI.E**	1	1			
Pelayos	PE.A	16	2	4	PE.1	3
	PE.B	3	3	3	PE.2	2
	PE.C(1)*	16				
	PE.C(2)*		4			

	ROB.A	11	5	8	ROB.1	5
Robledo	ROB.B	4	2	2	ROB.2	2
	ROB.C(1)*	4			ROB.3	2
	ROB.C(2)*		6			
	MA.A	13	15	7		
San Mames	MA.B	2	1	3	MA.1	1
	MA.C	2	10	5	MA.2	1
	MA.D(1,3)*	8		6		
	MA.D(2)*		8			
	MAD.E	14		9		
	MAD.F			2		

Supplementary Table 6 Hobs (Observed heterozygosity), Hexp (Expected heterozygosity), HW(Hardy-Weinberg equilibrium); Single locus P_{ID}; Muli-locus P_{ID}; Single locus $P_{ID\ (sib)}$; P_{ID}; Muli-locus $P_{ID\ (sib)}$ and estimation of the null frequency of alleles for each selected marker.

Marker	Hobs	Hexp	HW	Single-locus P_{ID} in increasing order	Multi-locus P_{ID} in increasing order of single-locus P_{ID}	Single-locus $P_{ID\ (sib)}$ in increasing order	Multi-locus $P_{ID(sib)}$ in increasing order of single-locus $P_{ID\ (sib)}$	Estimate of AN frequency
CPH5	0.481	0.852	ND	4,85E-02	4,85E-02	3,44E-01	3,44E-01	0.19
FH2054 (CXX/c2054)	0.707	0.840	ND	4,56E-02	2,21E-03	3,47E-01	1,19E-01	0.08
c2168	0.759	0.815	ND	6,42E-02	1,42E-04	3,65E-01	4,36E-02	0.00
DB1	0.269	0.806	ND	6,94E-02	9,85E-06	3,68E-01	1,61E-02	0.29
FH2001 (CXX/c2001)	0.474	0.795	NS	7,08E-02	6,97E-07	3,75E-01	6,02E-03	0.17
RENL05	0.298	0.764	***	9,07E-02	6,32E-08	3,94E-01	2,37E-03	0.25
CXX225 (u225)	0.367	0.703	***	1,33E-01	8,39E-09	4,35E-01	1,03E-03	0.18
PEZ03	0.460	0.683	*	1,32E-01	1,11E-09	4,44E-01	4,59E-04	0.11
CXX173 (u173)	0.324	0.685	*	1,61E-01	1,78E-10	4,53E-01	2,08E-04	0.20
INU030	0.119	0.673	***	1,64E-01	2,91E-11	4,59E-01	9,52E-05	0.33
C2140	0.473	0.665	NS	1,59E-01	4,62E-12	3,65E-01	4,38E-05	0.14
CPH9	0.241	0.580	***	1,93E-01	8,92E-13	4,97E-01	2,18E-05	0.20
DB3	0.096	0.543	***	3,15E-01	2,81E-13	5,60E-01	1,22E-05	0.28
CPH1	0.581	0.538	NS	3,19E-01	8,96E-14	5,65E-01	6,90E-06	0.00
C2004	0.173	0.420	ND	3,67E-01	3,29E-14	6,34E-01	4,37E-06	0.18
CXX109 (u109)	0.087	0.237	ND	6,02E-01	1,98E-14	7,84E-01	3,43E-06	0.16

CHAPTER 3

Food availability as an occupancy factor between the red fox and the stone marten and implications for predator coexistence.

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Manuscript in preparation

Keywords: intraguild coexistence; prey abundance; spatial segregation; top-predator.

Abstract

The spatial segregation is a pivotal mechanism to facility coexistence between species that share a same niche. In this vein, the study of factors that determine species occurrence is essential to identify this mechanism of coexistence. Here, we study the occupancy patterns of two abundant mesocarnivores in the central Iberian Peninsula, the fox (*Vulpes vulpes*) and the marten (*Martes foina*), as well as rodents and the rabbit (*Oryctolagus cuniculus)* as their main prey. We used camera traps and performed occupancy models to know the presence of these species in three study areas with different habitat composition. We examined vegetal variables and the relative abundance (total number of captures per 24h among the total number of capture occasions) of prey as a factor involved in the occurrence of red fox and stone marten. The results showed that both mesocarnivores selected similar habitat characteristics, related to the selection of prey habitat. The fox and the marten selected the same landscapes occupied by their prey (rodents and rabbits). The red fox selected sites with a higher abundance of rodents and rabbits as a predictor of its occurrence in the three areas. Nevertheless, the marten did not follow this pattern. These results suggest that prey availability may be a main factor determining fox occupancy in different habitats. Our results provide further evidence that red foxes and martens have a high overlap of habitat and food resources. In fact, spatial segregation does not seem to be the main mechanism of coexistence between the two species. Therefore, it is important to study other mechanisms, such as temporal segregation, that allow coexistence between both mesocarnivores.

Introduction

Identifying the competition, coexistence and predator-prey dynamics between animals living in the same habitat (the resources and conditions present in an area that produce occupancy, which may include survival and reproduction by a given organism (Krausman and Morrison 2016) is essential to understanding the bionomic variables that shape their ecological niche (Elton 1957; Hutchinson 1957). The competition between animal species and individuals is prominent in ecosystems where some reduce the survival or birth rate of others (Connell 1983; Schoener 1983). Intraguild predation is the most extreme competition between animals and a key component in structuring carnivore communities (Creel and Creel 1996). Empirical evidence of large carnivores killing other smaller as intraguild prey is well documented (Gese et al. 1996; Henke and Bryant 1999; Palomares and Caro 1999). When carnivores share common prey and the smaller carnivore is a more efficient hunter than the larger carnivore, the larger carnivore may need to kill its smaller competitor to persist (Rosenzweig 1966). Thus, in intraguild relationships, the dominant species could displace temporally and spatially a subordinate or even force it to shift prey (Björklund et al. 2016; Elbroch and Kusler 2018).

Following the decline of large predators across their distribution range during the 20th century (Ripple et al. 2014), the populations of mesocarnivores (species under 15 kg) increased in density and expanded in habitats once occupied by large carnivores. This process is termed mesopredator release (Ritchie and Johnson 2009; Brashares et al. 2010). Mesopredators play a major role in ecosystem function, structure and dynamics, including in the balance and imbalance of trophic cascades (Terborgh and Estes 2010). The replacement of large carnivore species by mesocarnivores resulted in new hierarchies and coexistence roles for the latter. However, little is known about the coexistence mechanisms regulating the interspecific interactions between mesocarnivores.

To compensate for competition, coexistence is one mechanism that allows species diversity (Schoener 1982; Chesson 2000; Chase and Leibold 2003). The coexistence mechanisms of terrestrial carnivores often consist of resource partitioning and spatial or temporal segregation (Ramesh et al. 2012; Torreta et al. 2016; Monterroso et al. 2020). Spatial segregation between carnivores can be modulated by habitat characteristics (such as vegetation composition, temperature, and precipitations), resource availability, or the fluctuations in species densities that share the same habitat and have an impact on the entire ecosystems (Linnell and Strand 2000; Monterroso et al. 2020).

Traditionally, species occurrence in habitats is analysed using habitat selection models (Virgós et al. 2003; McDonald et al. 2008; Santos and Santos-Reis 2010; Soto and Palomares 2015). These procedures mainly consider abiotic components (i.e. habitat characteristics). However, biotic components such as prey or other species abundance are often as important as the abiotic ones. Prey species modulate the occupancy of predator species by selecting areas of increasing prey abundance (Robison et al. 2014; Rabelo et al. 2019). However, predator abundance also impacts the relationship between intraguild species that share prey. The abundance of prey can drive the exclusion of dominant species in low-prey areas, the coexistence between dominant and subordinate species when the abundance of prey is intermediate, or the displacement of subordinate species when prey abundance is high to avoid agonistic encounters (Holt and Polis 1997; Robison et al. 2014). Other factors, such as the density of dominant species or type of habitats, can regulate the intensity of intraguild competition (Creel 2001; St-Pierre et al. 2006; Robison et al. 2014). Therefore, the characterization of habitat features and the quantification of resources is paramount to understanding how carnivores occupy and coexist in the same habitat (Karanth et al. 2017; Pokheral and Wegge 2019; Monterroso et al. 2020; Strampelli et al. 2023)

Occupancy models have been one of the most powerful tools to relate the occurrence of animals with the habitat and can incorporate spatial-temporal or biotic variables (Bailey et al. 2014) while accounting for the imperfect detection of species (i.e. when true occupancy of a specie in a site is not observed) (Royle 2006). Failing to consider the variation of detectability or detectability as perfect or constant can lead to biased estimates of habitat occupancy, especially when detectability differs between habitats (Guand Swihart 2004; MacKenzie and Royle 2005). Potential variations of detectability can change the effect of habitat attributes on detectability estimates. Therefore, identifying the factors that impact the detectability of species across the space is highly useful for building robust occupancy models. Using occupancy models can help detect factors that define the occurrence of species in different habitats. However, the identification of invariant factors that define the occupancy of a species in different habitats is poorly understood. Thus, this study encouraged to identify these constant relationships as well as those factors of high spatial and context dependence. This need is particularly prominent for species such as meso-predators due to their broad selection of habitat (Cavallini and Lovari 1991; Virgós et al. 2002; Pereira et al. 2012).

The red fox (*Vulpes vulpes*) and the stone marten (*Martes foina*) are two of the most abundant generalist mesocarnivores in the central Iberian Peninsula. These species occupied the role of the wolf (*Canis lupus*) and the Iberian Lynx (*Lynx pardinus*) after the disappearance of these large carnivores in most of their historical distribution (Blanco et al. 1992; Delibes et al. 2000; Molsher et al. 2017). The red fox and the stone marten show a high overlap of habitat and food resources, particularly rodents (*Apodemus sp., Mus spp*.) (Padial et al. 2002; Papakosta et al. 2010; Pereira et al. 2012). However, the fox is a facultative predator that consumes rabbits (*Oryctolagus cuniculus*) as staple prey when it is abundant (Delibes-Mateos et al. 2008; Díaz-Ruiz et al. 2013). Considering the competitive interactions between carnivores are driven by the body size of the species (Palomares and Caro 1999, Donadio and Buskirk 2006), the fox may have a dominant role over the marten due to its larger body size. As the result of the intraguild competition between these meso-predators in sympatric areas, the fox may predate (Polis et al. 1989) and potentially extirpate martens, as previously reported for the case of the pine marten, *Martes martes* (Storch et al. 1990; Lindström et al. 1995). The characteristic of the red fox and the stone marten as generalists inhabiting different habitats makes these species of great interest to study the invariable factors driving the occupation of both species in different habitats. In addition, both species share similar trophic and spatial requirements. Thus, using occupancy models can help identify whether spatial segregation is a coexistence mechanism.

We studied the occurrence of the red fox and the stone marten, and rodents and rabbits as their potential prey. For this objective, we carried out occupancy models of the four species in three areas of the central Iberian Peninsula. Each area encompassed different environmental characteristics. We studied the spatial segregation between foxes and stone martens, and due to their similar trophic and spatial requirements, we could expect that foxes and martens show low spatial segregation with occupancy models explained by similar variables. However, considering the fox as the dominant species, its occurrence would limit that of the stone marten and thus would occupy broader habitat characteristics. Within the range of habitat selected, both species would include the same habitats where their main prey, rodents and rabbits, occur. Therefore, we predicted that the abundance of prey was one invariant factor to explain the occupancy of red foxes and stone martens. Under this scenario, the spatial coexistence between the red fox and the stone marten would highly depend on the availability of rabbits (the most selected prey by the red fox (Delibes-Mateos et al. 2008)) in their habitats. Thus, we also predicted that the areas with a high abundance of rabbits showed increasing coexistence between both meso-predators. Our research highlights the assessment of invariant factors that define occupancy and determine the coexistence mechanisms between the red fox and stone marten in different habitat.

Material and methods

Study area and field sampling

We collected data at 24 locations in the Central Iberian Peninsula from 2013 to 2020 (Figure 1 of General Material and Methods). We included the locations into three geographical areas: North, Southeast and Southwest. The North area was characterized by a meso-supramediterranean climate, with a mean minimum temperature of 1.5ºC, a maximum of 28ºC, and an annual precipitation of 561 mm.

The Southeast area was a meso-mediterranean climate, with a mean minimum temperature of -0.4, a maximum of 33.2ºC, and annual precipitation of ~267.5 mm. The Southwest area was also a meso-Mediterranean climate with a mean minimum temperature of 2 and maximum of 33ºC and annual precipitation of ~382 mm. The most represented land uses in the North area were pasture, livestock and recreational areas. Agricultural and game hunting uses predominated in the Southeast area. Agricultural and pasture land, with some game hunting areas, were the predominant uses in the Southwest area. The common prey in the three areas was small mammals (*Apodemus sylvatucus, Mus spp*.) and rabbits. We studied the influence of season on species detection over different seasonal periods in each area. The north area included seven locations, four covering the warm (i.e. spring and summer) and three the cold (i.e. autumn and winter) seasons. The southeast area comprised eight locations, four covering the warm and four cold seasons. Lastly, the southwest area included nine locations, four covering the warm and five the cold seasons.

We deployed between eight to ten camera traps in each location for 20-35 days (an average of 31.25 days). We deployed a total of respectively, 60, 69 and 74 cameras in the North, Southeast and Southwest areas. Camera traps were spaced between 450 and 600 m apart, which covered a sufficiently large area to maximize the number of individuals photographed and reduce potential shades of detection of the species studied (similar to Sarmento et al. 2009). We generated a minimum convex polygon (MCP) by linking the camera locations and buffered the resulting polygon by 500 m. We considered the total sampled area contained both the MCP and the buffer area (Sarmento et al. 2009). The total area covered was 2595 ha in the north 3607 ha in the southeast and 3541 ha in southwest. The mean area of the sampled locations in each area was 370 ha, 450 ha, and 395 ha in the north, southeast and southwest, respectively; which is the average home-range area of the red fox reported in the mountains of Central Spain (López-Martín 2010).

The deployed cameras belonged to the following commercial models and brands to ensure similar trigger times (in brackets): Wildview Xtreme2 (not specified), Bushnell Trophy (1s), DLC Covert II (1s), Acorn LTL (1.1s), Cuddle Back Ambrush (not specified), HCO Scoutguard SG565 (1.2s), Scout Guard SG560K (1.2s), and Scout Guard SG562 (1.2s). We configured equally all the cameras to operate 24 hours a day, take three sequential photographs five seconds apart, use a normal PIR sensitivity, and record the date and time of each photograph. We placed two baits in front of each camera (~2 m), sardines (Heinlein et al. 2020; Sebastián-González et al. 2020) and commercial lure (HAGOPUR® Premium Attractant Fox) to maximize detection probability (Monterroso et al. 2013; Gil-Sánchez et al. 2021). We pierce the sardine cans and tie them to surfaces (rocks or vegetation). In this way, we tried to prevent them from accessing the bait and displacing it. We assumed baits did not affect the target species' behaviour and activity rates (Gerber et al. 2012; Braczkowski et al. 2016). We checked the cameras every four to seven days to refill baits and batteries and to download the photographs.

Predictor's selection

We modelled the relationship between a set of habitat predictors and fox and stone marten occupancy in each area. For this procedure, we first selected relevant habitat predictors identified in previous studies in Mediterranean ecosystems as important for both meso-predators (Cavallini and Lovari, 1994; Lucherini et al. 1995; Sarmento et al. 2009; Pereira et al. 2012). We also included the season of the year because it is considered to influence species activity and the probability of detection of the species (Andelt and Andelt, 1984; Vine et al. 2009).

We extracted predictors of vegetation cover from digital vegetation maps produced by the Autonomous Community of Madrid using QGis 3.26.3 (QGIS 2022). The vegetation extracted from maps was grouped into the following predictors: esparto grasses, scrublands, vineyards, crops, riparian forests, pine forests, *Quercus ilex* forests, pastures, ash tree forests, *Quercus pyrenaica* forests, olive trees and urbanized land habitats. Esparto grasses encompassed *Stipa tenacissima* together with other species, such as *Thymus vulgaris.* Shrubs encompassed species such as *Rosaceae sp, Genista scorpius*, *Retama sphaerocarpa*, *Quercus coccifera*, *Thymus vulgaris*, *Quercus ilex*, *Cistus clusii* and bushy riparian vegetation. The crops variable included irrigated and rained crops. Riparian forests included *Salix sp*., *Populus nigra* and *Rubus sp.* Pine forests included different species of pine (e.g. *Pinus nigra*, *Pinus pinea*, *Pinus pinaster* and *Pinus sylvestris*). Pastures encompassed high mountains with pastures and meadows.

We calculated the area (ha) of each vegetation patch in a buffer of 250 m radius around each camera. Food availability is critical in species' habitat selection (Heithaus 2001; Rauset et al. 2012). Thus, we also included the relative abundance of rodents and rabbits as predictors of occupancy for both mesocarnivores. The relative abundance of rodents and rabbits was estimated from the relative abundance index (RAI). RAI was calculated as the number of captures (photographs) of a species per total occasions. We considered a capture when any species was photographed per night. We used total occasions (i.e. total number of cameras times the total number of study nights) instead of nights (i.e. the total number of study nights) to control for bias due to differences in the number of nights and cameras between study areas (Martin-Garcia et al. 2022).

Because most habitat predictors were correlated with each other, we decided to use a principal component analysis (PCA) to summarize them for each area. PCA extracts the major axes of variation in a dataset and includes them into fewer orthogonal variables or principal components. The first principal component (PC) explains the most variation in the dataset (Abdi and Williams 2010). This method allowed us to account for covariation between predictors and reduced the dimensionality of our dataset (Garigal et al. 2000). We performed an independent PCA for each zone, as habitat predictors varied among the three areas. We included the relative abundance of rabbits and rodents in the PCAs to explain fox and marten occupancy. However, we only considered the habitat predictors in the PCAs to study the occupancy of rodents and rabbits without including the relative abundance of both prey. We selected as predictors the PCs of variance ratio > 1. Following Comrey and Lee (1992), we selected the most important variables that defined each PC by studying the contribution of each variable to the PC. The loadings represent the correlation between the original variables and the PCs. Therefore, a greater loading indicates that a component is a more accurate measure of the variable. According to these authors, loadings under 0.3 should not be considered when defining a PC (Escribano-Ávila et al. 2013). We selected the variables with loading (r) above 0.40. We used the 'factoextra' package in R Software (R Core Team 2022) and calculated the square of the coordinates ($\cos^2$) of the variables to estimate the quality of the representation of PCAs. We selected those variables with $\cos^2$ greater than 0.35 and r greater than 0.40 as they were the variables that contributed most in each PC (Comrey and Lee 1992).

Occupancy models

We performed a single-season occupancy model of fox, stone marten, rodents and rabbits from each area, considering the influence of detection (MacKenzie et al. 2002). Single-season occupancy models were parameterized in the 'Unmarked' package (Fiske and Chandler 2011) in R software using the *occu* function. *Occu* fits occupancy models based on zero-inflated binomial models (MacKenzie et al. 2006).

The occupancy state process (zi) of site i is modelled as,

$$zi \sim Bernoulli(\psi i)$$

The observation process is modelled as

$$yij\,|zi \sim Bernoulli(zipij\,)$$

Data for each species were arranged as matrices of sites by surveys (i.e. sampling occasion). Each entry indicated whether or not the species was observed at site i on survey j. If the species was observed at site i on survey j, then the entry received a score of 1. If the species was not observed, the entry received a score of 0. NA indicated the site i was not sampled on survey j. In our study, i depicts each camera site, and *j* is the sampling occasion (i.e. each day of camera operation).

We estimated occupancy ψ and detection probability (p) with and without covariates. We evaluated the selected PCs as occupancy covariates, whereas season was assessed as a detection covariate. Covariates of ψ and p were modelled using the logit link. We ran a global model with all covariates (PCs) and compared it with the null model, which assumes constant ψ and p (i.e. ψ (.), p (.)). We used the Akaike information criterion (AICc) to rank the candidate models and calculate their Akaike weights (Burhman and Anderson 2002). We applied a model averaging technique for top-ranked models with ∆AICc < 2 to estimate occupancy and predictors. We used the '*MuMIn'* package to select the model and calculate the relative importance of the model parameters (Barton 2022).

Results

We obtained fox presence in 90% of the cameras in the North area, 56% in the Southeast, and 67% in the Southwest. Stone marten was present in 76% of the cameras in the North area, 31% in the Southeast, and 66% in the Southwest. Rodent presence was registered in 65% of the cameras in the North area, 71% in the Southeast, and 62% in the Southwest. Rabbit's presence was scarce in the North and Southeast areas, while in the Southwest, it was present in 13% of the cameras. The relative abundance of target species varied among areas: Red fox showed a relative abundance of 0.19 in the North area, 0.04 in the Southeast, and 0.07 in the Southwest. Stone marten had a relative abundance of 0.17 in the North, 0.15 in the Southeast and 0.12 in the Southwest. The relative abundance of rodents was similar among areas, 0.23, 0.21 and 0.2 in the North, Southeast and Southwest, respectively. By contrast, the relative abundance of rabbits was lowest in the North area with 0.001, 0.01 in the Southeast, and highest in the Southwest with 0.012.

Predictor's selection

North area

The first five PCA axes explained 74.34% of the environmental data variation, with 19.2% for the first axis, 15.9% for the second axis, 15.04% for the third axis, 13.7% for the fourth axis, and 10.5% for the fifth axis. Axes were related to variables that characterized the type of landscapes. The variables that contributed most to the first axis were *Quercus ilex* forests (r = 0.45) with scrublands (r = 0.41) versus landscapes that included pine forests (r = -0.45) and a high relative abundance of rodents (r = -0.43). The second axis related to riparian landscapes, with riparian forests and ash tree forests as the most contributing variables (r = -0.61 and r = -0.55, respectively). The third axis was defined by landscapes where pine forests predominated (r = 0.44) versus *Quercus pyreniaca* forests (r = -0.48). The fourth axis was defined for *Quercus ilex* forest (r = 0.56), with a low relative abundance of rabbits (r = -0.50). The fifth axis defined landscapes of olive trees (r = 0.63) versus pasture (r = -0.56) (Figure 1a)

The first four PCA axes explained 72.50% of the environmental data variation in rodent occupancy. The first axis explained 21.39% of the variance and defined landscapes with *Quercus ilex* forest (r = 0.58) versus *Quercus pyreniaca* forest (r = -0.49). The second axis explained 19.74% of the variance and defined landscapes with riparian forests (r = 0.65) and ash tree forests (r = 0.59). The third axis explained 14.55% of the variance and defined landscapes lacking pine forest (r = -0.68). Finally, fourth axis explained 12.3% of the variance and defined landscapes lacking scrublands (r = -0.62) (**Figure 1b**).

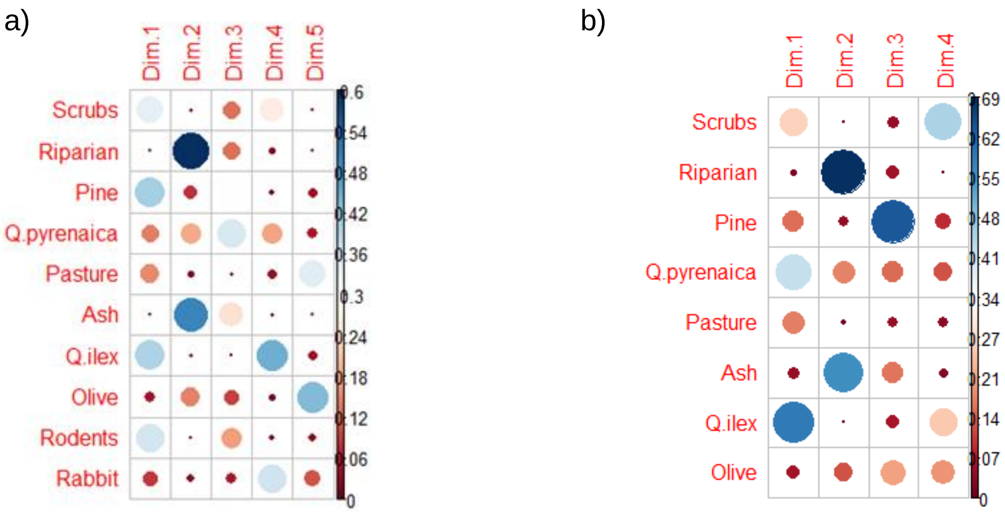

Figure 1 a) Square of the coordinates of the variables to estimate the quality of the representation of PCAs to the red fox and stone marten in the north area. b) Square of the coordinates of the variables to estimate the quality of the representation of PCAs to rodents in the north area. Values above 0.35 were selected to choose the variables that best explained each PC.

Southeast area

Five PCA axes explained 77.53% of environmental variation. The first, second, third, fourth and fifth axes explained 23.33%, 15.60%, 15.05%, 12.93% and 10.59% of the variation, respectively. Axis was related to variables that characterized types of landscapes. The first axis explained landscapes with riparian forest (r = 0.45) and vineyards (r = 0.50) and lacking *Quercus ilex* forest (r = -0.40). The second axis was more related to open areas with pastures (r = 0.58) and urbanized lands (r = 0.62). The third axis defined olive tree landscapes (r = 0.52). The fourth axis was defined for scrublands (r = 0.56), with a high relative abundance of rabbits (r = 0.51) versus *Quercus ilex* forest (r = -0.56). The fifth axis defined areas with a low relative abundance of rodents (r = -0.52) (Figure 2a).

The first four PCA axes explained 78.38% of the environmental data variation to explain rodent occupancy. The first axis explained 28.34% of the variance and defined landscapes with riparian forests (r = 0.45) and vineyards (r = 0.50) in contrast to *Quercus ilex* forest (r = -0.41). The second axis explained 18.75% of the variance and was more related to open areas with pastures (r = -0.55) and urbanized land (r = -

0.54). The third axis explained 16.88% of the variance and defined urbanized land (r = 0.41) and olive trees (r = 0.48). The fourth axis explained 14.39% of the variance and was defined for scrublands landscape (r = 0.74) versus *Quercus ilex* forest (r = -0.59) (Figure 2b).

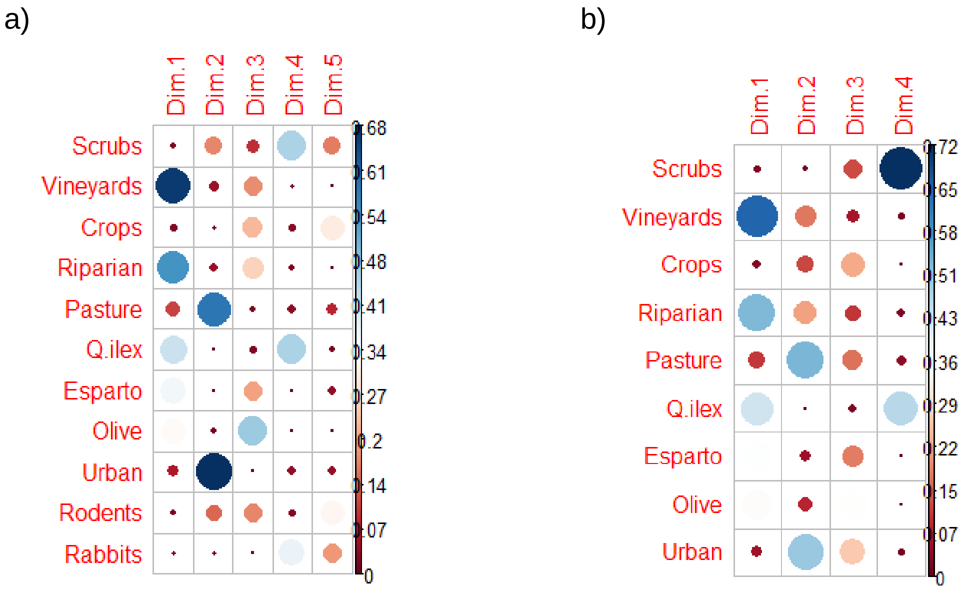

Figure 2 a) Square of the coordinates of the variables to estimate the quality of the representation of PCAs for the red fox and stone marten in the southeast area. b) Square of the coordinates of the variables to estimate the quality of the representation of PCAs to rodents in the southeast area. The values above 0.35 were selected to choose the variables that best explained each PC.

Southwest area

The first five PCA axes explained 69.82% of the environmental data variation: 21.5% for the first axis, 13.3% for the second axis, 12.8% for the third axis, 11.6% for the fourth axis, and 10.3% for the fifth axis. First axis was related to variables that characterized types of landscapes. The variables that contributed most to the first axis were *Quercus ilex* forest (r = 0.63) versus landscapes with scrublands (r = -0.42). The second axis was more related to areas with low relative abundance of rabbits (r = -0.50). The third axis was defined by landscapes where pine forests predominated (r = 0.69). The fourth axis defined riparian forests (r = 0.57) versus vineyards (r = -0.59), and the fifth axis defined landscapes of crops (r = 0.89) (Figure 3a).

The first four PCA axes explained 67.90% of the environmental data variation to explain rodent and rabbit occupancy. The first axis explained 24.21% of the variance and defined landscapes with *Quercus ilex* forest (r = 0.68) versus pine forest (r = -0.43) and scrublands (r = -0.45). The second axis explained 16.08% of the variance and defined landscapes with pine forests (r = 0.67) versus scrublands (r = -0.55). The third axis explained 14.62% of the variance and defined landscapes without pasture (r = -0.59) and vineyards (r = -0.61). The fourth axis explained 12.97% of the variance and defined the landscape of crops (r = 0.85) (Figure 3b).

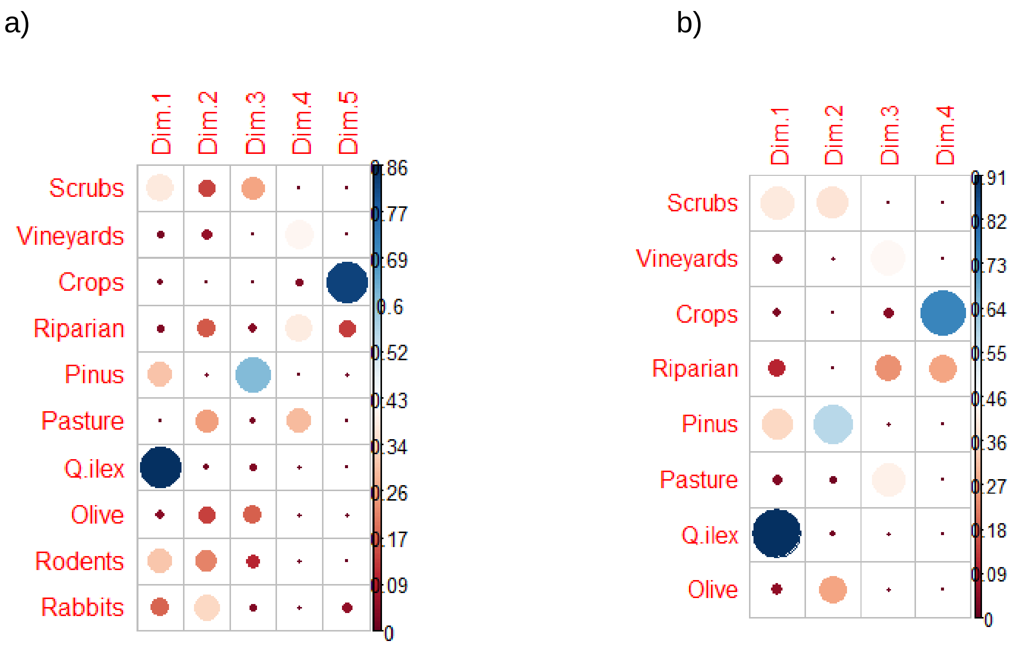

Figure 3 a) Square of the coordinates of the variables to estimate the quality of the representation of PCAs to the red fox and stone marten in the southwest area. b) Square of the coordinates of the variables to estimate the quality of the representation of PCAs to rodents and rabbits in the southwest area. The values above 0.35 were selected to choose the variables that best explained each PC.

Occupancy models

North area

According to the ΔAICc, our multimodel model selection revealed two top-ranked models with ΔAIC < 2 that explained the occupancy of the red fox (Table 1). Model-averaged coefficients showed a negative relationship between PC1 and fox occupancy (Table 2). The red fox selected pine forests with a high relative abundance of rabbits instead of *Quercus ilex* forests and shrubs (Table 3). However, this variable had non-significant relationship with red fox occupancy. Fox detection had a positive and significant relationship with the cold season.

Stone marten occupancy modelling selected a single model that contained the predictors PC3 explaining occupancy and season explaining detection (Table 1). Predictor PC3 showed a positive and significant relationship with the stone marten occupancy (Table 2). The stone marten selected pine forest landscapes instead of *Quercus pyreniaca* and ash tree forests (Table 3). The cold season showed a positive and significant relationship with stone marten detection.

Rodent occupancy modelling selected two models that explained its occupancy (Table 1). Model averaged coefficients showed that PC1 had a negative and significant relationship, and PC3 had a negative relationship with occupancy (Table 2). Rodents selected *Quercus pyreniaca* and pine forests instead of *Quercus ilex* forests (Table 3). Rodent detection had a positive and significant relationship with the cold season.

Southeast area

The multimodel selection revealed three top-ranked models in this area (ΔAIC < 2) that explained the occupancy of the red fox (Table 1). Model averaged coefficients showed that PC2 had a positive and significant relationship with fox occupancy (Table 2). The red fox selected pasture and urbanized land. PC4 and PC5 showed a negative but non-significant relationship with red fox occupancy. According to this result, the red fox selected landscapes with *Quercus ilex* forest and a high relative abundance of rodents instead of scrublands with a low relative abundance of rabbits (Table 3). Fox detection had a negative and significant relationship with the cold season.

According to the ΔAIC, model selection revealed four top-ranked models that explained the occupancy of stone marten (Table 1). Model averaged coefficients showed that PC2 had a positive and significant relationship with stone marten occupancy (Table 2). The stone marten selected pasture and urbanized land. PC4 showed a negative but non-significant relationship with stone marten occupancy. The stone marten selected landscape with *Quercus ilex* forest instead of scrublands with a low relative abundance of rabbits (Table 3). Stone marten detection had a negative but non-significant relationship with the cold season.

Our multimodel model selection revealed two top-ranked models with ΔAIC < 2 that explained the occupancy of rodents (Table 1). Model-averaged coefficients showed that PC3 had a positive and significant relationship with rodent occupancy (Table 2). Rodents preferred urbanized land and olive trees. PC4 showed a negative but non-significant relationship with rodent occupancy. Rodents selected landscapes with

Quercus ilex forest instead of scrublands (**Table 3**). Rodent detection had a negative and significant relationship with the cold season.

Southwest area

According to the ΔAIC, the multimodel selection yielded five top-ranked models with ΔAIC < 2 to explain red fox occupancy (Table 1). Model averaged coefficients showed that PC1, PC2, PC3 and PC5 had a negative but non-significant relationship with fox occupancy (Table 2). The red fox selected landscapes with shrubs and a high relative abundance of rabbits instead of *Quercus ilex* forests, pine forests and crops (Table 3). Fox detection had a negative and significant relationship with the cold season.

The multimodel selection yielded nine top-ranked models with ΔAIC < 2 that explained the occupancy of the stone marten (Table 1). The model averaging that resulted from the nine-ranked model coefficients showed that PC2, PC3 and PC5 had a negative relationship with stone marten occupancy (Table 1).

Table 1 Results of multimodel selection for red fox, stone marten, rodents and rabbits occupancy in each area. p defined detection probability and ψ is the occupancy probability. (.) indicates only the intercepts. Model selection based on Akaike's Information Criterion (AICc), degrees of freedom in the model (df), AICc difference of best fit models (ΔAIC < 2), model weights (wAICc).

Specie/Area	Models	df	AICc	ΔAICc	wAICc
Red fox/North	$p(\text{season}) \sim \psi\ (.)$	3	1744.87	0	0.52
	$p(\text{season}) \sim \psi\ (\text{PC1})$	4	1744.99	0.13	0.48
Stone marten/North	$p(\text{season}) \sim \psi\ (\text{PC3})$	4	1533.7	0	0.274
Rodents/North	$p(\text{season}) \sim \psi\ (\text{PC1+PC3})$	5	1498.54	0	0.7
	$p(\text{season}) \sim \psi\ (\text{PC1})$	4	1500.28	1.74	0.3
Red fox/Southeast	$p(\text{season}) \sim \psi\ (\text{PC2})$	4	795.64	0	0.5
	$p(\text{season}) \sim \psi\ (\text{PC2+PC4})$	5	796.57	0.93	0.31
	$p(\text{season}) \sim \psi\ (\text{PC2+PC5})$	5	797.52	1.89	0.19
Stone marten/Southeast	$p(\text{season}) \sim \psi\ (\text{PC2+PC4})$	5	604.92	0	0.38
	$p(\text{season}) \sim \psi\ (\text{PC2})$	4	605.62	0.69	0.27
	$p(.) \sim \psi\ (\text{PC2+PC4})$	4	606.14	1.22	0.21
	$p(.) \sim \psi\ (\text{PC2})$	3	606.82	1.89	0.15
Rodents/Southeast	$p(\text{season}) \sim \psi\ (\text{PC3+PC4})$	5	1990.99	0	0.6
	$p(\text{season}) \sim \psi\ (\text{PC3})$	4	1991.8	0.81	0.4
Red fox/Southwest	$p(\text{season}) \sim \psi\ (\text{PC2})$	4	1340.71	0	0.35
	$p(\text{season}) \sim \psi\ (\text{PC2+PC3})$	5	1342.08	1.37	0.17
	$p(\text{season}) \sim \psi\ (\text{PC2+PC5})$	5	1342.1	1.39	0.17
	$p(\text{season}) \sim \psi\ (.)$	3	1342.22	1.51	0.16
	$p(\text{season}) \sim \psi\ (\text{PC1+PC2})$	5	1342.49	1.77	0.14
Stone marten/Southwest	$p(.) \sim \psi\ (.)$	2	1734.81	0	0.14
	$p(\text{season}) \sim \psi\ (.)$	3	1734.9	0.09	0.14

	$p(.)\sim\psi$ (PC2)	3	1735.12	0.3	0.12
	$p(.)\sim\psi$ (PC5)	3	1735.2	0.39	0.12
	$p(\text{season})\sim\psi$ (PC2)	4	1735.27	0.46	0.11
	$p(\text{season})\sim\psi$ (PC5)	4	1735.36	0.55	0.11
	$p(.)\sim\psi$ (PC2+PC5)	4	1735.43	0.62	0.11
	$p(\text{season})\sim\psi$ (PC2+PC5)	5	1735.66	0.85	0.09
	$p(\text{season})\sim\psi$ (PC3)	3	1736.81	1.99	0.05
Rodents/Southwest	$p(\text{season})\sim\psi$ (PC1)	4	2090.99	0	0.57
	$p(\text{season})\sim\psi$ (PC1+PC2)	5	2092.97	1.98	0.21
	$p(\text{season})\sim\psi$ (PC1+PC4)	5	2092.99	2	0.21
Rabbit/Southwest	$p(.)\sim\psi$ (.)	2	246.71	0	0.4
	$p(.)\sim\psi$ (PC1)	3	247.57	0.86	0.26
	$p(.)\sim\psi$ (PC2)	3	248.47	1.76	0.17
	$p(.)\sim\psi$ (PC3)	3	248.52	1.81	0.16

However, all the selected PCAs had a non-significant relationship with the occupancy of the stone marten, with the null model in the first ranking position (Table 2). According to selected PCAs, the stone marten may prefer a landscape with a high relative abundance of rabbits instead of pine forests and crops (Table 3). Stone marten detection had a negative non-significant relationship with the cold season.

Rodent occupancy modelling selected two models (Table 1). Averaged model coefficients showed that PC1 had a positive and significant relationship, and PC2 had a positive but non-significant relationship with occupancy (Table 2). Rodents selected *Quercus ilex* forest and pine forest instead of shrubs (Table 3). Rodent detection had a positive and significant relationship with cold season.

According to the ΔAIC, model selection revealed four top-ranked models with ΔAIC < 2 that explained rabbit occupancy (Table 1). Model averaged coefficients showed that PC1 and PC3 had a positive relationship with rabbit occupancy while PC2 had a negative relationship (Table 2). Rabbits selected *Quercus ilex* forests and shrubs versus pine forests, pasture and vineyards (Table 3). However, both PCAs had non-significant relationship with rabbit's occupancy, with null model as first top-ranked model (Table 2).

Table 2 Predictor selection in the occupancy models for each species and area. The occupancy component (ψ) is defined by predictors that explain variations in species occupancy. The detection component (p) is defined by the predictors that explain variations in species detection. The regression coefficients (Estimate) are shown, and also the standard error (S.E) and p-value

North	Estimate	S.E.	p-value	Southeast	Estimate	S.E.	p-value	Southwest	Estimate	S.E.	p-value
Red fox				*Red fox*				*Red fox*			
ψ (Intercept)	2.44	0.56	<0.001	ψ (Intercept)	0.83	0.39	0.032	ψ (Intercept)	1.0	0.31	0.0014
p (Intercept)	-1.46	0.09	<0.001	p (Intercept)	-2.33	0.23	<0.001	p (Intercept)	-1.74	0.09	<0.001
p (cold season)	0.35	0.12	**0.005**	p (cold season)	-0.73	0.23	**0.002**	p (cold season)	-0.78	0.23	**<0.001**
ψ (PC1)	-0.27	0.40	0.50	ψ (PC2)	1.32	0.56	**0.017**	ψ (PC2)	-0.41	0.30	0.17
				ψ (PC4)	-0.12	0.25	0.64	ψ (PC3)	-0.04	0.13	0.76
Stone Marten				ψ (PC5)	-0.05	0.19	0.799	ψ (PC1)	-0.021	0.09	0.82
ψ (Intercept)	1.37	0.35	<0.001					ψ (PC5)	-0.043	0.14	0.76
p (Intercept)	-1.44	0.11	<0.001	*Stone Marten*							
p (cold season)	0.38	0.14	**0.0053**	ψ (Intercept)	-0.78	0.31	0.01	*Stone Marten*			
ψ (PC3)	0.66	0.29	**0.024**	p (Intercept)	-2.09	0.17	<0.001	ψ (Intercept)	0.68	0.24	0.006
				p (cold season)	-0.30	0.30	0.31	p (Intercept)	-1.39	0.11	<0.001
Rodents				ψ (PC2)	0.81	0.37	**0.03**	p (cold season)	-0.09	0.13	0.50
ψ (Intercept)	0.76	0.31	0.015	ψ (PC4)	-0.33	0.39	0.399	ψ (PC2)	-0.13	0.21	0.53
p (Intercept)	-0.99	0.09	<0.001					ψ (PC5)	-0.14	0.24	0.55
p (cold season)	0.57	0.12	**<0.001**	*Rodents*				ψ (PC3)	-0.005	0.05	0.92
ψ (PC1)	-0.57	0.24	**0.02**	ψ (Intercept)	1.18	0.34	<0.001				
ψ (PC3)	-0.43	0.39	0.27	p (Intercept)	-0.55	0.07	<0.001	*Rodents*			
				p (cold season)	-0.89	0.11	**<0.001**	ψ (Intercept)	0.53	0.25	0.036
				ψ (PC3)	0.97	0.35	**0.005**	p (Intercept)	-0.98	0.07	<0.001
				ψ (PC4)	-0.25	0.27	0.37	p (cold season)	0.62	0.10	**<0.001**

	ψ (PC1)	0.49	0.18	**0.007**
	ψ (PC2)	0.027	0.11	0.814
	ψ (PC4)	-0.03	0.12	0.816
	Rabbits			
	ψ (Intercept)	-1.76	0.36	<0.001
	p (Intercept)	-2.63	0.23	<0.001
	ψ (PC1)	0.084	0.20	0.687
	ψ (PC2)	-0.03	0.14	0.820
	ψ (PC3)	0.035	0.17	0.835

Table 3 Variables defining each principal component (PC) selected in each occupancy model. The occupancy component (ψ) is defined by predictors that explain species occupancy. The detection component (p) is determined by the predictors that explained variations in species detection.

	North	***Southeast***	***Southwest***
Red fox	ψ Pine forest (+) Rodent (+) *Q. ilex* forest (-) Shrubs (-) p Cold season (+) Warm season (-)	ψ Pastures (+) Urbanized land (+) Rodent (+) *Q. ilex* forest (+) Shrubs (-) Rabbits (-) P Cold season (-) Warm season (+)	ψ Rabbits (+) Shrubs (+) Crops (-) Pine forest (-) *Q. ilex* forest (-) p Cold season (-) Warm season (+)
Stone marten	ψ Pine forest (+) *Q. pyrenaica* forest (-) p Cold season (+) Warm season (-)	ψ Pastures (+) Urbanized land (+) *Q. ilex* forest (+) Shrubs (-) Rabbits (-) P Cold season (-) Warm season (+)	ψ Rabbits (+) Crops (-) Pine forest (-) p Cold season (-) Warm season (+)
Rodents	ψ Pine forest (+) *Q. ilex* forest (-) *Q. pyrenaica* forest (+) p Cold season (+) Warm season (-)	ψ Olive tree (+) *Q. ilex* forest (+) Urbanized land (+) Shrubs (-) P Cold season (-) Warm season (+)	ψ *Q. ilex* forest (+) Pine forest (+) Shrubs (-) Crops (-) p Cold season (-) Warm season (+)
Rabbits			ψ *Q. ilex* forest (+) Shrubs (+) Pine forest (-) Pasture (-) Vineyard (-)

Discussion

We assessed the strategy of spatial segregation as a coexistence mechanism between animal species. We focused on the case of the red fox and the stone marten, the most abundant mesocarnivores in the central Iberian Peninsula, where large carnivores are absent. We compared occupancy models of both mesocarnivores and their potential prey (rodents and rabbits) across three different habitats. Our findings revealed that the two mesocarnivores selected similar habitat characteristics and furthermore, this habitat selection is related to the selection of their prey habitat. The fox and the marten selected landscapes with high densities of rodents and rabbits. However, in contrast to the stone marten, the red fox exhibited a stronger correlation with prey abundance as a predictor of its presence across the north, southeast, and southwest areas. These results suggest that prey availability might be a main factor influencing fox occupancy in different habitats. Overall, our results provide evidence for a high degree of overlap in habitat and food resources between the red foxes and martens. This finding casts doubt on spatial segregation as the primary mechanism of coexistence between these two species. Consequently, exploring alternative mechanisms, such as temporal segregation, becomes crucial for understanding how these mesocarnivores coexist successfully.

Our analyses revealed variations in fox occupancy models across the different areas. However, prey availability emerged as a consistent factor influencing fox presence in all areas. While Sarmento et al. (2011) suggested that environmental factors hold minimal influence on fox occupancy, they did acknowledge a potential link between fox occupancy and proximity to vulture feeding grounds (indicating food availability).

Our results showed that high rodent abundance was the common factor of fox occupancy in the North and Southeast. In contrast, the Southwest region exhibited a stronger correlation between fox presence and high rabbit abundance. This aligns with the generalist mesopredator behaviour of the red fox, where it may prioritize abundant rabbits as prey (Delibes-Mateos et al. 2008; Diaz-Ruiz et al. 2013). Although the Southwest area had lower overall rabbit abundance compared to rodents, it offered a higher concentration of rabbits compared to the other regions where rodent populations declined. This result suggests that for foxes, selecting specific landscape features might be secondary to prioritizing areas with plentiful food sources. Numerous studies corroborated this strategy, highlighting how some predators often prioritize habitats rich in prey (Palomares et al. 2001; Spong 2002; Rauset et al. 2012; Wolff et al. 2015). In such cases, landscape composition plays a less significant influence in habitat selection, with predators selecting areas with higher prey concentrations. This explains why the red fox selected similar habitat predictors as their prey. In the North area, both foxes and rodents selected pine forest over *Quercus ilex* forest. Similarly, in the Southeast, foxes and rodents selected holm oak forest and urbanized lands over scrublands. *Apodemus sylvaticus,* a generalist occupying diverse habitats is known for its generalist habits, occupying diverse habitats, with a preference for forested and shrubby environments while avoiding open areas (Alcántara 1992). In the Southwest, foxes selected patterns aligned with increasing rabbit abundance and scrublands. While foxes and rabbits only overlapped in their selection of scrublands, previous research suggests a correlation between scrublands and higher rabbit abundance (Palomares et al. 2001).

Our results in the North and Southeast showed a high spatial overlap between the stone marten and the red fox, coinciding with previous studies (Pereira et al. 2012; Petrov et al. 2016; Roy et al. 2019). The stone marten selected the same habitats as foxes and rodents, with pine forest in the North and *Quercus ilex* forest and urbanized land in the Southeast. Sarmento et al. (2011) showed in occupancy models of stone martens that the habitat variables, landscape structure, and the wood mouse frequency from photographic captures were the most important occupancy drivers. Stone marten occupancy seems to be higher in areas of a patchy structure of pine forest and Mediterranean scrubland. Thus, in our study, the stone marten selected pine forest areas in the North area. However, in the Southeast, it selected *Quercus ilex* forest and urbanized land instead of scrubland. The stone marten occupancy model did not show a direct selection for a high relative abundance of rodents, as was the case for the red fox. The selection of the same landscapes as rodents may show a feeding strategy following higher rodent “catchability” rather than a high rodent abundance (Hopcraft et al. 2005; Balme et al. 2007). In the Southwest, the relative abundance of rabbits could explain stone marten occurrence. Previous studies showed that the stone marten can consume rabbits in its diet (Padial et al. 2002; Barrientos and Virgós 2006). However, this model was ranked third in the model selection, with the null model above it. Therefore, selecting the relative abundance of rabbits to define stone marten occupancy should be taken with caution. The factors selected had a low interference in stone marten occurrence in this area. Including factors in the model did not improve model prediction which emphasised the consideration of the stone marten as a generalist species (Virgós and García 2002; Santos and Santos-Reis 2010).

Season is considered an important factor influencing species detectability (Andelt and Andelt, 1984; Vine et al. 2009). We observed an opposite pattern in fox and stone marten detectability between the northern and southeast areas and the southwest. In the North area, detectability was higher in the cold season than in the warm season. However, the opposite pattern was observed in the southeast and southwest areas. This finding may be due to different reasons. In the case of the red fox, activity seemed affected by the increased human disturbance (Díaz-Ruiz et al. 2015). Game hunting has an important presence in the southeast and southwest during the cold season. In this vein, the persecution of the fox by hunters might affect its behaviour resulting in more wary and cautious individuals being more difficult to detect (lower probability of detection). During spring (birth/ lactation) and summer (mothers accompanied by cubs), the likelihood of detection was higher, likely due to the behavioural changes that occur during these periods. During the denning period, female foxes were more active during the daytime (Phillips and Catling 1991). The presence of cubs and juveniles during spring and summer could also increase detection due to their curious and exploratory behaviour. In the north, without game hunting pressure, the dispersion of juveniles during the cold season could improve the detection of the red fox (Macdonald 1987). In the case of the stone marten, Ferreti et al. (2023) found the detection rate of Martes spp. had a positive association with that of the red fox and a negative with human detection rates. In addition, the detection rate of Martes spp. was higher in the warm season (spring and summer) and lower in the cold season (autumn and winter). According to our results, the red fox and the stone marten had the same detection patterns in the three areas. They might avoid humans and have the highest detection during the warm season in the southeast and areas.

Although martens and foxes share habitats, the fox might limit stone martens in selecting areas of high rodent abundance. This pressure might also show the role of the red fox and the stone marten as dominant and subordinate mesocarnivores, respectively. Thus, a subordinate species might be displaced when prey abundance is high, consequently avoiding agonistic encounters (Holt and Polis 1997). The landscape of fear (Laundré et al. 2001; Laundré et al. 2010) occurs when smaller species perceive the risk of predation by a top predator in the shared area. Decisions on predatory species might be trade-offs between the risk of predation and the benefits obtained from a given activity (i.e. habitat selection, sociability, vigilance) (Lima and Dill 1990). Particularly, subordinate species attempt to adapt their behaviour to select low-risk habitat conditions versus food resources (Heithaus 2001; Björklund et al. 2016; Virgós et al. 2020). Intraguild predation between the red fox and *Martes sp*. was identified in previous research (Padial et al. 2002; Remonti et al. 2012). Lindström et al. (1995) observed that foxes strongly limit marten numbers through predation in

Scandinavia. Although the fox may be dominant over martens, there is still a high spatial overlap between both mesocarnivores. In fact, spatial segregation does not seem to be the main mechanism of coexistence between both species, so other mechanisms, such as temporal segregation, might be driving this coexistence. Chapter 4 of this thesis focused on comparing activity patterns between the red fox and stone martens. We found that the red fox and the stone marten had a low overlap of daily activity patterns. Furthermore, the occupancy in cameras between foxes and stone martens was more significant as marten and fox relative abundance increased; however, we observed a more significant difference in activity patterns between the two species in this scenario.

Overall, our research supports the importance of identifying the invariant factors that define species occupancy patterns in different habitats. The selection of these factors depends on the coexistence of the species living in the same habitat. Thus, dominant species can select landscapes based primarily on food abundance, while subordinate species exhibit more complex habitat selections depending on their relationships with dominant competitors. Our research assists in assessing the emerging new roles, dynamics and mechanisms of coexistence between mesocarnivores communities in different and changeable habitat conditions.

CHAPTER 4

Spatio-temporal mechanisms of coexistence between two generalist mesocarnivores, the red fox and the stone marten

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Abstract

The study of the mechanisms of coexistence between animals and their determinants is essential to understand the role of species in different ecosystems. Spatial and temporal segregation allows the coexistence of carnivores in interspecific competition. Here, we study the activity and occupancy patterns of two abundant mesocarnivores in the central Iberian Peninsula, the red fox (*Vulpes vulpes*) and the stone marten (*Martes foina).* We also include their main prey species, rodents and the European rabbit (*Oryctolagus cuniculus*). Camera traps were used in three study areas across two seasons to record the presence and activity patterns of these species. Multispecies occupancy models were employed to analyse co-occurrence and interactions between foxes and martens. The R package "overlap" was used to estimate activity pattern overlap coefficients among all four species. Additionally, relative abundance (captures per 24 hours relative to total capture occasions) was examined as a factor influencing coexistence mechanisms. The results showed a positive spatial interaction: marten occupancy increased in areas where foxes were present. Occupancy also increased when both predators were more abundant. However, temporal overlap between foxes and martens was low, with greater activity pattern divergence when both were more abundant. Temporal overlap between foxes and rodents followed a seasonal pattern. Martens and rodents showed a higher temporal overlap when the temporal overlap between foxes and rodents was lower. These findings suggest that foxes may exert dominance over martens in food selection, with temporal segregation as the primary mechanism enabling coexistence between these two mesocarnivores.

Introduction

Competition highly drives the structure and dynamics of animal communities (Connell 1983; Schoener 1983). Interspecific competition occurs when different species compete for the same resources; consequently, threatening or killing subordinate species can occur (Schoener 1983). As a result, animals have developed mechanisms of coexistence to alleviate interspecific competition, such as niche partitioning through different food resources, or the spatial and temporal segregation of resource use (Schoener 1982; Chesson et al. 2000; Chase and Leibold 2003) through character displacement (i.e. behavioural evolutionary changes among similar species within the same environment) (Dayan and Simberloff 2005).

Terrestrial carnivores are representative animals for coexistence mechanisms (Ramesh et al. 2012; Torreta et al. 2016; Monterroso et al. 2020). Competitive interactions among carnivores are driven by the body size of the species (Monterroso et al. 2020). Thus, most studies on coexistence have focused either on large carnivores (Karanth et al. 2017; Miller et al. 2018; Evers et al. 2022) or on mesocarnivores (i.e. species of carnivores < 15 kilograms [kg]) coexisting with top-predators (Wang et al. 2015; Gómez-Ortiz et al. 2019; Gil-Sánchez et al. 2021). After the decline of top-predator populations during the 20th century (Ripple et al. 2014), new hierarchies and coexistence roles between mesocarnivores arose, influencing ecosystem function, structure, and dynamics (Monterroso et al. 2020).

The coexistence mechanisms between mesocarnivores have been less studied in environments lacking top-predator species (but see Vilella et al. 2020; Ferreiro-Arias et al. 2021; Hernandez-Puentes et al. 2022). The Iberian Peninsula has historically been home to top predators like the wolf (*Canis lupus*) and Iberian lynx (*Lynx pardis*) (Blanco et al. 1992; Delibes et al. 2000; Molsher et al. 2017). However, their disappearance in some areas, particularly central Spain, has allowed mesocarnivore species to fill the vacant top predator niche. The red fox (*Vulpes vulpes*) competes with the abundant stone marten (*Martes foina*) (Virgós and Casanovas, 1998, Dudús, 2014; Petrov et al. 2016; Roy et al. 2019) due to a high overlap of their used habitat and food resources, particularly rodents (Padial et al. 2002; Papakosta et al. 2010, Pereira et al. 2012). However, the fox is a facultative predator that consumes rabbits (*Oryctolagus cuniculus*) as staple prey when it is abundant in Iberian Peninsula (Delibes-Mateos et al. 2008; Diaz-Ruiz et al. 2013). Intraguild competition in sympatric areas could lead to fox predation on martens. Polis et al. (1989) found marten remains in fox scats (however, Brzeziński et al. (2014) suggest red fox predation might not be the sole driver of marten decline, citing similar observations between red fox and pine marten, Martes martes (Storch et al. 1990; Lindström et al. 1995)). More studies are needed to definitively assess the impact of foxes on marten populations. Considering the body mass ratio is the most important factor related to the strength of competitive interactions (Palomares and Caro 1999, Donadio and Buskirk 2006), red fox and stone marten can be considered dominant and subordinate species, respectively. Dominant species can influence subordinate species' population size, distribution and behaviour (Vanak et al. 2013; Fedriani et al. 2000; Monterroso et al. 2020).

Spatial, diet and activity segregation enables the coexistence of carnivores (Garneau et al. 2007; Di Betetti et al. 2010; Monterroso et al. 2014; Karanth et al. 2017). However, these mechanisms may be difficult to maintain in sympatric species such as the red fox and the stone marten. Due to their high spatial and diet overlap (Padial et al. 2002; Pereira et al. 2012) the segregation of their activity patterns becomes the principal mechanism modulating their coexistence (Monterroso et al. 2014). Thus, when sharing the same specific resource (e.g. a prey species), carnivores can use it at different times (Garneau et al. 2007). Thus, the activity patterns of a predator are often driven by the activity patterns of its staple prey, adjusting their daily activity to periods of increased prey availability (Linkie and Ridout 2011; Foster et al. 2013). However, the dominant species potentially cause shifts in the activity patterns of subordinate competitors. Dominant species can modify the timing of activity patterns of the subordinate species with its prey and reduce food availability (Kronfeld-Schor and Dayan 2003). Consequently, subordinate species need to assess the risk of agonistic interactions despite the increasing availability of prey (Fedriani et al. 2000).

Beyond prey abundance and top predator presence, additional factors like climate and habitat composition can also influence and define mesocarnivore activity patterns (Chutipong et al. 2017; Rosalino et al. 2005; Suraci et al. 2016; Monterroso et al. 2013). Studies on the activity patterns regarding mesocarnivore coexistence have increased in recent years (Blake et al. 2012; Ferreiro-Arias et al. 2021; Hernandez-Puentes et al. 2022). However, a crucial gap remains: a comparative analysis of activity patterns across different habitats. Such an analysis, considering variations in interspecific abundance and food availability, would be key to fully understanding how mesocarnivores coexist.

This study investigated spatial and temporal segregation as potential mechanisms of coexistence between the red fox and stone marten in central Spain. We examined occupancy and activity patterns of both mesocarnivores across three areas (north, southeast, and southwest) during warm and cold seasons. Each area represented a distinct habitat with unique plant composition and climatic conditions. We further explored potential factors influencing activity pattern overlap and occupancy, including the relative abundance of both mesocarnivores and their prey species (*Apodemus sp*., *Mus spp*., and *Oryctolagus cuniculus*).Considering the red fox as the dominant and the stone marten as the subordinate, we specifically tested the following predictions: 1) the red fox adjust its activity patterns to the seasonal, daily activity patterns and abundance of its prey species; 2) The stone marten avoids foxes spatially and/or temporally. Thus, because the fox and stone marten share common prey, the overlapping of activity patterns between martens and prey is determined by the relationship between foxes and prey. We expect that the overlapping of activity patterns between martens and rodents is less when the overlap of activity patterns between foxes and rodents is more similar. Our research assists in assessing the emerging new roles and mechanisms of coexistence between mesocarnivores in different and changeable habitat conditions. Understanding the diversity and dynamics of mesocarnivore communities is paramount for specific conservation and management measures without compromising the balance of the ecosystem.

Material and Methods

Study area

We collected data at 24 locations in the central Iberian Peninsula between 2013 and 2020 (Figure 1 of General Material and methods). The locations were grouped into three geographical areas: North, Southeast and Southwest. Each area represented a habitat covering different climatic conditions, land uses and predominant plant communities within supramediterranean and mesomediterranean bioclimatic environments (Ministry of Environment and Spatial Planning, 2001). The most represented land uses were pastures, small game, livestock and recreational areas (Table 1 of General material and methods).

Each location was camera-trapped for 20-35 days during either the warm (spring and summer) or cold season (autumn and winter). Six locations were exceptions, being sampled twice in different years and seasons. The locations were sampled during different seasons to study the influence of seasonality on temporal movement patterns. The distribution of sampling across seasons varied by area. In the north, four of the seven locations were sampled during the warm season, while three were sampled during the cold season. The southeast area had an even split, with four locations sampled in each season. Finally, the southwest area included four locations sampled during the warm season and five during the cold season (Table 1).

Table 1 Camera sampling details. The Area (North, Southeast and Southwest); Period of sampling (Period) and Season (summer, spring, autumn and winter) of each location are shown. The number of camera-trapping days and cameras in each location are specified. The numbers along with the locations correspond to the locations represented on the map in Figure 1 of General material and methods

Location	Area	Year	Month	Season	Camera-trapping (days)	Number of camera traps
(16)Manzanares del Real	North	2013	10/04-30/04	Spring	20	10
(17) La Berzosa	North	2013	04/05-24/05	Spring	20	9
(19) La Berzosa	North	2017	27/09-31/10	Autumn	35	9
(18) Miraflores de la Sierra	North	2013	1/06-20/06	Spring	20	8
(20)San Mames	North	2017	1/08-5/09	Summer	35	8
(21) Madarcos	North	2019	17/09-21/10	Autumn	35	8
(22) Braojos	North	2020	8/02-14/03	Winter	35	8
(2) Carabaña	Southeast	2014	3/11-8/12	Autumn	35	8
(6) Carabaña	Southeast	2017	04/06-9/07	Summer	35	10
(4) Ambite	Southeast	2014	12/02-7/03	Winter	23	9
(7) Ambite	Southeast	2019	04/06-9/07	Summer	35	8
(3) Villarejo de Salvanés	Southeast	2014	18/12-22/01	Winter	35	10
(8) Villarejo de Salvanés	Southeast	2018	13/03-17/04	Spring	35	8
(1)Valdaracete	Southeast	2014	03/11-8/12	Autumn	35	8
(5) Torres de la	Southeast	2014	04/04-	Spring	21	8

Alameda			25/04			
(14) Robledo	Southwest	2017	21/11-26/12	Autumn	35	10
(11) Pelayos de la Presa	Southwest	2018	19/06-24/07	Summer	35	8
(9) Quijorna	Southwest	2018	01/05-05/06	Spring	35	8
(23) Quijorna	Southwest	2019	16/07-20/08	Summer	35	8
(10)Cenicientos	Southwest	2016	22/11-15/12	Autumn	23	8
(24)Cenicientos	Southwest	2019	26/03-30/04	Spring	35	8
(13)Chapineria	Southwest	2019	29/10-03/12	Autumn	35	8
(12)Fresnedillas de la Oliva	Southwest	2019	17/12-21/01	Winter	35	8
(15) Navas del Rey	Southwest	2016	21/02-20/03	Winter	28	8

Field sampling

We deployed eight to ten camera-traps in each location for 20-35 days (an average of 31.25 days). Camera-traps were spaced 450-600m apart, covering an area sufficiently large to maximize the number of individuals photographed and reduce potential shades of detection of the species studied (similar to Sarmento et al. 2009). We created a minimum convex polygon (MCP) by connecting camera locations and buffered it by 500 meters, considering the total sampled area as the MCP plus buffer (Sarmento et al. 2009). This resulted in sampled areas of 2595 ha, 3607 ha, and 3541 ha in the north, southeast, and southwest, respectively. The mean area per location within each region (north: 370 ha, southeast: 450 ha, southwest: 395 ha) aligns with the average red fox home range reported in central Spanish mountains (López-Martín 2010).

Eight camera models were used with similar trigger time: Wildview Xtreme2 (not specified), Bushnell Trophy (1s), DLC Covert II (1s), Acorn LTL (1.1s), Cuddle Back Ambrush (not specified), HCO Scoutguard SG565 (1.2s), Scout Guard SG560K (1.2s), and Scout Guard SG562 (1.2s). We configured cameras following the same parameters (cameras operated 24 hours a day, taking three sequential photographs five seconds apart , normal PIR sensitivity and recording the date and time of photograph). To maximize detection probability (Monterroso et al., 2013; Gil-Sánchez et al., 2021), two baits were placed 1-2 meters in front of each camera: sardines (Heinlein et al., 2020; Sebastián-González et al., 2020) and a commercial fox lure (HAGOPUR® Premium Attractant Fox). We secured the sardines by piercing the cans and tying them to rocks or vegetation, preventing access and bait displacement. Following Gerber et al. (2012) and Braczkowski et al. (2016), we assumed the baits did not influence target species behaviour or activity rates. Cameras were checked every 4-7 days for bait/battery replacement and image download.

We studied seasonal effects in each area by selecting locations in different seasons: The warm season, which included spring and summer (April to September) and the cold season, which included autumn and winter (October to March) (Vilella et al. 2020) (Table 1). The locations that coincided with part of their sampling in both stations (the case of Villarejo de Salvanés 2018 and Madarcos), were classified within the station with more sampling days. The resulting scenarios were six: Warm season in the North area (Nwarm); Cold season in the North area (Ncold); Warm season in the Southeast area (SEwarm); Cold season in the Southeast area (SEcold); Warm season in the Southwest area (SWwarm) and, cold season in the Southwest area (SWcold).

Multispecies occupancy models

We conducted multispecies occupancy models to study the occurrence and the interaction between red fox and stone marten. We followed the Rota et al. (2016) occupancy model using the function *occuMulti* in the 'Unmarked' package of R software (Fiske and Chandler 2011). This model assumes the latent occupancy state at site i for a set of s potentially interacting species is a vector Zi of length s containing a sequence of the values 0 or 1 (0 when species is not detected, 1 when species is detected). The latent state is modelled as a multivariate Bernoulli random variable:

$$Zi \sim MVB\ (\psi i)$$

where ψi is a vector of length 2^s containing the probability of each possible combination of 0s and 1s, such that $\sum \psi i=1$. We studied the occurrence and interaction between red fox and stone marten (s = 2) having three natural parameters.

$$fred\,fox = log(\psi 10/\psi 00)$$

$$fstone\,marten = log(\psi 01/\psi 00)$$

$$fred\ fox/stone\ marten\ = log((\psi 11 * \psi 00)/(\psi 10 * \psi 01))$$

where the possible states are [11], [10], [01], or [00], corresponding to both species present, only species 1 or species 2 present, or both species absent, respectively.

The observations yij at site i on occasion j are vectors of length s and there are independent values of detection probability (p) for each species s in the observation process.

$$yij|Zi \sim Bernoulli(Zi * psij)$$

We focused on occupancy probability (psi) and strength of interaction between species ($fred\ fox/stone\ marten$) and the effect of relative abundance of mesocarnivores and preyon this natural parameter. We run a total of 16 models combining four variables in $fred\ fox/stone\ marten$: relative abundance of red fox, stone marten rodents and rabbits ($\text{RAI}_{\text{red fox}}$, $\text{RAI}_{\text{stone marten}}$, $\text{RAI}_{\text{rodents}}$ and $\text{RAI}_{\text{rabbit}}$, respectively). We considered intercept-only (~1) in $fred\ fox$, $fstone\ marten$ parameters and detection probability modelling. Each species' relative abundance index (RAI) was calculated as the number of captures (photographs) of a species per total occasion. We considered a capture whenever any of the species was photographed in a camera-trap every 24h, and an occasion as the number of cameras per day of the camera-trapping campaign. We used Akaike's Information Criterion (AIC) (Burnham and Anderson 2012) to select models with ΔAIC < 2. We used the *optimizePenalty* function to choose the best value of penalty using K-fold cross-validation, and re-fit the models using the optimal penalty term value. The use of penalized likelihood helps with separation/boundary issues, eliminate unreasonably large estimates, and reduce error (Clipp et al. 2021). We predicted occupancy probability of four possible states, marginal occupancy of both mesocarnivores and conditional occupancy of stone marten under dominant red fox.

Assessment of activity pattern and overlap of activity pattern

Photographic captures were manually tagged by location, camera, species, and time (UTC) by the same researcher. For each camera, we considered an independent detection when photographs of the same species were separated by at least one hour (Silveira et al. 2003; Linkie and Ridout 2009). Captures of more than one individual were considered multiple detections (Ridout and Linkie 2009). We identified target mesocarnivores at the species level. Small mammals (*Apodemus sylvaticus* and *Mus spp.*) were classified altogether as rodents.

We used the ‘overlap’ package (Ridout and Linkie 2009) in R 3.4.4 software (R Development Core Team 2017) to estimate the overlap coefficients between fox, stone marten and their potential prey (rodents and rabbits) by assessing the activity patterns of target species. *Activity pattern*: the independent detection records for each target species were regarded as a random sample from the underlying continuous temporal distribution (Ridout and Linkie 2009). Activity pattern is the probability density function of this temporal distribution fit with Kernel density functions (Ridout and Linkie 2009).
Overlap coefficient: comparisons of the pairwise activity pattern of the combined target species in each area and season (i.e. the area shared by the two functions) with confidence intervals.

The overlap coefficient i (Δ) takes values from zero to one ($\Delta \sim 1$ indicates a higher overlap of activity patterns). We used the estimators $\Delta 1$, and $\Delta 4$ recommended for small (<50 independent detections) and large (>50 independent detections) sample sizes, respectively (Ridout and Linkie 2009). Confidence intervals were obtained as intervals of percentiles from 999 bootstrap samples. Next, we assessed the overlap of the activity patterns values related to the overall pairwise comparisons made in the three areas. We considered values below the 50th percentile as low activity overlap and values above the 75th percentile as a high overlap. Values in between were regarded as moderate activity overlap of activity patterns (see Monterroso et al. 2014).

The overlap coefficient is only descriptive; thus, to test for significant differences in the activity pattern, we calculated in the R package 'CircStats' (Agostinelli and Lund 2018) a Watson's two-sample test for homogeneity of activity patterns between species (Jammalamadaka and Sengupta 2001). A p-value ≤ 0.05 depicted significant differences between activity patterns.

Results

We had a total of 750 sampled days with a total of 6328 occasions of capture (number of days per number of cameras). We obtained 1036 photographs of foxes and 1176 of stone martens separated by a minimum time interval of 1 hour. We also recorded 4007 photographs of rodents (including *Apodemus sylvaticus* and *Mus spp*.) and 126 of rabbits. Due to a low number of rabbit captures, we could only perform the interaction fox-rabbit in the Southeast and Southwest areas (Table 2).

Although genet (*Genetta genetta*) and badger (*Meles meles*) were also detected in all three areas, these two species presented a low number of captures (photographs). We decided to exclude them from the study and focus on the coexistence relationships of the two most abundant mesocarnivores in these areas.

Table 2: Number of independent detections of each carnivore and potential prey detected in the sampling areas concerning North, Southeast and Southwest areas and seasons. *Vulpes vulpes* (red fox); *Martes foina* (Stone Marten); small mammals (includes *Apodemus sp*., *Mus spp*); *Oryctolagus cuniculus* (rabbit); *Genetta genetta* (Genet) and *Meles meles* (Badger).

	North		**Southeast**		**Southwest**	
	Warm season	Cold season	Warm season	Cold season	Warm season	Cold season
Vulpes vulpes	216	429	91	46	175	79
Martes foina	147	363	72	46	154	394
Rodents	452	475	1084	625	574	797
Oryctolagus cuniculus	1	1	71	19	15	19
Genetta genetta	16	22	16	52	23	148
Meles meles	13	47	10	2	1	4

Occupancy and interaction of red fox and stone marten

We fitted models with a penalty value of 0.5. Model selection showed an interspecific dependence among red fox and stone marten. The two top models assume a positive interaction between both mesocarnivores. The first top model (AIC = 9095.19; AICwt = 0.32) showed that the probability of two species' occupancy varied as a function of the relative abundance of red fox and stone marten. The second top model (AIC = 9095.54; AICwt = 0.27) selected the relative of both mesocarnivores and rodents to explain two species occupancy. Nevertheless, while variables RAI_{redfox} and $RAI_{stone\ marten}$ showed a significant relationship, RAIrodents had a non-significant relationship (Table 3).

Hereafter we report results from our first-ranked model with significant variables. We estimated occupancy probability, and marginal and conditional occupancy of red fox and stone marten from each site (Supplementary material 1). In addition, we predicted occupancy probability and marginal and conditional occupancy of red fox and stone marten from all sites. Red fox showed a marginal occupancy higher than the stone marten (Table 4).

Furthermore, the marginal occupancy of both mesocarnivores increased as the relative abundance of both mesocarnivores increased (Figure 2). The marginal occupancy of martens was similar to foxes with high abundances of both species (Figure 2). The probability of two mesocarnivores being presented (psi [11]) was higher than the probability of red fox presence and stone marten absence (psi [10]). This was also reflected in the conditional occupancy where marten occupancy was higher in areas where foxes were present (Table 4). The probability of detection of both mesocarnivores was similar

Table 3 Predictor selection in the multispecies occupancy models. Occupancy probability (psi) in defined for the tree natural parameters ($fred\ fox$; $fstone\ marten$; $fred\ fox/stone\ marten$). Selected predictors explain variations in $f$red fox/stone marten occupancy probability. $fred\ fox$ and $fstone\ marten$ is defined by the intercept. The detection probability (p) is defined by the intercept. The regression coefficients (Estimate) are shown, and also the standard error (S.E) and the p-value (α=0.05).

Model	Natural parameter	Estimate	SE	p-value
	psi (red fox) Intercept	0.358	0.190	5.92e-02
	psi (stone marten) Intercept	-0.931	0.270	5.68e-04
$fred\ fox$ (~1)	psi (redfox:stonemarten) Intercept	0.882	0.317	5.46e-03
$fstone\ marten$ (~1)	psi (redfox:stonemarten) RAI_{redfox}	2.161	0.741	3.54e-03
$fred\ fox/stone\ marten$ (~RAI_{redfox} + $\text{RAI}_{stonemarten}$)	psi (redfox:stonemarten) $\text{RAI}_{stonemarten}$	5.834	0.553	5.15e-26
	p (red fox) Intercept	-1.45	0.0894	6.56e-59
	p (stone marten) Intercept	-1.48	0.1057	1.73e-44
	psi (red fox) Intercept	0.355	0.259	1.70e-01
$fred\ fox$ (~1)	psi (stone marten) Intercept	-0.938	0.279	7.74e-04
$fstone\ marten$ (~1)	psi (redfox:stonemarten) Intercept	0.743	0.302	1.37e-02
$fred\ fox/stone\ marten$ (~RAI_{redfox} + $\text{RAI}_{rodents}$)	psi (redfox:stonemarten) RAI_{redfox}	2.182	0.883	1.35e-02
	psi (redfox:stonemarten) $\text{RAI}_{stonemarten}$	5.755	0.525	5.33e-28
	psi (redfox:stonemarten) $\text{RAI}_{rodents}$	0.693	0.419	9.80e-02
	p (red fox) Intercept	-1.45	0.0861	2.89e-63
	p (stone marten) Intercept	-1.48	0.0941	9.95e-56

Table 4 Predicted occupancy probability (psi) and detection probability (p) of red fox and stone marten from all sites. Probability occupancy was predicted in the four states [11], [10], [01], or [00], corresponding to both species present, only red fox or stone marten present, or both species absent, respectively. Marginal occupancy of both mesocarnivores and conditional occupancy probability with/without presence of red fox was showed. Predicted values (Predicted) are shown, and also the standard error (S.E) and the lower and upper interval coefficient (CI [2.5, 97.5%]).

	Predicted	SE	CI lower	Clupper
$\boldsymbol{psi}$[11]	0.325	0.025	0.279	0.382
$\boldsymbol{psi}$[10]	0.342	0.035	0.278	0.399
$\boldsymbol{psi}$[01]	0.094	0.020	0.059	0.129
$\boldsymbol{psi}$[00]	0.239	0.041	0.178	0.322
$\boldsymbol{p}$ [red fox]	0.191	0.014	0.165	0.219
$\boldsymbol{p}$[stone marten]	0.186	0.012	0.162	0.211
marginal $\boldsymbol{psi}$ [red fox]	0.667	0.040	0.584	0.729
marginal $\boldsymbol{psi}$[stone marten]	0.419	0.033	0.366	0.488
conditional $\boldsymbol{psi}$ with fox	0.488	0.031	0.443	0.548
conditional $\boldsymbol{psi}$ without fox	0.283	0.063	0.172	0.430

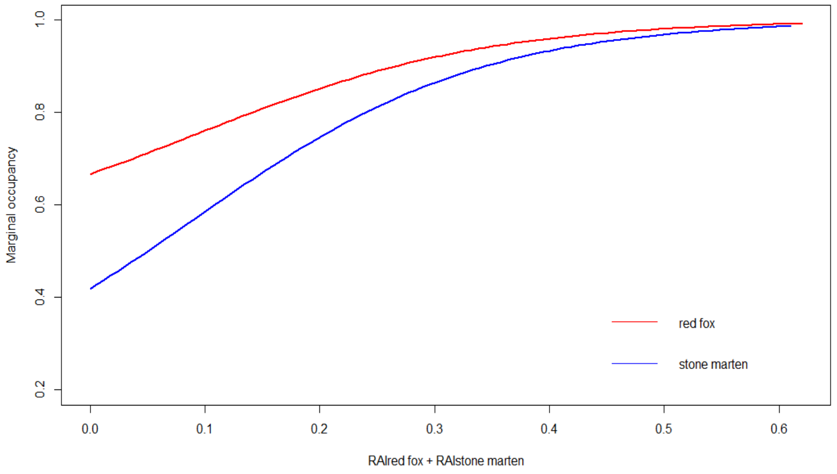


Figure 2 Marginal occupation of foxes (*Vulpes vulpes*) and martens (*Martes foina*) according to the relative abundance of both mesocarnivores. Red line represents fox and blue line represents marten.

Activity patterns

We identified significant differences in the activity patterns of the considered species across areas and seasons (Table 5). The red fox was predominantly nocturnal, although its activity pattern was not uniform across seasons and areas. In SEwarm and

SWwarm scenarios, the activity pattern of the red fox was unimodal, with maximum activity peaks at 0:00hr and between 21:00hr to 2:00hr, respectively (Figure 3).

Table 5 Pairwise comparisons of activity patterns of red fox, stone marten, rodents and rabbit studied species across areas in two seasonal periods (warm and cold seasons). The following statistic is shown: Watson.two test value and signification (Watson.two).

Species	Season	Area	watson.two
Red fox	Warm	N-SE	0.167
		N-SW	0.308**
		SE-SW	0.051
	Cold	N-SE	0.077
		N-SW	0.159
		SE-SW	0.087
Stone marten	Warm	N-SE	0.138
		N-SW	0.179
		SE-SW	0.054
	Cold	N-SE	0.804***
		N-SW	0.732***
		SE-SW	0.281**
Rodents	Warm	N-SE	0.413***
		N-SW	0.208*
		SE-SW	0.713***
	Cold	N-SE	0.506***
		N-SW	0.681***
		SE-SW	0.091
Rabbit	Warm	SE-SW	0.118
	Cold	SE-SW	0.157

* 0.01 < p-value < 0.05

**0.001 < p-value < 0.01

*** p-value < 0.001

However, the activity pattern was only more diurnal in Nwarm. In the Nwarm scenario, the activity of the red fox tended to a trimodal pattern of three peaks of maximum activity at 16:00hr, 23:00hr and 4:00hr (Figure 3). However, we only found significant differences in the fox activity patterns between Nwarm and SWwarm. During the autumn-winter season, the pattern of fox activity was nocturnal and similar between areas (Table 5), with increased activity hours concentrated between 18:00h and 7:00h (Figure 3). We found no significant differences in the activity pattern between areas this season.

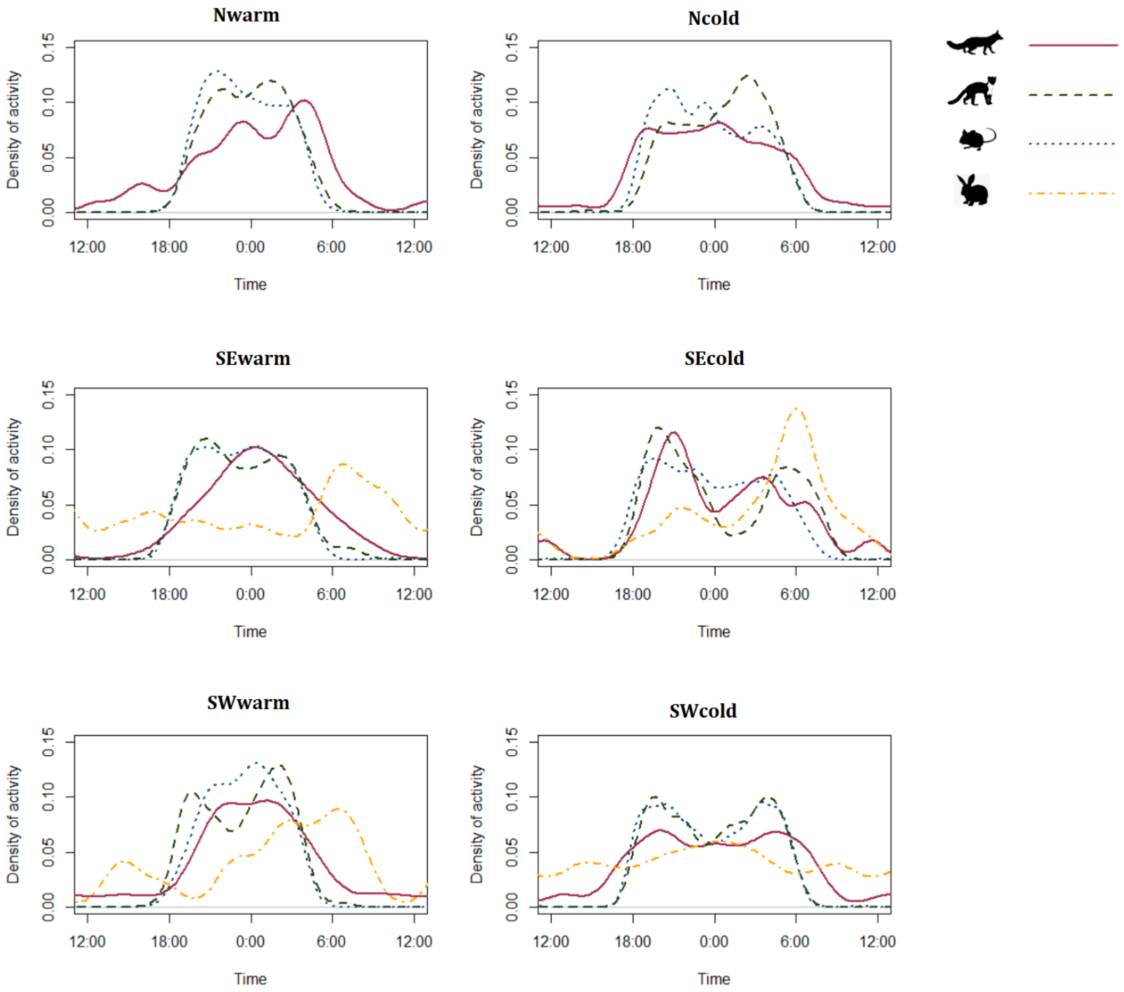


Figure 3 Activity patterns of red fox, stone marten, rodents and rabbits in each area (North, Southeast and Southwest) and seasonal period (warm and cold seasons). The red and continuous line represents the pattern of activity of the red fox (*Vulpes vulpes*); the green and discontinuous line represents the pattern of activity of the stone marten (*Martes foina*); blue dotted line represents the pattern of activity of rodents. The yellow dotted and discontinuous line represents the patterns of activity of rabbits (*Oryctolagus cuniculus*).

The activity pattern of the stone marten was bimodal and nocturnal in each area and season. However, significant differences in activity patterns were only found in all areas during the cold season (Table 5). During the warm season, the pattern had two activity peaks at 19:00hr and 3:00hr. However, the activity pattern was shorter in the northern area during the cold season. It showed two peaks of activity at 20:00hr and 3:00hr in Ncold, two peaks of activity at 19:00hr and 6:00hr in SEcold, and two peaks of activity at 19:00hr and 4:00hr in the SWcold scenarios (Figure 3).

Rodents exhibited a predominant nocturnal activity pattern. However, we only found significant differences in the activity pattern between SEcold and SWcold scenarios (Table 6). In Nwarm and SWwarm scenarios, the rodent activity pattern was bimodal with two peaks at 21:00h and 3:00hr and 21:00hr and 1:00hr, respectively (Figure 3). In contrast, the activity showed a trimodal pattern in SEwarm scenario with three peaks of activity at 20:00hr, 1:00hr and 3:00hr (Figure 3). The activity pattern of rodents showed a trimodal pattern in Ncold scenario with peaks at 21:00hr; 23:00hr and 3:00hr. This activity pattern was a uniform pattern between 19:00hr to 4:00hr in SEcold and SWcold scenarios (Figure 3).

Overlap of activity pattern.

We considered the 50th percentile (Δ = 0.795) of the range of the overlap coefficient values as the threshold for separating low and moderate overlapping activity patterns. Similarly, we used the 75th percentile (Δ = 0.832) to separate between a moderate and high overlap. Overlap of activity patterns between a red fox and stone marten was low in Nwarm, SEcold, SWwarm and SWcold scenarios (Δ= 0.744; Δ= 0.767 and Δ= 0.793, respectively) and moderate in Ncold (Δ= 0.798) and SEwarm scenarios (Δ= 0.807) (Table 6). Results from the Watson's two-sample test showed that the activity pattern between the stone marten and the red fox was only significantly different in Nwarm, Ncold and SWwarm scenarios (Table 6).

The overlap of activity patterns between the red fox and rodents was low in Nwarm (Δ= 0.714) and SWcold (Δ= 0.785); moderate in SEwarm (Δ= 0.803), SE-cold (Δ= 0.813) and SWwarm (Δ= 0.798) and high in Ncold (Δ= 0.845) scenarios (Table 6). Fox and rodents showed significant differences in the activity pattern in all areas and seasons, with the exception of SEcold scenario (Table 6).

The overlap of activity patterns between stone martens and rodents was high in all the scenarios (Δ > 0.832) except for SEcold, which was low (Δ= 0.779) (Table 6). Despite the high temporal overlap between the two species, we observed significant differences in activity patterns in Ncold and SWwarm scenarios (Table 6).

The overlap of activity patterns between the red fox and rabbits was low in the Southeast and Southwest during all seasons (Δ< 0.795) (Table 6). However, significant differences in the pattern of activity were only observed during the warm season in both areas (Table 6).

Our analysis revealed significant differences in activity patterns between the two species in scenarios with higher relative abundance of both mesocarnivores (Nwarm Ncold, and SWcold). These scenarios had the highest relative abundance values (1.35; 2.06; 1.45, respectively) (Table 6). Conversely, in areas with lower relative abundance of mesocarnivores (SEwarm, SEcold, and SWwarm), where the relative abundance values were much lower (0.41; 0.28; 0.42, respectively), we found no significant differences in activity patterns between fox and stone marten (Table 6).

Table 6 Pairwise comparisons of overlap of activity patterns between red fox, stone marten, rodents and rabbits in each area in two seasonal periods (warm and cold seasons). The following statistics are shown: Activity coefficient for large samples Dhat4 (Dhat); degree of overlap of activity pattern (Overlap); lower and upper interval coefficient (CI [2.5, 97.5%]) and Watson.two test value and signification (watson.two)

Area	Season	Species interaction	Dhat	Overlap	CI[97,5%-2,5%]	watson.two
N	Warm	Red fox - Stone marten	0.744	Low	[0.642,0.796]	0.891***
		Red fox - Rodents	0.714	Low	[0.634,0.764]	1.531***
		Stone marten - Rodents	0.912	High	[0.868,0.991]	0.086
	Cold	Red fox - Stone marten	0.798	Moderate	[0.742,0.839]	1.132***
		Red fox - Rodents	0.845	High	[0.804,0.884]	0.710***
		Stone marten - Rodents	0.842	High	[0.778,0.897]	0.648***
SE	Warm	Red fox - Stone marten	0.807	Moderate	[0.717,0.928]	0.123
		Red fox - Rodents	0.803	Moderate	[0.761,0.906]	0.195*
		Stone marten - Rodents	0.898	High	[0.881,1.000]	0.035
		Red fox - Rabbit	0.536	Low	[0.373,0.618]	1.241***
	Cold	Red fox - Stone marten	0.767[1]	Low	[0.686, 0.914]	0.079
		Red fox - Rodents	0.813[1]	Moderate	[0.733, 0.910]	0.056
		Stone marten - Rodents	0.779[1]	Low	[0.686, 0.888]	0.193*
		Red fox - Rabbit	0.632[1]	Low	[0.468,0.868]	0.173
SW	Warm	Red fox - Stone marten	0.793	Low	[0.711,0.854]	0.140
		Red fox - Rodents	0.798	Moderate	[0.747,0.872]	0.421***
		Stone marten - Rodents	0.858	High	[0.778,0.919]	0.436***
		Red fox - Rabbit	0.617[1]	Low	[0.432,0.827]	0.223*
	Cold	Red fox - Stone marten	0.780	Low	[0.714,0.869]	0.301**
		Red fox - Rodents	0.785	Low	[0.725,0.876]	0.286**
		Stone marten - Rodents	0.936	High	[0.931,0.993]	0.030
		Red fox - Rabbit	0.726[1]	Low	[0.634,0.933]	0.059

[1] Dhat1

* 0.01 < p-value < 0.05

**0.001 < p-value < 0.01

*** p-value < 0.001

Discussion

This study investigated temporal segregation as a key mechanism for coexistence between red fox and stone marten by analysing their activity patterns and occurrence alongside potential prey. Using the overlap of activity patterns between pairwise target species, we found that red fox and stone marten had a low overlap of activity patterns suggesting avoidance between them. Additionally, the red fox exhibited a seasonal pattern linked to rodent activity, while the overlap between martens and rodents may be influenced by the risk of fox predation. These observed differences suggest that the red fox acts as the dominant predator in these ecosystems, where wolves and lynxes have been absent for decades. Interestingly, we found a positive interaction between mesocarnivore occupancy, with higher occurrences of both fox and stone marten when their relative abundances were high. However, despite increased co-occurrence, activity patterns remained largely segregated. These findings support the importance of differential day-cycle use in promoting red fox and stone marten coexistence, aligning with previous observations (Di Bitetti et al. 2010).

Despite their differing activity patterns, both red fox, stone marten, and their rodent prey primarily exhibit nocturnal behaviour, aligning with previous research (fox: Meek & Saunders 2000, Díaz-Ruíz et al. 2013; marten: Monterroso et al. 2014, Torretta et al. 2017; rodents: Galsworthy et al. 2005, Bennie et al. 2014). However, seasonal and regional variations influence these patterns. Their range of activity was broader during the cold season and more concentrated in the warm season, according to other studies in Mediterranean environments (Tester 1987; Posillico et al. 1995; Vilella et al. 2020). Yearly variations in daylight hours also play a role, with rodents generally active for fewer hours in spring and summer compared to autumn and winter (Flowerdew 2000). Additionally, temperature, precipitation, and cloud cover significantly impact rodent activity patterns (Stokes et al. 2001; Wróbel & Bogdziewicz 2015). These factors can lead to subtle differences in peak activity times between regions during the same season. Notably, the red fox's broader activity range in the cold season might be a response to prey behaviour strategies (Azevedo et al. 2018). Indeed, our findings show greater overlap in activity patterns between foxes and rodents during the colder months compared to the warmer season. Red foxes likely consume more rodents during colder months due to increased prey availability (Padial et al. 2002; Carvalho and Gomes 2004; Barrull et al. 2014). Conversely, their diet becomes more varied in warm months with the inclusion of fruits and insects (Carvalho and Gomes 2004). This suggests a potential predator-prey relationship driving red fox activity patterns, aligning with rodent activity shifts during colder seasons (Mukherjee et al. 2020). Although red fox had mainly nocturnal activity, it showed some diurnal activity in the North area during the warm season. Other studies have observed this pattern, assuming that the fox may have a diurnal activity during the breeding period (Servín et al. 1991), also during lactation, and after a succession of rainy days (Meek and Saunders 2000).

The influence of seasonality on activity patterns between martens and rodents appears weaker compared to the pressure exerted by foxes on rodents. Martens and rodents showed more similar activity patterns and greater overlap of activity patterns when activity patterns between foxes and rodents were more different and had less overlap. The red fox and stone marten are considered generalist species (Barrientos and Virgós 2006; Díaz-Ruiz et al. 2013). They select different food resources and have large diet variability depending on the temporal availability of food. However, both species can have a high overlap in their diet (Barrull et al. 2014), with rodents as an essential part of the diet of both species (Padial et al. 2002; Carvalho and Gomes 2004; Barrull et al. 2014). Although the two species may share some dietary overlap, the potential for intraguild predation by red fox could be influencing the activity patterns of the stone marten. We observed low to moderate overlap in activity between the two mesocarnivores, with stone marten activity decreasing or starting later when red fox activity peaked. This phenomenon aligns with the concept of the "landscape of fear" (Laundré et al. 2001; Laundré et al. 2010), where smaller prey species adjust their behaviour based on the perceived risk of predation by larger predators within a shared space. This can influence factors like habitat use, diversity, and abundance. Previous research supports the existence of intraguild predation between red fox and Martes sp. (Padial et al. 2002; Remonti et al. 2012). These studies documented dietary overlap, with marten remains found in fox scats during spring and summer, suggesting asymmetric predation by foxes. Additionally, Lindström et al. (1995) observed strong limitation of marten populations through fox predation in Scandinavia. Within the landscape of fear, prey species face trade-offs between the risk of predation and the benefits associated with specific activities (e.g., habitat selection, social interactions, vigilance) (Lima and Dill 1989). Notably, subordinate species often prioritize low-risk habitats over readily available food resources (Heithaus 2001; Björklund et al. 2016; Virgós et al. 2020).

Our results of the occurrence and activity patterns relationship between the red fox and stone marten could also show the roles of dominant and subordinate mesocarnivores, respectively. The relative abundance of stone marten and red fox determined the occurrence between the red fox and stone marten; scenarios with a higher occupancy were those with a higher relative abundance of both mesocarnivores. Red fox and stone marten showed a positive interaction. Both species could have a significant spatial overlap indicating the exploration of the same general habitat conditions (Pereira et al. 2012; Petrov et al. 2016). However, the stone marten's arboreal habits likely minimize predation risk from red fox despite potential spatial overlap (Pereira et al., 2012). Importantly, activity patterns diverged in areas with higher mesocarnivore abundance, suggesting that temporal segregation is the key driver of coexistence. By minimizing potential intraguild predation, spatial and food competition, temporal segregation allows both mesocarnivores to coexist (Petrov et al. 2016).

The red fox can be a facultative carnivore that selects rabbits as its staple food when these are abundant but selects rodents, seeds, and fruits when rabbits are scarce (Delibes-Mateos et al. 2008; Diaz-Ruiz et al. 2013). However, due to the very low rabbit presence in our study areas, we cannot definitively assess its influence on rodent selection and its potential impact on activity pattern overlap between rodents and stone martens. We observed higher overlap in activity patterns between red fox and rodents during the cold season in the North compared to the Southwest and Southeast regions. Notably, rabbit presence in the North was practically nonexistent (2 observations), while the other two areas had a higher relative abundance. This pattern suggests that areas with available rabbits may experience less pressure on rodent populations, reflecting the red fox's dietary flexibility. However, these results require cautious interpretation. Only diet analysis could confirm whether increased temporal overlap between predator and prey translates to higher prey consumption in those areas.

Overall, our research supports the importance of temporal segregation as a mechanism of coexistence between the red fox and stone marten. This mechanism allows for a dynamic balance between occupancy and competition, adapting to seasonal and local changes while maintaining individual fitness (Chesson 2000). Furthermore, our results suggest that the fox can play a dominant predator role (mainly in food selection), driving the coexistence mechanism with subordinate species where large carnivores are absent. The ecological plasticity of mesocarnivores underscores the importance of studying their coexistence and the factors influencing it. Understanding these mechanisms can provide valuable insights into the functional role of mesocarnivores within various ecosystems. Notably, knowledge of inter-mesocarnivore coexistence can also be highly relevant to reintroduction programs for large carnivores.

Supporting information chapter 4

a) Marginal occupancy of stone marten

Site	Predicted	SE	lower	upper
1	0.419	0.034	0.371	0.493
2	0.538	0.027	0.494	0.590
3	0.634	0.022	0.599	0.679
4	0.694	0.019	0.659	0.732
5	0.843	0.016	0.811	0.867
6	0.499	0.030	0.454	0.560
7	0.587	0.042	0.519	0.667
8	0.867	0.017	0.831	0.894
9	0.762	0.025	0.709	0.808
10	0.440	0.034	0.393	0.512
11	0.651	0.057	0.540	0.754
12	0.462	0.036	0.409	0.538
13	0.585	0.026	0.546	0.637
14	0.612	0.070	0.481	0.739
15	0.815	0.023	0.770	0.856
16	0.749	0.018	0.711	0.780
17	0.922	0.019	0.883	0.950
18	0.650	0.025	0.601	0.690
19	0.709	0.025	0.656	0.753
20	0.697	0.088	0.510	0.840
21	0.479	0.039	0.425	0.559
22	0.440	0.034	0.393	0.512
23	0.811	0.016	0.778	0.836
24	0.610	0.047	0.526	0.699
25	0.626	0.031	0.577	0.687
26	0.524	0.048	0.448	0.615
27	0.566	0.058	0.466	0.676
28	0.588	0.024	0.550	0.637
29	0.811	0.020	0.773	0.848
30	0.688	0.029	0.637	0.742
31	0.666	0.025	0.629	0.716
32	0.601	0.033	0.550	0.667
33	0.864	0.019	0.821	0.897
34	0.827	0.016	0.795	0.851
35	0.941	0.012	0.916	0.959
36	0.515	0.046	0.444	0.602
37	0.539	0.030	0.496	0.602
38	0.530	0.038	0.475	0.604
39	0.732	0.018	0.697	0.765

b) Marginal occupancy of red fox

Site	Predicted	SE	lower	upper
1	0.667	0.032	0.593	0.721
2	0.735	0.029	0.672	0.787
3	0.790	0.022	0.746	0.829
4	0.825	0.020	0.786	0.861
5	0.910	0.014	0.880	0.932
6	0.713	0.028	0.653	0.765
7	0.763	0.024	0.715	0.808
8	0.924	0.014	0.890	0.945
9	0.864	0.023	0.814	0.898
10	0.679	0.030	0.613	0.733
11	0.800	0.027	0.751	0.854
12	0.691	0.028	0.633	0.745
13	0.762	0.024	0.714	0.802
14	0.778	0.032	0.720	0.845
15	0.894	0.014	0.865	0.919
16	0.856	0.018	0.821	0.888
17	0.955	0.013	0.925	0.972
18	0.799	0.026	0.747	0.840
19	0.833	0.025	0.785	0.870
20	0.826	0.041	0.747	0.902
21	0.701	0.027	0.646	0.751
22	0.679	0.030	0.613	0.733
23	0.891	0.015	0.861	0.917
24	0.776	0.024	0.725	0.824
25	0.786	0.021	0.745	0.824
26	0.727	0.026	0.675	0.777
27	0.751	0.028	0.696	0.807
28	0.764	0.024	0.713	0.806
29	0.892	0.014	0.864	0.915
30	0.821	0.019	0.785	0.857
31	0.808	0.020	0.772	0.843
32	0.771	0.022	0.728	0.812
33	0.922	0.015	0.887	0.945
34	0.901	0.014	0.871	0.925
35	0.966	0.007	0.953	0.978
36	0.722	0.026	0.671	0.771
37	0.736	0.025	0.685	0.781
38	0.730	0.025	0.681	0.775
39	0.846	0.019	0.812	0.879

40	0.557	0.056	0.463	0.662	40	0.746	0.028	0.690	0.799
41	0.631	0.074	0.486	0.762	41	0.788	0.034	0.726	0.859
42	0.883	0.014	0.854	0.906	42	0.933	0.011	0.911	0.951
43	0.857	0.021	0.816	0.894	43	0.918	0.013	0.894	0.940
44	0.953	0.009	0.935	0.968	44	0.973	0.006	0.961	0.983
45	0.876	0.014	0.847	0.899	45	0.929	0.011	0.904	0.948
46	0.902	0.028	0.839	0.941	46	0.944	0.014	0.914	0.966
47	0.895	0.015	0.867	0.919	47	0.940	0.010	0.920	0.956
48	0.734	0.028	0.681	0.786	48	0.847	0.017	0.813	0.880
49	0.811	0.016	0.781	0.839	49	0.892	0.014	0.865	0.917
50	0.910	0.020	0.869	0.940	50	0.948	0.011	0.929	0.966
51	0.980	0.006	0.968	0.988	51	0.989	0.003	0.981	0.994
52	0.828	0.028	0.771	0.876	52	0.902	0.015	0.874	0.928
53	0.543	0.052	0.457	0.642	53	0.738	0.027	0.682	0.789
54	0.730	0.019	0.690	0.762	54	0.845	0.020	0.807	0.879
55	0.675	0.026	0.633	0.727	55	0.813	0.019	0.777	0.849
56	0.444	0.035	0.396	0.517	56	0.681	0.030	0.617	0.735
57	0.675	0.026	0.633	0.727	57	0.813	0.019	0.777	0.849
58	0.625	0.022	0.588	0.670	58	0.785	0.023	0.737	0.825
59	0.652	0.032	0.597	0.714	59	0.800	0.020	0.761	0.839
60	0.489	0.032	0.443	0.556	60	0.707	0.028	0.650	0.759
61	0.419	0.034	0.371	0.493	61	0.667	0.032	0.593	0.721
62	0.419	0.034	0.371	0.493	62	0.667	0.032	0.593	0.721
63	0.419	0.034	0.371	0.493	63	0.667	0.032	0.593	0.721
64	0.419	0.034	0.371	0.493	64	0.667	0.032	0.593	0.721
65	0.453	0.036	0.403	0.528	65	0.687	0.029	0.626	0.741
66	0.430	0.034	0.383	0.503	66	0.673	0.031	0.604	0.727
67	0.430	0.034	0.383	0.503	67	0.673	0.031	0.604	0.727
68	0.419	0.034	0.371	0.493	68	0.667	0.032	0.593	0.721
69	0.419	0.034	0.371	0.493	69	0.667	0.032	0.593	0.721
70	0.430	0.034	0.383	0.503	70	0.673	0.031	0.604	0.727
71	0.419	0.034	0.371	0.493	71	0.667	0.032	0.593	0.721
72	0.494	0.029	0.449	0.557	72	0.710	0.029	0.645	0.762
73	0.540	0.027	0.497	0.597	73	0.736	0.027	0.680	0.785
74	0.641	0.021	0.601	0.680	74	0.794	0.024	0.744	0.835
75	0.419	0.034	0.371	0.493	75	0.667	0.032	0.593	0.721
76	0.462	0.032	0.415	0.528	76	0.691	0.030	0.623	0.744
77	0.419	0.034	0.371	0.493	77	0.667	0.032	0.593	0.721
78	0.447	0.032	0.400	0.515	78	0.683	0.032	0.610	0.736
79	0.429	0.034	0.382	0.502	79	0.673	0.031	0.603	0.727
80	0.547	0.026	0.505	0.598	80	0.740	0.028	0.681	0.789
81	0.476	0.030	0.429	0.538	81	0.699	0.031	0.629	0.752
82	0.457	0.032	0.411	0.524	82	0.689	0.030	0.620	0.742
83	0.419	0.034	0.371	0.493	83	0.667	0.032	0.593	0.721
84	0.429	0.034	0.382	0.502	84	0.673	0.031	0.603	0.727

85	0.723	0.023	0.674	0.763	85	0.841	0.023	0.795	0.876
86	0.440	0.034	0.392	0.512	86	0.679	0.030	0.613	0.733
87	0.449	0.035	0.400	0.523	87	0.684	0.029	0.622	0.738
88	0.449	0.035	0.400	0.523	88	0.684	0.029	0.622	0.738
89	0.419	0.034	0.371	0.493	89	0.667	0.032	0.593	0.721
90	0.434	0.034	0.386	0.507	90	0.675	0.031	0.607	0.729
91	0.419	0.034	0.371	0.493	91	0.667	0.032	0.593	0.721
92	0.434	0.034	0.386	0.507	92	0.675	0.031	0.607	0.729
93	0.546	0.053	0.459	0.646	93	0.739	0.027	0.683	0.791
94	0.419	0.034	0.371	0.493	94	0.667	0.032	0.593	0.721
95	0.508	0.033	0.461	0.576	95	0.718	0.026	0.663	0.767
96	0.419	0.034	0.371	0.493	96	0.667	0.032	0.593	0.721
97	0.419	0.034	0.371	0.493	97	0.667	0.032	0.593	0.721
98	0.419	0.034	0.371	0.493	98	0.667	0.032	0.593	0.721
99	0.419	0.034	0.371	0.493	99	0.667	0.032	0.593	0.721
100	0.419	0.034	0.371	0.493	100	0.667	0.032	0.593	0.721
101	0.472	0.030	0.425	0.535	101	0.697	0.031	0.627	0.750
102	0.419	0.034	0.371	0.493	102	0.667	0.032	0.593	0.721
103	0.419	0.034	0.371	0.493	103	0.667	0.032	0.593	0.721
104	0.501	0.043	0.438	0.585	104	0.714	0.026	0.663	0.762
105	0.499	0.034	0.450	0.569	105	0.712	0.027	0.657	0.762
106	0.612	0.022	0.572	0.655	106	0.778	0.024	0.725	0.821
107	0.590	0.024	0.552	0.639	107	0.765	0.024	0.714	0.807
108	0.565	0.025	0.523	0.614	108	0.750	0.027	0.693	0.799
109	0.612	0.022	0.572	0.655	109	0.778	0.024	0.725	0.821
110	0.419	0.034	0.371	0.493	110	0.667	0.032	0.593	0.721
111	0.442	0.035	0.394	0.514	111	0.680	0.030	0.615	0.734
112	0.419	0.034	0.371	0.493	112	0.667	0.032	0.593	0.721
113	0.451	0.032	0.404	0.519	113	0.685	0.032	0.613	0.738
114	0.453	0.036	0.403	0.528	114	0.687	0.029	0.626	0.741
115	0.442	0.035	0.394	0.514	115	0.680	0.030	0.615	0.734
116	0.430	0.034	0.383	0.503	116	0.673	0.031	0.604	0.727
117	0.484	0.029	0.438	0.545	117	0.704	0.031	0.635	0.757
118	0.453	0.036	0.403	0.528	118	0.687	0.029	0.626	0.741
119	0.477	0.039	0.423	0.556	119	0.700	0.027	0.644	0.751
120	0.451	0.032	0.404	0.519	120	0.685	0.032	0.613	0.738
121	0.419	0.034	0.371	0.493	121	0.667	0.032	0.593	0.721
122	0.912	0.013	0.885	0.932	122	0.949	0.009	0.928	0.965
123	0.442	0.035	0.394	0.514	123	0.680	0.030	0.615	0.734
124	0.465	0.037	0.412	0.542	124	0.693	0.028	0.635	0.747
125	0.477	0.039	0.423	0.556	125	0.700	0.027	0.644	0.751
126	0.430	0.034	0.383	0.503	126	0.673	0.031	0.604	0.727
127	0.474	0.032	0.428	0.541	127	0.699	0.029	0.636	0.752
128	0.824	0.017	0.791	0.855	128	0.899	0.013	0.873	0.923
129	0.419	0.034	0.371	0.493	129	0.667	0.032	0.593	0.721

130	0.555	0.055	0.462	0.659	130	0.745	0.027	0.688	0.798
131	0.443	0.035	0.395	0.515	131	0.680	0.030	0.616	0.734
132	0.504	0.043	0.440	0.588	132	0.715	0.026	0.664	0.764
133	0.581	0.062	0.470	0.696	133	0.759	0.029	0.705	0.819
134	0.491	0.041	0.433	0.573	134	0.708	0.026	0.657	0.757
135	0.454	0.036	0.404	0.529	135	0.687	0.029	0.627	0.741
136	0.479	0.039	0.425	0.558	136	0.701	0.027	0.646	0.751
137	0.466	0.037	0.413	0.543	137	0.694	0.028	0.636	0.747
138	0.504	0.043	0.440	0.588	138	0.715	0.026	0.664	0.764
139	0.419	0.034	0.371	0.493	139	0.667	0.032	0.593	0.721
140	0.568	0.058	0.466	0.678	140	0.752	0.028	0.697	0.808
141	0.443	0.035	0.395	0.515	141	0.680	0.030	0.616	0.734
142	0.602	0.055	0.503	0.705	142	0.772	0.027	0.719	0.825
143	0.466	0.037	0.413	0.543	143	0.694	0.028	0.636	0.747
144	0.443	0.035	0.395	0.515	144	0.680	0.030	0.616	0.734
145	0.491	0.041	0.433	0.573	145	0.708	0.026	0.657	0.757
146	0.867	0.023	0.818	0.905	146	0.924	0.018	0.882	0.947
147	0.419	0.034	0.371	0.493	147	0.667	0.032	0.593	0.721
148	0.720	0.025	0.667	0.765	148	0.839	0.024	0.791	0.876
149	0.750	0.025	0.696	0.796	149	0.856	0.023	0.807	0.892
150	0.760	0.023	0.711	0.801	150	0.862	0.021	0.817	0.896
151	0.750	0.025	0.696	0.796	151	0.856	0.023	0.807	0.892
152	0.803	0.025	0.750	0.848	152	0.887	0.021	0.839	0.918
153	0.827	0.025	0.775	0.869	153	0.901	0.020	0.854	0.928
154	0.727	0.020	0.694	0.768	154	0.843	0.017	0.812	0.876
155	0.419	0.034	0.371	0.493	155	0.667	0.032	0.593	0.721
156	0.419	0.034	0.371	0.493	156	0.667	0.032	0.593	0.721
157	0.638	0.022	0.604	0.683	157	0.792	0.022	0.751	0.830
158	0.419	0.034	0.371	0.493	158	0.667	0.032	0.593	0.721
159	0.475	0.032	0.429	0.542	159	0.699	0.029	0.637	0.752
160	0.525	0.038	0.471	0.600	160	0.728	0.025	0.679	0.772
161	0.625	0.022	0.589	0.670	161	0.785	0.023	0.738	0.825
162	0.419	0.034	0.371	0.493	162	0.667	0.032	0.593	0.721
163	0.419	0.034	0.371	0.493	163	0.667	0.032	0.593	0.721
164	0.894	0.019	0.851	0.924	164	0.939	0.014	0.905	0.958
165	0.794	0.022	0.745	0.832	165	0.882	0.020	0.838	0.912
166	0.949	0.014	0.920	0.969	166	0.971	0.009	0.950	0.982
167	0.844	0.017	0.807	0.871	167	0.910	0.015	0.876	0.933
168	0.664	0.025	0.627	0.715	168	0.808	0.020	0.771	0.842
169	0.500	0.029	0.455	0.557	169	0.713	0.030	0.646	0.766
170	0.680	0.020	0.640	0.716	170	0.816	0.022	0.769	0.854
171	0.763	0.017	0.727	0.793	171	0.864	0.017	0.831	0.895
172	0.656	0.025	0.606	0.695	172	0.802	0.026	0.751	0.842
173	0.656	0.025	0.606	0.695	173	0.802	0.026	0.751	0.842
174	0.688	0.025	0.637	0.731	174	0.821	0.025	0.773	0.859

175	0.419	0.034	0.371	0.493
176	0.475	0.032	0.429	0.542
177	0.582	0.029	0.539	0.641
178	0.569	0.028	0.529	0.626
179	0.753	0.018	0.712	0.782
180	0.451	0.032	0.404	0.519
181	0.700	0.022	0.653	0.737
182	0.668	0.022	0.623	0.705
183	0.684	0.021	0.651	0.728
184	0.750	0.025	0.696	0.796
185	0.509	0.029	0.464	0.569
186	0.734	0.018	0.699	0.768
187	0.547	0.032	0.501	0.613
188	0.556	0.027	0.515	0.611
189	0.886	0.017	0.849	0.913
190	0.487	0.033	0.442	0.556
191	0.463	0.031	0.417	0.529
192	0.832	0.016	0.801	0.857
193	0.509	0.029	0.464	0.569
194	0.910	0.017	0.873	0.936
195	0.543	0.026	0.501	0.600
196	0.586	0.025	0.541	0.633
197	0.500	0.029	0.455	0.557
198	0.671	0.025	0.620	0.711
199	0.419	0.034	0.371	0.493
200	0.459	0.031	0.412	0.525
201	0.459	0.031	0.412	0.525
202	0.419	0.034	0.371	0.493
203	0.419	0.034	0.371	0.493

175	0.667	0.032	0.593	0.721
176	0.699	0.029	0.637	0.752
177	0.760	0.023	0.716	0.799
178	0.753	0.024	0.705	0.794
179	0.858	0.019	0.820	0.890
180	0.685	0.032	0.613	0.738
181	0.828	0.023	0.782	0.864
182	0.810	0.024	0.761	0.848
183	0.819	0.019	0.785	0.854
184	0.856	0.023	0.807	0.892
185	0.718	0.028	0.660	0.770
186	0.848	0.018	0.814	0.881
187	0.740	0.024	0.693	0.782
188	0.745	0.025	0.693	0.790
189	0.935	0.013	0.902	0.955
190	0.706	0.028	0.649	0.759
191	0.692	0.030	0.624	0.745
192	0.903	0.014	0.876	0.927
193	0.718	0.028	0.660	0.770
194	0.948	0.013	0.919	0.965
195	0.738	0.027	0.683	0.787
196	0.762	0.028	0.704	0.811
197	0.713	0.030	0.646	0.766
198	0.811	0.026	0.761	0.850
199	0.667	0.032	0.593	0.721
200	0.689	0.031	0.618	0.742
201	0.689	0.031	0.618	0.742
202	0.667	0.032	0.593	0.721
203	0.667	0.032	0.593	0.721

c) Conditional occupancy with red fox

Site	Predicted	SE	lower	upper
1	0.488	0.028	0.431	0.535
2	0.630	0.027	0.573	0.675
3	0.728	0.022	0.678	0.758
4	0.782	0.020	0.737	0.811
5	0.898	0.015	0.864	0.918
6	0.587	0.025	0.529	0.624
7	0.682	0.040	0.605	0.743
8	0.916	0.015	0.882	0.936
9	0.838	0.025	0.781	0.877
10	0.515	0.028	0.455	0.558
11	0.743	0.054	0.642	0.822
12	0.542	0.031	0.480	0.596

d) Conditional occupancy without red fox

Site	Predicted	SE	lower	upper
1-203	0.283	0.064	0.168	0.436

13	0.679	0.023	0.624	0.712
14	0.707	0.069	0.584	0.807
15	0.878	0.021	0.829	0.908
16	0.827	0.019	0.785	0.854
17	0.952	0.014	0.917	0.972
18	0.742	0.027	0.679	0.784
19	0.794	0.026	0.733	0.835
20	0.784	0.083	0.626	0.891
21	0.563	0.035	0.494	0.630
22	0.515	0.028	0.455	0.558
23	0.875	0.016	0.839	0.896
24	0.704	0.045	0.622	0.772
25	0.720	0.029	0.661	0.766
26	0.615	0.047	0.528	0.695
27	0.660	0.058	0.556	0.752
28	0.682	0.023	0.629	0.712
29	0.875	0.019	0.830	0.901
30	0.776	0.027	0.722	0.815
31	0.757	0.024	0.702	0.793
32	0.696	0.031	0.633	0.746
33	0.913	0.017	0.878	0.937
34	0.887	0.016	0.852	0.908
35	0.964	0.009	0.944	0.975
36	0.605	0.044	0.521	0.681
37	0.631	0.027	0.573	0.670
38	0.621	0.035	0.551	0.683
39	0.813	0.019	0.771	0.841
40	0.650	0.056	0.549	0.740
41	0.724	0.072	0.593	0.828
42	0.926	0.013	0.896	0.942
43	0.909	0.018	0.862	0.934
44	0.972	0.007	0.955	0.981
45	0.921	0.013	0.891	0.939
46	0.939	0.022	0.882	0.964
47	0.934	0.013	0.907	0.950
48	0.815	0.026	0.760	0.850
49	0.876	0.016	0.839	0.897
50	0.944	0.016	0.902	0.964
51	0.988	0.004	0.978	0.993
52	0.888	0.024	0.830	0.921
53	0.635	0.052	0.540	0.721
54	0.812	0.020	0.766	0.841
55	0.765	0.025	0.711	0.803
56	0.520	0.028	0.460	0.566
57	0.765	0.025	0.711	0.803

58	0.719	0.022	0.669	0.748
59	0.744	0.030	0.684	0.789
60	0.574	0.027	0.514	0.617
61	0.488	0.028	0.431	0.535
62	0.488	0.028	0.431	0.535
63	0.488	0.028	0.431	0.535
64	0.488	0.028	0.431	0.535
65	0.531	0.030	0.471	0.583
66	0.502	0.028	0.444	0.543
67	0.502	0.028	0.444	0.543
68	0.488	0.028	0.431	0.535
69	0.488	0.028	0.431	0.535
70	0.502	0.028	0.444	0.543
71	0.488	0.028	0.431	0.535
72	0.580	0.026	0.523	0.620
73	0.632	0.024	0.576	0.666
74	0.734	0.022	0.683	0.766
75	0.488	0.028	0.431	0.535
76	0.541	0.027	0.483	0.585
77	0.488	0.028	0.431	0.535
78	0.523	0.028	0.466	0.570
79	0.501	0.028	0.443	0.542
80	0.639	0.025	0.585	0.677
81	0.559	0.027	0.502	0.603
82	0.536	0.027	0.478	0.580
83	0.488	0.028	0.431	0.535
84	0.501	0.028	0.443	0.542
85	0.806	0.024	0.750	0.839
86	0.514	0.028	0.455	0.557
87	0.526	0.029	0.466	0.575
88	0.526	0.029	0.466	0.575
89	0.488	0.028	0.431	0.535
90	0.507	0.028	0.448	0.548
91	0.488	0.028	0.431	0.535
92	0.507	0.028	0.448	0.548
93	0.638	0.053	0.542	0.725
94	0.488	0.028	0.431	0.535
95	0.596	0.028	0.535	0.641
96	0.488	0.028	0.431	0.535
97	0.488	0.028	0.431	0.535
98	0.488	0.028	0.431	0.535
99	0.488	0.028	0.431	0.535
100	0.488	0.028	0.431	0.535
101	0.554	0.027	0.497	0.598
102	0.488	0.028	0.431	0.535

103	0.488	0.028	0.431	0.535
104	0.589	0.041	0.511	0.661
105	0.586	0.029	0.524	0.633
106	0.706	0.023	0.656	0.738
107	0.684	0.023	0.631	0.713
108	0.659	0.025	0.605	0.695
109	0.706	0.023	0.656	0.738
110	0.488	0.028	0.431	0.535
111	0.517	0.028	0.457	0.561
112	0.488	0.028	0.431	0.535
113	0.528	0.028	0.471	0.574
114	0.531	0.030	0.471	0.583
115	0.517	0.028	0.457	0.561
116	0.502	0.028	0.444	0.543
117	0.568	0.027	0.512	0.613
118	0.531	0.030	0.471	0.583
119	0.560	0.034	0.492	0.626
120	0.528	0.028	0.471	0.574
121	0.488	0.028	0.431	0.535
122	0.945	0.011	0.920	0.960
123	0.517	0.028	0.457	0.561
124	0.546	0.032	0.483	0.601
125	0.560	0.034	0.492	0.626
126	0.502	0.028	0.444	0.543
127	0.557	0.027	0.498	0.594
128	0.885	0.016	0.846	0.905
129	0.488	0.028	0.431	0.535
130	0.648	0.055	0.548	0.737
131	0.518	0.028	0.458	0.562
132	0.592	0.041	0.513	0.664
133	0.675	0.062	0.565	0.771
134	0.577	0.038	0.503	0.648
135	0.533	0.030	0.471	0.585
136	0.562	0.035	0.493	0.629
137	0.547	0.032	0.484	0.604
138	0.592	0.041	0.513	0.664
139	0.488	0.028	0.431	0.535
140	0.662	0.058	0.557	0.754
141	0.518	0.028	0.458	0.562
142	0.697	0.054	0.601	0.778
143	0.547	0.032	0.484	0.604
144	0.518	0.028	0.458	0.562
145	0.577	0.038	0.503	0.648
146	0.915	0.019	0.872	0.945
147	0.488	0.028	0.431	0.535

148	0.804	0.026	0.743	0.844
149	0.828	0.025	0.770	0.868
150	0.836	0.022	0.784	0.870
151	0.828	0.025	0.770	0.868
152	0.869	0.023	0.817	0.906
153	0.887	0.022	0.837	0.921
154	0.809	0.020	0.766	0.839
155	0.488	0.028	0.431	0.535
156	0.488	0.028	0.431	0.535
157	0.731	0.022	0.680	0.762
158	0.488	0.028	0.431	0.535
159	0.558	0.027	0.499	0.595
160	0.616	0.035	0.546	0.678
161	0.719	0.022	0.669	0.748
162	0.488	0.028	0.431	0.535
163	0.488	0.028	0.431	0.535
164	0.933	0.016	0.900	0.957
165	0.862	0.021	0.815	0.894
166	0.969	0.010	0.945	0.983
167	0.899	0.016	0.863	0.920
168	0.755	0.024	0.701	0.793
169	0.587	0.027	0.531	0.632
170	0.769	0.022	0.718	0.801
171	0.839	0.018	0.799	0.864
172	0.747	0.027	0.684	0.789
173	0.747	0.027	0.684	0.789
174	0.777	0.026	0.714	0.817
175	0.488	0.028	0.431	0.535
176	0.558	0.027	0.499	0.595
177	0.676	0.027	0.615	0.717
178	0.663	0.025	0.606	0.697
179	0.830	0.019	0.785	0.857
180	0.528	0.028	0.471	0.574
181	0.787	0.024	0.730	0.819
182	0.759	0.024	0.701	0.792
183	0.773	0.021	0.723	0.804
184	0.828	0.025	0.770	0.868
185	0.597	0.025	0.540	0.634
186	0.816	0.019	0.774	0.844
187	0.640	0.029	0.578	0.687
188	0.649	0.024	0.593	0.684
189	0.928	0.014	0.897	0.949
190	0.573	0.028	0.513	0.617
191	0.543	0.027	0.485	0.586
192	0.890	0.015	0.856	0.910

193	0.597	0.025	0.540	0.634
194	0.944	0.014	0.914	0.964
195	0.636	0.024	0.580	0.669
196	0.680	0.027	0.619	0.724
197	0.587	0.027	0.531	0.632
198	0.761	0.026	0.697	0.802
199	0.488	0.028	0.431	0.535
200	0.538	0.027	0.481	0.583
201	0.538	0.027	0.481	0.583
202	0.488	0.028	0.431	0.535
203	0.488	0.028	0.431	0.535

e)Predicted probability of occupancy of the four states

Site	psi[11]	psi[10]	psi[01]	psi[00]
1	0.325	0.342	0.094	0.239
2	0.463	0.272	0.075	0.190
3	0.575	0.215	0.059	0.150
4	0.644	0.180	0.050	0.126
5	0.817	0.093	0.025	0.065
6	0.418	0.295	0.081	0.206
7	0.520	0.243	0.067	0.170
8	0.846	0.078	0.021	0.055
9	0.724	0.140	0.039	0.098
10	0.349	0.330	0.091	0.230
11	0.595	0.205	0.057	0.144
12	0.374	0.317	0.087	0.222
13	0.517	0.244	0.067	0.171
14	0.550	0.228	0.063	0.159
15	0.785	0.109	0.030	0.076
16	0.708	0.148	0.041	0.103
17	0.909	0.046	0.013	0.032
18	0.594	0.206	0.057	0.144
19	0.662	0.171	0.047	0.120
20	0.648	0.178	0.049	0.125
21	0.395	0.307	0.084	0.214
22	0.349	0.330	0.091	0.230
23	0.780	0.112	0.031	0.078
24	0.547	0.229	0.063	0.160
25	0.566	0.220	0.061	0.154
26	0.447	0.280	0.077	0.196
27	0.496	0.255	0.070	0.179
28	0.521	0.243	0.067	0.170

f) SE of probability of occupancy of the four states

Site	psi[11]	psi[10]	psi[01]	psi[00]
1	0.026	0.027	0.028	0.025
2	0.030	0.020	0.024	0.020
3	0.024	0.018	0.019	0.015
4	0.026	0.016	0.017	0.013
5	0.024	0.012	0.010	0.008
6	0.025	0.024	0.025	0.021
7	0.033	0.028	0.019	0.018
8	0.026	0.012	0.010	0.009
9	0.037	0.017	0.016	0.014
10	0.025	0.027	0.026	0.023
11	0.048	0.034	0.016	0.020
12	0.026	0.028	0.025	0.023
13	0.024	0.021	0.021	0.017
14	0.059	0.041	0.017	0.024
15	0.023	0.015	0.010	0.008
16	0.027	0.014	0.015	0.011
17	0.026	0.012	0.008	0.009
18	0.035	0.017	0.020	0.017
19	0.037	0.017	0.018	0.015
20	0.079	0.048	0.014	0.029
21	0.028	0.029	0.024	0.022
22	0.025	0.027	0.026	0.023
23	0.024	0.013	0.012	0.009
24	0.038	0.030	0.018	0.019
25	0.026	0.022	0.018	0.015
26	0.036	0.033	0.021	0.021
27	0.047	0.036	0.019	0.022
28	0.025	0.020	0.021	0.017

29	0.781	0.111	0.031	0.078	29	0.022	0.014	0.011	0.008
30	0.637	0.184	0.051	0.129	30	0.025	0.020	0.016	0.013
31	0.612	0.197	0.054	0.137	31	0.024	0.019	0.017	0.013
32	0.537	0.235	0.065	0.164	32	0.027	0.024	0.019	0.016
33	0.842	0.080	0.022	0.056	33	0.029	0.013	0.010	0.010
34	0.799	0.102	0.028	0.071	34	0.024	0.012	0.011	0.009
35	0.932	0.035	0.010	0.024	35	0.013	0.007	0.004	0.004
36	0.437	0.285	0.079	0.199	36	0.034	0.032	0.022	0.021
37	0.465	0.271	0.075	0.190	37	0.024	0.024	0.022	0.019
38	0.453	0.277	0.076	0.194	38	0.028	0.028	0.022	0.020
39	0.688	0.158	0.044	0.110	39	0.026	0.015	0.015	0.011
40	0.485	0.261	0.072	0.182	40	0.045	0.036	0.019	0.022
41	0.571	0.217	0.060	0.152	41	0.064	0.043	0.016	0.025
42	0.864	0.069	0.019	0.048	42	0.019	0.010	0.008	0.006
43	0.834	0.084	0.023	0.059	43	0.021	0.013	0.008	0.007
44	0.946	0.028	0.008	0.019	44	0.012	0.006	0.004	0.004
45	0.856	0.073	0.020	0.051	45	0.021	0.011	0.008	0.007
46	0.886	0.058	0.016	0.040	46	0.025	0.015	0.006	0.008
47	0.878	0.062	0.017	0.043	47	0.018	0.010	0.007	0.006
48	0.690	0.157	0.043	0.110	48	0.025	0.019	0.014	0.011
49	0.781	0.111	0.031	0.078	49	0.023	0.013	0.011	0.008
50	0.895	0.053	0.015	0.037	50	0.019	0.012	0.006	0.006
51	0.977	0.012	0.003	0.008	51	0.007	0.004	0.002	0.002
52	0.801	0.101	0.028	0.071	52	0.026	0.017	0.009	0.009
53	0.469	0.269	0.074	0.188	53	0.041	0.034	0.020	0.022
54	0.687	0.159	0.044	0.111	54	0.028	0.015	0.016	0.012
55	0.622	0.192	0.053	0.134	55	0.024	0.019	0.016	0.013
56	0.354	0.327	0.090	0.229	56	0.025	0.027	0.026	0.023
57	0.622	0.192	0.053	0.134	57	0.024	0.019	0.016	0.013
58	0.565	0.221	0.061	0.154	58	0.025	0.018	0.020	0.015
59	0.596	0.205	0.056	0.143	59	0.027	0.023	0.017	0.014
60	0.406	0.301	0.083	0.210	60	0.025	0.025	0.024	0.021
61	0.325	0.342	0.094	0.239	61	0.026	0.027	0.028	0.025
62	0.325	0.342	0.094	0.239	62	0.026	0.027	0.028	0.025
63	0.325	0.342	0.094	0.239	63	0.026	0.027	0.028	0.025
64	0.325	0.342	0.094	0.239	64	0.026	0.027	0.028	0.025
65	0.365	0.322	0.089	0.225	65	0.025	0.028	0.026	0.023
66	0.338	0.335	0.092	0.234	66	0.025	0.027	0.027	0.024
67	0.338	0.335	0.092	0.234	67	0.025	0.027	0.027	0.024
68	0.325	0.342	0.094	0.239	68	0.026	0.027	0.028	0.025
69	0.325	0.342	0.094	0.239	69	0.026	0.027	0.028	0.025
70	0.338	0.335	0.092	0.234	70	0.025	0.027	0.027	0.024
71	0.325	0.342	0.094	0.239	71	0.026	0.027	0.028	0.025
72	0.412	0.298	0.082	0.208	72	0.026	0.023	0.025	0.021
73	0.465	0.271	0.075	0.189	73	0.025	0.021	0.023	0.019

74	0.583	0.211	0.058	0.148	74	0.028	0.017	0.020	0.015
75	0.325	0.342	0.094	0.239	75	0.026	0.027	0.028	0.025
76	0.374	0.317	0.087	0.222	76	0.026	0.025	0.026	0.023
77	0.325	0.342	0.094	0.239	77	0.026	0.027	0.028	0.025
78	0.357	0.326	0.090	0.228	78	0.027	0.025	0.027	0.023
79	0.337	0.336	0.092	0.235	79	0.025	0.027	0.027	0.024
80	0.473	0.267	0.073	0.187	80	0.028	0.020	0.023	0.019
81	0.391	0.309	0.085	0.216	81	0.027	0.023	0.026	0.022
82	0.369	0.319	0.088	0.223	82	0.026	0.025	0.026	0.023
83	0.325	0.342	0.094	0.239	83	0.026	0.027	0.028	0.025
84	0.337	0.336	0.092	0.235	84	0.025	0.027	0.027	0.024
85	0.678	0.163	0.045	0.114	85	0.034	0.016	0.017	0.014
86	0.349	0.330	0.091	0.231	86	0.025	0.027	0.026	0.023
87	0.360	0.324	0.089	0.227	87	0.025	0.027	0.026	0.023
88	0.360	0.324	0.089	0.227	88	0.025	0.027	0.026	0.023
89	0.325	0.342	0.094	0.239	89	0.026	0.027	0.028	0.025
90	0.342	0.333	0.092	0.233	90	0.025	0.027	0.027	0.024
91	0.325	0.342	0.094	0.239	91	0.026	0.027	0.028	0.025
92	0.342	0.333	0.092	0.233	92	0.025	0.027	0.027	0.024
93	0.472	0.267	0.074	0.187	93	0.042	0.034	0.020	0.022
94	0.325	0.342	0.094	0.239	94	0.026	0.027	0.028	0.025
95	0.428	0.290	0.080	0.203	95	0.025	0.025	0.023	0.020
96	0.325	0.342	0.094	0.239	96	0.026	0.027	0.028	0.025
97	0.325	0.342	0.094	0.239	97	0.026	0.027	0.028	0.025
98	0.325	0.342	0.094	0.239	98	0.026	0.027	0.028	0.025
99	0.325	0.342	0.094	0.239	99	0.026	0.027	0.028	0.025
100	0.325	0.342	0.094	0.239	100	0.026	0.027	0.028	0.025
101	0.386	0.311	0.086	0.217	101	0.027	0.024	0.026	0.022
102	0.325	0.342	0.094	0.239	102	0.026	0.027	0.028	0.025
103	0.325	0.342	0.094	0.239	103	0.026	0.027	0.028	0.025
104	0.420	0.294	0.081	0.205	104	0.031	0.031	0.023	0.022
105	0.417	0.295	0.081	0.206	105	0.025	0.026	0.024	0.021
106	0.549	0.228	0.063	0.160	106	0.027	0.018	0.021	0.016
107	0.523	0.241	0.066	0.169	107	0.025	0.020	0.021	0.017
108	0.494	0.256	0.071	0.179	108	0.028	0.020	0.023	0.018
109	0.549	0.228	0.063	0.160	109	0.027	0.018	0.021	0.016
110	0.325	0.342	0.094	0.239	110	0.026	0.027	0.028	0.025
111	0.351	0.328	0.090	0.230	111	0.025	0.027	0.026	0.023
112	0.325	0.342	0.094	0.239	112	0.026	0.027	0.028	0.025
113	0.362	0.323	0.089	0.226	113	0.027	0.025	0.027	0.023
114	0.365	0.322	0.089	0.225	114	0.025	0.028	0.026	0.023
115	0.351	0.328	0.090	0.230	115	0.025	0.027	0.026	0.023
116	0.338	0.335	0.092	0.234	116	0.025	0.027	0.027	0.024
117	0.400	0.304	0.084	0.212	117	0.028	0.023	0.026	0.022
118	0.365	0.322	0.089	0.225	118	0.025	0.028	0.026	0.023

119	0.392	0.308	0.085	0.215	119	0.027	0.029	0.024	0.022
120	0.362	0.323	0.089	0.226	120	0.027	0.025	0.027	0.023
121	0.325	0.342	0.094	0.239	121	0.026	0.027	0.028	0.025
122	0.897	0.052	0.014	0.036	122	0.018	0.009	0.006	0.006
123	0.351	0.328	0.090	0.230	123	0.025	0.027	0.026	0.023
124	0.378	0.315	0.087	0.220	124	0.026	0.028	0.025	0.022
125	0.392	0.308	0.085	0.215	125	0.027	0.029	0.024	0.022
126	0.338	0.335	0.092	0.234	126	0.025	0.027	0.027	0.024
127	0.389	0.309	0.085	0.216	127	0.025	0.025	0.025	0.022
128	0.795	0.104	0.029	0.072	128	0.021	0.013	0.010	0.008
129	0.325	0.342	0.094	0.239	129	0.026	0.027	0.028	0.025
130	0.483	0.262	0.072	0.183	130	0.044	0.035	0.019	0.022
131	0.352	0.328	0.090	0.229	131	0.025	0.027	0.026	0.023
132	0.423	0.292	0.080	0.204	132	0.032	0.031	0.022	0.022
133	0.513	0.247	0.068	0.173	133	0.051	0.038	0.018	0.023
134	0.409	0.300	0.082	0.209	134	0.030	0.030	0.023	0.022
135	0.366	0.321	0.088	0.224	135	0.025	0.028	0.026	0.023
136	0.394	0.307	0.085	0.214	136	0.028	0.029	0.024	0.022
137	0.380	0.314	0.086	0.220	137	0.026	0.028	0.025	0.022
138	0.423	0.292	0.080	0.204	138	0.032	0.031	0.022	0.022
139	0.325	0.342	0.094	0.239	139	0.026	0.027	0.028	0.025
140	0.498	0.254	0.070	0.178	140	0.047	0.037	0.019	0.022
141	0.352	0.328	0.090	0.229	141	0.025	0.027	0.026	0.023
142	0.538	0.234	0.064	0.164	142	0.045	0.034	0.018	0.021
143	0.380	0.314	0.086	0.220	143	0.026	0.028	0.025	0.022
144	0.352	0.328	0.090	0.229	144	0.025	0.027	0.026	0.023
145	0.409	0.300	0.082	0.209	145	0.030	0.030	0.023	0.022
146	0.846	0.078	0.022	0.055	146	0.033	0.015	0.011	0.011
147	0.325	0.342	0.094	0.239	147	0.026	0.027	0.028	0.025
148	0.675	0.165	0.045	0.115	148	0.037	0.017	0.018	0.015
149	0.709	0.147	0.041	0.103	149	0.037	0.017	0.017	0.015
150	0.721	0.141	0.039	0.099	150	0.034	0.016	0.016	0.013
151	0.709	0.147	0.041	0.103	151	0.037	0.017	0.017	0.015
152	0.771	0.116	0.032	0.081	152	0.037	0.016	0.014	0.013
153	0.798	0.102	0.028	0.071	153	0.036	0.016	0.013	0.013
154	0.682	0.161	0.044	0.112	154	0.023	0.016	0.015	0.011
155	0.325	0.342	0.094	0.239	155	0.026	0.027	0.028	0.025
156	0.325	0.342	0.094	0.239	156	0.026	0.027	0.028	0.025
157	0.579	0.213	0.059	0.149	157	0.024	0.018	0.019	0.014
158	0.325	0.342	0.094	0.239	158	0.026	0.027	0.028	0.025
159	0.390	0.309	0.085	0.216	159	0.025	0.025	0.025	0.022
160	0.448	0.279	0.077	0.195	160	0.028	0.028	0.022	0.020
161	0.565	0.220	0.061	0.154	161	0.025	0.018	0.020	0.015
162	0.325	0.342	0.094	0.239	162	0.026	0.027	0.028	0.025
163	0.325	0.342	0.094	0.239	163	0.026	0.027	0.028	0.025

164	0.877	0.063	0.017	0.044
165	0.760	0.121	0.033	0.085
166	0.941	0.030	0.008	0.021
167	0.818	0.092	0.025	0.064
168	0.610	0.198	0.054	0.138
169	0.419	0.294	0.081	0.206
170	0.628	0.188	0.052	0.132
171	0.725	0.139	0.038	0.097
172	0.600	0.203	0.056	0.142
173	0.600	0.203	0.056	0.142
174	0.638	0.183	0.051	0.128
175	0.325	0.342	0.094	0.239
176	0.390	0.309	0.085	0.216
177	0.514	0.246	0.068	0.172
178	0.499	0.254	0.070	0.177
179	0.713	0.145	0.040	0.102
180	0.362	0.323	0.089	0.226
181	0.652	0.176	0.049	0.123
182	0.614	0.195	0.054	0.137
183	0.632	0.186	0.051	0.130
184	0.709	0.147	0.041	0.103
185	0.429	0.289	0.080	0.202
186	0.691	0.156	0.043	0.109
187	0.474	0.267	0.073	0.186
188	0.484	0.261	0.072	0.183
189	0.868	0.067	0.018	0.047
190	0.404	0.302	0.083	0.211
191	0.376	0.316	0.087	0.221
192	0.804	0.099	0.027	0.069
193	0.429	0.289	0.080	0.202
194	0.895	0.053	0.015	0.037
195	0.469	0.269	0.074	0.188
196	0.519	0.244	0.067	0.170
197	0.419	0.294	0.081	0.206
198	0.617	0.194	0.053	0.136
199	0.325	0.342	0.094	0.239
200	0.371	0.319	0.088	0.223
201	0.371	0.319	0.088	0.223
202	0.325	0.342	0.094	0.239
203	0.325	0.342	0.094	0.239

f) Lower CI of probability of occupancy of the four states

164	0.028	0.013	0.009	0.009
165	0.033	0.015	0.014	0.012
166	0.019	0.009	0.005	0.006
167	0.026	0.012	0.011	0.009
168	0.024	0.019	0.017	0.013
169	0.028	0.022	0.025	0.021
170	0.029	0.016	0.018	0.014
171	0.026	0.014	0.014	0.011
172	0.035	0.017	0.020	0.017
173	0.035	0.017	0.020	0.017
174	0.036	0.017	0.019	0.016
175	0.026	0.027	0.028	0.025
176	0.025	0.025	0.025	0.022
177	0.024	0.022	0.020	0.017
178	0.024	0.022	0.021	0.017
179	0.028	0.014	0.015	0.012
180	0.027	0.025	0.027	0.023
181	0.033	0.016	0.018	0.015
182	0.032	0.016	0.019	0.015
183	0.023	0.017	0.017	0.013
184	0.037	0.017	0.017	0.015
185	0.025	0.023	0.024	0.020
186	0.026	0.015	0.015	0.011
187	0.025	0.025	0.022	0.019
188	0.024	0.021	0.022	0.018
189	0.026	0.012	0.009	0.009
190	0.025	0.026	0.024	0.021
191	0.026	0.025	0.026	0.023
192	0.023	0.012	0.011	0.008
193	0.025	0.023	0.024	0.020
194	0.025	0.011	0.008	0.008
195	0.025	0.021	0.023	0.019
196	0.032	0.019	0.022	0.018
197	0.028	0.022	0.025	0.021
198	0.036	0.017	0.020	0.016
199	0.026	0.027	0.028	0.025
200	0.027	0.024	0.027	0.023
201	0.027	0.024	0.027	0.023
202	0.026	0.027	0.028	0.025
203	0.026	0.027	0.028	0.025

f) Upper CI of probability of occupancy of the four states

Site	psi[11]	psi[10]	psi[01]	psi[00]
1	0.276	0.285	0.055	0.189
2	0.403	0.229	0.042	0.148
3	0.518	0.182	0.034	0.122
4	0.586	0.155	0.028	0.101
5	0.764	0.076	0.013	0.052
6	0.363	0.246	0.047	0.165
7	0.455	0.193	0.041	0.142
8	0.787	0.061	0.010	0.042
9	0.644	0.119	0.019	0.076
10	0.299	0.274	0.053	0.183
11	0.499	0.147	0.035	0.106
12	0.325	0.263	0.052	0.178
13	0.462	0.206	0.039	0.139
14	0.432	0.159	0.039	0.112
15	0.737	0.083	0.017	0.063
16	0.652	0.127	0.022	0.083
17	0.845	0.030	0.005	0.020
18	0.523	0.177	0.030	0.112
19	0.583	0.149	0.024	0.094
20	0.485	0.097	0.026	0.076
21	0.342	0.254	0.050	0.173
22	0.299	0.274	0.053	0.183
23	0.728	0.093	0.016	0.063
24	0.471	0.176	0.040	0.130
25	0.511	0.180	0.036	0.130
26	0.375	0.223	0.048	0.161
27	0.402	0.192	0.045	0.139
28	0.463	0.205	0.038	0.137
29	0.734	0.088	0.017	0.065
30	0.584	0.148	0.030	0.110
31	0.557	0.163	0.031	0.116
32	0.481	0.192	0.039	0.138
33	0.773	0.062	0.010	0.041
34	0.747	0.084	0.015	0.058
35	0.900	0.025	0.005	0.019
36	0.369	0.229	0.049	0.163
37	0.411	0.226	0.044	0.155
38	0.398	0.228	0.046	0.159
39	0.632	0.136	0.024	0.088
40	0.396	0.199	0.046	0.144
41	0.445	0.145	0.036	0.104
42	0.821	0.056	0.010	0.039
43	0.790	0.063	0.013	0.049
44	0.919	0.020	0.004	0.014

Site	psi[11]	psi[10]	psi[01]	psi[00]
1	0.381	0.393	0.164	0.280
2	0.514	0.306	0.134	0.225
3	0.611	0.251	0.108	0.177
4	0.682	0.215	0.093	0.149
5	0.850	0.120	0.056	0.083
6	0.462	0.339	0.142	0.244
7	0.575	0.307	0.112	0.204
8	0.882	0.104	0.050	0.074
9	0.779	0.177	0.079	0.129
10	0.392	0.384	0.157	0.271
11	0.680	0.284	0.094	0.180
12	0.415	0.376	0.151	0.263
13	0.552	0.286	0.120	0.203
14	0.658	0.321	0.102	0.204
15	0.818	0.138	0.055	0.093
16	0.746	0.180	0.080	0.125
17	0.944	0.076	0.035	0.053
18	0.645	0.241	0.106	0.177
19	0.716	0.208	0.092	0.154
20	0.778	0.290	0.080	0.181
21	0.440	0.367	0.144	0.256
22	0.392	0.384	0.157	0.271
23	0.814	0.141	0.064	0.096
24	0.615	0.299	0.104	0.196
25	0.604	0.267	0.106	0.184
26	0.516	0.351	0.127	0.235
27	0.584	0.337	0.112	0.221
28	0.561	0.281	0.120	0.200
29	0.809	0.138	0.058	0.094
30	0.673	0.224	0.089	0.153
31	0.643	0.237	0.098	0.161
32	0.577	0.286	0.112	0.197
33	0.882	0.109	0.052	0.077
34	0.833	0.130	0.060	0.089
35	0.949	0.051	0.019	0.033
36	0.501	0.354	0.131	0.238
37	0.502	0.320	0.131	0.227
38	0.499	0.336	0.131	0.231
39	0.725	0.192	0.083	0.132
40	0.568	0.340	0.115	0.225
41	0.686	0.315	0.097	0.198
42	0.890	0.090	0.041	0.062
43	0.864	0.111	0.043	0.073
44	0.961	0.042	0.018	0.027

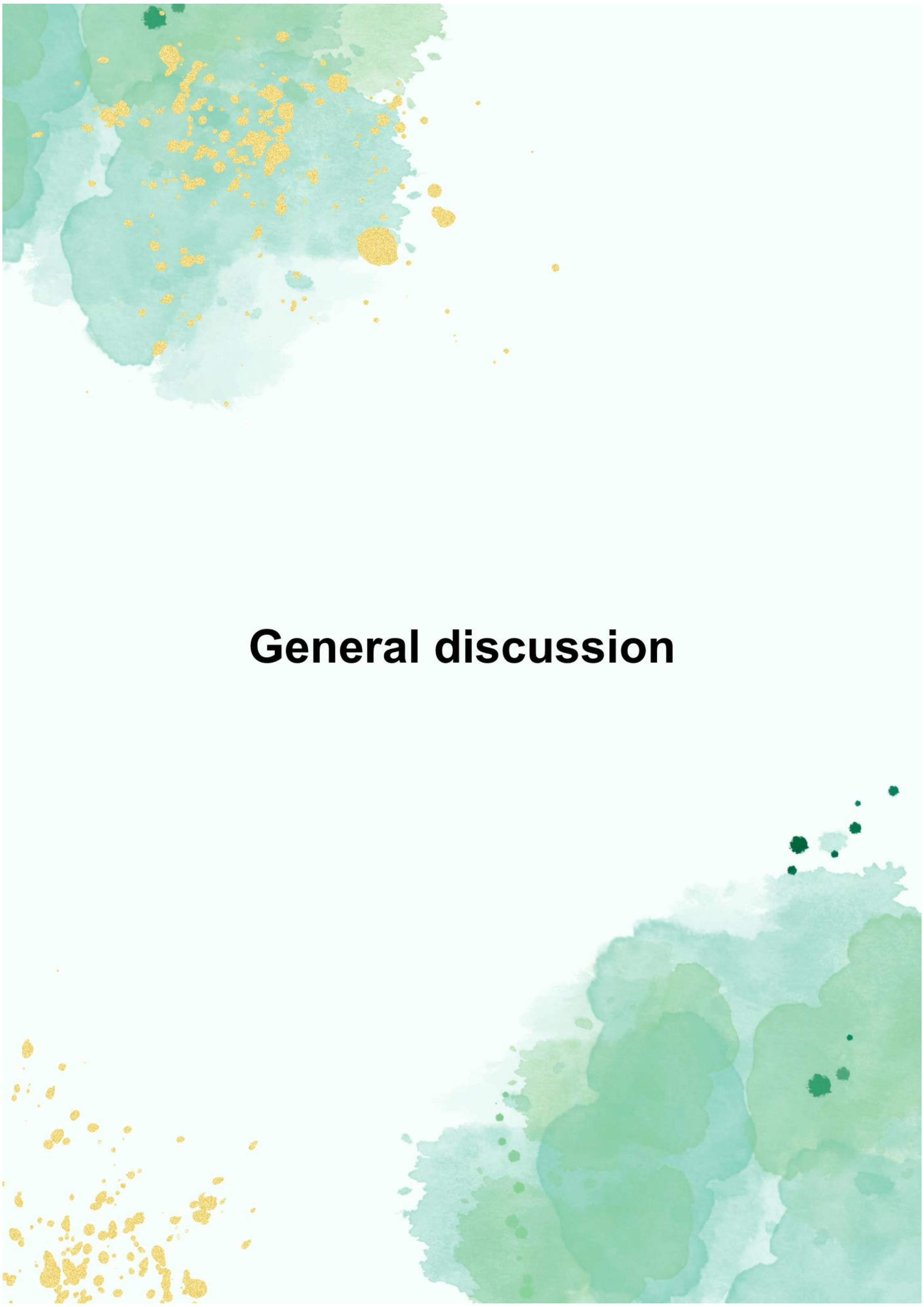
45	0.810	0.059	0.011	0.041	45	0.883	0.095	0.044	0.066
46	0.835	0.037	0.009	0.028	46	0.918	0.090	0.030	0.058
47	0.840	0.048	0.009	0.035	47	0.902	0.082	0.035	0.055
48	0.638	0.123	0.026	0.093	48	0.727	0.193	0.076	0.131
49	0.732	0.092	0.017	0.063	49	0.813	0.139	0.062	0.095
50	0.853	0.036	0.008	0.028	50	0.921	0.079	0.028	0.050
51	0.961	0.008	0.002	0.006	51	0.985	0.021	0.007	0.013
52	0.750	0.073	0.017	0.057	52	0.837	0.134	0.050	0.089
53	0.387	0.209	0.047	0.153	53	0.545	0.345	0.120	0.230
54	0.626	0.137	0.023	0.089	54	0.726	0.192	0.084	0.134
55	0.568	0.157	0.031	0.114	55	0.657	0.231	0.094	0.157
56	0.303	0.272	0.053	0.182	56	0.395	0.382	0.156	0.270
57	0.568	0.157	0.031	0.114	57	0.657	0.231	0.094	0.157
58	0.505	0.187	0.034	0.124	58	0.606	0.255	0.111	0.181
59	0.540	0.164	0.034	0.122	59	0.636	0.252	0.098	0.172
60	0.353	0.251	0.049	0.169	60	0.445	0.352	0.144	0.250
61	0.276	0.285	0.055	0.189	61	0.381	0.393	0.164	0.280
62	0.276	0.285	0.055	0.189	62	0.381	0.393	0.164	0.280
63	0.276	0.285	0.055	0.189	63	0.381	0.393	0.164	0.280
64	0.276	0.285	0.055	0.189	64	0.381	0.393	0.164	0.280
65	0.314	0.267	0.052	0.180	65	0.404	0.379	0.153	0.266
66	0.289	0.279	0.054	0.186	66	0.387	0.388	0.160	0.275
67	0.289	0.279	0.054	0.186	67	0.387	0.388	0.160	0.275
68	0.276	0.285	0.055	0.189	68	0.381	0.393	0.164	0.280
69	0.276	0.285	0.055	0.189	69	0.381	0.393	0.164	0.280
70	0.289	0.279	0.054	0.186	70	0.387	0.388	0.160	0.275
71	0.276	0.285	0.055	0.189	71	0.381	0.393	0.164	0.280
72	0.356	0.249	0.047	0.165	72	0.458	0.340	0.144	0.247
73	0.407	0.227	0.043	0.151	73	0.507	0.310	0.132	0.224
74	0.521	0.181	0.032	0.116	74	0.627	0.245	0.107	0.176
75	0.276	0.285	0.055	0.189	75	0.381	0.393	0.164	0.280
76	0.321	0.265	0.051	0.176	76	0.423	0.364	0.152	0.261
77	0.276	0.285	0.055	0.189	77	0.381	0.393	0.164	0.280
78	0.305	0.272	0.052	0.180	78	0.409	0.372	0.157	0.268
79	0.287	0.280	0.054	0.186	79	0.386	0.388	0.161	0.276
80	0.414	0.225	0.041	0.147	80	0.521	0.302	0.131	0.221
81	0.335	0.258	0.048	0.170	81	0.439	0.350	0.150	0.255
82	0.317	0.267	0.051	0.177	82	0.419	0.367	0.153	0.263
83	0.276	0.285	0.055	0.189	83	0.381	0.393	0.164	0.280
84	0.287	0.280	0.054	0.186	84	0.386	0.388	0.161	0.276
85	0.606	0.142	0.023	0.090	85	0.726	0.199	0.087	0.145
86	0.299	0.275	0.053	0.183	86	0.392	0.384	0.157	0.272
87	0.309	0.270	0.053	0.181	87	0.399	0.381	0.154	0.267
88	0.309	0.270	0.053	0.181	88	0.399	0.381	0.154	0.267
89	0.276	0.285	0.055	0.189	89	0.381	0.393	0.164	0.280

90	0.293	0.277	0.054	0.185	90	0.389	0.386	0.159	0.274
91	0.276	0.285	0.055	0.189	91	0.381	0.393	0.164	0.280
92	0.293	0.277	0.054	0.185	92	0.389	0.386	0.159	0.274
93	0.388	0.207	0.047	0.151	93	0.549	0.344	0.119	0.229
94	0.276	0.285	0.055	0.189	94	0.381	0.393	0.164	0.280
95	0.374	0.241	0.047	0.164	95	0.468	0.343	0.139	0.241
96	0.276	0.285	0.055	0.189	96	0.381	0.393	0.164	0.280
97	0.276	0.285	0.055	0.189	97	0.381	0.393	0.164	0.280
98	0.276	0.285	0.055	0.189	98	0.381	0.393	0.164	0.280
99	0.276	0.285	0.055	0.189	99	0.381	0.393	0.164	0.280
100	0.276	0.285	0.055	0.189	100	0.381	0.393	0.164	0.280
101	0.331	0.260	0.049	0.171	101	0.434	0.353	0.151	0.257
102	0.276	0.285	0.055	0.189	102	0.381	0.393	0.164	0.280
103	0.276	0.285	0.055	0.189	103	0.381	0.393	0.164	0.280
104	0.359	0.240	0.049	0.167	104	0.477	0.359	0.136	0.245
105	0.364	0.245	0.048	0.167	105	0.456	0.350	0.141	0.245
106	0.489	0.194	0.035	0.126	106	0.594	0.261	0.114	0.188
107	0.465	0.204	0.038	0.136	107	0.563	0.280	0.119	0.199
108	0.434	0.216	0.040	0.141	108	0.542	0.290	0.127	0.212
109	0.489	0.194	0.035	0.126	109	0.594	0.261	0.114	0.188
110	0.276	0.285	0.055	0.189	110	0.381	0.393	0.164	0.280
111	0.300	0.273	0.053	0.183	111	0.393	0.383	0.157	0.271
112	0.276	0.285	0.055	0.189	112	0.381	0.393	0.164	0.280
113	0.309	0.270	0.051	0.178	113	0.413	0.369	0.156	0.266
114	0.314	0.267	0.052	0.180	114	0.404	0.379	0.153	0.266
115	0.300	0.273	0.053	0.183	115	0.393	0.383	0.157	0.271
116	0.289	0.279	0.054	0.186	116	0.387	0.388	0.160	0.275
117	0.344	0.255	0.048	0.167	117	0.448	0.344	0.148	0.251
118	0.314	0.267	0.052	0.180	118	0.404	0.379	0.153	0.266
119	0.340	0.255	0.050	0.173	119	0.437	0.369	0.145	0.257
120	0.309	0.270	0.051	0.178	120	0.413	0.369	0.156	0.266
121	0.276	0.285	0.055	0.189	121	0.381	0.393	0.164	0.280
122	0.855	0.040	0.007	0.029	122	0.920	0.070	0.033	0.049
123	0.300	0.273	0.053	0.183	123	0.393	0.383	0.157	0.271
124	0.329	0.261	0.051	0.177	124	0.420	0.375	0.149	0.262
125	0.340	0.255	0.050	0.173	125	0.437	0.369	0.145	0.257
126	0.289	0.279	0.054	0.186	126	0.387	0.388	0.160	0.275
127	0.336	0.258	0.050	0.173	127	0.432	0.359	0.148	0.256
128	0.750	0.085	0.016	0.060	128	0.824	0.130	0.057	0.088
129	0.276	0.285	0.055	0.189	129	0.381	0.393	0.164	0.280
130	0.394	0.200	0.046	0.145	130	0.565	0.341	0.116	0.226
131	0.301	0.273	0.053	0.183	131	0.393	0.383	0.156	0.270
132	0.360	0.238	0.049	0.166	132	0.481	0.358	0.135	0.244
133	0.411	0.182	0.043	0.130	133	0.607	0.332	0.109	0.215
134	0.352	0.247	0.050	0.170	134	0.459	0.363	0.140	0.250

135	0.316	0.267	0.052	0.180	135	0.405	0.379	0.153	0.265
136	0.342	0.254	0.050	0.173	136	0.440	0.368	0.144	0.256
137	0.330	0.261	0.051	0.176	137	0.422	0.374	0.149	0.261
138	0.360	0.238	0.049	0.166	138	0.481	0.358	0.135	0.244
139	0.276	0.285	0.055	0.189	139	0.381	0.393	0.164	0.280
140	0.403	0.191	0.044	0.138	140	0.586	0.336	0.112	0.220
141	0.301	0.273	0.053	0.183	141	0.393	0.383	0.156	0.270
142	0.448	0.175	0.041	0.127	142	0.621	0.312	0.104	0.202
143	0.330	0.261	0.051	0.176	143	0.422	0.374	0.149	0.261
144	0.301	0.273	0.053	0.183	144	0.393	0.383	0.156	0.270
145	0.352	0.247	0.050	0.170	145	0.459	0.363	0.140	0.250
146	0.770	0.057	0.009	0.038	146	0.891	0.112	0.052	0.079
147	0.276	0.285	0.055	0.189	147	0.381	0.393	0.164	0.280
148	0.595	0.144	0.023	0.091	148	0.729	0.201	0.089	0.149
149	0.630	0.126	0.020	0.081	149	0.765	0.184	0.082	0.135
150	0.648	0.122	0.020	0.078	150	0.769	0.177	0.079	0.127
151	0.630	0.126	0.020	0.081	151	0.765	0.184	0.082	0.135
152	0.692	0.095	0.015	0.061	152	0.823	0.153	0.069	0.110
153	0.719	0.081	0.013	0.052	153	0.849	0.137	0.063	0.098
154	0.628	0.135	0.025	0.093	154	0.715	0.195	0.083	0.133
155	0.276	0.285	0.055	0.189	155	0.381	0.393	0.164	0.280
156	0.276	0.285	0.055	0.189	156	0.381	0.393	0.164	0.280
157	0.523	0.180	0.033	0.122	157	0.614	0.250	0.107	0.175
158	0.276	0.285	0.055	0.189	158	0.381	0.393	0.164	0.280
159	0.337	0.258	0.050	0.173	159	0.432	0.358	0.148	0.256
160	0.394	0.231	0.046	0.160	160	0.494	0.339	0.132	0.233
161	0.506	0.187	0.034	0.124	161	0.605	0.255	0.110	0.181
162	0.276	0.285	0.055	0.189	162	0.381	0.393	0.164	0.280
163	0.276	0.285	0.055	0.189	163	0.381	0.393	0.164	0.280
164	0.808	0.045	0.007	0.030	164	0.915	0.093	0.044	0.065
165	0.686	0.102	0.016	0.067	165	0.807	0.156	0.070	0.110
166	0.890	0.019	0.003	0.012	166	0.966	0.053	0.026	0.038
167	0.759	0.074	0.013	0.051	167	0.854	0.119	0.057	0.084
168	0.556	0.164	0.032	0.116	168	0.642	0.238	0.098	0.162
169	0.362	0.247	0.046	0.162	169	0.466	0.332	0.144	0.244
170	0.565	0.162	0.028	0.104	170	0.673	0.222	0.098	0.158
171	0.670	0.119	0.021	0.078	171	0.761	0.172	0.076	0.118
172	0.528	0.175	0.029	0.110	172	0.651	0.238	0.105	0.174
173	0.528	0.175	0.029	0.110	173	0.651	0.238	0.105	0.174
174	0.562	0.159	0.026	0.100	174	0.691	0.219	0.097	0.161
175	0.276	0.285	0.055	0.189	175	0.381	0.393	0.164	0.280
176	0.337	0.258	0.050	0.173	176	0.432	0.358	0.148	0.256
177	0.458	0.206	0.039	0.142	177	0.547	0.295	0.120	0.205
178	0.444	0.213	0.041	0.145	178	0.532	0.299	0.124	0.211
179	0.653	0.125	0.021	0.081	179	0.751	0.179	0.079	0.125

180	0.309	0.270	0.051	0.178	180	0.413	0.369	0.156	0.266
181	0.583	0.153	0.025	0.097	181	0.698	0.212	0.093	0.153
182	0.548	0.169	0.029	0.107	182	0.661	0.230	0.101	0.166
183	0.575	0.157	0.029	0.107	183	0.666	0.221	0.095	0.154
184	0.630	0.126	0.020	0.081	184	0.765	0.184	0.082	0.135
185	0.373	0.242	0.046	0.162	185	0.472	0.333	0.140	0.240
186	0.635	0.134	0.024	0.087	186	0.728	0.190	0.083	0.130
187	0.420	0.222	0.043	0.153	187	0.511	0.319	0.128	0.222
188	0.427	0.219	0.042	0.148	188	0.520	0.304	0.128	0.217
189	0.806	0.051	0.009	0.034	189	0.903	0.094	0.045	0.066
190	0.352	0.251	0.049	0.170	190	0.443	0.354	0.145	0.250
191	0.323	0.264	0.051	0.176	191	0.425	0.363	0.152	0.261
192	0.756	0.082	0.015	0.056	192	0.835	0.126	0.057	0.086
193	0.373	0.242	0.046	0.162	193	0.472	0.333	0.140	0.240
194	0.833	0.038	0.006	0.025	194	0.929	0.081	0.039	0.057
195	0.411	0.226	0.043	0.150	195	0.510	0.308	0.131	0.223
196	0.454	0.209	0.037	0.132	196	0.571	0.277	0.122	0.205
197	0.362	0.247	0.046	0.162	197	0.466	0.332	0.144	0.244
198	0.543	0.167	0.028	0.106	198	0.669	0.229	0.101	0.168
199	0.276	0.285	0.055	0.189	199	0.381	0.393	0.164	0.280
200	0.317	0.266	0.050	0.176	200	0.420	0.363	0.154	0.262
201	0.317	0.266	0.050	0.176	201	0.420	0.363	0.154	0.262
202	0.276	0.285	0.055	0.189	202	0.381	0.393	0.164	0.280
203	0.276	0.285	0.055	0.189	203	0.381	0.393	0.164	0.280

Supplementary material 1. Occupancy probabilities for each site. a) Predicted marginal occupancy of stone marten for each site. b) Predicted marginal occupancy of red fox for each site. d) Predicted conditional occupancy of stone marten in presence of red fox in each site e) Predicted conditional occupancy of stone marten in absence or red fox. Standard error (SE) and the lower and upper interval coefficient (CI [2.5, 97.5%]) are shown. f) Predicted occupancy for four states in each site. [11], [10], [01], or [00], corresponding to both species present, only red fox or stone marten present, or both species absent, respectively. g) Standard error (SE) of predicted occupancy for four states in each site. h) Lower confidence interval of predicted occupancy for four states in each site. i) Upper confidence interval of predicted occupancy for four states in each site.



General discussion

Accurately assessing and understanding population size and the factors influencing its fluctuations are crucial for determining the conservation status of a wildlife species. However, obtaining reliable abundance data can be challenging and expensive to obtain (Soberón and Peterson 2004). Two of the main difficulties include the need for sufficient recaptures per individual animal (Otis et al.1978) and the requirement for a high number of spatially replicated surveys (Kéry and Schaub 2012). In some cases, relative abundance can be a valuable tool for tracking changes in population size and abundance. Real abundance refers to the actual/absolute number of individuals in a population species at a specific time and place, whereas relative abundance allows comparisons of abundance between different situations (Walker et al. 2000; O'Brien 2011). However, it is important to remember that the relationship between relative and real abundance is not always positive and constant (O'Brien et al. 2011). Furthermore, controlling variations in species detection is also critical (Royle 2004; Veech et al. 2016) to obtain reliable abundance estimates. Fortunately, numerous techniques have been developed to study species abundance (O'Brien et al. 2003; Kinnaird and O'Brien 2012; Efford 2014; Royle et al. 2014; Ficetola et al. 2018). However, the choice of method depends on several factors, including the specific requirements of each technique, budget constraints, environmental characteristics of the study area, and the target species itself, among others (Silveira et al. 2003; Balme et al. 2009).

Species abundance can also be a driver of ecological processes and mechanisms. Abundance can influence the intensity and direction of interactions between species (Chase et al.2002; Amarasekare, 2008; Kendall et al.2012; Barrull et al.2014). Cost-effective methods for obtaining abundance data would allow us to better assess this factor and understand its implications, particularly regarding coexistence between species. For instance, the abundance of resources (e.g., prey) or competing species can influence spatial segregation as a coexistence mechanism (Linnell and Strand, 2000; Monterroso et al.2020). Dominant species may select habitats with higher food abundance and availability, displacing subordinate species that share the same resources (Donadio and Buskirk 2006; Lonsinger et al. 2017; Marneweck et al. 2019). However, the density of coexisting species within the same habitat can also affect the intensity of this spatial displacement (Monterroso et al. 2020). Thus, when dominant species abundance is lower, the spatial overlap between dominant and subordinate species can be greater (Fedriani et al. 2000). However, other coexistence mechanisms, such as temporal segregation, can play a more significant role in relationships between species of the same guild. This allows for spatial overlap and the use of the same resources (Torretta et al. 2016; Ferreiro-Arias et al. 2021).

General discussion

Building on the ideas above, this thesis examined the effectiveness of different non-invasive sampling techniques in explaining changes in species abundance. We aimed to identify cost-effective, time-efficient, and reliable methods for studying abundance estimation. Our results revealed that different sampling methods can produce contrasting patterns in explaining variations in relative abundance, potentially leading to biased abundance estimates. Specifically, chapters 1 and 2 demonstrated that some relative abundance indices lack positive correlations with each other or with actual abundance. Additionally, some indices appeared to be influenced by variations in detectability, rendering the chosen predictors unreliable for explaining abundance variations. These observed discrepancies in abundance-related predictors suggest that management or conservation guidelines based on abundance indices should not be considered directly comparable.

Furthermore, our study emphasizes the importance of guild species abundance and their prey availability as modulators of spatial and temporal coexistence mechanisms. We observed in chapters 3 and 4 that the abundance of co-occurring species significantly impacts habitat occupancy, with greater spatial overlap when both species are abundant. However, dominant species preferentially select areas with higher prey abundance, aligning with their temporal patterns and potentially restricting access for subordinate species. Additionally, when overall abundance of species was high, temporal segregation appeared to be the primary coexistence mechanism between dominant and subordinate species, even with substantial spatial overlap. These findings highlighted the critical role of studying species abundance as a potential driver in coexistence relationships among species sharing the same spatial and trophic niche.

Use of Relative Abundance Indices

Monitoring carnivore populations requires the evaluation of multiple sampling methods to identify the most suitable ones to assist in effective conservation strategies (Caughley and Sinclair 1994; Sadlier et al. 2004; Barea-Azcón et al. 2007). Camera-trapping and trail surveys for scat detection are two of the most widely used non-invasive techniques for carnivore studies (Trolle et al. 2007; O’Connell et al. 2011; Sollmann et al. 2013; Rodgers et al. 2014). This thesis employed both methodologies to collect relative abundance indices. Chapter 1 compared the relationships between these indices, while chapter 2 examined their relationship with estimated abundance. However, the results did not reveal a consistently significant and positive relationship between all the indices and the abundance estimates.

General discussion

Our study revealed that camera-trapping indices, including the Relative Abundance Index (RAI) and the minimum number of individually photo-identified animals (NI), captured similar patterns of variation in fox relative abundance (Chapter 1). Additionally, the NI photo-identified index exhibited a positive relationship with the estimated abundance (Chapter 2). However, these camera-trapping indices differed from scat detection indices in explaining abundance changes. Specifically, locations with a higher number of scat segments (NSE) showed low values for RAI and NI photo-identified (Chapter 1). Furthermore, no correlation was found between the NI detected by faecal DNA and NI identified through camera-trapping (Chapter 2). In fact, there was even a non-significant negative relationship between NI detected by faecal DNA and abundance estimates.

Previous studies have assessed the link between RAI and abundance estimates, finding that areas with higher RAI typically harbour greater abundance (Carbone et al. 2001 on *Panthera tigris*; Palmer et al. 2018 on African herbivore species). Individual identification through capture-recapture methods has been established as a reliable technique for abundance estimation (Karanth 1995; Silver et al. 2004; Jackson et al. 2006; Sarmento et al. 2010). However, utilizing individual identification data as a separate relative abundance index within abundance models is a novel approach.

Our findings suggest that the number of individuals photo-identified (NI) can be a reliable index for studying variations in abundance, particularly when more complex methods are not feasible. Capture-recapture (CR), commonly used for abundance estimation, requires a sufficient number of recaptures per individual for accurate results (Otis et al. 1978). Similarly, spatial capture-recapture (SCR) approaches necessitate at least 20-25 recaptures, including those involving spatial data; to effectively describe movement patterns (Efford et al. 2004). Alternatively, telemetry data from tracked animals using telemetry can be incorporated to enhance abundance estimates (Jiménez et al. 2019).

Other methods, such as *N-Mixture* models, offer an alternative approach for estimating abundance using count data without requiring individual identification or defining the effective trapping area (Royle 2004). These models rely on count data, and their reliability has been demonstrated through comparisons with SCR (Basile et al. 2016) and capture-mark-recapture methods (Ficetola et al. 2018), often yielding similar abundance estimates. However, implementing *N-Mixture* models requires significant investment in terms of effort and resources. To account for imperfect detection, a substantial number of spatially replicated surveys are necessary, typically exceeding

20 sites (Kéry and Schaub 2012). Additionally, a high probability of detection is crucial for reliable abundance estimates (Royle 2004; Veech et al. 2016). Furthermore, the assumption of independent counts within a sampling occasion may not always hold true (Link et al. 2018).

Interestingly, the usefulness of the NI photo-identified index as a relative abundance measure appeared to be dependent on the sampling method employed. Our findings suggest that the NI indices obtained from scats DNA and NSE (Number of Scat Segments) through scat surveys may not reflect actual abundance. This lack of relationship between the NI identified by both sampling methods might be explained by variations in territorial marking behaviour among individuals. This can lead to missed detections of some individuals and biased abundance estimates (Gorman and Trowbridge 1989; Webbon et al. 2004).

Scat-sampling methods for abundance estimation in carnivores have faced criticism due to the primary function of scats in communication and territorial marking (Gorman and Trowbridge 1989; Gese 2004). Defecation rates can fluctuate during mating and dispersal seasons (Barja et al. 2008), and vary between males, females, adults, and juveniles (Goszczyński 1990; Peterson et al. 2002; Ralls et al. 2010; Fawcett et al. 2012), influencing detection rates. Additionally, seasonal changes and diet can also affect scat deposition (Andelt and Andelt 1984; Goszczynski 1990). Furthermore, marking frequency may exhibit non-random distribution along paths (Macdonald 1980; Gorman 1990; Vila et al. 1994; Barja and List 2014).

To mitigate marking bias and increase individual detection, scat sampling should encompass diverse landscapes with varied compositions and configurations. Thus, randomly selected transects within the study area might be preferable over well-defined paths (Güthlin et al. 2012). Moreover, the relationship between abundance and NI detected by faecal DNA could potentially be improved by incorporating other genomic techniques. Single Nucleotide Polymorphisms (SNPs) analysis, such as RAD-seq, can enhance DNA amplification precision, reduce sample loss, and consequently improve abundance estimates (Andrews et al.2016; De Barba et al.2017; Erwin et al.2021). Another promising method is the SNP genotyping using Fluidigm's Dynamic Array™, a real-time PCR technique particularly suited for degraded samples like scats and those applied in DNA from ancient samples (Kraus et al.2015).

The importance of controlling detection in abundance studies

General discussion

The choice of index in abundance studies can significantly impact the interpretation of environmental factors influencing species populations. While sensitivity to habitat characteristics is important, detection variability is another crucial consideration (Pollock et al. 2002; Archaux et al. 2012). Discrepancies between abundance models and relative abundance indices may not necessarily reflect true abundance variations, but rather inconsistencies in detection probability. Indices with detection probability below 1 and temporal variation can underestimate population size (O'Brien 2011). Our study revealed that different indices favoured distinct models for explaining abundance changes. This suggests that some indices might be particularly susceptible sensitive to variations in detection. As a result, predictors of significant importance in relative abundance models might primarily capture detection variation rather than true abundance fluctuations.

Gu and Swihart (2004) studied the influence of random and non-random detection on habitat relationships using occupancy models. Their simulations revealed that models based on random detection errors at occupied sites underestimated the significance of habitat variables positively linked to occupancy. Conversely, when detection was non-random and related to habitat characteristics, models often overestimated the importance of habitat variables positively associated with detection probability as drivers of occupancy. These findings from occupancy models parallel our observations with *N-Mixture* abundance models. *N-Mixture* models integrate variables that control both detection and abundance variation to study changes in species abundance (Royle 2004). However, some relative abundance indices lack this functionality. When is non-random, this limitation can introduce biases. These indices might select habitat variables influencing detection as indicators of abundance changes, leading to misinterpretations.

The RAI index selected abundance predictors identified by the *N-Mixture* model as detection factors. However, RAI also captured additional factors influencing abundance changes according to the *N-Mixture* models. This suggests that the RAI index might be susceptible to detection bias, potentially due to its dependence on factors affecting animals entry into camera traps. An illustrative example obtained in this study, is the negative relationship between small game presence and fox abundance identified by the RAI index, while the *N-Mixture* models linked it to detection probability. This selection by RAI could be driven by behavioural differences. Areas with abundant small game are considered "scary landscapes" for foxes. Thus, shyer individuals within the fox population might avoid interaction with cameras, leading to a lower capture rate by camera traps and a potential underestimation of fox abundance in those areas (Díaz-Ruíz et al. 2015).

The NSE index exhibited the strongest evidence of sensitivity to detection variations. The predictors it selected to explain fox abundance mirrored those chosen by the *N-Mixture* models selected to explain fox detection, but with an inverse relationship. For instance, NSE positively selected hunting areas and negatively selected summer and spring seasons, suggesting it might capture variation in fox detection linked to marking behaviour rather than true abundance changes. Hunting areas likely provide more prey resources, potentially leading to increased marking activity by foxes (Burgos et al. 2019). Additionally, recolonization dynamics might be higher in these areas, causing foxes to mark their territories more frequently compared to non-hunting areas (Murdoch et al. 2016). The influence of seasonality on scat detection is not unique to this study. Schauster et al. (2002) and Dempsey et al. (2014) similar findings in other fox species, with scat detection peaking during the mating season (winter) and dropping to its lowest point during the breeding season (summer).

The NI photo-identified index selected the same predictors as the *N-Mixture* models, with the same directional relationships, to explain fox abundance variations. This suggests minimal detection bias in the NI index. Consequently, NI photo-identified emerges as a valuable relative abundance index for studying abundance patterns of red fox populations, particularly when other more complex methods are not feasible. Such limitations might arise due to a low number of individuals or captures (Otis et al. 1978), insufficient spatial replicates, or very low detection probability, hindering reliable abundance estimates (Efford et al. 2004; Royle 2004; Kéry and Schaub 2012; Veech et al. 2016).

While chapter 1 highlighted a positive relationship between RAI and NI photo-identified), both indices ultimately yielded distinct models for explaining abundance changes. For species where individual identification is not achievable, necessitating capture-based methods, controlling detection variations becomes crucial to identify factors influencing abundance. *N-Mixture* abundance models offer a powerful alternative, despite their inherent assumptions (Royle 2004).

Abundance of food and species as determinants of occupation.

While abiotic factors have traditionally dominated ecological niche research (Soberón and Peterson 2005; Soberón 2007), biotic factors also play a crucial role in shaping species niche and interactions between species (Elton 1957; Hutchinson 1957). Among biotic factors, prey abundance, availability, and competitor density can significantly influence species occupancy within a habitat and drive interspecific relationships (Holt and Polis 1997; Creel 2001; St-Pierre et al. 2006; Robison et al. 2014; Rabelo et al. 2019). Occupancy models are a valuable tool to analyse the combined effect of abiotic and biotic factors on species' occupancy in a habitat. These models can also account for detection variations, allowing us to distinguish between factors influencing presence and those affecting detection probability (Royle 2006). In our study, prey abundance (rodents and rabbits) emerged as a main determinant of fox occupancy. We found that foxes preferentially selected vegetation compositions chosen by their prey across different habitat types (Chapter 3). Furthermore, Chapter 4 revealed a positive relationship between the spatial overlap of foxes and stone martens with increasing relative abundance of both species.

Our findings suggest that prey abundance is a consistent factor influencing fox occupancy across diverse habitats. Furthermore, this biotic factor might act as a secondary filter on top of other factors shaping fox occupancy models. Numerous studies support the notion that some predators select foraging areas based on prey abundance (Palomares et al. 2001; Spong 2002; Rauset et al. 2012; Wolff et al. 2015). For example, Sarmento et al. (2011) found that while environmental factors played a lesser role, fox occupancy had a relationship with proximity to vulture feeding sites, suggesting a link to food availability. Goldyn et al. (2003) observed that red foxes primarily foraged in habitats with high abundance of *Apodemus sylvaticus*, and Pereira et al. (2012) reported foxes selecting coniferous forests with increased density of rodents.

Similar to the fox, stone marten occupancy also correlated with rodent occupancy patterns. However, unlike the fox, martens did not directly select for high rodent relative abundance. Selecting the same landscapes as their prey might suggest a feeding strategy focused on exploiting "capturability" of rodents rather than simply seeking high abundance (Hopcraft et al.2005; Balme et al.2006). Alternatively, this behaviour could reflect the competition between the red fox (dominant) and the stone marten (subordinate) (Holt and Polis 1997). In this scenario, the results might indicate displacement of the stone marten by the red fox, even in areas with abundant prey, to avoid encounters and confrontations (Holt and Polis 1997).

While dominant species can supress subordinate competitors (Palomares et al. 1996), coexistence within the same area without population suppression is also possible (Miller et al. 2018). Interestingly, in our study, the fox population did not suppress the stone marten population. In fact, a positive correlation emerged between their relative abundance and spatial overlap. This spatial overlap between the fox and the stone marten might be a strategy by the marten to minimize predation risk. By utilizing the vertical component of the habitat, the marten leverages its arboreal abilities to potentially avoid the primarily terrestrial red fox by utilizing the vertical component of the habitat (Pereira et al. 2012; Padial et al. 2002). The selection of pine and oak forests by both mesocarnivores and rodents further supports this hypothesis. The presence of arboreal forest mice (Montgomery 1980; Rosalino et al. 2010) in these habitats could benefit both predators, potentially explaining the higher abundance of stone marten in these environments. Alternatively, the high spatial overlap may be facilitated by temporal segregation, another potential coexistence mechanism.

Occupancy models applied to both mesocarnivores suggest a link between occupancy patterns and species roles within the shared habitat. Dominant species may prioritize landscapes based on food abundance, while subordinate species have more complex habitat selections influenced by their relationship with dominant competitors. Therefore, understanding these factors, along with characterizing habitat features and quantifying resources, is crucial to deciphering how carnivores coexist within the same space (Karanth et al. 2017; Pokheral and Wegge 2018; Monterroso et al. 2020; Strampelli et al. 2023). This knowledge is essential for a deeper understanding of species' ecological niche, informing conservation and management strategies that promote ecosystem balance, as previously discussed.

Temporal segregation as a coexistence mechanism in highly overlapping spatial niches

High spatial and trophic overlap between coexisting species in the same habitat can be mitigated by temporal segregation, allowing subordinate species to share resources with dominant competitors (Garneau et al. 2007; Monterroso et al. 2014). Our findings support this concept, as shown in chapter 3 by occupancy models and the selection of same landscapes than their prey. Also, chapter 4 revealed a spatial overlap between fox and stone marten that coincided with more disparate activity patterns between the two species. These results, along with previous research (Pereira et al. 2012; Petrov et al. 2016), suggest that temporal segregation might be the key mechanism enabling coexistence between these mesocarnivores despite of sharing a spatial and trophic niche.

Both the fox and the stone marten selected similar habitats to their rodent prey (Chapter 3), but they adjusted their activity patterns differently (Chapter 4). The fox showed greater temporal overlap with rodents during the colder months, when it presumably consumes more rodents (Padial et al. 2002; Carvalho and Gomes 2004; Barrull et al. 2014). This overlap likely reflects the fox's hunting behaviour (Azevedo et al. 2018) driven by the predator-prey dynamics (Mukherjee et al. 2020). In contrast, the stone marten's activity patterns showed no such seasonal link to rodent activity. Interestingly, the stone marten and rodent activity patterns became more similar when the fox and rodent activity diverged (i.e. less overlap). Additionally, the fox and stone marten showed low to moderate activity patterns overlap. These results, coupled with the stone marten's lack of selection for high rodent abundance in occupancy models (Chapter 3), which suggest a potential dominance hierarchy with the red fox as the superior competitor. Within the concept of the "landscape of fear" (Laundré et al. 2001; Laundré et al. 2010), predation implies trade-offs between the risk of predation and the benefits of specific activity (i.e. habitat use, social interactions, vigilance) (Lima and Dill 1989). Notably, subordinate species often prioritize to low-risk habitats over food resources (Heithaus 2001; Björklund et al. 2016; Virgós et al. 2020). The stone marten's activity patterns suggest a potential adaptation to minimize encounters with the dominant red fox.

Future Applications

Reliable data abundance on species abundance is essential to understand their status and developing effective conservation programs. Moreover, cost-effective and rapid methods for gathering such data would enable researcher to study a wider range of species and implement long-term monitoring programs. This thesis highlights the importance of abundance in species interactions and coexistence, an aspect often overlooked due to the challenges of studying it. However, incorporating abundance into studies of species interactions is crucial for generating more conclusive results.

The Non-invasive Index (NI) described in this thesis offers a promising tool as a relative abundance index for other identifiable species. This index exhibits a positive relationship with true abundance changes and is not affected by detection probability. Moreover, its application requires less intensive sampling (both spatially and temporally) compared to other density estimation methods like mark-recapture (SCR). Additionally, camera-trapping might be a more cost-effective alternative to using microsatellites for DNA genotyping from faecal samples.

The current general scenario presents the paradox of biodiversity loss alongside species expansion and recolonization of historical habitats. Monitoring these species is crucial. For instance, if we resort to the case of an emblematic and conflictual species, the Iberian wolf (*Canis lupus*) is reclaiming its lost distribution in Central Spain as the result of recent decades of protection (Blanco 2017). Similar to the fox, studies like Galaverni et al. (2012) have demonstrated that camera traps can be used to identify individual Iberian wolves based on their unique morphological characteristics. Additionally, this thesis explored scats-based sampling methods, which are widely used for study of wolf (Caniglia et al. 2012; Piaggio et al. 2016; Mattioli et al. 2018). The wolf's role as a top carnivore within trophic networks and its contribution to ecosystem health are well-established (Miller et al. 2012; Beschta and Ripple 2016). Extensive research in Yellowstone has documented the long-term population increase of wolves, as well as their impact on coexistence networks among carnivores where they were previously absent (Garrott et al. 2010; Bartnick et al. 2013; Beschta and Ripple 2016). However, the potential effect of wolf recolonization in Mediterranean environments remains unknown, making it a topic of great interest for further research, which would highly benefit from using accurate abundance indices.

General Conclusions

1. Our research highlights the critical role of selecting appropriate sampling methods for abundance studies. Different methods can yield different results due to inherent limitations. Therefore, carefully considering on the limitations of potential techniques in relation to the specific research objectives and the species of study is highly important. Additionally, controlling for detection variability is essential for accurate abundance modelling.
2. When alternative methods are unavailable, the minimum photo-identified Non-Invasive Index (NI) can be a reliable tool for studying abundance variation. This index exhibits a positive correlation with true abundance and is not influenced by detection bias.
3. If methods based on capture per occasion (RAI) are chosen, we recommend using session-based data processing to account for variation in detectability.
4. Improvements in scats sampling methods are needed to estimate population size and explore its relationship with camera trap data. Sampling designs that incorporate transects placed away from existing trails will likely increase the number of scats found. Moreover, transects can help reduce bias caused by individuals that mark more intensely along trails. Further research is recommended to compare the cost-effectiveness of new genetic methods with camera-trapping.
5. The ecological adaptability of mesocarnivores makes studying their coexistence and the factors driving it highly interesting for understanding their role within

different ecosystems. Incorporating data on prey abundance and the species involved in interactions is crucial to explain the mechanisms of coexistence.

6. Dominant species' occupancy patterns may be primarily driven by landscapes with abundant food sources, while subordinate species will exhibit more complex habitat selection strategies based on their interactions with dominant competitors.
7. When two species have significant spatial and trophic overlap, temporal segregation is a likely the mechanism for coexistence. Dominant species may adjust their activity patterns to match their prey availability, while subordinate species may adapt their behaviour to prioritize low-risk habitats over available food resources.
8. The red fox can exhibit top carnivore behaviour, playing a dominant role over other mesocarnivores like the stone marten. In the absence of pressure from other apex predators, red foxes can significantly influence coexistence relationships with stone martens.

References

Abdi H, Williams LJ (2010) Principal component analysis. Wiley Interdiscip Rev Comput Stat 2:433–459.

Acevedo, P., Ferreres, J., Escudero, M. A., Jimenez, J., Boadella, M., & Marco, J. (2017). Population dynamics affect the capacity of species distribution models to predict species abundance on a local scale. Diversity and Distributions, 23(9), 1008-1017.

Agostinelli, C., & Lund, U. (2018). R package 'circular': circular statistics. R package version 0.4-93.

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Autom Control 19(6):716–723.

Alcántara, M. (1992). Distribución y preferencias de hábitat de los micromamíferos (insectivora yrodentia) de la sierra de Guadarrama. Tesis Doctoral, Universidad Complutense de Madrid.

Aliperti, J. R., Jenderseck, K., & Van Vuren, D. H. (2022). Habitat selection in a fluctuating ground squirrel population: Density-dependence and fitness consequences. Ecology and Evolution, 12(8), e9241.

Amarasekare, P. (2008). Coexistence of intraguild predators and prey in resource-rich environments. Ecology, 89(10), 2786-2797.

Andelt, W.F., Andelt, S.H., (1984). Diet bias in scat deposition-rate surveys of coyote density. Wildlife Society Bull. (1973-2006) 12 (1), 74–77.

Anderson, D.R., (2003). Response to Engeman: index values rarely constitute reliable information. Wildlife Society Bull. 31 (1), 288–291.

Andrews KR, Good JM, Miller MR, Luikart G, Hohenlohe PA (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. Nat Rev Genet 17:81–92.

Arandjelovic M, Guschanski K, Schubert G, Harris TR, Thalmann O, Siedel H, Vigilant L (2009) Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. Mol Ecol Resour 9(1):28–36.

References

Archaux, F., Henry, P.Y., Gimenez, O., (2012). When can we ignore the problem of imperfect detection in comparative studies? Methods Ecol. Evol. 3 (1), 188–194.

Azevedo, F. C., Lemos, F. G., Freitas-Junior, M. C., Rocha, D. G., & Azevedo, F. C. C. (2018). Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil. Journal of Zoology, 305(4), 246-255.

Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. Methods in Ecology and Evolution, 5(12), 1269-1279.

Bailey, L., & Adams, M. J. (2005). Occupancy models to study wildlife (No. 2005-3096). US Geological Survey.

Bakaloudis, D. E., Vlachos, C. G., Papakosta, M. A., Bontzorlos, V. A., & Chatzinikos, E. N. (2012). Diet composition and feeding strategies of the stone marten (Martes foina) in a typical Mediterranean ecosystem. The Scientific World Journal, 2012.

Balme GA, Hunter LT, Slotow R (2009) Evaluating methods for counting cryptic carnivores. J Wildl Manag 73(3):433–441.

Balme, G., Hunter, L., & Slotow, R. O. B. (2007). Feeding habitat selection by hunting leopards Panthera pardus in a woodland savanna: prey catchability versus abundance. Animal Behaviour, 74(3), 589-598.

Barea-Azcón JM, Virgós E, Ballesteros-Duperon E, Moleón M, Chirosa M (2007) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodivers Conserv 16(4):1213–1230.

Barja I, De Miguel FJ, Bárcena F (2001) Distribución espacial de los excrementos de zorro rojo (Vulpes vulpes, Linnaeus 1758) en los Montes do Invernadeiro (Ourense). Galemys 13:171–178

Barja I, List R (2014) The role of spatial distribution of scats in coyote scent marking behaviour. Pol J Ecol 62(2):373–384.

Barja, I., de Miguel, F.J., Bárcena, F., (2004). The importance of crossroads in faecal marking behaviour of the wolves (Canis lupus). Naturwissenschaften 91 (10), 489–492.

Barja, I., Silván, G., Illera, J.C., (2008). Relationships between sex and stress hormone levels in feces and marking behavior in a wild population of Iberian wolves (Canis lupus signatus). J. Chem. Ecol. 34 (6), 697–701.

References

Barrientos, R., & Virgós, E. (2006). Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. Acta Oecologica, 30(1), 107-116.

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J. G., Gosàlbez, J., & Salicrú, M. (2014). Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: an integrated study based on camera trapping and diet. Mammalian Biology, 79, 123-131.

Barrull, J., Mate, I., Salicrú, M., Palet, J., Casanovas, J. G., Gosàlbez, J., & Ruiz-Olmo, J. (2014). Differential response of a carnivore community to predator control: A spatio-temporal observational study. Italian Journal of Zoology, 81(2), 271-279.

Barton, K. (2022). MuMIn: Multi-model inference. R package version 1.46.0. https://cran.r-project.org/package=MuMIn

Basile M, Balestrieri R, Posillico M, Mancinelli A, Altea T, Matteucci G (2016) Measuring bird abundance—a comparison of methodologies between capture/recapture and audio-visual surveys. Avocetta 40:55–61

Bateman, P.W., Fleming, P.A., Le Comber, S., (2012). Big city life: carnivores in urban environments. J. Zool. 287 (1), 1–23.

Becerra López, Jorge Luis, et al. "Evidence of niche shift and invasion potential of Lithobates catesbeianus in the habitat of Mexican endemic frogs." Plos One 12.9 (2017): e0185086.

Beja P, Gordinho L, Reino L, Loureiro F, Santos-Reis M, Borralho R (2009) Predator abundance in relation to small game management in southern Portugal: conservation implications. Eur J Wildl Res 55(3):227–238.

Bellemain EVA, Swenson JE, Tallmon D, Brunberg S, Taberlet P (2005) Estimating population size of elusive animals with DNA from hunter-collected feces: four methods for brown bears. Conserv Biol 19(1):150–161.

Bengsen, A.J., Leung, L.K.P., Lapidge, S.J., Gordon, I.J., (2011). Using a general index approach to analyze camera-trap abundance indices. J. Wildlife Manage. 75 (5), 1222–1227.

References

Bennie, J. J., Duffy, J. P., Inger, R., & Gaston, K. J. (2014). Biogeography of time partitioning in mammals. Proceedings of the National Academy of Sciences, 111(38), 13727-13732.

Bermúdez, F. L. (2001). Cambio climático y desertificación, amena-zas para la sostenibilidad de las tierras del Arco Mediterráneo. Situación y perspectiva. Revista valenciana d'estudis autonòmics, 36, 108.

Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological conservation, 142(11), 2401-2414.

Björklund, H., Santangeli, A., Blanchet, F. G., Huitu, O., Lehtoranta, H., Lindén, H., ... & Laaksonen, T. (2016). Intraguild predation and competition impacts on a subordinate predator. Oecologia, 181(1), 257-269.

Blake, J. G., Mosquera, D., Loiselle, B. A., Swing, K., Guerra, J., & Romo, D. (2012). Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. Ecotropica, 18(2), 137-146.

Blanco, J. C., Reig, S., & de la Cuesta, L. (1992). Distribution, status and conservation problems of the wolf Canis lupus in Spain. Biological Conservation, 60(2), 73-80.

Borchers, D. L., and M. G. Efford. (2008). Spatially explicit maximum likelihood methods for capture-recapture studies. Biometrics 64:377–385.

Braczkowski, A. R., Balme, G. A., Dickman, A., Fattebert, J., Johnson, P., Dickerson, T., ... & Hunter, L. (2016). Scent lure effect on camera-trap based leopard density estimates. PloS one, 11(4), e0151033.

Brashares, J. S., Prugh, L. R., Stoner, C. J., & Epps, C. W. (2010). Ecological and conservation implications of mesopredator release. Trophic cascades: predators, prey, and the changing dynamics of nature, 221-240

Brown, C. H., & Griscom, H. P. (2022). Differentiating between distribution and suitable habitat in ecological niche models: A red spruce (Picea rubens) case study. *Ecological Modelling*, *472*, 110102.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. The american naturalist, 124(2), 255-279.

References

Buchalski MR, Benjamin N, Sacks KD, Ahrens, Kyle D, Gustafson JL, Rudd HB, Ernest, Justin A (2022) Dellinger. “Development of a 95 SNP panel to individually genotype mountain lions (Puma concolor) for microfluidic and other genotyping platforms. Conserv Genet Resour (1–4).

Buhr, E. D., & Takahashi, J. S. (2013). Molecular components of the Mammalian circadian clock. Circadian clocks, 3-27.

Burgar, J. M., Stewart, F. E., Volpe, J. P., Fisher, J. T., & Burton, A. C. (2018). Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models. Global Ecology and Conservation, 15, e00411.

Burgos, T., Virgós, E., Valero, E.S., Arenas-Rojas, R., Rodríguez-Siles, J., Recio, M.R., (2019). Prey density determines the faecal-marking behaviour of a solitary predator, the Iberian lynx (Lynx pardinus). Ethol. Ecol. Evol. 31 (3), 219–230.

Burnham KP, Anderson DR (2002) A Practical Information-Theoretic Approach. Model Selection and Multimodel Inference, 2nd ed. Springer, New York, p. 2

Campos CM, Ojeda RA (1997) Dispersal and germination of Prosopis flexuosa (Fabaceae) seeds by desert mammals in Argentina. J Arid Environ 35(4):707–714.

Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., Laidlaw, R., Lynam, A., Macdonald, D.W., Martyr, D., McDougal, C., Nath, L., O’Brien, T., Seidensticker, J., Smith, D.J.L., Sunquist, M., Tilson, R., Shahruddin, W.N., (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim. Conserv. 4 (1), 75–79.

Carbone, C., Pettorelli, N., & Stephens, P. A. (2011). The bigger they come, the harder they fall: body size and prey abundance influence predator–prey ratios. Biology letters, 7(2), 312-315.

Carroll EL, Bruford MW, DeWoody JA, Leroy G, Strand A, Waits L, Wang J (2018) Genetic and genomic monitoring with minimally invasive sampling methods.698. Evol Appl 11(7):1094–1119.

References

Carvalho, J. C., & Gomes, P. (2004). Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). Journal of zoology, 263(3), 275-283.

Carvalho, J. C., & Gomes, P. (2004). Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). Journal of zoology, 263(3), 275-283.

Caughley G, Sinclair ARE (1994) Wildlife Ecology and Management. Blackwell Science: Melbourne)Chapuis MP, Estoup A (2009) FreeNA.

Cavallini P (1994) Faeces count as an index of fox abundance. Acta Theriol 39:417–417

Cavallini P, Lovari S (1991) Environmental factors influencing the use of habitat in the red fox, Vulpes vulpes. J Zool 223:323–339

Cavallini, P., Lovari, S., (1994). Home range, habitat selection and activity of the red fox in a Mediterranean coastal ecotone. Acta Theriol. 39 (3), 279–287.

Chase, J. M., Abrams, P. A., Grover, J. P., Diehl, S., Chesson, P., Holt, R. D., ... & Case, T. J. (2002). The interaction between predation and competition: a review and synthesis. Ecology letters, 5(2), 302-315.

Chase, Jonathan M., and Mathew A. Leibold. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, 2003.

Chautan M, Pontier D, Artois M (2000) Role of rabies in recent demographic changes in red fox (Vulpes vulpes) populations in Europe. Mammalia 64(4):391–410

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual review of Ecology and Systematics, 343-366.

Chutipong, W., Steinmetz, R., Savini, T., & Gale, G. A. (2017). Assessing resource and predator effects on habitat use of tropical small carnivores. Mammal Research, 62(1), 21-36.

Clark, J. D., Dunn, J. E., & Smith, K. G. (1993). A multivariate model of female black bear habitat use for a geographic information system. The Journal of wildlife management, 519-526.

References

Clipp, H. L., Evans, A. L., Kessinger, B. E., Kellner, K., & Rota, C. T. (2021). A penalized likelihood for multispecies occupancy models improves predictions of species interactions. Ecology, 102(12), e03520.

Comrey, A. L., & Lee, H. B. (1992). Interpretation and application of factor analytic results. Comrey AL, Lee HB. A first course in factor analysis, 2, 1992.

Connell, J. H. (1983). On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist, 122(5), 661-696.

Cortázar-Chinarro, M., Halvarsson, P., Virgós, E., (2019). Sign surveys for red fox (Vulpes vulpes) censuses: evaluating different sources of variation in scat detectability. Mamm. Res. 64, 183–190.

Costa A, Romano A, Salvidio S (2020) Reliability of multinomial N-Mixture models for estimating abundance of small terrestrial vertebrates. Biodivers Conserv 29(9):2951–2965.

Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. Conservation Biology, 15(1), 271-274.

Creel, S., & Creel, N. M. (1996). Limitation of African wild dogs by competition with larger carnivores. Conservation Biology, 10(2), 526-538.

Cruz, J., & Sarmento, P., (1998). Some ecological aspects of the red fox at Serra da Malcata. In Proceedings of the Euro-American Mammal Congress: challenges in holarctic mammalogy (pp. 19-24). Santiago de Compostela, Spain: 19–24 July 1998, Universidad de Santiago de Compostela.

Cruz, P., Paviolo, A., Bó, R. F., Thompson, J. J., & Di Bitetti, M. S. (2014). Daily activity patterns and habitat use of the lowland tapir (Tapirus terrestris) in the Atlantic Forest. Mammalian Biology, 79(6), 376-383.

Curveira-Santos, G., Marques, T. A., Björklund, M., & Santos-Reis, M. (2017). Mediterranean mesocarnivores in spatially structured managed landscapes: community organization in time and space. Agriculture, ecosystems & environment, 237, 280-289.

References

Dakin EE, Avise JC (2004) Microsatellite null alleles in parentage analysis. Heredity 93(5):504–509.

Dallas, T. A., & Hastings, A. (2018). Habitat suitability estimated by niche models is largely unrelated to species abundance. Global Ecology and Biogeography, 27(12), 1448-1456.

Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. Ecology letters, 20(12), 1526-1533.

Davis, R. S., Gentle, L. K., Stone, E. L., Uzal, A., & Yarnell, R. W. (2022). A review of spotted hyaena population estimates highlights the need for greater utilisation of spatial capture-recapture methods. Journal of Vertebrate Biology, 71(22017), 22017-1.

Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: the next generation. Ecology letters, 8(8), 875-894.

De Barba M, Miquel C, Lobréaux S, Quenette PY, Swenson JE, Taberlet P (2017) High-throughput microsatellite genotyping in ecology: improved accuracy, efficiency, standardization and success with low quantity and degraded DNA. Mol Ecol Resour 17:492–507.

De la Fuente, A., Hirsch, B. T., Cernusak, L. A., & Williams, S. E. (2021). Predicting species abundance by implementing the ecological niche theory. Ecography, 44(11), 1723-1730.

Del Rio, C. M., Dugelby, B., Foreman, D., Miller, B., Noss, R., & Phillips, M. (2001). The importance of large carnivores to healthy ecosystems. Endangered species update, 18(5), 202-210.

Delibes, M., Rodrıguez, A., & Ferreras, P. (2000). Action Plan for the Conservation of the Iberian Lynx (Lynx pardinus) in Europe, no. 111. Council of Europe.

Delibes-Mateos, M., Fernandez de Simon, J., Villafuerte, R., & Ferreras, P. (2008). Feeding responses of the red fox (Vulpes vulpes) to different wild rabbit (Oryctolagus cuniculus) densities: a regional approach. European Journal of Wildlife Research, 54(1), 71-78.

References

Della Rocca, F., Milanesi, P., Magna, F., Mola, L., Bezzicheri, T., Deiaco, C., Bracco, F., (2020). Comparison of two sampling methods to estimate the abundance of lucanus cervus with application of N-Mixture models. Forests 11 (10), 1085.

Dempsey, S.J., Gese, E.M., Kluever, B.M., Maldonado, J.E., (2014). Finding a fox: an evaluation of survey methods to estimate abundance of a small desert carnivore. PLoS ONE 9 (8), e105873.

Di Bitetti, M. S. (2008). Depredadores tope y cascadas tróficas en ambientes terrestres.

Di Bitetti, M. S., De Angelo, C. D., Di Blanco, Y. E., & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica, 36(4), 403-412.

Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B., Ferreras, P., (2015). Drivers of red fox (Vulpes vulpes) daily activity: prey availability, human disturbance or habitat structure? J. Zool. 298 (2), 128–138.

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 V ulpes vulpes in the Iberian P eninsula. Mammal Review, 43(1), 59-70.

Díaz-Ruiz, F., Ferreras, P., (2013). Conocimiento científico sobre gestión de depredadores generalistas en España: el caso del zorro (Vulpes vulpes) y la urraca (Pica pica). Ecosistemas 22 (2), 40–47.

Donadio, E., & Buskirk, S. W. (2006). Diet, morphology, and interspecific killing in Carnivora. The American Naturalist, 167(4), 524-536.

Dorning J, Harris S (2019) The challenges of recognising individuals with few distinguishing features: identifying red foxes Vulpes vulpes from camera-trap photos.PloS one, 14(5), e0216531.

Duduś, L., Zalewski, A., Kozioł, O., Jakubiec, Z., & Król, N. (2014). Habitat selection by two predators in an urban area: The stone marten and red fox in Wrocław (SW Poland). Mammalian Biology, 79(1), 71-76.

Efford MG (2004) Density estimation in live-trapping studies. Oikos 106:598–610.

References

Efford MG, Dawson DK, Robbins CS (2004) DENSITY: Software for analysing capture-recapture data from passive detector arrays. Anim Biodivers Conserv 27:217–228

Efford, M. G., D. L. Borchers, and A. E. Byrom. (2009). Density estimation by spatially explicit capture–recapture: likelihood-based methods. Pages 255–269 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York, New York, USA.

Elbroch, L. M., & Kusler, A. (2018). Are pumas subordinate carnivores, and does it matter?. PeerJ, 6, e4293.

Elton, C. 1927. Animal ecology. Sidgwick and Jackson, London, England.

Erwin JA, Robert R, Fitak, Culver M (2021) PumaPlex100: an expanded tool for puma SNP genotyping with low-yield DNA. Conserv Genet Resour 13(3):341–343.

Escribano-Avila, G., Pettorelli, N., Virgós, E., Lara-Romero, C., Lozano, J., Barja, I., ... & Puerta, M. (2013). Testing Cort-Fitness and Cort-Adaptation hypotheses in a habitat suitability gradient for roe deer. Acta Oecologica, 53, 38-48.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Wardle, D. A. (2011). Trophic downgrading of planet Earth. science, 333(6040), 301-306.

Evers, E. E., Pretorius, M. E., Venter, J. A., Honiball, T. L., Keith, M., Mgqatsa, N., & Somers, M. J. (2022). Varying degrees of spatio-temporal partitioning among large carnivores in a fenced reserve, South Africa. Wildlife Research.

Fa, J.E., Sharples, C.M., Bell, D.J., 1999. Habitat correlates of European rabbit (Oryctolagus cuniculus) distribution after the spread of RVHD in Cadiz Province, Spain. J. Zool. 249 (1), 83–96.

Fedriani, J. M., Fuller, T. K., Sauvajot, R. M., & York, E. C. (2000). Competition and intraguild predation among three sympatric carnivores. Oecologia, 125(2), 258-270.

Fedriani, J. M., Palomares, F., & Delibes, M. (1999). Niche relations among three sympatric Mediterranean carnivores. Oecologia, 121, 138-148.

Fernandez-de-Simon, J., Díaz-Ruiz, F., Rodríguez-de la Cruz, M., Delibes-Mateos, M., Villafuerte, R., Ferreras, P., (2015). Can widespread generalist predators affect keystone prey? A case study with red foxes and European rabbits in their native range. Popul. Ecol. 57 (4), 591–599.

Ferreiro-Arias, I., Isla, J., Jordano, P., & Benítez-López, A. (2021). Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. Ecology and Evolution, 11(22), 15520-15533.

Ferreras P, Jiménez J, Tobajas J, Ramos S, Descalzo E, Mateo R (2017) Estimating red fox (Vulpes vulpes) abundance with spatial mark-resight models and camera traps: the effects of tagging, observer and individual recognition

Ferreras, P., Díaz-Ruiz, F., Alves, P.C., Monterroso, P., (2017). Optimizing camera-trapping protocols for characterizing mesocarnivore communities in south-western Europe. J. Zool. 301 (1), 23–31.

Ferretti, F., Oliveira, R., Rossa, M., Belardi, I., Pacini, G., Mugnai, S., ... & Lazzeri, L. (2023). Interactions between carnivore species: limited spatiotemporal partitioning between apex predator and smaller carnivores in a Mediterranean protected area. Frontiers in Zoology, 20(1), 20.

Ficetola GF, Barzaghi B, Melotto A, Muraro M, Lunghi E, Canedoli C, Lo Parrino E, Nanni V, Silva-Rocha I, Urso A, Carretero MA, Salvi D, Scali S, Scarì G, Pennati R, Andreone F, Manenti R (2018) N-Mixture models reliably estimate the abundance of small vertebrates. Sci Rep 8(1).

Fiske I, Chandler R (2011) Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J Stat Softw 43(10):1–23.

Flagstad Ø, Hedmark EVA, Landa A, Brøseth H, Persson J, Andersen R, …, Ellegren H (2004) Colonization history and noninvasive monitoring of a reestablished wolverine population. Conserv Biol 18(3):676–688.

Flowerdew, J. R. (2000). Wood mice—small granivores/insectivores with seasonally variable patterns. In Activity Patterns in Small Mammals (pp. 177-189). Springer, Berlin, Heidelberg.

Foster RJ, Harmsen BJ (2012) A critique of density estimation from camera-trap data. J Wildl Manag 76(2):224–236.

References

Foster, V. C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A. T., Negrões, N., ... & Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. Biotropica, 45(3), 373-379.

Francisco LV, Langsten AA, Mellersh CS, Neal CL, Ostrander EA (1996) A class of highly polymorphic tetranucleotide repeats for canine genetic mapping. Mamm Genome 7(5):359–362.

Frantz AC, Pope LC, Carpenter PJ, Roper TJ, Wilson GJ, Delahay RJ, Burke T (2003) Reliable microsatellite genotyping of the eurasian badger (Meles meles) using faecal DNA. Mol Ecol 12(6):1649–1661.

Fraterrigo, J.M., Wiens, J.A., (2005). Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. Landscape Urban Plann. 71 (2–4), 263–275.

Fredholm M, Winterø AK (1995) Variation of short tandem repeats within and between species belonging to the Canidae family. Mamm Genome 6(1):11–18.

Gaidet-Drapier N, Fritz H, Bourgarel M, Renaud PC, Poilecot P, Chardonnet P, Le Bel S (2006) Cost and efficiency of large mammal census techniques: comparison of methods for a participatory approach in a communal area, Zimbabwe. Biodivers Conserv 15(2):735–754.

Galaverni M, Palumbo D, Fabbri E, Caniglia R, Greco C, Randi E (2012) Monitoring wolves (Canis lupus) by non-invasive genetics and camera trapping: a small-scale pilot study. Eur J Wildl Res 58(1):47–58.

Galsworthy, M. J., Amrein, I., Kuptsov, P. A., Poletaeva, I. I., Zinn, P., Rau, A., ... & Lipp, H. P. (2005). A comparison of wild-caught wood mice and bank voles in the Intellicage: assessing exploration, daily activity patterns and place learning paradigms. Behavioural brain research, 157(2), 211-217.

Garneau, D. E., Post, E., Boudreau, T., Keech, M., & Valkenburg, P. (2007). Spatio-temporal patterns of predation among three sympatric predators in a single-prey system. Wildlife Biology, 13(2), 186-194.

Genovesi, P., Secchi, M., & Boitani, L. (1996). Diet of stone martens: an example of ecological flexibility. Journal of Zoology, 238(3), 545-555.

References

Gerber, B. D., Karpanty, S. M., & Kelly, M. J. (2012). Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology, 54, 43-54

Gergs, A., Preuss, T. G., & Palmqvist, A. (2014). Double trouble at high density: cross-level test of resource-related adaptive plasticity and crowding-related fitness. PloS one, 9(3), e91503.

Gese, E. M., Stotts, T. E., & Grothe, S. (1996). Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. Journal of Mammalogy, 77(2), 377-382.

Gese, E.M., (2004). Survey and census techniques for canids. USDA National Wildlife Research Center-Staff Publications 337.

Gil-Sánchez, J. M., Mañá-Varela, B., Herrera-Sánchez, F. J., & Urios, V. (2021). Spatio-temporal ecology of a carnivore community in middle atlas, NW of Morocco. Zoology, 146, 125904.

Gittleman JL, Funk SM, MacDonald DW, Wayne RK (eds) (2001) Carnivore conservation, vol 5. Cambridge University Press, Cambridge

Gittleman, J. L., & Gompper, M. E. (2005). Plight of predators: the importance of carnivores for understanding patterns of biodiversity and extinction risk. Ecology of predator–prey interactions, 370-388.

Gómez-Ortiz, Y., Monroy-Vilchis, O., & Castro-Arellano, I. (2019). Temporal coexistence in a carnivore assemblage from central Mexico: temporal-domain dependence. Mammal Research, 64(3), 333-342.

Gompper ME, Kays RW, Ray JC, Lapoint SD, Bogan DA, Cryan JR (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. Wildl Soc Bull 34(4):1142–1151.

Gorman ML (1990) Scent marking strategies in mammals. Rev Suisse Zool 97:3–30

Gorman ML, Trowbridge BJ (1989) The role of odor in the social lives of carnivores. Carnivore behaviour, ecology, and evolution. Springer, Boston, MA, pp 57–88.

Goszczyński J (1990) Scent marking by red foxes in Central Poland during the winter season. ActaTheriologica 35(1–2):7–16

References

Graham, M.H., (2003). Confronting multicollinearity in ecological multiple regression. Ecology 84 (11), 2809–2815.

Grinnell, Joseph. "The niche-relationships of the California Thrasher." The Auk 34.4 (1917): 427-433.

Gu, W., Swihart, R.K., (2004). Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biol. Conserv. 116 (2), 195–203.

Güthlin D, Kröschel M, Küchenhoff H, Storch I (2012) Faecal sampling along trails: a questionable standard for estimating red fox Vulpes vulpes abundance. Wildl Biology 18(4):374–382.

Güthlin D, Storch I, Küchenhoff H (2014). Is it possible to individually identify red foxes from photographs? Wildl Soc Bull 38(1):205–210.

Güthlin, D., Storch, I., Küchenhoff, H., (2013). Landscape variables associated with relative abundance of generalist mesopredators. Landscape Ecol. 28 (9), 1687–1696.

Habibullah, M. S., Din, B. H., Tan, S. H., & Zahid, H. (2022). Impact of climate change on biodiversity loss: global evidence. Environmental Science and Pollution Research, 29(1), 1073-1086.

Hansen, M.M., Jacobsen, L., (1999). Identification of mustelid species: otter (Lutra lutra), American mink (Mustela vison) and polecat (Mustela putorius), by analysis of DNA from faecal samples. J. Zool. 247 (2), 177–181.

Harding, E.K., Doak, D.F., Albertson, J.D., (2001). Evaluating the effectiveness of predator control: the non-native red fox as a case study. Conserv. Biol. 15 (4), 1114–1122.

Harrell Jr, F.E., Lee, K.L., Mark, D.B., (1996). Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. Stat. Med. 15 (4), 361–387.

Hayward, M. W., & Slotow, R. (2009). Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research-24-month delayed open access, 39(2), 109-125.

References

Heinlein BW, Urbanek RE, Olfenbuttel C, Dukes CG (2020) Effects of different attractants and human scent on mesocarnivore detection at camera traps. Wildl Res 47(4):338–348.

Heithaus, M. R. (2001). Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos, 92(3), 542-554.

Hemami, M. R., Esmaeili, S., Brito, J. C., Ahmadi, M., Omidi, M., & Martínez-Freiría, F. (2018). Using ecological models to explore niche partitioning within a guild of desert felids. Hystrix, (2), 216.

Henke, S. E., & Bryant, F. C. (1999). Effects of coyote removal on the faunal community in western Texas. The Journal of Wildlife Management, 1066-1081.

Hernandez-Puentes, C., Torre, I., & Vilella, M. (2022). Spatio-temporal interactions within a Mediterranean community of Mesocarnivores. Mammalian Biology, 1-17.

Herrera, C. M. (1989). Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos, 250-262.

Hirzel, Alexandre H., and Gwenaëlle Le Lay. "Habitat suitability modelling and niche theory." Journal of applied ecology 45.5 (2008): 1372-1381.

Holmes NG, Humphreys SJ, Binns MM, Holliman A, Curtis R, Mellersh CS, Sampson I (1993) Isolation and characterization of microsatellites from the canine genome. Anim Genet 24(4):289–292.

Holt, R. D., and G. A. Polis. (1997). A theoretical framework forintraguild predation. American Naturalist 149:745–764

Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology, 74(3), 559-566.

Huang K, Ritland K, Dunn DW, Qi X, Guo S, Li B (2016) Estimating relatedness in the presence of null alleles. Genetics 202(1):247–260.

Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

References

Jackson RM, Roe JD, Wangchuk R, Hunter DO (2006) Estimating snow leopard population abundance using photography and capture-recapture techniques. Wildl Soc Bull 34(3):772–781.

Jammalamadaka, S. R., & Sengupta, A. (2001). Topics in circular statistics (Vol. 5). world scientific.

Janečka JE, Munkhtsog B, Jackson RM, Naranbaatar G, Mallon DP, Murphy WJ (2011) Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. J Mammal 92(4):771–783.

Jankowiak, Ł., Malecha, A. W., & Krawczyk, A. J. (2016). Garbage in the diet of carnivores in an agricultural area. European Journal of Ecology, 2(1), 81-86.

Jędrzejewski, W., Jędrzejewska, B., & Szymura, A. (1989). Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. Acta theriologica, 34(34), 487-496.

Jimenez J, Chandler R, Tobajas J, Descalzo E, Mateo R, Ferreras P (2019a) Generalized spatial mark–resight models with incomplete identification: an application to red fox density estimates. Ecol Evol 9(8):4739–4748.

Jiménez J, Nuñez-Arjona JC, Mougeot F, Ferreras P, González LM, García-Domínguez F, Muñoz-Igualada J, Palacios MJ, Pla S, Rueda C, Villaespesa F, Nájera F, Palomares F, López-Bao JV (2019b) Restoring apex predators can reduce mesopredator abundances. Biol Conserv 238:108234.

Jiménez J, Nuñez-Arjona JC, Rueda C, González LM, García-Domínguez F, Muñoz-Igualada J, López-Bao JV (2017) Estimating carnivore community structures. Sci Rep 7:1–10.

Jiménez-Valverde, A., Nakazawa, Y., Lira-Noriega, A., & Peterson, A. T. (2009). Environmental correlation structure and ecological niche model projections. Biodiversity Informatics, 6, 28-35.

Johansson Ö, Samelius G, Wikberg E, Chapron G, Mishra C, Low M (2020) Identification errors in camera-trap studies result in systematic population overestimation. Sci Rep 10(1):1–10.

Johnson, Chris. Australia's mammal extinctions: a 50,000-year history. Cambridge University Press, 2006.

References

Jordano, P., García, C., Godoy, J. A., & Garcia-Castaño, J. (2007). Differential contribution of frugivores to complex seed dispersal patterns. Proceedings of the National Academy of Sciences, 104(9), 3278-3282.

Juan T, Sagrario A, Jesús H, Cristina CM (2006) Red fox (Vulpes vulpes L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (Celtis australis L). Acta Oecol 30(1):39–45.

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16(5):1099–1106.

Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79(8):2852–2862

Karanth, K. U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., & Kumar, N. S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B: Biological Sciences, 284(1848), 20161860.

Karanth, K.U., 1995. Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. Biol. Conserv. 71 (3), 333–338.

Karanth, K.U., Nichols, J.D., 2011. Estimating tiger abundance from camera trap data: field surveys and analytical issues. In: O'Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology. Springer Japan, Tokyo, pp. 97–117.

Keever, A.C., McGowan, C.P., Ditchkoff, S.S., Acker, P.K., Grand, J.B., Newbolt, C.H., 2017. Efficacy of N-Mixture models for surveying and monitoring white-tailed deer populations. Mammal Res. 62 (4), 413–422.

Kendall, C., Virani, M. Z., Kirui, P., Thomsett, S., & Githiru, M. (2012). Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. The Condor, 114(3), 523-531.

Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS. A hierarchical perspective. Academic Press / Elsevier

References

Kéry, M., Royle, J.A., Schmid, H., (2005). Modeling avian abundance from replicated counts using binomial mixture models. Ecol. Appl. 15 (4), 1450–1461.

Kidwai Z, Jimenez J, Louw CJ, Nel HP, Marshal JP (2019) Using N-Mixture models to estimate abundance and temporal trends of black rhinoceros (Diceros bicornis L.) populations from aerial counts. Global Ecol Conserv 19:e00687.

Kinnaird, M.F., O'brien, T.G., (2012). Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. Conserv. Biol. 26 (6), 1026–1039.

Kohn, M.H., Wayne, R.K., (1997). Facts from feces revisited. Trends Ecol. Evol. 12 (6), 223-227.

Kraus RH, Vonholdt B, Cocchiararo B, Harms V, Bayerl H, Kühn R, Nowak C (2015) A single-nucleotide polymorphism-based approach for rapid and cost-effective genetic wolf monitoring in Europe based on noninvasively collected samples. Mol Ecol Resour 15(2):295–305. https://doi.org/10.1111/1755-0998.12307

Krausman, P. R., & Morrison, M. L. (2016). Another plea for standard terminology. The Journal of Wildlife Management, 80(7), 1143-1144.

Kronfeld-Schor, N., & Dayan, T. (2003). Partitioning of time as an ecological resource. Annual review of ecology, evolution, and systematics, 34(1), 153-181.

Kruuk H (1978) Spatial organization and territorial behaviour of the european badger Meles meles. J Zool 184(1):1–19. https://doi.org/10.1111/j.1469-7998.1978.tb03262.x

Kruuk, H., Conroy, J.W.H., Glimmerveen, U., Ouwerkerk, E.J., (1986). The use of spraints to survey populations of otters Lutra lutra. Biol. Conserv. 35 (2), 187–194.

Large Carnivores Initiative for Europe, http://www.lcie. org/Home.aspx; accessed 18 August 2013. 87.

Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. The Open Ecology Journal, 3(1).

Laundré, JW, Hernández, L, & Altendorf, KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology, 79, 1401-1409.

References

Letnic, Mike, and Christopher R. Dickman. "Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats." Biological Reviews 85.3 (2010): 501-521.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian journal of zoology, 68(4), 619-640.

Lindsø LK, Dupont P, Rød-Eriksen L, Andersskog IPØ, Ulvund KR, Flagstad Ø, …, Eide NE (2022) Estimating red fox density using non-invasive genetic sampling and spatial capture–recapture modelling. Oecologia 198(1):139–151.

Lindström, E. R., Brainerd, S. M., Helldin, J. O., & Overskaug, K. (1995, January). Pine marten—red fox interactions: a case of intraguild predation?. In Annales Zoologici Fennici (pp. 123-130). Finnish Zoological and Botanical Publishing Board.

Link WA, Schofield MR, Barker RJ, Sauer JR (2018) On the robustness of N-Mixture models. Ecology 99(7):1547–1551.

Linkie, M., & Ridout, M. S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. Journal of Zoology, 284(3), 224-229.

Linnell JD, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. Divers Distrib 6(4):169–176.

Lloyd HG (1980) Habitat requirements of the red fox. InThe red fox. Springer, Dordrecht, pp 7–25

López-Bao, J. V., Godinho, R., Rocha, R. G., Palomero, G., Blanco, J. C., Ballesteros, F., & Jiménez, J. (2020) Consistent bear population DNA-based estimates regardless molecular markers type. Biological Conservation, 248, 108651.

López-Martín, J.M., (2010). Zorro – Vulpes vulpes. En: Enciclopedia Virtual de los Vertebrados Españoles. In: Salvador, A., Cassinello, J. (Eds.), Museo Nacional de Ciencias Naturales, Madrid.

Lozano, J., Olszańska, A., Morales-Reyes, Z., Castro, A. A., Malo, A. F., Moleón, M., ... & Martín-López, B. (2019). Human-carnivore relations: a systematic review. Biological Conservation, 237, 480-492.

Lucherini M, Lovari S, Crema G (1995) Habitat use and ranging behaviour of the red fox (Vulpes vulpes) in a Mediterranean rural area: is shelter availability a key factor? J Zool 237(4):577–591.

References

Lyra-Jorge, M.C., Ciocheti, G., Pivello, V.R., Meirelles, S.T., (2008). Comparing methods for sampling large-and medium-sized mammals: camera traps and track plots. Eur. J. Wildl. Res. 54 (4), 739–744.

MacDonald DW (1980) Patterns of scent marking with urine and faeces amongst carnivore communities. In Symposia of the Zoological Society of London (Vol 45(107):e139

Macdonald DW (1985) The carnivores: order Carnivora. In: Brown RE (ed) Social Odours in Mammals/Eds.

Macdonald DW. MacKay, P., Zielinski, W.J., Long, R., Ray, J.C., (2008). Noninvasive research and carnivore conservation. Noninvasive survey methods for carnivores. Island Press, Washington, DC, USA, pp. 1–7.

Macdonald, D. W. (1987). Running with the fox. London: Unwin Hyman

MacKenzie, D. I. et al. (2006). Occupancy Estimation and Modeling. Amsterdam: Academic Press.

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. Journal of applied Ecology, 42(6), 1105-1114.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., (2002). Estimating site occupancy rates when detection probabilities are less than one. Ecology 83 (8), 2248–2255.

Maguire Jr, B. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist*, *107*(954), 213-246.

Mangas, J.G., Lozano, J., Cabezas-Díaz, S., Virgós, E., (2008). The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. Biodivers. Conserv. 17 (1), 43–51.

Mangas, J.G., Rodríguez-Estival, J., 2010. Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. For. Ecol. Manage. 260 (8), 1274–1281.

Martínez-Meyer, E., Díaz-Porras, D., Peterson, A. T., & Yáñez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology letters*, *9*(1), 20120637.

References

Martin-Garcia S, Rodríguez-Recio M, Peragón I, Bueno I, Virgós E (2022) Comparing relative abundance models from different indices, a study case on the red fox. Ecol Ind 137:108778.

Mazerolle MJ, Mazerolle MMJ (2017) Package 'AICcmodavg'.R package,281

McDonald, P. J., Griffiths, A. D., Nano, C. E., Dickman, C. R., Ward, S. J., & Luck, G. W. (2015). Landscape-scale factors determine occupancy of the critically endangered central rock-rat in arid Australia: the utility of camera trapping. Biological Conservation, 191, 93-100.

McGarigal K, Cushman S, Stafford S (2000) Multivariate statistics for wildlife and ecology research. New York: Springer.

Meek PD, Ballard GA, Fleming PJ (2015) The pitfalls of wildlife camera trapping as a survey tool in Australia. Australian Mammalogy 37(1):13–22.

Meek PD, Ballard GA, Fleming PJ, Schaefer M, Williams W, Falzon G (2014) Camera traps can be heard and seen by animals. PLoS ONE 9(10).

Meek, P. D., & Saunders, G. (2000). Home range and movement of foxes (Vulpes vulpes) in coastal New South Wales, Australia. Wildlife Research, 27(6), 663-668.

Miller, J. R., Pitman, R. T., Mann, G. K., Fuller, A. K., & Balme, G. A. (2018). Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. Journal of Animal Ecology, 87(6), 1709-1726.

Mills LS, Citta JJ, Lair KP, Schwartz MK, Tallmon DA (2000) Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. Ecol Appl 10(1):283–294.

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(1), e0168460.

Monclús, R., Arroyo, M., Valencia, A., De Miguel, F.J., (2009). Red foxes (Vulpes vulpes) use rabbit (Oryctolagus cuniculus) scent marks as territorial marking sites. J. Ethol. 27 (1), 153–156.

References

Mondol S, Karanth KU, Kumar NS, Gopalaswamy AM, Andheria A, Ramakrishnan U (2009) Evaluation of non-invasive genetic sampling methods for estimating tiger population size. Biol Conserv 142(10):2350–2360.

Monterroso, P., Alves, P. C., & Ferreras, P. (2013). Catch me if you can: diel activity patterns of mammalian prey and predators. Ethology, 119(12), 1044-1056.

Monterroso, P., Alves, P. C., & Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behavioral Ecology and Sociobiology, 68(9), 1403-1417.

Monterroso, P., Díaz-Ruiz, F., Lukacs, P. M., Alves, P. C., & Ferreras, P. (2020) Ecological traits and the spatial structure of competitive coexistence among carnivores. Ecology, 101(8), e03059.

Morin, D. J., Kelly, M. J., & Waits, L. P. (2016). Monitoring coyote population dynamics with fecal DNA and spatial capture–recapture. The Journal of Wildlife Management, 80(5), 824-836.

Morris, D. W. (1989). Density-dependent habitat selection: testing the theory with fitness data. Evolutionary Ecology, 3, 80-94.

Mosquera D, Blake JG, Swing K, Romo D (2016) Ocelot (Leopardus pardalis) density in Eastern Ecuador based on capture–recapture analyses of camera trap data. Neotropical Biodivers 2(1):51–58.

Mukherjee, D. (2020). Role of fear in predator–prey system with intraspecific competition. Mathematics and Computers in Simulation, 177, 263-275.

Murdoch, J.D., Davie, H., Galbadrah, M., Reading, R.P., (2016). Factors influencing red fox occupancy probability in central Mongolia. Mammalian Biol. 81 (1), 82–88.

Murphy MA, Kendall KC, Robinson A, Waits LP (2007) .The impact of time and field conditions on brown bear (Ursus arctos) faecal DNA amplification. Conserv Genet 8(5):1219–1224

Nielsen, S. E., Johnson, C. J., Heard, D. C., & Boyce, M. S. (2005). Can models of presence-absence be used to scale abundance? Two case studies considering extremes in life history. Ecography, 28(2), 197-208.

References

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T., & Paquet, P. C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology, 10(4), 949-963.

Nsubuga AM, Robbins MM, Roeder AD, Morin PA, Boesch C, Vigilant L (2004) Factors affecting the amount of genomic DNA extracted from ape faeces and the identification of an improved sample storage method. Mol Ecol 13(7):2089–2094.

O'Brien, T.G., (2011). Abundance, density and relative abundance: a conceptual framework. In Camera traps in animal ecology. In: O', A.F., Nichols, J.D., Karanth, K.U. (Eds.), Camera Traps in Animal Ecology. Springer Japan, Tokyo, pp. 71–96.

O'Brien, T.G., Kinnaird, M.F., Wibisono, H.T., (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. Anim. Conserv. 6 (2), 131–139.

O'Connell AF, Nichols JD, Karanth KU (2011) Camera traps in animal ecology: methods and analyses (p. 271). Tokyo: Springer. odours in Mammals. Clarendon Press, Oxford: 619–722

O'Brien, T. G., & Kinnaird, M. F. (2011). Density estimation of sympatric carnivores using spatially explicit capture–recapture methods and standard trapping grid. Ecological Applications, 21(8), 2908-2916.

Osorio-Olvera, L. A., Falconi, M., & Soberón, J. (2016). Sobre la relación entre idoneidad del hábitat y la abundancia poblacional bajo diferentes escenarios de dispersión. Revista mexicana de biodiversidad, 87(3), 1080-1088.

Osorio-Olvera, L., Soberón, J., & Falconi, M. (2019). On population abundance and niche structure. *Ecography*, *42*(8), 1415-1425.

Ostrander EA, Sprague Jr GF, Rine J (1993) Identification and characterization of dinucleotide repeat (CA) n markers for genetic mapping in dog. Genomics 16(1):207–213.

Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations.Wildlife monographs, (62),3–135

Padial, J. M., Avila, E., & Sanchez, J. M. (2002). Feeding habits and overlap among red fox (Vulpes vulpes) and stone marten (Martes foina) in two Mediterranean mountain habitats. Mammalian Biology, 67(3), 137-146.

Palmer, M.S., Swanson, A., Kosmala, M., Arnold, T., Packer, C., (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. Afr. J. Ecol. 56 (4), 791–803..

Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. The American Naturalist, 153(5), 492-508.

Palomares, F., Delibes, M., Revilla, E., Calzada, J., & Fedriani, J. M. (2001). Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. Wildlife Monographs, 1-36.

Palomares, F., Ferreras, P., Fedriani, J. M., & Delibes, M. (1996). Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. Journal of Applied Ecology, 5-13.

Papakosta, M., Bakaloudis, D., Kitikidou, K., Vlachos, C., & Chatzinikos, E. (2010). Dietary overlap among seasons and habitats of red fox and stone marten in Central Greece. European Journal of Scientific Research, 45(1), 122-127.

Papp, C. R., Egerer, H., Kuraś, K., & Nagy, G. (2020). International action plan on conservation of large carnivores and ensuring ecological connectivity in the Carpathians. In UNEP Vienna Programme Office-Secretariat of the Carpathian Convention, WWF Romania, CEEWeb, Eurac Research. 22pp.

Parker LD, Campana MG, Quinta JD, Cypher B, Rivera I, Fleischer RC, Maldonado JE (2021) An efficient noninvasive method for simultaneous species, individual, and sex identification of sympatric Mojave Desert canids via in-solution SNP capture. Authorea Preprints

Pascual Rosa V, Aguilera Benavente F, Rocha P, Gómez Delgado W, M., Bosque Sendra J (2010) Simulación de modelos de crecimiento urbano: métodos de comparación con los mapas reales. In Congreso Nacional de Tecnologías de la Información Geográfica (14. 2010. Sevilla) (2010), p 1.000-1.013. Universidad de Sevilla

References

Pearce, J., & Ferrier, S. (2001). The practical value of modelling relative abundance of species for regional conservation planning: a case study. Biological conservation, 98(1), 33-43.

Peñuelas, J., Sardans, J., Filella, I., Estiarte, M., Llusià, J., Ogaya, R., ... & Terradas, J. (2017). Impacts of global change on Mediterranean forests and their services. *Forests*, *8*(12), 463.

Pereira, P., Da Silva, A.A., Alves, J., Matos, M., Fonseca, C., (2012). Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. Ecol. Res. 27 (4), 745–753.

Peterson RO, Jacobs AK, Drummer TD, Mech LD, Smith DW (2002) Leadership behaviour in relation to dominance and reproductive status in gray wolves, Canis lupus. Can J Zool 80(8):1405–1412.

Peterson, A. T. (2011). Ecological niche conservatism: A time-structured review of evidence. Journal of Biogeography, 38(5), 817-827.

Petrov, P. R., Popova, E. D., & Zlatanova, D. P. (2016). Niche partitioning among the red fox Vulpes vulpes (L.), stone marten Martes foina (Erxleben) and pine marten Martes martes (L.) in two mountains in Bulgaria. Acta Zoologica Bulgarica, 68(3), 375-390.

Phillips, M., Catling, P.C., (1991). Home range and activity patterns of red foxes in Nadgee Nature Reserve. Wildlife Res. 18 (6), 677–686.

Pilot M, Dąbrowski MJ, Hayrapetyan V, Yavruyan EG, Kopaliani N, Tsingarska E, Bogdanowicz W (2014) Genetic variability of the grey wolf Canis lupus in the Caucasus in comparison with Europe and the Middle East: distinct or intermediary population? PLoS ONE 9(4):e93828.

Pita, R., Mira, A., Moreira, F., Morgado, R., & Beja, P. (2009). Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. Agriculture, Ecosystems & Environment, 132(1-2), 57-65.

Pokheral, C. P., & Wegge, P. (2019). Coexisting large carnivores: spatial relationships of tigers and leopards and their prey in a prey-rich area in lowland Nepal. Ecoscience, 26(1), 1-9.

References

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual review of ecology and systematics, 297-330.

Pollock KH (1976) Building models of capture-recapture experiments. J Royal Stat Soc Ser D (The Statistician) 25(4):253–259.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L., Sauer, J.R., (2002). Large scale wildlife monitoring studies: statistical methods for design and analysis. Environ.: Offic. J. Int. Environ. Society 13 (2), 105–119.

Pörtner, H. O., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E., ... & Ibrahim, Z. Z. (2022). Climate change 2022: impacts, adaptation and vulnerability. IPCC.

Posillico, M., Serafini, P., & Lovari, S. (1995). Activity patterns of the stone marten Martes foina Erxleben, 1777, in relation to some environmental factors. Hystrix, the Italian Journal of Mammalogy, 7(1-2).

Prion S, Haerling KA (2014) Making sense of methods and measurement: Pearson product- moment correlation coefficient. Clin Simul Nurs 11(10):587–588.

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS, Brashares JS (2009) The rise of the mesopredator. Bioscience 59(9):779–791.

Prugh, L. R., & Sivy, K. J. (2020). Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecology Letters, 23(5), 902-918.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

QGIS.org, %Y. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rabelo, R. M., Aragón, S., & Bicca-Marques, J. C. (2019). Prey abundance drives habitat occupancy by jaguars in Amazonian floodplain river islands. Acta Oecologica, 97, 28-33.

References

Ralls K, Sharma S, Smith DA, BREMNER-HARRISON S, Cypher BL, Maldonado JE (2010) Changes in kit fox defecation patterns during the reproductive season: implications for noninvasive surveys. J Wildl Manag 74(7):1457–1462.

Ramesh, T., Downs, C.T., (2015). Impact of land use on occupancy and abundance of terrestrial mammals in the Drakensberg Midlands, South Africa. J. Nature Conserv. 23, 9–18.

Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2012). Spatio-temporal partitioning among large carnivores in relation to major prey species in W estern G hats. Journal of Zoology, 287(4), 269-275.

Rauset, G. R., Kindberg, J., & Swenson, J. E. (2012). Modeling female brown bear kill rates on moose calves using global positioning satellite data. The Journal of Wildlife Management, 76(8), 1597-1606.

Ray, J., Redford, K. H., Steneck, R., & Berger, J. (Eds.). (2013). Large carnivores and the conservation of biodiversity. Island Press.

Recio, M.R., Arija, C.M., Cabezas-Díaz, S., Virgós, E., (2015). Changes in Mediterranean mesocarnivore communities along urban and ex-urban gradients. Curr. Zool. 61 (5), 793–801.

Remonti, L., Balestrieri, A., Ruiz-González, A., Gómez-Moliner, B. J., Capelli, E., & Prigioni, C. (2012). Intraguild dietary overlap and its possible relationship to the coexistence of mesocarnivores in intensive agricultural habitats. Population Ecology, 54(4), 521-532.

Remonti, L., Ruiz-González, A., & Balestrieri, A. (2022). Colonization of Agricultural Landscapes by the Pine Marten: Influence of Habitat Constraints and Interspecific Competition. Small Carnivores: Evolution, Ecology, Behaviour, and Conservation, 275-292.

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics, 14(3), 322-337.

Ríos-Muñoz, C. A., Vega-Flores, M., Vega-Flores, K. M., Hernández-Rubio, S., & Martínez, D. V. E. (2021). DEL CONCEPTO A SU APLICACIÓN: EL PROCESO DEL MODELADO DE NICHOS ECOLÓGICOS Y SUS ALGORITMOS: El proceso del modelado de nichos ecológicos y sus algoritmos. Revista Latinoamericana de Herpetología, 4(1), 11-25.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science, 343(6167), 1241484.

Ripple, W. J., Wirsing, A. J., Wilmers, C. C., & Letnic, M. (2013). Widespread mesopredator effects after wolf extirpation. Biological Conservation, 160, 70-79.

Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA (2012) Ecosystem restoration with teeth: what role for predators? Trends Ecol Evol 27(5):265–271.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. Ecology letters, 12(9), 982-998.

Robinson, E. M., Lunt, J., Marshall, C. D., & Smee, D. L. (2014). Eastern oysters Crassostrea virginica deter crab predators by altering their morphology in response to crab cues. Aquatic Biology, 20(2), 111-118.

Rodgers TW, Giacalone J, Heske EJ, Janečka JE, Phillips CA, Schooley RL (2014) Comparison of noninvasive genetics and camera trapping for estimating population density of ocelots (Leopardus pardalis) on Barro Colorado Island, Panama. Trop Conserv Sci 7(4):690–705.

Roemer, G. W., Gompper, M. E., & Van Valkenburgh, B. (2009). The ecological role of the mammalian mesocarnivore. BioScience, 59(2), 165-173.

Roffler, G. H., Waite, J. N., Pilgrim, K. L., Zarn, K. E., & Schwartz, M. K. (2019). Estimating abundance of a cryptic social carnivore using spatially explicit capture–recapture. Wildlife Society Bulletin, 43(1), 31-41.

Romesburg HC (1981) Wildlife science: gaining reliable knowledge.The Journal of Wildlife

Rosalino, L. M., Macdonald, D. W., & Santos-Reis, M. (2005). Activity rhythms, movements and patterns of sett use by badgers, Meles meles, in a Mediterranean woodland.

References

Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Marois, J. J., & Jaffee, B. A. (1995). Intraguild predation among biological-control agents: theory and evidence. Biological control, 5(3), 303-335.

Rosenzweig, M. L. (1966). Community structure in sympatric Carnivora. Journal of mammalogy, 47(4), 602-612.

Rota, C. T., M. A. R. Ferreira, R. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. (2016). A multi-species occupancy model for two or more interacting species. Methods in Ecology and Evolution 7:1164–1173.

Roy, S., Ghoshal, A., Bijoor, A., & Suryawanshi, K. (2019). Distribution and activity pattern of stone marten Martes foina in relation to prey and predators. Mammalian Biology, 96(1), 110-117.

Royle JA (2004) N-Mixture models for estimating population size from spatially replicated counts. Biometrics 60(1):108–115.

Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Spatial capture-recapture. Elsevier, Academic Press, Waltham, Massachusetts

Royle, A.J. Andrew. et al. Spatial Capture-Recapture. Boston: Elsevier, 2013. Print.

Royle, J. A. (2006). Site occupancy models with heterogeneous detection probabilities. Biometrics, 62(1), 97-102.

Royle, J.A., Nichols, J.D., Kéry, M., (2005). Modelling occurrence and abundance of species when detection is imperfect. Oikos 110 (2), 353–359.

Sacks BN, Moore M, Statham MJ, Wittmer HU (2011). A restricted hybrid zone between native and introduced red fox (Vulpes vulpes) populations suggests reproductive barriers and competitive exclusion. Mol Ecol 20(2):326–341.

Sadlier LM, Webbon CC, Baker PJ, Harris S (2004) Methods of monitoring red foxes Vulpes vulpes and badgers Meles meles: are field signs the answer? Mammal Rev 34(1–2):75–98.

Sagarin, R. D. and Gaines, S. D. 2002. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. – J. Biogeogr. 29: 985

References

Sagarin, R. D., & Gaines, S. D. (2002). The ‘abundant centre’distribution: to what extent is it a biogeographical rule?. Ecology letters, 5(1), 137-147.

Santini, L. et al. 2018. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. – Ecography doi:10.1111/ecog.04027

Santos, F., Carbone, C., Wearn, O. R., Rowcliffe, J. M., Espinosa, S., Lima, M. G. M., ... & Peres, C. A. (2019). Prey availability and temporal partitioning modulate felid coexistence in Neotropical forests. PloS one, 14(3), e0213671.

Santos, M. J., & Santos-Reis, M. (2010). Stone marten (Martes foina) habitat in a Mediterranean ecosystem: effects of scale, sex, and interspecific interactions. European Journal of Wildlife Research, 56, 275-286.

Sarmento P, Cruz J, Eira C, Fonseca C (2009) Evaluation of camera trapping for estimating red fox abundance. J Wildl Manag 73(7):1207–1212.

Sarmento, P. B., Cruz, J., Eira, C., & Fonseca, C. (2011). Modeling the occupancy of sympatric carnivorans in a Mediterranean ecosystem. European Journal of Wildlife Research, 57, 119-131.

Sarmento, P.B., Cruz, J.P., Eira, C.I., Fonseca, C., (2010). Habitat selection and abundance of common genets Genetta genetta using camera capture-mark-recapture data. Eur. J. Wildl. Res. 56 (1), 59–66.

Scandura M, Apollonio M, Mattioli L (2001) Recent recovery of the italian wolf population: a genetic investigation using microsatellites. Mammalian Biology 66:321–331

Schauster, E.R., Gese, E.M., Kitchen, A.M., (2002). An evaluation of survey methods for monitoring swift fox abundance. Wildl. Soc. Bull. 464–477.

Schmidt, B.R., Schmidt, B.R., Gschwend, G., Schmidt, B.R., Gschwend, G., Bachmann, J. A., Schmidt, B.R., Gschwend, G., Bachmann, J.A., Dermond, P., (2015). Use of removal sampling to estimate abundance of larval salamanders (Salamandra salamandra) in streams. Amphibia-Reptilia 36 (1), 87–92.

Schoener, T. W. (1974). Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. Science, 185(4145), 27-39.

References

Schoener, T. W. (1982). The controversy over interspecific competition: despite spirited criticism, competition continues to occupy a major domain in ecological thought. American Scientist, 70(6), 586-595.

Schoener, T. W. (1983). Field experiments on interspecific competition. The american naturalist, 122(2), 240-285.

Sebastián-González E, Morales-Reyes Z, Naves-Alegre L, Alemañ CJD, Lima LG, Lima LM, Sánchez-Zapata JA (2020) Which bait should I use? Insights from a camera trap study in a highly diverse cerrado forest. Eur J Wildl Res 66(6):1–8.

Seoane, J., Carrascal, L. M., Alonso, C. L., & Palomino, D. (2005). Species-specific traits associated to prediction errors in bird habitat suitability modelling. Ecological Modelling, 185(2-4), 299-308.

Servín, J., Rau, J. R., & Delibes, M. (1991). Activity pattern of the red fox Vulpes vulpes in Dońana, SW Spain. Acta Theriologica, 36(3-4), 369-373.

Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C. G., Sousa-Guedes, D., Martínez-Freiría, F., ... & Barbosa, A. M. (2021). Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. Ecological Modelling, 456, 109671.

Silveira L, Jacomo AT, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: a comparative evaluation. Biol Conserv 114(3):351–355.

Silver, S.C., Ostro, L.E.T., Marsh, L.K., Maffei, L., Noss, A.J., Kelly, M.J., Wallace, R.B., Gómez, H., Ayala, G., (2004). The use of camera traps for estimating jaguar Panthera onca abundance and density using capture/recapture analysis. Oryx 38 (2), 148–154.

Silverstein, R. P. (2005). Germination of native and exotic plant seeds dispersed by coyotes (Canis latrans) in southern California. The Southwestern Naturalist, 50(4), 472-478.

Soberón, J. M. (2010). Niche and area of distribution modeling: a population ecology perspective. Ecography, 33(1), 159-167.

Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas.

References

Soisalo MK, Cavalcanti SM (2006) Estimating the density of a jaguar population in the brazilian pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biol Conserv 129(4):487–496.

Soler, L., Lucherini, M., Manfredi, C., Ciuccio, M., Casanave, E.B., (2009). Characteristics of defecation sites of the Geoffroy's cat Leopardus geoffroyi. Mastozoología Neotropical 16 (2), 485–489.

Sollmann R, Tôrres NM, Furtado MM, de Almeida Jácomo AT, Palomares F, Roques S, Silveira L (2013) Combining camera-trapping and noninvasive genetic data in a spatial capture–recapture framework improves density estimates for the jaguar. Biol Conserv 167:242–247.

Sollmann, R., B. Gardner, and J. L. Belant. (2012). How does spatial study design influence density estimates from spatial capture-recapture models? PLoS ONE 7(4):e34575.

Sorace, A., Gustin, M., (2009). Distribution of generalist and specialist predators along urban gradients. Landscape Urban Plann. 90 (3–4), 111–118.

Soto, C., & Palomares, F. (2015). Coexistence of sympatric carnivores in relatively homogeneous Mediterranean landscapes: functional importance of habitat segregation at the fine-scale level. Oecologia, 179, 223-235.

Spong, G. (2002). Space use in lions, Panthera leo, in the Selous Game Reserve: social and ecological factors. Behavioral Ecology and Sociobiology, 52, 303-307.

Srbek-Araujo AC, Chiarello AG (2005) Is camera-trapping an efficient method for surveying mammals in neotropical forests? A case study in south-eastern Brazil. J Trop Ecol 21(1):121–125

Stokes, M. K., Slade, N. A., & Blair, S. M. (2001). Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. Canadian Journal of Zoology, 79(6), 966-972.

Storch, I., Lindström, E., & De Jounge, J. (1990). Diet and habitat selection of the pine marten in relation to competition with the red fox. Acta Theriologica, 35(3-4), 311-320.

References

St-Pierre, C., Ouellet, J. P., & Crête, M. (2006). Do competitive intraguild interactions affect space and habitat use by small carnivores in a forested landscape?. Ecography, 29(4), 487-496.

Strampelli, P., Henschel, P., Searle, C. E., Macdonald, D. W., & Dickman, A. J. (2023). Spatial co-occurrence patterns of sympatric large carnivores in a multi-use African system. Plos one, 18(1), e0280420.

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. Nature communications, 7(1), 1-7.

Taberlet P, Griffin S, Goossens B, Questiau S, Manceau V, Escaravage N, Bouvet J (1996) Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Res 24(16):3189–3194.

Tellería, J. L., Santos, T., Refoyo, P., & Muñoz, J. (2012). Use of ring recoveries to predict habitat suitability in small passerines. Diversity and Distributions, 18(11), 1130-1138.

Terborgh, J., Estes, J. A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B. J., & Noss, R. F. (1999). The role of top carnivores in regulating terrestrial ecosystems. Continental conservation: scientific foundations of regional reserve networks, 39-64.

Terborgh, J., Holt, R. D., Estes, J. A., Terborgh, J., & Estes, J. (2010). Trophic cascades: what they are, how they work, and why they matter (pp. 1-18). Island Press, Washington, DC.

Tester, J. R. (1987). Changes in daily activity rhythms of some freeranging animals. Can. FieZd-Nat, 101, 13-21.

Torres, R. T., Virgós, E., Santos, J., Linnell, J. D., & Fonseca, C. (2012). Habitat use by sympatric red and roe deer in a Mediterranean ecosystem. Animal Biology, 62(3), 351-366.

Torretta, E., Mosini, A., Piana, M., Tirozzi, P., Serafini, M., Puopolo, F., ... & Balestrieri, A. (2017). Time partitioning in mesocarnivore communities from different habitats of NW Italy: insights into martens' competitive abilities. Behaviour, 154(2), 241-266.

References

Torretta, E., Serafini, M., Puopolo, F., & Schenone, L. (2016). Spatial and temporal adjustments allowing the coexistence among carnivores in Liguria (NW Italy). acta ethologica, 19, 123-132.

Tourani, M. (2022). A review of spatial capture–recapture: Ecological insights, limitations, and prospects. Ecology and Evolution, 12(1), e8468.

Travaini, A., Aldama, J.J., Laffitte, R., Delibes, M., (1993). Home range and activity patterns of red fox Vulpes vulpes breeding females. Acta Theriol. 38, 427–434.

Trolle M, Noss AJ, Lima EDS, Dalponte JC (2007) Camera-trap studies of maned wolf density in the Cerrado and the Pantanal of Brazil. Biodivers Conserv 16(4):1197–1204.

Trouwborst, A. (2015). Global large carnivore conservation and international law. Biodiversity and Conservation, 24, 1567-1588.

Valière N (2003) GIMLET v. 1.3. 2 guide. Laboratoire de Biométrie et biologie Evolutive-UMR5558-43, boulevard du 11 novembre 1918-F69622, Villeurbanne, France

Valladares, F. (2007). El hábitat mediterráneo continental: un sistema humanizado, cambiante y vulnerable. En, Paracuellos (coord. de la ed.). Ambientes mediterráneos. Funcionamiento, biodiversidad y conservación de los ecosistemas mediterráneos. Colección Medio Ambiente, 2.

Vanak, A. T., Fortin, D., Thaker, M., Ogden, M., Owen, C., Greatwood, S., & Slotow, R. (2013). Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. Ecology, 94(11), 2619-2631.

Vandermeer, John H. "Niche theory." Annual review of Ecology and Systematics 3.1 (1972): 107-132.

VanDerWal, J., Shoo, L. P., Johnson, C. N., & Williams, S. E. (2009). Abundance and the environmental niche: environmental suitability estimated from niche models predicts the upper limit of local abundance. The American Naturalist, 174(2), 282-291.

Veech JA, Ott JR, Troy JR (2016) Intrinsic heterogeneity in detection probability and its effect on N-Mixture models. Methods Ecol Evol 7(9):1019–1028.

References

Velli E, Bologna MA, Silvia C, Ragni B, Randi E (2015) Non-invasive monitoring of the european wildcat (Felis silvestris silvestris Schreber, 1777): comparative analysis of three different monitoring techniques and evaluation of their integration. Eur J Wildl Res 61(5):657–668

Vilà C, Urios V, Castroviejo J (1994) Use of faeces for scent marking in Iberian wolves (Canis lupus). Can J Zool 72(2):374–377.

Vilella, M., Ferrandiz-Rovira, M., & Sayol, F. (2020). Coexistence of predators in time: Effects of season and prey availability on species activity within a Mediterranean carnivore guild. Ecology and Evolution, 10(20), 11408-11422.

Villafuerte, R., Viñuela, J., Blanco, J.C., (1998). Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain. Biol. Conserv. 84 (2), 181–188.

Vine, S.J., Crowther, M.S., Lapidge, S.J., Dickman, C.R., Mooney, N., Piggott, M.P., English, A.W., (2009). Comparison of methods to detect rare and cryptic species: a case study using the red fox (Vulpes vulpes). Wildlife Res. 36 (5), 436–446.

Virgós E, Telleria J, Santos T (2002) A comparison on the responseto forest fragmentation by medium-sized Iberian carnivores in central Spain. Biodivers Conserv 11:1063–1079

Virgós E, Travaini A (2005) Relationship between small-game hunting and carnivore diversity in central Spain. Biodivers Conserv 14(14):3475–3486.

Virgós, E., & Casanovas, J. G. (1998). Distribution patterns of the stone marten (Martes foina Erxleben, 1777) in Mediterranean mountains of central Spain. Zeitschrift fur Saugetierkunde, 63(4), 193-199.

Virgós, E., & García, F. J. (2002). Patch occupancy by stone martens Martes foina in fragmented landscapes of central Spain: the role of fragment size, isolation and habitat structure. Acta Oecologica, 23(4), 231-237.

Virgós, E., (2001) a. Relative value of riparian woodlands in landscapes with different forest cover for medium-sized Iberian carnivores. Biodivers. Conserv. 10 (7), 1039–1049.

References

Virgós, E., (2001) b. Role of isolation and habitat quality in shaping species abundance: a test with badgers (Meles meles L.) in a gradient of forest fragmentation. J. Biogeogr. 28 (3), 381–389.

Virgós, E., Baniandrés, N., Burgos, T., & Recio, M. R. (2020). Intraguild predation by the eagle owl determines the space use of a mesopredator carnivore. Diversity, 12(9), 359.

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

Virgós, E., Recio, M.R., Cortés, Y., (2000). Stone marten (Martes foina) use of different landscape types in the mountains of central Spain. Zeitschrift für Saügetierkunde 65, 375–379.

Waits LP, Luikart G, Taberlet P (2001) Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Mol Ecol 10(1):249–256.

Wang, Y., Allen, M. L., & Wilmers, C. C. (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation, 190, 23-33.

Webbon, C.C., Baker, P.J., Harris, S., (2004). Faecal density counts for monitoring changes in red fox numbers in rural Britain. J. Appl. Ecol. 41 (4), 768–779

Weber, M.M., Stevens, R.D., Diniz-Filho, J.A.F., Grelle, C.E.V., (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. Ecography 40 (7), 817–828.

Wegge P, Bakke BB, Odden M, Rolstad J (2019) DNA from scats combined with capture recapture modeling: a promising tool for estimating the density of red foxes a pilot study in a boreal forest in southeast Norway. Mammal Res 64(1):147–154.

Wiens, John J., et al. "Niche conservatism as an emerging principle in ecology and conservation biology." Ecology letters 13.10 (2010): 1310-1324.

Williams, B. K., Nichols, J. D., & Conroy, M. J. (2002). Analysis and management of animal populations. Academic press.

References

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. Royal Society open science, 4(7), 170052.

Wolf, Christopher, and William J. Ripple. "Prey depletion as a threat to the world's large carnivores." Royal Society open science 3.8 (2016): 160252.

Wolff, J.O., Caughley, G., Sinclair, A.R.E., (1995). Wildlife ecology and management. Blackwell Sci. 64 (3), 420.

Wolff, P. J., Taylor, C. A., Heske, E. J., & Schooley, R. L. (2015). Habitat selection by American mink during summer is related to hotspots of crayfish prey. Wildlife Biology, 21(1), 9-17.

Wróbel, A., & Bogdziewicz, M. (2015). It is raining mice and voles: which weather conditions influence the activity of Apodemus flavicollis and Myodes glareolus?. European Journal of Wildlife Research, 61(3), 475-478.

Zabala, J., Zuberogoitia, I., & Martínez-Climent, J. A. (2009). Testing for niche segregation between two abundant carnivores using presence-only data. Folia Zoologica, 58(4), 385.

Zaman, M., Tolhurst, B., Zhu, M., Heng, B., Jiang, G., (2019). Do Red Foxes (Vulpes vulpes) Increase the Detectability of Scent Marks by Selecting Highly Conspicuous Substrates? J. Ethol.and Animal Sci. 2 (2), 000113.

Zanin M, Adrados B, González N, Roques S, Brito D, Chávez C, Palomares F (2016) Gene flow and genetic structure of the puma and jaguar in Mexico. Eur J Wildl Res 62(4):461–469.

Zielinski, W. J., Tucker, J. M., & Rennie, K. M. (2017). Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. Biological Conservation, 209, 533-545.

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