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Ecological Interactions and Species Coexistence in Iberian Mesocarnivore Communities

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Resumo

Em comunidades de predadores, a biomassa dos mesopredadores excede a dos predadores de topo. Consequentemente, os requisitos energéticos dos mesocarnívoros (como comunidade) sugerem que o seu impacto sobre os níveis tróficos inferiores são significativos. Vários casos de desregulação nos ecossistemas têm sido descritos como resultado de alterações nas comunidades de mesocarnívoros (*e.g.* a explosão demográfica de espécies presa após a supressão da predação, ou imposição de um efeito de poço de predação imposto por predadores em espécies presa). No entanto, a estrutura das comunidades de mesocarnívoros é complexa e resulta de uma teia multidimensional de interações entre os diferentes níveis tróficos existentes, através de efeitos de regulação superior e inferior, interações com espécies do mesmo nível trófico ou qualidade do habitat. Assim, a compreensão dos factores que atuam para estruturar estes sistemas revela-se fundamental para uma adequada gestão e planeamento de ações de conservação.

As características ecológicas e comportamentais dos mesocarnívoros fazem com que estas espécies sejam particularmente difíceis de estudar. Por outro lado, estudos sobre comunidades ou sobre múltiplas espécies em simultâneo revelam-se especialmente difíceis de implementar. No entanto, os progressos recentes em técnicas não-invasivas têm promovido a sua implementação, tornando-as mais comuns no estudo de mamíferos carnívoros terrestres. Adicionalmente, desenvolvimentos nas tecnologias associadas a estas amostragens, nomeadamente ao nível dos métodos moleculares, têm permitido uma maior acessibilidade a este tipo de aproximações. Na presente dissertação são focadas duas questões fundamentais: a avaliação da adequabilidade e desenvolvimento de metodologias não-invasivas para o estudo de mesocarnívoros e a investigação das estratégias utilizadas pelos mesocarnívoros presentes nas comunidades terrestres que permitem a sua coexistência no Sudoeste (SW) da Europa.

Ao nível metodológico, identificou-se que a urina de lince, combinada com extracto de valeriana, atraem com eficiência a maioria das espécies presentes nas comunidades de carnívoros do SW Europeu, podendo ser usadas em associação a metodologias de detecção remota para aumentar as probabilidades de detecção. Identificou-se também

que a identificação de excrementos de mesocarnívoros com base nas suas características morfológicas são sujeitas a taxas de erro variáveis (entre 5 e 100%). Estas taxas de erro são dependentes da abundancia das espécies alvo, das características dos excrementos e de factores contexto-dependentes. Este facto impede a sua extrapolação entre áreas e enfatiza que as metodologias tradicionais (principalmente as baseadas na identificação morfológica dos excrementos) são favoráveis à produção de resultados incorretos, potencialmente perigosos para a conservação da natureza. É sugerido que as metodologias moleculares não-invasivas representam uma ferramenta essencial para a minimização deste tipo de enviesamentos. Finalmente, é sugerido que as amostragens com estações de pêlo poderão representar uma alternativa eficaz e de reduzidos custos para a monitorização de mesocarnívoros a largo prazo, com a vantagem adicional de permitir obter informação profunda sobre vários parâmetros populacionais através da análise genética das amostras recolhidas. No entanto, a reduzida detectabilidade deste método indica que são necessários ainda desenvolvimentos significativos para aumentar a sua eficiência.

Ao nível ecológico, verificou-se que, apesar do elevado aporte energético associado à captura de coelho-bravo, a comunidade de mesocarnívoros sincroniza o seu ritmo circadiano de atividade com a dos roedores. A sua atividade é apenas parcialmente sobreposta com do coelho-bravo. Foi possível identificar três grupos de mesocarnívoros no que respeita à sua atividade circadiana: espécies estritamente noturnas, espécies facultativamente noturnas e espécies estritamente diurnas. No entanto, apesar do tipo de atividade que exibem, todas as espécies apresentam plasticidade suficiente alterar os seus padrões de atividade dentro do período preferido.

Os resultados obtidos sugerem que as relações interespecíficas entre potenciais competidores são dinâmicas, podendo variar entre períodos e com a localização geográfica. Foram observados ajustes no eixo espacial do nicho ecológico em comunidades dominadas por mesocarnívoros, onde as espécies possuem tamanhos similares. No entanto, podem ocorrer respostas comportamentais em áreas de coocorrência, que potencialmente se expressam através de um comportamento mais ilusivo. Nesta comunidade, relações potencialmente stressantes são geridas através de ajustes ao nível do nicho trófico e temporal. Verificou-se assim, que a segregação

temporal desempenha um papel fundamental facilitando a coexistência entre espécies de mesocarnívoros, especialmente com o aumento da complexidade das comunidades. Adicionalmente, verificou-se que os recursos tróficos estão envolvidos na mediação das relações interespecíficas entre mesocarnívoros ibéricos, especialmente quando espécies potencialmente competidoras partilham a mesma espécie presa. Finalmente verificou-se que a dominância competitiva da marta (*Martes martes*) sobre a fuinha (*Martes foina*) não se verifica no Parque Nacional da Peneda-Gerês, contrastando com a teoria vigente.

No contexto atual de degradação dos ecossistemas a nível mundial e de alterações climáticas, há uma tendência generalizada para a simplificação das comunidades de vertebrados terrestres, com consequências potencialmente desastrosas para a conservação da natureza e economia mundial. Assim, torna-se relevante e urgente adquirir conhecimento sobre as relações interespecíficas entre os predadores, que são peças estruturantes dos ecossistemas. Com o presente trabalho contribui-se para este conhecimento nas comunidades de carnívoros terrestres da Península Ibérica e sugerem-se passos futuros conducentes a uma adequada visão da importância destas espécies no ecossistemas onde se inserem, que permita o desenvolvimento de medidas de conservação e gestão devidamente sustentadas.

Palavras-chave

Mesocarnívoros, Sudoeste Europeu, Amostragens não-invasivas, Identificação genética não invasiva, Armadilhagem fotográfica, Competição, Interações interespecífica, Coexistência

Abstract

In predator communities, mesopredator biomass typically exceeds that of apex predators. Consequently, the energetic requirements of mesocarnivores (as a community) suggest that their impact on lower trophic levels should be significant. Several cases of ecosystem disruptions have been described as a result of changes in predator communities (e.g. irruptions of prey species released from top-down regulation, or over-suppression of prey via a predator-pit effect). However, the structure of mesocarnivore communities is complex, and results from a multidimensional web of interactions with several trophic levels, upheld through top-down and bottom-up effects, intraguild interactions and habitat quality. Therefore, understanding the factors that act together in structuring such systems is crucial for adequate planning and management of conservation policies.

The ecological and behavioral traits of carnivores deem them particularly difficult to study. Additionally, community-wide or multiple species research studies are particularly difficult to implement. Yet, non-invasive techniques have become commoner and technological advances, namely in the field of molecular genetics, have made for such studies more accessible. In this research we aimed to address two fundamental questions: to assess the reliability and improve current sampling methods for ecological studies of mesocarnivores in Southwestern Europe; and to evaluate the strategies used by mesocarnivores that facilitate their coexistence in SW European communities.

At the methodological level, we found that lynx urine, combined with valerian extract area efficient attractants SW European carnivores, and may be used to increase detection probabilities when coupled with remote detection methods. We also found that traditional expert-based identification of carnivore scats is prone to highly variable accuracy rates (ranging from 0 to 95%). Accuracy is dependent on target species abundance, scat characteristics and context-dependent factors. This prevents the extrapolation of accuracy rates over time and sampling areas. We suggest that recently developed non-invasive molecular methods consist of a fundamental tool for minimizing such biases, which are potentially hazardous for nature conservation. Finally, while requiring higher sampling efforts, hair-snaring methods are suggested as a cost-effective method for large scale and long term monitoring of Iberian

mesocarnivores while providing deeper insights into population parameters attained through adequate analysis of genetic information. Finally, we suggest that hair snaring sampling may provide a valuable cost-effective method for large scale and long term monitoring of Iberian mesocarnivores while providing deeper insights into population parameters attained through adequate analysis of genetic information. However, further refinements are required to increase efficiency and detectability rates.

At the ecological level, we verified that, although providing higher energetic inputs provided by preying on European rabbits, mesocarnivores (as a community) preferentially track the activity of small mammals (rodents). We were able to identify three distinct groups of Iberian mesocarnivores regarding their activity patterns: strictly nocturnal, facultative nocturnal and strictly diurnal species. However, the activity patterns exhibited by mesocarnivores were not constant, as we observed activity shifts, even though such shifts were contained within the preferred parts each species' circadian cycle.

Our results suggest that the interactions between co-occurring Iberian mesocarnivores are dynamic, and their strength and direction may vary seasonally and geographically. Adjustments along the spatial dimension of the ecological niche are not a frequent strategy among co-occurring similar sized mesocarnivores in the Iberian Peninsula. However, behavioral responses may take place in areas of co-occurrence, where subordinate species may adopt higher elusiveness. In these situations, potentially stressful interactions are preferably handled by displacements along the temporal and trophic niche dimensions, allowing sympatric intraguild competitors to spatially co-occur. We verified that segregation along the temporal niche constitutes a recurrent strategy in facilitating carnivores' coexistence and that it is more pronounced in more complex communities. Additionally, our results have shown that feeding resources are involved in mediating interspecific relations among potential intraguild competitors, especially when they share the same prey species. Finally, we detected that the stone marten (*Martes foina*) appears to be the dominant competitor over the pine marten (*Martes martes*) in the Peneda-Gerês National Park, contrasting to what has been reported in other areas of sympatry.

In the current context of worldwide environmental degradation and climate change, there is a generalized tendency for a simplification of vertebrate communities, with potentially disastrous consequences for the conservation of nature and world economy.

Therefore, it is highly relevant and urgent the need to gather knowledge about interspecific relations among predators, which are fundamental pieces in structuring ecosystems. With this work, we provide new information about interspecific relations in Iberian carnivore communities, and suggest future steps towards an adequate assessment of these species' function in terrestrial ecosystems, which could lead to suitable conservation and management strategies.

Keywords

Mesocarnivores, SW Europe, Non-invasive sampling, Camera trapping, Non-invasive genetic species identification, Competition, Interspecific interactions, Coexistence

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General Introduction

1 General Introduction

1.1 The role of carnivores in ecosystems

1.1.1 Carnivore function and cascading effects in ecosystems

While eliciting diverging opinions in humans, predators are fundamental elements of natural ecosystems (Estes et al. 2011; Kruuk 2002; Ritchie et al. 2012). Increasing evidence from natural experiments and observational studies have sustained their crucial role as ecosystem engineers (Ritchie et al. 2012) that, directly or otherwise, provide a variety of ecosystem services such as enforcing top-down regulation on lower trophic levels (Estes et al. 2011; Prugh et al. 2009; Ritchie and Johnson 2009), promoting ecosystem resilience against introduced species (Carlsson et al. 2009; Salo et al. 2008), reducing the impact of wildlife diseases (Roemer et al. 2009) or by promoting seed dispersal (Rosalino and Santos-Reis 2009).

One of the most systematically advocated functions of carnivores is the enforcing of top-down regulation, which has cascading effects over the entire ecosystem and has the potential for producing fundamental changes in it (Levi and Wilmers 2012; Prugh et al. 2009; Ripple et al. 2010; Ripple and Beschta 2008; Ripple and Beschta 2006a). Although growing evidences have been published in recent years supporting such theory and describing its effects on ecosystem processes, the full implications of predators' removal or re-establishment are still underevaluated and most likely underestimated (Estes et al. 2011; Ripple et al. 2010). Top-down control imposed by carnivores act on two levels: on a demographic level (density-mediated effects), by constraining prey population numbers (Melis et al. 2009; Ripple and Beschta 2012); and on a behavioral level, by imposing constraints in the spatial and temporal activity patterns of subordinate species (Cozzi et al. 2012; Laundré et al. 2001; Ripple and Beschta 2006b). These effects act synergistically on prey populations by constraining their biomass and spatial distribution.

Upon a meta-analysis of the predatory impacts of the wolf and brown bear (*Ursus arctos*), Ripple and Beschta (2012) found that top down forces exherted by these predators was relatively strong in systems where they were present, as mean density of cervids was significantly lower in areas where wolves were functionally present than in areas where they were rare or absent. They further found that predation by brown bears on cervids was additive to that of wolves, rather than compensatory. In a parallel study, Melis et al. (2009) identified top-down control of roe deer (*Capreolus capreolus*) populations as a result of the predatory impact of wolves and Eurasian lynxes (*Lynx lynx*). Another example of top-down density-mediated control was described by Ripple and Beschta (2006a), who linked a decline in cougar (*Puma concolor*) densities to disproportionate irruptions of mule deer (*Odocoileus hemionus*) as a result of release from top-down control. Simultaneously, resent research has also reported behavioral-mediated effects of predators on prey populations via implementation of a landscape of fear (Laundré et al. 2001), which is a visual model of how fear could alter an animal's use of an area as it tries to reduce its vulnerability to predation (Laundre et al. 2010; Ripple and Beschta 2004). However, the top-down processes described above for predator-prey relations are also applied in the context of intraguild competitors. Dominant competitors have the ability to suppress subordinate species populations or constrain their access to the most beneficial resources, which can be optimal prey, habitat, or period of the day.

1.1.2 Intraguild interactions among mammalian carnivores

The composition and structure of carnivore communities is strongly influenced by interspecific competitive interactions (Donadio and Buskirk 2006; Ritchie and Johnson 2009). Intraguild predation (IGP) constitutes an intense form of pre-emptive interference competition (Ritchie and Johnson 2009), and is a widespread biological interaction, especially in carnivore communities (Arim and Marquet 2004; Palomares and Caro 1999). Its intensity is mediated by relative body size (being more intense at intermediate body size differences), feeding ecology, prey availability and predatory habits of the species involved (Donadio and Buskirk 2006; Palomares and Caro 1999). IGP is a non-random phenomenon and its occurrence is considered to be largely mediated by the exploitation of a shared resource, which is more efficiently explored by the subordinate/victim (Arim and Marquet 2004; Palomares and Caro 1999).

Several cases of density-mediated effects of apex predators on subordinate species have been reported all over the world and, at times, have provided counterintuitive patterns. Eurasian lynxes had been extirpated from large areas of their former range in Scandinavia, and were close to extinction in the 1950s (Elmhagen et al. 2010; Elmhagen and Rushton 2007). This decline of the Eurasian lynx was inversely related to red fox (*Vulpes vulpes*) abundance, which increased their numbers steeply (Elmhagen and Rushton 2007; Pasanen-Mortensen et al. 2013). The posterior recolonization of Eurasian lynxes provided further support for their ability to control fox populations, which varied with system productivity according to the exploitation ecosystems hypothesis (EEH) (Oksanen et al. 1981). Ritchie et al. (2012) suggested that these effects might have further ramifications depending on carnivore community complexity. Red foxes may limit pine martens' (*Martes martes*), American minks' (*Neovison vison*) and artic foxes (*Alopex lagopus*) populations by actively pursuing and killing them (Carlsson et al. 2009; Frafjord et al. 1989; Lindström et al. 1995). Therefore, in complex systems where Eurasian lynxes suppress red foxes through top-down control, pine martens could be released from a control enforced by red foxes and increase in abundance. A similar process could happen in arctic systems with Eurasian lynxes, red foxes and arctic foxes. However, the strength of these interactions is context-dependent, being affected by the landscape structure, system productivity and prey availability (Estes et al. 2011; Ritchie et al. 2012; Ritchie and Johnson 2009). Nonetheless, the effect of top-down control by Eurasian lynxes could have also undesirable effects, if the suppression of red fox populations releases the American minks, which is an invasive species in Europe (Kauhala 1996). However, if Eurasian otters (*Lutra lutra*) are present, they may compensate the effect of the reduced red fox abundance, by controlling minks themselves (Bonesi et al. 2004). Similar findings were obtained in a different system involving wolves, coyotes (*Canis latrans*) and foxes (*Vulpes vulpes* and *Vulpes velox*) in the North American continent. During the 19th and early 20th centuries, wolf populations were widely persecuted in the United States, which led to significant contraction of their distributional range (Laliberte and Ripple 2004; Ripple et al. 2010). Increasing evidence suggests that the wolf presence is negatively related with the densities of coyotes (Berger and Gese 2007; Levi and Wilmers 2012; Ripple et al. 2013). Therefore, wolf extirpation from the American west led to dramatic increases in coyote densities (Ripple et al. 2013). However, in areas where coyotes have claimed the role of top predators because of the absence of wolves, they have the potential to suppress fox populations (Levi and Wilmers 2012; Ripple et al. 2013). In the Iberian Peninsula (IP), southwestern Europe (SW Europe), Iberian lynxes have been reported to suppress Egyptian mongoose (*Herpestes ichneumon*) (Palomares et al. 1998; Palomares et al. 1995) following a similar cascade of density-mediated effects as that identified with Eurasian lynxes and red foxes in Scandinavia, or with wolves and coyotes in North America.

When apex predators are removed from a system, and subordinate species (i.e. mesopredators) are released from their suppression effect, their abundance will most likely increase disproportionally (Ritchie and Johnson 2009). This effect was coined as the mesopredator release hypothesis (MRH) (Soule et al. 1988), and has been intensively described in terrestrial and marine ecosystems, although the full extent of its ecological impacts is just beginning to be understood (Estes et al. 2011; Prugh et al. 2009; Ripple et al. 2010; Roemer et al. 2009).

Competitive interactions among coexisting carnivores, however, are not restricted to density-mediated interactions, such as IGP. These direct lethal encounters are most likely just a small part of all competitive interactions among coexisting carnivores (Ritchie and Johnson 2009), and although IGP is responsible for a large proportion of deaths in predator communities (Palomares and Caro 1999), the effects of other forms of interference interactions are most likely underestimated in community ecology, because their effects are less conspicuous (Elmhagen et al. 2010; Ritchie and Johnson 2009). The “ecology of fear” (Brown et al. 1999) and its spatially explicit representation - the landscape of fear (Laundré et al. 2001) - is also applicable in the framework of intraguild competitive interactions (Scheinin et al. 2006). Dominant competitors (apex predators) can influence the distribution and behavior of subordinate competitors (mesocarnivores) either directly, through IGP, or indirectly, through the fear of IGP (Roemer et al. 2009). Therefore, behavioral adjustments in foraging strategies may also play a critical role in reducing agonistic encounters, therefore promoting coexistence and biodiversity (Linnell and Strand 2000). Examples of such behavioral-mediated effects have been reported in several systems across the world as a means to promote coexistence among sympatric competitors (Ritchie et al. 2012). The behavioral effects most frequently reported are the limitation of accessibility to the most favorable habitats (Harrington and Macdonald 2008; Mitchell and Banks 2005; Palomares et al. 1996; Wilson et al. 2010) or/and to the most profitable prey (Cupples et al. 2011; Hass 2009; Moreno et al. 2006) or the temporal segregation (Di Bitetti et al. 2009; Cozzi et al. 2012; Gerber et al. 2012; Harrington and Macdonald 2008).

1.1.3 Trophic downgrading of terrestrial ecosystems

Carnivore occupancy and persistence is dependent on a variety of factors, namely their biotic traits and anthropogenic impacts (Cardillo et al. 2004; Diniz-Filho et al. 2009). Direct or indirect human-related impacts in ecosystems such persecution (Casanovas et al. 2012; Woodroffe et al. 2008), degradation of natural habitats (Brooks et al. 2002) or disruption of ecosystem processes (Shepard et al. 2008), have led to worldwide declines of apex predator populations, and consequent extinction in most of their original range leading to a process denoted as “trophic downgrade”, which refers to the consequences of removing apex consumers from nature (Estes et al. 2011). The frequency of apex predator extinctions has transferred the role of top-down effects to subordinate levels in trophic webs all over the globe (Prugh et al. 2009). Yet, most species “promoted” to the apex predator status cannot completely replace “true” apex predators because they tend to have fundamentally different relations with people and ecosystems (Cove et al. 2012; Levi and Wilmers 2012; Prugh et al. 2009). Evidence of fundamental changes in ecosystems due to changes of top-down regulation have only recently became evident, and have just appeared in literature since the beginning of the 21st century (Estes et al. 2011). Given that the strength and relative dominance position of interspecific competitors is dependent on their relative body size, availability of prey and habitat (Donadio and Buskirk 2006; Ritchie and Johnson 2009), the removal of apex predators will contribute to the homogenization of body sizes among species within the affected guild. Therefore, in these apex predator deprived ecosystems, the web of competitive relations among similar sized sympatric mesocarnivores can change between areas as a result of local conditions.

While asymmetrical competitive relations among predator species have been a fairly common focus of recent research (Fedriani et al. 1999; Pasanen-Mortensen et al. 2013), mutual reciprocal competitive interactions within carnivore communities have rarely been addressed. Given that most of the world’s ecosystems are partially or completely deprived of apex predators, understanding intraguild mesopredator relations should be a major concern because they are likely to have a significant impact on ecosystem structure (Laundre et al. 2010; Prugh et al. 2009; Roemer et al. 2009). In these communities, where interference competition can be mutual, an increase in predator diversity should result in prey release (Roemer et al. 2009). Understanding which forces act and in which direction to shape ecosystems is crucial for adequate conservation planning and management (Ripple et al. 2013). Within the current worldwide context of climate change and human-related habitat destruction, the ability to foresee potential community responses to expected changes in the environment is vital for the conservation of biodiversity.

1.2 Ecological interactions among mammalian carnivores

1.2.1 Ecological niche and limiting similarity

The fundamental ecological niche refers to the full range of conditions (biotic and abiotic) and resources in which an organism can survive and reproduce (Elton 2001). However, local environmental pressures act on individuals narrowing the breadth of utilization of at least one of the niche dimensions or resources, promoting coexistence (Hutchinson 1957). Among these locally implemented environmental pressures, interspecific interactions play an important role.

Hardin’s competitive exclusion principle hypothesis (CEPY) states that “complete competitors cannot coexist” (Hardin 1960). This statement means that if two non-interbreeding populations occupy exactly the same ecological niche in Elton’s sense (Elton 2001), are sympatric, and have different growth rates, then the population growing faster will ultimately displace the other, which will become extinct. Further refinements to this theory were added by MacArthur and Levins (1967), in the form of the limiting similarity theory (LST), which states that competing species must segregate, at least partially, along one or more dimensions of their ecological niche in order to maintain sustainable coexistence. Since then, this topic has been the focus of intense theoretic and empirical research, which provide contrasting results (Abrams 1983; Abrams and Rueffler 2009; Szabó and Meszeéna 2006). However, Gurevitch et al. (1992) identified a dramatic lack of research on competition among both herbivores and carnivores, and referred that the question of how often organisms compete in nature was still largely unknown.

In his review of resource partitioning in ecological communities Schoener (1974) found that the separation among species niches is generally multidimensional, and two is the most common number of dimensions separating species. Further, he argued that in competitive systems, increased complexity in ecological communities, i.e. with higher species diversity, would force coexisting species to segregate on more niche dimensions in order to preserve minimal resource overlap. The most important niche dimensions over which competing species segregate have been identified, in order of importance, as: habitat dimensions (spatial), food-type dimensions (trophic) and temporal dimensions (Schoener 1974). Interspecific competition has been identified in all types of systems (freshwater, marine and terrestrial) and this kind of interaction is considered quite frequent in nature (Connell 1983; Schoener 1983). Moreover, exploitation competition (consumption competition, *sensu* Schoener 1983), was identified as prevailing among top carnivores and in terrestrial animals, but that interference competition (territorial and encounter competition, *sensu* Schoener 1983) was also very common.

1.2.2 The spatial dimension in carnivore interactions

Reports of the spatial interactions among sympatric mammalian carnivores have been a particularly common focus in the attempt to evaluate competitive relations. Reported patterns of spatially explicit responses among competitors include complete exclusion (Balestrieri et al. 2010; Rosellini et al. 2008), changes in habitat selection at the landscape scale (Fedriani et al. 2000; Fedriani et al. 1999; Fisher et al. 2012; Scognamillo et al. 2003; Wilson et al. 2010), or behaviourally-mediated spatial avoidance (Broekhuis et al. 2013; Harmsen et al. 2009; Macdonald et al. 2004). However, the spatial relations among species are not constant, as they may display different patterns of spatial coexistence under different circumstances. For example, the jaguar (*Panthera onca*) and the puma are two large felids that have overlapping distribution areas across most of the South American continent (Haines 2006). However, different studies on the spatial relations between these species in areas of co-occurrence revealed distinct patterns. Davis et al. (2011) found a positive but non-significant association between jaguars and pumas in Belize. Also in Belize, Harmsen et al. (2009) reported sequential use of the same areas between the two co-occurring cats. Scognamillo et al. (2003) identified highly overlapping home ranges between these two felids with interspecific avoidance exhibited at fine-scale, and Sollmann et al. (2012) found that differences in habitat selection mediated the spatial partitioning between jaguars and pumas in central Brazil. Similarly, upon the analysis of European mesocarnivore guilds, Sarmento et al. (2010) found no effect of the presence of intraguild competitors in the distribution patterns of mammalian mesocarnivores in central Portugal. Analogous findings were reported by Šálek et al. (2013), who found no evidence of spatially segregated distribution of mesocarnivores in Czech Republic. However, also in Portugal, Pereira et al. (2012) suggested that mesocarnivores coexistence was mediated by fine-scale spatial partitioning. Regardless of the potential diversity of spatial responses exhibited by sympatric competing mammalian carnivores, the spatial niche dimension remains as one of the most important mediating competitive interactions because it entangles accessibility not only to adequate habitats, but also to prey (Fedriani et al. 2000; Ritchie and Johnson 2009; Wilson et al. 2010).

1.2.3 The trophic dimension in carnivore interactions

Food acquisition and consumption is one of the most important activities for any living being. In the case of mammalian carnivores, prey biomass is a major determinant of predator density both within and between species (Carbone and Gittleman 2002; Gittleman and Harvey 1982). Furthermore, the area secured by a mammalian carnivore, i.e. home range, is directly related to its metabolic needs and diet composition, where predominantly carnivorous species require bigger areas than predominantly frugivorous or insectivorous species (Gittleman and Harvey 1982). The intensity of the relation between carnivores' requirements and prey availability determine the competitive stress among sympatric predators that share the same prey (Carbone et al. 1999; Gittleman and Harvey 1982), especially when prey availability is limiting (Donadio and Buskirk 2006; Linnell and Strand 2000; Ritchie and Johnson 2009). Several measures of niche overlap, such as the Pianka's index (Pianka 1974), were frequently used to make inferences about exploitative competition among coexisting species. However, while such measures provide compact descriptions of community patterns, they may not directly relate to interspecific competition given the multidimensional nature of species' ecological niches (Holt 1987). Most recent research on the evaluation of competition between carnivores along the trophic niche dimension, often consist of two or three-dimensional approaches by evaluating dietary and spatial (and/or temporal) patterns simultaneously (Fedriani et al. 2000; Harrington et al. 2009; Hass 2009; Mitchell and Banks 2005; Scognamillo et al. 2003). Alternatively, the competitive stress induced by the presence of a dominant competitor may be assessed by evaluating the competitive release effect in the diets of subordinate species when the former is removed (Moreno et al. 2006).

For example, in Australia, Mitchell and Banks (2005) found that the competitive stress induced by similar dietary patterns is lessened by fine-scale spatial segregation between wild dogs (*Canis lupus familiaris* and *C. l. dingo*) and red foxes. Similar findings were obtained by Fedriani et al. (2000) in Santa Monica Mountains (California, USA) with coyotes and gray foxes (*Urocyon cinereoargenteus*), that shared their main prey (small mammals), and consequently led the latter to avoid habitats were coyotes were more abundant. In South Spain, Fedriani et al. (1999) reported that coexisting Iberian lynxes, red foxes and Eurasian badgers (*Meles meles*) shared their main prey, the European rabbit (*Oryctolagus cuniculus*). According to these authors, red foxes avoided agonistic encounters with Iberian lynxes by habitat segregation during the periods of lynx activity, while no niche segregation was detected between badgers and lynxes.

Contrasting examples in mammalian carnivores include trophic niche shifts by the subordinate species. Near Oxford (England), American minks changed their diets following the recovery of the Eurasian otter population, by intensifying the exploitation of terrestrial resources (Harrington et al. 2009). Likewise, Hass (2009) suggested that, in the Huachuca Mountains (Arizona, USA), interspecific competition between sympatric pumas and bobcats (*Lynx rufus*) was lessened via modification of their diets and fine-scale habitat segregation.

These examples depict the variability of trophic relationships among coexisting mammalian carnivores, and emphasize that the complexity of such interactions can only be understood when evaluated in a multidimensional framework. In light of the optimal foraging theory (Brown et al. 1999) and the risk allocation hypothesis (Lima and Bednekoff 1999), we anticipate that coexisting mammalian competitors that share a staple prey should: (*i*) avoid each other spatially, when prey availability is widely distributed in the landscape; or (*ii*) segregate temporally, when prey distribution is clustered in specific habitats therefore minimizing risks of agonistic encounters. However,if at least one of the species is not a specialist and alternative feeding resources are available, then (*iii*) trophic niche segregation could provide a better alternative to reduce competitive stress.

1.2.4 The temporal dimension in carnivore interactions

Time is another niche dimension over which interacting animals might segregate to reduce the effect of agonistic encounters (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 2003; Schoener 1974). The temporal niche can be analysed at several scales: daily, seasonally, or yearly (Halle and Stenseth 2000). However, the diel activity pattern is the most well studied of animal activity cycles, despite being the shorter period of analysis (Halle and Stenseth 2000; Kronfeld-Schor et al. 2001; Schoener 1974). This is the cycle that we will be addressing throughout this work. Despite being regarded as the least important of the three main niche dimensions (Schoener 1974), the temporal niche is particularly important in the case of predator species as they often segregate across the diel cycle, promoting coexistence (e.g. Di Bitetti et al. 2009; Harrington et al. 2009; Wang and Fisher 2012). Further, the presence of competitors frequently influences activity patterns through interference competition, which is expected to be stronger whenever similarity in other niche dimensions and body mass are high (Schoener 1974; Linnell and Strand 2000; Donadio and Buskirk 2006; Ritchie and Johnson 2009). However, the activity pattern exhibited by a mammalian carnivore is context-dependent, as it is determined by its endogenous regulation (Kronfeld-Schor et al. 2001; Kronfeld-Schor and Dayan 2003) and by external abiotic and biotic factors, such as the presence of competitors (Cozzi et al. 2012; Harrington et al. 2009), human disturbance (Kitchen et al. 2000; Theuerkauf 2009) or accessibility to prey, that often have their own well defined activity patterns (Arias-Del Razo et al. 2011; Halle 2000). The interaction with these factors can change the ultimate expression of a species nycthemeral activity. Therefore the observed overlap between two co-occurring species can change according to their location or period of time analysed. To further puzzle the evaluation of the temporal niche dimension for ecological separation among competing species, an additional constrain is that temporal partitioning can be rapidly exhausted with increasing species diversity (Schoener 1974). The predation risk allocation hypothesis proposed by Lima & Bednekoff (1999) advocates that through a reasonably accurate perception of predation risk, prey species adapt their activity strategies to avoid being active in high-risk periods. This theory should equally apply to competitive relations, as the risk of IGP or other forms of interference competition also constitutes a risk to physical integrity and individual fitness. Therefore, by allocating strong anti-predator behaviours to such periods, competing species could then compensate by focusing their feeding effort in low-risk situations. However, if the diel cycle is already saturated by the activity of competitors, or if prey is only accessible at a certain period of the day, then an animal has little choice but to be active under high-risk periods (Broekhuis et al. 2013; Lima and Bednekoff 1999).

The temporal segregation in diel activity patterns appears to be particularly important for predators (Ritchie and Johnson 2009; Schoener 1974). This kind of temporal partitioning has been reported among several carnivore assemblages, and it can be exhibited by a clear asynchrony in their foraging patterns (Di Bitetti et al. 2009; Gerber et al. 2012; Harrington et al. 2009; Lucherini et al. 2009), suggesting a predictive response to risk. Alternatively, activity segregation may be reactive, induced by the detection of the competitor (Broekhuis et al. 2013; Harmsen et al. 2009). The diel temporal niche should be important for ecological separation among potentially competing carnivores when: (*i*) carnivores are spatially clustered; (*ii*) they have high trophic niche overlap, i.e. feed mainly on the same prey; and (*iii*) the shared feeding resource is limited.

1.2.5 The definition of mesocarnivore

Before going further, it is important to define the term “mesocarnivore”. Three distinct definitions of the term “mesocarnivore” have been described in the scientific literature. A first definition of mesocarnivore is diet-based, and considers mesocarnivores as the category of mammalian carnivores that include 50–70% meat in diet, with the balance made up of non-vertebrate foods (Van Valkenburgh 2007; Valkenburgh 1988). Buskirk (1999) used a bodyweight-based definition of mesocarnivores, which consisted of midranking mammalian carnivores with weight between 1 and 15kg. Finally, Prugh et al. (2009) suggested a food web-based definition, in which a mesocarnivore should be defined as any midranking mammalian predator in a food web, regardless of its size or taxonomy. Although I feel the food web-based definition (Prugh et al. 2009) to be more adequate, because it refers to the relative position in the trophic environment where the animal is included, I will use the term “mesocarnivore” in consistency to what is most often described in the literature, which is the bodyweight-based definition. Therefore, throughout the entire document, I address all mammalian carnivore species with an average bodyweight over 1kg and below 15kg as mesocarnivores, regardless of coexisting or not with apex predators.

1.2.6 Iberian mammalian carnivore communities

Southwestern (SW) European terrestrial carnivore communities include a total of 17 species (Cabral et al. 2005; Mitchell-Jones et al. 1999; Palomo et al. 2007). Two of these species are clear apex predators: the brown bear (*Ursus arctos*) and the wolf. While having a bodyweight under 15kg, the Iberian lynx plays the role of an apex predator in Mediterranean ecosystems because it has no sympatric predators and has been documented to suppress or exclude smaller carnivore species (Fedriani et al. 1999; Palomares et al. 1996). However, in the Iberian Peninsula (IP), the distribution of these apex predators is highly restricted. The Iberian lynx distribution is currently restricted to two natural unconnected populations, and two others that have been reintroduced, all in the south of Spain (Gil-Sánchez and McCain 2011; Sarmento et al. 2009). The Iberian distribution of the wolf corresponds to nearly 1/3 of the NW Iberian territory, although their populations are frequently scattered in a metapopulation-like system (Blanco et al. 2007; Cabral et al. 2005). Finally, the brown bear is restricted to the Pyrenean and Cantabric mountains, and surrounding areas (Naves and Fernández-Gil 2007). Given the limited distributional range of apex predators in the IP, carnivore communities across a large portion of Iberia are strictly comprised of meso and small carnivores. Eight mesocarnivore species (six native and two introduced) occur in Iberia: The red fox, the European wildcat (*Felis silvestris*), the pine marten (*Martes martes*), the stone marten (*Martes foina*), the Eurasian badger, the Eurasian otter, the common genet and the Egyptian mongoose. However, they do not always occur in sympatry or coexist spatially within their distribution areas (Cabral et al. 2005; Mitchell-Jones et al. 1999; Palomo et al. 2007). While most mesocarnivore species are widespread in the IP, two have particularly limited ranges: the pine marten is restricted to the northern fringe (López-Martin 2007), and the Egyptian mongoose only occurs in the southwest (Balmori and Carbonell 2012; Barros and Fonseca 2011; Palomares 2007). As a consequence, mesocarnivore communities vary geographically in composition and structure, potentially resulting in interspecific relations between the same species pairs to change from one area to another. Within the SW European mesocarnivore communities, the potential for exploitation and/or interference competition exists among several species pairs along various niche dimensions (table 1). However, only a few studies have been conducted directly evaluating the ecological interactions among these coexisting species (Fedriani et al. 1999; López-Martin 2003; Palomares et al. 1998; Palomares et al. 1996; Sarmento et al. 2010; Zabala et al. 2009), and none that I am aware of evaluates these interactions at a community-wide scale using a multidimensional approach. Therefore, a substantial lack of knowledge still exists regarding the ecological interactions governing carnivore communities across the southwest of Europe.

A complementary characteristic that increases the biological diversity across the Iberian Peninsula is the fact that it includes two distinct bioclimatic regions (European Environmental Agency 2012; Rivas-Martínez et al. 2004): the Atlantic region, which extends through a northern strip, from the Pyrenees, through the Cantabric mountains and occupies all the northwestern region of Spain and Portugal; and the Mediterranean region, which occupies most of the Iberian territory (figure 1). This bioclimatic division of the Iberian Península is particularly important for the structure and functioning of mammalian carnivore communities because, among other reasons, of the differential availability of European rabbits. Another relevant feature, is the fact that the European rabbit is a keystone species in the Mediterranean region of the IP (Delibes-Mateos et al. 2007b), where it is the staple prey of a diversity of predators (Delibes-Mateos et al. 2008; Jaksic and Delibes 1987). The high energetic profits of hunting rabbits (Aldama et al. 1991; Aldama and Delibes 1990; Malo et al. 2004) are linked to the presence of rabbit specialist species, such as the Iberian lynx (Palomares 2001), and other mesocarnivore species that preferably prey on rabbits whenever they are available (Delibes-Mateos et al. 2007a; Lozano et al. 2006; Virgós et al. 2005). The differences in the availability of prey between the two bioclimatic regions of the Iberian peninsula, should provide interesting contrasts in the interspecific interactions among carnivores.

Table 1.2.6.1. Predicted first-order species interactions in Iberian mesocarnivore communities and respective factors leading to potential inter-specific competition (Data obtained from Wilson and Mittermeier 2009). D - Dominant species; S - Subordinate species.

Species pair (Dominant ↔ subordinate)	Bodyweight (kg)		Bodyweight ratio	Feeding specialization		Preferred prey		Preferred habitat		Factors motivating interaction
	D	S		D	S	D	S	D	S	
Iberian lynx ↔ red fox	10.5	6.0	1.75	Spl	Gnr	ER	ER$_{MD}$ /	SCRB/WDL	SCRB/WDL	F + H
Iberian lynx ↔ European wildcat	10.5	4.7	2.23*	Spl	FcSpl	ER	ER$_{MD}$ /	SCRB/WDL	SCRB$_{MD}$/WDL$_{ATL}$	F + H
Iberian lynx ↔ stone marten	10.5	1.5	7.00	Spl	Gnr	ER	SM	SCRB/WDL	SCRB$_{MD}$/WDL$_{ATL}$	H
Iberian lynx ↔ common genet	10.5	1.9	5.53	Spl	FcSpl	ER	SM	SCRB/WDL	WDL	H
Iberian lynx ↔ Eurasian badger	10.5	7.3	1.44	Spl	Gnr	ER	ER$_{MD}$ /	SCRB/WDL	SCRB$_{MD}$/WDL$_{ATL}$	F + H
Iberian lynx ↔ Egyptian mongoose	10.5	2.8	3.75*	Spl	Gnr	ER	ER$_{MD}$ /	SCRB/WDL	SCRB	F + H
Red fox ↔ European wildcat	6.0	4.7	1.28	Gnr	FcSpl	ER$_{MD}$ /	ER$_{MD}$ /	SCRB/WDL	Scrublands	F + H
Red fox ↔ stone marten	6.0	1.5	4.00*	Gnr	Gnr	ER$_{MD}$ /	SM	SCRB/WDL	SCRB$_{MD}$/WDL$_{ATL}$	F$_{ATL}$ + H
Red fox ↔ pine marten	6.0	1.1	5.45	Gnr	Gnr	ER$_{MD}$ /	SM	SCRB/WDL	WDL	F$_{ATL}$ + H$_{ATL}$
Red fox ↔ common genet	6.0	1.9	3.16*	Gnr	FcSpl	ER$_{MD}$ /	SM	SCRB/WDL	WDL	F$_{ATL}$ + H
Red fox ↔ Egyptian mongoose	6.0	2.8	2.14*	Gnr	Gnr	ER$_{MD}$ /	ER$_{MD}$ /	SCRB/WDL	SCRB	F + H
Eurasian badger ↔ red fox	7.3	6.0	1.22	Gnr	Gnr	Several	ER$_{MD}$ /	SCRB$_{MD}$/WDL$_{ATL}$	SCRB/WDL	F$_{MD}$ + H
Eurasian badger ↔ European	7.3	4.7	1.55	Gnr	FcSpl	ER$_{MD}$ /	ER$_{MD}$ /	SCRB$_{MD}$/WDL$_{ATL}$	SCRB$_{MD}$/WDL$_{ATL}$	F$_{MD}$ + H
Eurasian badger ↔ stone marten	7.3	1.5	4.87*	Gnr	Gnr	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	SCRB$_{MD}$/WDL$_{ATL}$	H
Eurasian badger ↔ pine marten	7.3	1.1	6.64	Gnr	Gnr	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	WDL	H
Eurasian badger ↔ common genet	7.3	1.9	3.84*	Gnr	FcSpl	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	WDL	H$_{ATL}$
Eurasian badger ↔ Egyptian	7.3	2.8	2.61*	Gnr	Gnr	ER$_{MD}$ /	ER$_{MD}$ /	SCRB$_{MD}$/WDL$_{ATL}$		F$_{MD}$ + H$_{MD}$
European wildcat ↔ stone marten	4.7	1.5	3.13*	FcSpl	Gnr	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	SCRB$_{MD}$/WDL$_{ATL}$	F$_{ATL}$ + H
European wildcat ↔ pine marten	4.7	1.1	4.27*	FcSpl	Gnr	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	WDL	F$_{ATL}$ + H$_{ATL}$
European wildcat ↔ common	4.7	1.9	2.47*	FcSpl	FcSpl	ER$_{MD}$ /	SM	SCRB$_{MD}$/WDL$_{ATL}$	WDL	F$_{ATL}$ + H$_{ATL}$
European wildcat ↔ Egyptian	4.7	2.8	1.68	FcSpl	Gnr	ER$_{MD}$ /	ER$_{MD}$ /	SCRB$_{MD}$/WDL$_{ATL}$	SCRB	F$_{MD}$ + H$_{MD}$
Pine marten ↔ stone marten	1.1	1.5	0.73	Gnr	Gnr	SM	SM	WDL	SCRB$_{MD}$/WDL$_{ATL}$	F$_{ATL}$ + H$_{ATL}$
Pine marten ↔ common genet	1.1	1.9	0.58	Gnr	FcSpl	SM	SM	WDL	WDL	F$_{ATL}$ + H$_{ATL}$
Common genet ↔ stone marten	1.9	1.5	1.27	FcSpl	Gnr	SM	SM	WDL	SCRB$_{MD}$/WDL$_{ATL}$	F$_{ATL}$ + H$_{ATL}$
Egyptian mongoose ↔ common	2.8	1.9	1.47	Gnr	FcSpl	ER$_{MD}$ /	SM	SCRB	SCRB$_{MD}$/WDL$_{ATL}$	H$_{MD}$
Egyptian mongoose ↔ stone	2.8	1.5	1.87	Gnr	Gnr	ER$_{MD}$ /	SM	SCRB	SCRB$_{MD}$/WDL$_{ATL}$	H$_{MD}$

Spl - Specialist; FcSpl - Facultative specialist; Gnr - Generalist; ER - European rabbit; SM - Small mammals; SCRB - Scrublands; WDL - Woodlands; $_{MD}$- Any given characteristic in the Mediterranean region; $_{ATL}$- Any given characteristic in the Atlantic region; F - Feeding resources; H - Habitat.

* High potential for intraguild predation, according to (Donadio and Buskirk 2006).

1.3 Current methodological limitations in mesocarnivore studies: can we trust our data?

Carnivores have cascading effects on entire ecosystems, acting as ecosystems' engineers by enforcing top-down control on lower trophic levels (Estes et al. 2011; Ray et al. 2005; Ripple et al. 2010; Wilson and Mittermeier 2009). However, these species typically occur in low densities, have elusive behaviors and have large home ranges, which make population or demographic parameters especially difficult to estimate (Gittleman and Harvey 1982; Long et al. 2008; O'Connell et al. 2011; Wilson and Delahay 2001). Consequently, the challenges involved in monitoring carnivores make the use of direct and invasive methods laborious, often inefficient and potentially hazardous for the animals (Kelly et al. 2012; Long et al. 2008).

Traditional methods of studying carnivores include direct methods such as observation, capture-recapture or radiotracking (Boitani and Fuller 2000). However, such methods are often impractical to apply across large spatial scales since they are time-consuming, have high costs, and involve complex logistical requirements.

Non-invasive techniques provide alternative means of monitoring such species. Non-invasive techniques are those that "do not require target animals to be directly observed or handled by the surveyor" (Long et al. 2008). Broadly these methods include tracking natural signs such as scats, tracks, or dens; recording tracks at track stations; collecting hair at hair stations; employing camera-traps, and using scat detection dogs (Long et al. 2008).

The recent technological advances both in conservation genetics (Beja-Pereira et al. 2009; Shehzad et al. 2012) and field techniques (McCallum 2013; O'Connell et al. 2011), coupled with developments in statistical methods such occupancy models (Mackenzie et al. 2006) or modeling of daily routines (Ridout and Linkie 2009) have enhanced the value of non-invasive methods. The widespread use of these methods has promoted their much more common use to monitor multiple carnivore species across large areas at a relatively modest cost (Johnson et al. 2009; Long et al. 2007; Weaver et al. 2005; Zielinski et al. 2006).

Among the non-invasive methods, camera trapping and scat searching are particularly common in studies of mammalian carnivore species (Boitani and Fuller 2000; Kelly et al. 2012; Long et al. 2008; O'Connell et al. 2011). However, hair collection methods have gained renewed interest with the possibility of extracting and amplifying bad-quality DNA from donor species (Davoli et al. 2012; Dreher et al. 2009; Kendall and Mckelvey 2008).

Due to its reduced costs, scat searching is one of the survey methods most frequently used (Davison et al. 2002; Prugh and Ritland 2005), and it has been argued as being one of the most efficient methods for the detection and monitoring of European mammalian mesocarnivores (Barea-Azcón et al. 2006; Lozano et al. 2003; Rosellini et al. 2008; Sadlier et al. 2004). Moreover, scat-based research provides the possibility to address many ecological aspects of the target species such as the evaluation of conservation status (Janecka et al. 2008; Sarmento et al. 2004), distribution (Rosellini et al. 2008), abundance (Mondol et al. 2009), spatial interactions (Dalen et al. 2004), dietary patterns of the population (Posluszny et al. 2007; Shehzad et al. 2012) or diets of individual animals (Fedriani and Kohn 2001).

Along with an increase in research possibilities provided by the advances in non-invasive molecular methods, the application of molecular scatology has highlighted the fact that, although reliable at times (Prugh and Ritland 2005), the evaluation of scat morphology alone is prone to misidentifications among sympatric carnivore species, even when evaluated by experienced field technicians (Davison et al. 2002; Harrington et al. 2010; Janecka et al. 2008). However, because morphology-based scat searching methods are often the only available alternative for conducting large-scale surveys on carnivore species because of the reduced costs and labor (Barea-Azcón et al. 2006; Wilson and Delahay 2001), they cannot be readily discarded. Nevertheless, potential sources of bias need to be identified and accounted for so that reliable inferences can be obtained.

Camera traps and hair collection methods consist of fixed stations that require animals to directly encounter them while actively moving (Kendall and Mckelvey 2008; O'Connell et al. 2011). These methods can either be used alone, detecting animals passively, or in combination with specific attractants, consisting in baited stations (Kays and Slauson 2008; Kendall and Mckelvey 2008). An adequate sampling design using these methods can provide previously unattained information about wide-ranging secretive species. However, the continuous developments in statistical inference and refinement of these sampling methods promote enduring debate regarding their reliability. For instance, for the last two decades countless studies have reported estimations of population densities based on individual identification of coat patterns examined from camera-trapping records (Karanth et al. 2006; Karanth 1995; Núñez-Pérez 2011; Silver et al. 2004). However, animals with indistinctive coat patterns deem their individual identification impossible from photographic records. Therefore, camera-trapping detection rates have also been suggested as good proxies of target species' population abundance (Carbone et al. 2001; Rovero and Marshall 2009). Further improvements in statistical methods for estimating population densities without the requirement of individual identification were introduced by Rowcliffe et al. (2008). Nevertheless, the novelty of such approaches and relatively untested status elicit scientific criticism (Foster and Harmsen 2012; Kelly 2008; Rowcliffe and Carbone 2008; Sollmann et al. 2013).

The combined use of hair collection methods with molecular genetics, warrants species individual and sex identification, and recently have been extensively used to detect several mammal species (Kendall and Mckelvey 2008; Mills 1996; Ruell and Crooks 2007). Particularly, the individual identification provided by hair snaring can be used for detailed demographic and population monitoring (Davoli et al. 2012; Zielinski et al. 2006). However, generally, hair snaring methods tend to have relatively low detection rates (Comer et al. 2011; Long et al. 2007), which limits their employment for detecting rare or wide ranging species, and motivates the development and testing of new hair collection structures (Heurich et al. 2012; Schmidt and Kowalczyk 2006; Zielinski et al. 2006)

The challenges that involve carnivore monitoring are numerous, and the recent methodological advances in species monitoring research suggest that traditional sampling methods are bias prone, potentially leading to misadjusted interpretations of biological patterns. Therefore, a constant re-evaluation of such sampling methods in light of recent molecular and technological advances is not only useful, but also required to assess their validity and propose further refinements, by incorporating recent developments and new sampling methods in wildlife biology research and conservation.

1.4 Objectives

The challenges that involve carnivore monitoring are several, and the recent methodological advances stress the need not only to incorporate new technologies in ecological methods, but also to use these new methods to re-assess the adequateness of traditional sampling methods. With the advent of recent methodological advances, new and more detailed information regarding mesocarnivore ecology becomes achievable providing an opportunity to develop deeper research focusing on multispecies interactions and strategies for species coexistence. In this context, we defined two main objectives for this thesis, that are addressed in two distinct chapters:

I. To assess the reliability and improve current sampling methods for ecological studies of mesocarnivores in Southwestern Europe;

II. To study the strategies that allow coexistence among mesocarnivores in SW European communities.

In order to achieve these main research goals, a set of subsidiary objectives were also defined:

1. To improve the detection rates of remote sampling methods by identifying lures that could efficiently attract most mesocarnivore species in SW European communities;
2. To evaluate the level of reliability traditional sampling methods based on expert identification of mesocarnivore scats, and assess the potential bias in ecological studies on mesocarnivores using these methodologies.
3. To evaluate the efficiency of hair snares as a cost-effective method for long term mesocarnivore monitoring programs in SW Europe.
4. To assess the level of synchrony in activity patterns between mesocarnivores and their main prey, and to evaluate the dynamic organization of predator-prey systems, the bidirectional system of mesocarnivore-mediated predation risk and variable prey diel availability;

5. To evaluate the level of plasticity in the activity patterns of mesocarnivore species present at SW European communities, and whether ecological shifts along the temporal axis can promote coexistence by reducing the overlap in activity periods with competitors;

6. To investigate spatial co-occurrence patterns between mesocarnivores, and to evaluate the levels of spatial avoidance or association among species in SW mesocarnivore communities, namely: if the occurrence of subordinate species is conditional on the presence of superior competitors; and if the presence of a superior competitor influences the behaviour of subordinate species.

7. Using the stone marten / pine marten complex as a case study, for evaluating along which of the three main niche axes (spatial, temporal or feeding resources) does ecological separation occur, and identify the factors that influence that relationship.

1.5 Study areas

In order to address the exposed objectives, five sampling sites in the Iberian Peninsula were defined. These sites were selected based on criteria of ecosystem integrity and representation of the existing carnivore communities. Particularly, we aimed: to represent both bioclimatic regions present in the Iberian Peninsula (Mediterranean and Atlantic; figure 1); to represent communities with and without apex predator presence; and that the selected sites exhibited varying abundances of the main prey species, the European rabbit. These study sites were selected based on previous knowledge about their mammalian communities and considering the logistic constraints for field sampling. Within each study site, a sampling area of approximately 6000 ha within each of the study sites was selected, based on criteria of ecosystem conservation status and logistic factors. The selected study sites are described below.

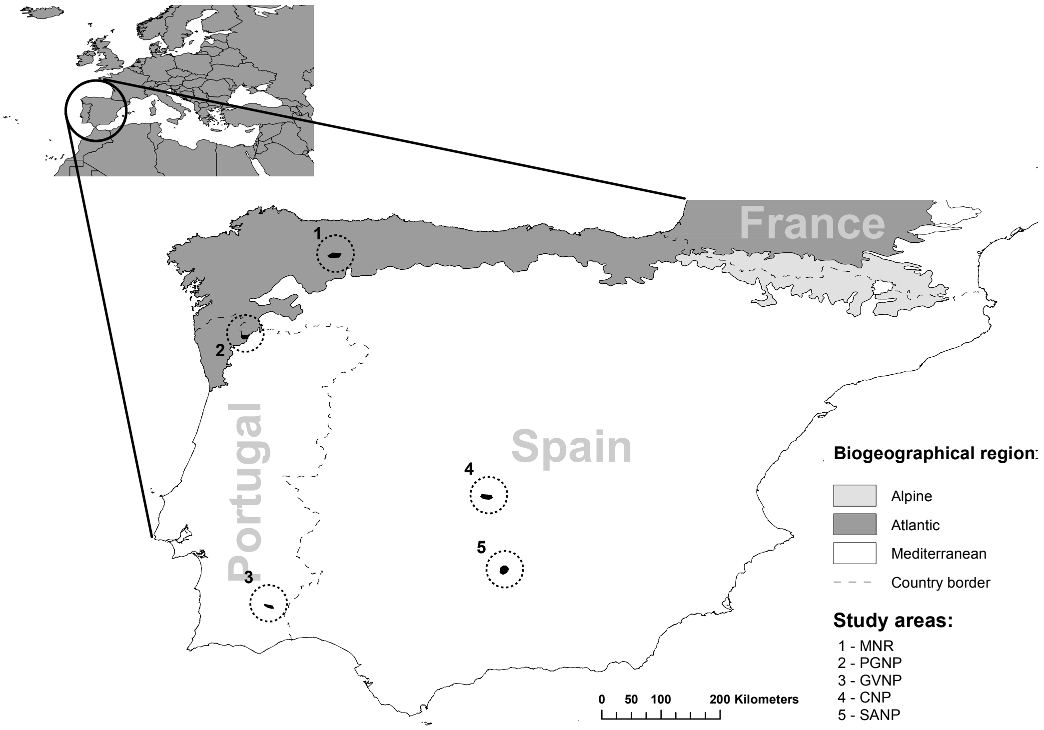

Figure 1.5.1. Locations of the study areas in the Iberian Peninsula, and spatial distribution of the biogeographical regions. MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park; SANP - Serra de Andújar Natural Park.

1.5.1 Guadiana Valley Natural Park (GVNP)

The Guadiana Valley Natural Park (GVNP) is a protected area located in Southern Portugal. The climate is classified as attenuated thermo-Mediterranean (Alcoforado et al. 1982). The landscape is highly fragmented with cereal croplands and agroforestry systems (Montado) of *Pinus pinea* L. and *Quercus ilex* L. Scrubland patches are mainly associated with steeper slopes and elevation ridges. The vegetation is dominated by the *Myrto communis–Querco rotundifoliae* S. series but other sub-serial stages can also be found (Costa et al. 1998). Hunting activity is extremely important in this region and about 86% of the land is included in hunting estates. The most revelant game species include the red-legged partridge (*Alectoris rufa*) and the European rabbit. The red fox, stone marten, Egyptian mongoose and European wildcat are the most common mammalian mesocarnivore species present, despite the presence, in lower densities, are the Eurasian badger and common genet (Monterroso et al. 2009; Monterroso 2006; Monterroso et al. 2006). Predator control directed towards red fox and Egyptian mongoose is legally conducted.

Figure 1.5.1.1. Landscape at the Guadiana Valley Natural Park study area.

1.5.2 Cabañeros National Park (CNP)

The Cabañeros National Park (CNP) is a protected area located in Central Spain. Like the GVNP, it is located in the Mediterranean pluviseasonal continental bioclimate region (Rivas-Martínez et al. 2004). The vegetation is dominated by the *Pyro-Quercetum rotundifoliae* series and other subserial stages (Rivas-Martinez 1981), especially associated with the steeper slopes, higher elevations and main water bodies. The landscape at the central lower part of this study area constitutes a savannah-like system, with holm oak (*Quercus ilex*) trees scattered within a grassland matrix (García-Canseco 1997). The red fox, stone marten and common genet are the most abundant mammalian carnivore species, while European wildcats, Eurasian badgers and Egyptian mongooses are also found, but in lower densities (Guzmán 1997). Neither hunting activity nor predator control is allowed.

Figure 1.5.2.1. Landscape at the Cabañeros National Park study area.

1.5.3 Sierra de Andújar Natural Park (SANP)

Located in the same bioclimatic region as the GVNP and CNP (Rivas-Martínez et al. 2004), the studied area at SANP has grossly a similar vegetation structure as the other two Mediterranean areas. The main difference is that stone pine (*Pinus pinea*) and maritime pine (*Pinus pinaster*) forests with and without understory dominate the areas with gentler slopes (Gil-Sánchez et al. 2006). Because it is included in one of the last natural areas for the Iberian lynx (Gil-Sánchez and McCain 2011; Simón et al. 2009), this study area is managed for the conservation of this critically endangered feline (IUCN 2013; Simón et al. 2009). Therefore, intense European rabbit recovery actions, such as restocking operations, are implemented to maintain the required prey availability for the breeding lynx population. The Iberian lynx, the red fox and the Eurasian badger are the most abundant mammalian carnivore species, while European wildcats, common genets and stone martens are rare and geographically limited (authors, unpl. work; Gil-Sánchez, personal communication). Neither predator control nor small game hunting is allowed. Big game hunting (red reed, *Cervus elaphus,* and wild boar, *Sus scrofa*) is allowed, but controlled.

Figure 1.5.3.1. Landscape at the Sierra de Andújar Natural Park study area.

1.5.4 Peneda-Gerês National Park (PGNP)

The Peneda-Gerês National Park (PGNP) is located in the northwestern border of Portugal. It is a part of the Cantabrian-Atlantic subprovince, Juresian-Queixensean Sector and Amarela-Gerês district, and is included in the montane bioclimatic level with a hyper-humid and ultra-hyper-humid ombroclimate (Costa et al. 1998; Honrado 2003; Rivas-Martínez et al. 2002). Diverse types of granitic soils and a great topographic complexity result in a diversification of ecological conditions, which are reflected in the presence of several climacic forests, particularly, mature forests of European oak (*Quercus robur*), especially associated with steeper slopes, valleys and riverbeds (Honrado 2003). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Carvalho and Gomes 2004). High levels of tourist visitation also characterize this area, which are mainly focused in the warmer months. Hunting is allowed, but geographically restricted. This area harbors one of the best populations of wolves and pine martens in Portugal (Álvares and Brito 2006; Pimenta et al. 2005). Other present carnivores include the stone marten, the common genet and the European wildcat (Carvalho and Gomes 2004).

Figure 1.5.4.1. Landscape at the Peneda-Gerês National Park study area.

1.5.5 *Muniellos Natural Reserve (MNR)*

Figure 1.5.5.1. Landscape at the Muniellos Natural Reserve study area.

The Muniellos Natural Reserve is located in the northwestern region of Spain, in the western range of the Cantabrian Mountains. It has a temperate oceanic submediterranean bioclimate (Rivas-Martínez et al. 2004) and is one of the best representations of Atlantic native forests of western Europe (Suárez-Eoane and García-Ovés 2004). The landscapes consist of mountainous agricultural–forest mosaic, where mountain tops are mostly dominated by scrublands with Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially dominated by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* sp. and *Fagus* sp.) (Prieto and Sánchez 1996). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations. Hunting and predator control is forbidden inside the integral reserve. Human access is also restricted to 20 persons per day. However, hunting is allowed in the reserve surroundings, where roe deer and wild boar are the most hunted species. Two apex predators, the wolf and the brown bear, are present in this study area (Blanco et al.

2007; Clevenger et al. 1999; Naves and Fernández-Gil 2007). The most frequent mesocarnivore is the pine marten, however other species like the red fox, European wildcat and common genet are also present. Stone martens appear to have a more restricted distribution in this study area.

1.6 References

Abrams P (1983) The theory of limiting similarity. Annu Rev Ecol Syst 14:359–376.

Abrams PA, Rueffler C (2009) Coexistence and limiting similarity of consumer species competing for a linear array of resources. Ecology 90:812–822.

Alcoforado MJ, Alegria MF, Pereira AR, Sirgado C (1982) Domínios Bioclimáticos em Portugal, definidos por comparação dos Índices de Gaussen et d'Emberger. Linha de Acção de Geografia Física. Report nr.14. 30pp+2 maps.

Aldama J, Beltrán JF, Delibes M (1991) Energy expenditure and prey requirements of free-ranging Iberian lynx in southwestern Spain. J Wildl Manage 55:635–641.

Aldama J, Delibes M (1990) Some preliminary results on rabbit energy utilization by the Spanish lynx. Donana Acta Vertebr 17:116–121.

Álvares F, Brito JC (2006) Habitat requirements and potential areas of occurrence for the pine marten in North-Western Portugal: Conservation implications. In: Santos-Reis M, Birks JDS, O'Doherty EC, Proulx G (eds) Martes Carniv. Communities. Alpha Wildlife Publications, Alberta, Canada, pp 27–43

Arias-Del Razo I, Hernández L, Laundré JW, Myers O (2011) Do predator and prey foraging activity patterns match? A study of coyotes (*Canis latrans*), and lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*). J Arid Environ 75:112–118.

Arim M, Marquet P a. (2004) Intraguild predation: a widespread interaction related to species biology. Ecol Lett 7:557–564.

Balestrieri A, Remonti L, Ruiz-González A, et al. (2010) Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mamm Biol - Zeitschrift für Säugetierkd 75:412–419.

Balmori A, Carbonell R (2012) Expansion and distribution of the Egyptian mongoose (*Herpestes ichneumon*) in the Iberian Peninsula. Galemys, Spanish J Mammal 24:1–3.

Barea-Azcón JM, Virgós E, Ballesteros-Duperón E, et al. (2006) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodivers Conserv 16:1213–1230.

Barros T, Fonseca C (2011) Expansão do sacarrabos *Herpestes ichneumon* (Linnaeus , 1758) em Portugal. Galemys 23:9–15.

Beja-Pereira A, Oliveira R, Alves PC, et al. (2009) Advancing ecological understandings through technological transformations in noninvasive genetics. Mol Ecol Resour 9:1279–301.

Berger KM, Gese EM (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? J Anim Ecol 76:1075–1085.

Di Bitetti MS, Di Blanco YE, Pereira J a., et al. (2009) Time Partitioning Favors the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes (*Lycalopex gymnocercus*). J Mammal 90:479–490.

Blanco JC, Buruaga MS, Llaneza L (2007) *Canis lupus*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 272–276

Boitani L, Fuller T (2000) Research Techniques in Animal Ecology Methods: Controversies and Consequences. Columbia Univ Press, New York.

Bonesi L, Chanin P, Macdonald DW (2004) Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. Oikos 106:19–26.

Broekhuis F, Cozzi G, Valeix M, et al. (2013) Risk avoidance in sympatric large carnivores: reactive or predictive? J Anim Ecol 82:1098–1105.

Brooks TM, Mittermeier RA, Mittermeier CG, et al. (2002) Habitat Loss and Extinction in the Hotspots of Biodiversity. Conserv Biol 16:909–923.

Brown JS, Laundre JW, Mahesh G (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399.

Buskirk SW (1999) Mesocarnivores of Yellowstone. In: Clark TW, Curlee AP, Minta SC, Kareiva PM (eds) Carniv. Ecosyst. Yellowstone Exp. Yale University Press, pp 165–188.

Cabral MJ, Almeida J, Almeida PR, et al. (2005) Livro Vermelho dos Vertebrados de Portugal, 2nd ed. Instituto da Conservação da Natureza/Assírio Alvim, Lisboa.

Carbone C, Christie S, Conforti K, et al. (2001) The use of photographic rates to estimate densities of tigers and other cryptic mammals. Anim Conserv 4:75–79.

Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. Science 295:2273–2276. doi: 10.1126/science.1067994

Carbone C, Mace GM, Roberts SC, Macdonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Cardillo M, Purvis A, Sechrest W, et al. (2004) Human population density and extinction risk in the world’s carnivores. PLoS Biol 2:E197.

Carlsson NOL, Jeschke JM, Holmqvist N, Kindberg J (2009) Long-term data on invaders: when the fox is away, the mink will play. Biol Invasions 12:633–641.

Carothers JH, Jaksić FM (1984) Time as a Niche Difference: The Role of Interference Competition. Oikos 42:403–406.

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool 263:275–283.

Casanovas JG, Barrull J, Mate I, et al. (2012) Shaping carnivore communities by predator control: competitor release revisited. Ecol Res 27:603–614.

Clevenger A, Purroy F, Naves J, Nores C (1999) Status and management of the brown bear in eastern and western Cantabria, Spain. In: Servheen C, Herrero S, Peyton B (eds) Bears Status Surv. Conserv. Action Plan. IUCN/SSC Bear and Polar Bear Specialist Groups, Gland, Switzerland and Cambridge, UK, pp 100–110

Comer CE, Symmank ME, Kroll JC (2011) Bobcats Exhibit Low Detection Rates at Hair Collection Stations in East Texas. Wildl Biol Pract 7:116–122.

Connell J (1983) On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments. Am Nat 122:661–696.

Costa JC, Aguiar C, Capelo JH, et al. (1998) Biogeografia de Portugal continental. Quercetea 0:5–56.

Cove M, Jones B, Bossert A (2012) Use of Camera Traps to Examine the Mesopredator Release Hypothesis in a Fragmented Midwestern Landscape. Am Midl Nat 168:456–465.

Cozzi G, Broekhuis F, McNutt JW, et al. (2012) Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa’s large carnivores. Ecology 93:2590–2599.

Cupples JB, Crowther MS, Story G, Letnic M (2011) Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? J Mammal 92:590–600.

Dalen L, Elmhagen B, Angerbjorn A (2004) DNA analysis on fox faeces and competition induced niche shifts. Mol Ecol 13:2389–92.

Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Anim Conserv 14:56–65.

Davison A, Birks JDS, Brookes RC, et al. (2002) On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. J Zool 257:141–143.

Davoli F, Schmidt K, Kowalczyk R, Randi E (2012) Hair snaring and molecular genetic identification for reconstructing the spatial structure of Eurasian lynx populations. Mamm Biol - Zeitschrift für Säugetierkd 78:118–126.

Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot. Conserv Biol 22:1106–17.

Delibes-Mateos M, Fernandez de Simon J, Villafuerte R, Ferreras P (2007a) Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. Eur J Wildl Res 54:71–78.

Delibes-Mateos M, Redpath S, Angulo E, et al. (2007b) Rabbits as a keystone species in southern Europe. Biol Conserv 137:149–156.

Diniz-Filho JAF, Rodríguez MÁ, Bini LM, et al. (2009) Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. J Biogeogr 36:2222–2236.

Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat 167:524–36.

Dreher BP, Rosa GJM, Lukacs PM, et al. (2009) Subsampling Hair Samples Affects Accuracy and Precision of DNA-Based Population Estimates. J Wildl Manage 73:1184–1188.

Elmhagen B, Ludwig G, Rushton SP, et al. (2010) Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. J Anim Ecol 79:785–794.

Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett 10:197–206.

Elton CS (2001) Animal Ecology. University of Chicago Press, Chicago.

Estes JA, Terborgh J, Brashares JS, et al. (2011) Trophic downgrading of planet Earth. Science 333:301–6.

European Environmental Agency (2012) Biogeographic regions in Europe. http://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe. Accessed 25 Jan 2013.

Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fedriani JM, Kohn MH (2001) Genotyping faeces links individuals to their diet. Ecol Lett 4:477–483.

Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric Mediterranean carnivores. Oecologia 121:138–148.

Fisher JT, Anholt B, Bradbury S, et al. (2012) Spatial segregation of sympatric marten and fishers: the influence of landscapes and species-scapes. Ecography (Cop) no–no.

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

Frafjord K, Becker D, Angerbjorn A (1989) Interactions between Arctic and Red Foxes in Scandinavia - Predation and Aggression. Arctic 42:354–356.

García-Canseco V (1997) Parque Nacional de Cabañeros, 1st editio. Ecohabitat, Madrid.

Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. J Mammal 93:667–676.

Gil-Sánchez JM, Ballesteros-Duperón E, Bueno-Segura J (2006) Feeding ecology of the Iberian lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). Acta Theriol (Warsz) 51:1–6.

Gil-Sánchez JM, McCain EB (2011) Former range and decline of the Iberian lynx (*Lynx pardinus*) reconstructed using verified records. J Mammal 92:1081–1090.

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. Behav Ecol Sociobiol 10:57–63.

Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A Meta-Analysis of Competition in Field Experiments. Am Nat 140:539–572.

Guzmán JN (1997) Mamíferos. In: García-Canseco V (ed) Parq. Nac. Cabañeros, 1st editio. Ecohábitat, Madrid, Spain, pp 225–268.

Haines A (2006) Is there competition between sympatric jaguar *Panthera onca* and puma *Puma concolor*? Acta Zool Sin 52:1142–1147.

Halle S (2000) Ecological Relevance of Daily Activity Patterns. In: Halle S, Stenseth NC (eds) Act. Patterns Small Mamm. An Ecol. Approach. Springer, New York, pp 67–90.

Halle S, Stenseth NC (2000) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York.

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297.

Harmsen BJ, Foster RJ, Silver SC, et al. (2009) Spatial and Temporal Interactions of Sympatric Jaguars (*Panthera onca*) and Pumas (*Puma concolor*) in a Neotropical Forest. J Mammal 90:612–620.

Harrington LA, Harrington AL, Hughes J, et al. (2010) The accuracy of scat identification in distribution surveys: American mink, *Neovison vison*, in the northern highlands of Scotland. Eur J Wildl Res 56:377–384.

Harrington LA, Harrington AL, Yamaguchi N, et al. (2009) The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–16.

Harrington LA, Macdonald DW (2008) Spatial and temporal relationships between invasive American mink and native European polecats in the southern United Kingdom. J Mammal 89:991–1000.

Hass CC (2009) Competition and coexistence in sympatric bobcats and pumas. J Zool 278:174–180.

Heurich M, Müller J, Burg M (2012) Comparison of the effectivity of different snare types for collecting and retaining hair from Eurasian Lynx (*Lynx lynx*). Eur J Wildl Res.

Holt R (1987) On the relation between niche overlap and competition: the effect of incommensurable niche dimensions. Oikos 48:110–114.

Honrado J (2003) Flora e Vegetação do Parque Nacional da Peneda-Gerês. Universidade do Porto, Porto.

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol 22:415–427.

IUCN (2013) The IUCN Red List of Threatened Species. In: Version 2013.1. http://www.iucnredlist.org. Accessed 1 Sep 2013

Jaksic F, Delibes M (1987) A comparative analysis of food-niche relationships and trophic guild structure in two assemblages of vertebrate predators differing in species richness: cause, correlations, and consequences. Oecologia 71:461–472.

Janecka JE, Jackson R, Yuquang Z, et al. (2008) Population monitoring of snow leopards using noninvasive collection of scat samples: a pilot study. Anim Conserv 11:401–411.

Johnson A, Vongkhamheng C, Saithongdam T (2009) The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. Oryx 43:626–633.

Karanth KU (1995) Estimating tiger *Panthera tigris* populations from camera-trap data using capture–recapture models. Biol Conserv 71:333–338.

Karanth KU, Nichols JD, Kumar NS, Hines JE (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. Ecology 87:2925–37.

Kauhala K (1996) Introduced carnivores in Europe with species reference to central and northern Europe. Wildlife Biol 2:197–204.

Kays RW, Slauson KM (2008) Remote cameras. In: Long RA, Mackay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, pp 110–140.

Kelly MJ (2008) Design, evaluate, refine: camera trap studies for elusive species. Anim Conserv 11:182–184.

Kelly MJ, Betsch J, Wultsch C, et al. (2012) Noninvasive sampling for carnivores. In: Boitani L, Powell RA (eds) Carniv. Ecol. Conserv. A Handb. Tech. Oxford University Press, Oxford, pp 47–69

Kendall KC, Mckelvey KS (2008) Hair collection. In: Long RA, MacKay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, pp 141–182.

Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. Can J Zool 78:853–857.

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu Rev Ecol Evol Syst 34:153–181.

Kronfeld-Schor N, Dayan T, Elvert R, et al. (2001) On the Use of the Time Axis for Ecological Separation: Diel Rhythms as an Evolutionary Constraint. Am Nat 158:451–457.

Kruuk H (2002) Hunter and hunted: relationships between carnivores and people. Cambridge Univ Press, Cambridge.

Laliberte AS, Ripple WJ (2004) Range Contractions of North American Carnivores and Ungulates. Bioscience 54:123.

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Can J Zool 79:1401–1409.

Laundre JW, Hernandez L, Ripple WJ (2010) The Landscape of Fear: Ecological Implications of Being Afraid. Open Ecol J 3:1–7.

Levi T, Wilmers CC (2012) Wolves-coyotes-foxes: a cascade among carnivores. Ecology 93:921–929.

Lima SL, Bednekoff PA (1999) Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. Am Nat 153:649–659.

Lindström E, Brainerd S, Helldin JO, Overskaiig K (1995) Pine marten - red fox interactions: a case of intraguild predation? Ann Zool Fennici 32:123–130.

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

Long R a., Donovan TM, Mackay P, et al. (2007) Comparing Scat Detection Dogs, Cameras, and Hair Snares for Surveying Carnivores. J Wildl Manage 71:2018–2025.

Long RA, Mackay, Zielinski WJ, Ray J (2008) Noninvasive survey methods for carnivores. Island Press, Washignton DC.

López-Martin JM (2007) *Martes martes*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 302–304

López-Martin JM (2003) Comparación de la ecología de la Marta (*Martes martes* L. 1758) y la Garduña (M. foina Erx.1777) en el N.E. Ibérico, e interacciones con la Gineta. Universitat de Barcelona, Bracelona.

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

Lozano J, Virgós E, Malo A, et al. (2003) Importance of scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (*Felis silvestris*). Biodivers Conserv 12:921–935.

Lucherini M, Reppucci J, Walker R, et al. (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal 90:1404–1409.

MacArthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat 101:377–385.

Macdonald DW, Buesching CD, Stopka P, et al. (2004) Encounters between two sympatric carnivores: red foxes (*Vulpes vulpes*) and European badgers (*Meles meles*). J Zool 263:385–392.

Mackenzie DI, Nichols JD, Royle JA, et al. (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press

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

McCallum J (2013) Changing use of camera traps in mammalian field research: habitats, taxa and study types. Mamm Rev 43:196–206.

Melis C, Jędrzejewska B, Apollonio M, et al. (2009) Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. Glob Ecol Biogeogr 18:724–734.

Mills MGL (1996) Methodological advances in capture, census, and food-habits studies of large African carnivores. In: Gittleman JL (ed) Carniv. Behav. Ecol. Evol. Cornell University Press, New York, USA, pp 223–242.

Mitchell BD, Banks PB (2005) Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. Austral Ecol 30:581–591.

Mitchell-Jones AG, Amori G, Bogdanowicz W, et al. (1999) The Atlas of European Mammals. T and AD Poyser Natural History, London.

Mondol S, Ullas Karanth K, Samba Kumar N, et al. (2009) Evaluation of non-invasive genetic sampling methods for estimating tiger population size. Biol Conserv 142:2350–2360.

Monterroso P (2006) Distribuição, selecção de habitat e actividade do gato-bravo (*Felis silvestris*) no Parque Natural do Vale do Guadiana. Universidade do Porto, Porto.

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

Monterroso P, Moreira P, Castro D, et al. (2006) Predação sobre o coelho-bravo (*Oryctolagus cuniculus*) em ecossistemas mediterrâneos. In: Ferreira C, Alves PC (eds) Gestão Popul. coelho-bravo (*Oryctolagus cuniculus algirus*). Federação alentejana de caçadores, pp 51–79.

Moreno RS, Kays RW, Samudio R (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. J Mammal 87:808–816.

Naves J, Fernández-Gil A (2007) *Ursus arctos*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 321–326

Núñez-Pérez R (2011) Estimating jaguar population density using camera-traps: a comparison with radio-telemetry estimates. J Zool 285:39-45.

O’Connell AF, Nichols JD, Karanth KU (2011) Camera Traps in Animal Ecology: Methods and Analyses. Springer.

Oksanen L, Fretwell S, Arruda J, Niemela P (1981) Exploitation ecosystems in a gradient of primary productivity. Am Nat 118:240–261.

Palomares F (2001) Vegetation structure and prey abundance requirements of the Iberian lynx: implications for the design of reserves and corridors. J Appl Ecol 38:9–18.

Palomares F (2007) *Herpestes ichneumon*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 327–329

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508.

Palomares F, Ferreras P, Fedriani JM, Delibes M (1996) Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. J Appl Ecol 33:5–13.

Palomares F, Ferreras P, Travaini A, Delibes M (1998) Co-existence between Iberian lynx and Egyptian mongooses: estimating interaction strength by structural equation modelling and testing by an observational study. J Anim Ecol 67:967–978.

Palomares F, Gaona P, Ferreras P, Delibes M (1995) Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits. Conserv Biol 9:295–305.

Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain

Pasanen-Mortensen M, Pyykönen M, Elmhagen B (2013) Where lynx prevail, foxes will fail - limitation of a mesopredator in Eurasia. Glob Ecol Biogeogr 22:868–877.

Pereira P, Alves da Silva A, Alves J, et al. (2012) Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. Ecol Res 27:745–753.

Pianka E (1974) Niche Overlap and Diffuse Competition. Proc Natl Acad 71:2141–2145.

Pimenta V, Barroso I, Álvares F, et al. (2005) Situação populacional do lobo em Portugal, resultados do censo nacional de 2002/2003. Instituto para a Conservação da Natureza / Grupo Lobo, Lisboa.

Posluszny M, Pilot M, Goszczyński J, Gralak B (2007) Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. Ann Zool Fennici 44:269–284.

Prieto JAF, Sánchez ÁB (1996) La reserva integral de Muniellos: Flora y vegetación. 206.

Prugh LR, Ritland CE (2005) Molecular testing of observer identification of carnivore feces in the field. Wildl Soc Bull 33:189–194.

Prugh LR, Stoner CJ, Epps CW, et al. (2009) The Rise of the Mesopredator. Bioscience 59:779–791

Ray JC, Redford KH, Steneck RS, Berger J (2005) Large carnivores and the conservation of biodiversity. Island Press, Washington DC.

Ridout M, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat 14:322–337.

Ripple WJ, Beschta RL (2008) Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biol Conserv 141:1249–1256.

Ripple WJ, Beschta RL (2006a) Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biol Conserv 133:397–408.

Ripple WJ, Beschta RL (2012) Large predators limit herbivore densities in northern forest ecosystems. Eur J Wildl Res 58:733–742.

Ripple WJ, Beschta RL (2006b) Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. For Ecol Manage 230:96–106.

Ripple WJ, Beschta RL (2004) Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? Bioscience 54:755–766.

Ripple WJ, Rooney TP, Beschta RL (2010) Large predators, deer, and trophic cascades in boreal and temperate ecosystems. In: Terborgh J, Estes J (eds) Trophic cascades predators, prey, Chang. Dyn. Nat. Island Press, Washignton DC, pp 141–161.

Ripple WJ, Wirsing AJ, Wilmers CC, Letnic M (2013) Widespread mesopredator effects after wolf extirpation. Biol Conserv 160:70–79.

Ritchie EG, Elmhagen B, Glen AS, et al. (2012) Ecosystem restoration with teeth: what role for predators? Trends Ecol Evol 27:265–271.

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998.

Rivas-Martinez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique. An del Jard Bot Madrid 37:251–268.

Rivas-Martínez S, Díaz TE, Fernández-González F, et al. (2002) Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. Itinera Geobot 15:5–922.

Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas. In: Serv. Cart. la Univ. León Madrid, Spain. http://www.ucm.es/info/cif/form/maps.htm.

Roemer GW, Gompper ME, Van Valkenburgh B (2009) The Ecological Role of the Mammalian Mesocarnivore. Bioscience 59:165–173.

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. Mamm Rev 39:67–78.

Rosellini S, Osorio E, Ruiz-González A, et al. (2008) Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. Wildl Res 35:434–440.

Rovero F, Marshall AR (2009) Camera trapping photographic rate as an index of density in forest ungulates. J Appl Ecol 46:1011–1017.

Rowcliffe JM, Carbone C (2008) Surveys using camera traps: are we looking to a brighter future? Anim Conserv 11:185–186.

Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. J Appl Ecol 45:1228–1236.

Ruell EW, Crooks KR (2007) Evaluation of Noninvasive Genetic Sampling Methods for Felid and Canid Populations. J Wildl Manage 71:1690–1694.

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

Šálek M, Červinka J, Padyšáková E, Kreisinger J (2013) Does spatial co-occurrence of carnivores in a Central European agricultural landscape follow the null model? Eur J Wildl Res.

Salo P, Nordström M, Thomson RL, Korpimäki E (2008) Risk induced by a native top predator reduces alien mink movements. J Anim Ecol 77:1092–8.

Sarmento P, Cruz J, Monterroso P, et al. (2004) The Iberian Lynx in Portugal: Status survey and conservation action plan. Instituto para a Conservação da Natureza, Lisboa.

Sarmento P, Cruz J, Monterroso P, et al. (2009) Status survey of the critically endangered Iberian lynx *Lynx pardinus* in Portugal. Eur J Wildl Res 55:247–253.

Sarmento PB, Cruz J, Eira C, Fonseca C (2010) Modeling the occupancy of sympatric carnivorans in a Mediterranean ecosystem. Eur J Wildl Res 57:119–131.

Scheinin S, Yom-Tov Y, Motro U, Geffen E (2006) Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment. Anim Behav 71:577–584.

Schmidt K, Kowalczyk R (2006) Using Scent-Marking Stations to Collect Hair Samples to Monitor Eurasian Lynx Populations. Wildl Soc Bull 34:462–466.

Schoener T (1983) Field experiments on interspecific competition. Am Nat 122:240–285.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39.

Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. J Zool 259:269–279.

Shehzad W, Riaz T, Nawaz MA, et al. (2012) Carnivore diet analysis based on next-generation sequencing: application to the leopard cat (*Prionailurus bengalensis*) in Pakistan. Mol Ecol 21:1951–65.

Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA (2008) Roads as barriers to animal movement in fragmented landscapes. Anim Conserv 11:288–296.

Silver SC, Ostro LET, Marsh LK, et al. (2004) The use of camera traps for estimating jaguar *Panthera onca* abundance and density using capture/recapture analysis. Oryx 38:148–154.

Simón MA, Cadenas R, Gil-Sánchez JM, et al. (2009) Conservation of free-ranging Iberian lynx (*Lynx pardinus*) populations in Andalusia. In: Vargas A, Breitenmoser C, Breitenmoser U (eds) Iber. Lynx Ex Situ Conserv. An Interdiscip. Approach. Fundación Biodiversidad in collaboration with IUCN Cat Specialist Group, Madrid, pp 43–55.

Sollmann R, Furtado MM, Hofer H, et al. (2012) Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mamm Biol - Zeitschrift für Säugetierkd 77:41–46.

Sollmann R, Mohamed A, Samejima H, Wilting A (2013) Risky business or simple solution – Relative abundance indices from camera-trapping. Biol Conserv 159:405–412.

Soule ME, Bolger DT, Alberts AC, et al. (1988) Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. Conserv Biol 2:75–92.

Suárez-Eoane S, García-Ovés P (2004) Do disturbances in surrounding areas affect a core population of cantabrian capercaillie *Tetrao urogallos cantabricus*? The case of the natural Reserve of Muniellos (Asturias, NW Spain). Ardeola 51:395–409.

Szabó P, Meszeéna G (2006) Limiting similarity revisited. Oikos 112:612–619.

Theuerkauf J (2009) What Drives Wolves: Fear or Hunger? Humans, Diet, Climate and Wolf Activity Patterns. Ethology 115:649–657.

Valkenburgh BV (1988) Trophic diversity in past and present guilds of large predatory mammals. Paleobiology 14:155–173.

Valkenburgh BV (2007) Deja vu: the evolution of feeding morphologies in the Carnivora. Integr Comp Biol 47:147–63.

Virgós E, Revilla E, Mangas JG, et al. (2005) Revisión de la dieta del Téjon (*Meles meles*) en la Península Ibérica: comparación con otras localidades de su área de distribución natural. In: Virgós E, Mangas JG, Revilla E, Roura X-D (eds) Ecol. Distrib. y estatus Conserv. del tejón Ibérico. Sociedad Española para la Conservación y Estudio de los Mamíferos, Málaga, pp 67–80.

Weaver JL, Wood P, Paetkau D, Laack LL (2005) Use of scented hair ocelots to detect Ocelots. Wildl Soc Bull 33:1384–1391.

Wilson DE, Mittermeier RA (2009) Handbook of the carnivores of the world. Vol. I - Carnivores. Lynx editions, Barcelona

Wilson GJ, Delahay RJ (2001) A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildl Res 28:151–164.

Wilson RR, Blankenship TL, Hooten MB, Shivik JA (2010) Prey-mediated avoidance of an intraguild predator by its intraguild prey. Oecologia 164:921–929.

Woodroffe R, Gilks P, Johnston WT, et al. (2008) Effects of culling on badger abundance: implications for tuberculosis control. J Zool 274:28–37.

Zabala J, Zuberogoitia I, Martínez-climent JA (2009) Testing for niche segregation between two abundant carnivores using presence-only data. Folia Zool 58:385–395.

Zielinski WJ, Schlexer F V., Pilgrim KL, Schwartz MK (2006) The Efficacy of Wire and Glue Hair Snares in Identifying Mesocarnivores. Wildl Soc Bull 34:1152–1161.

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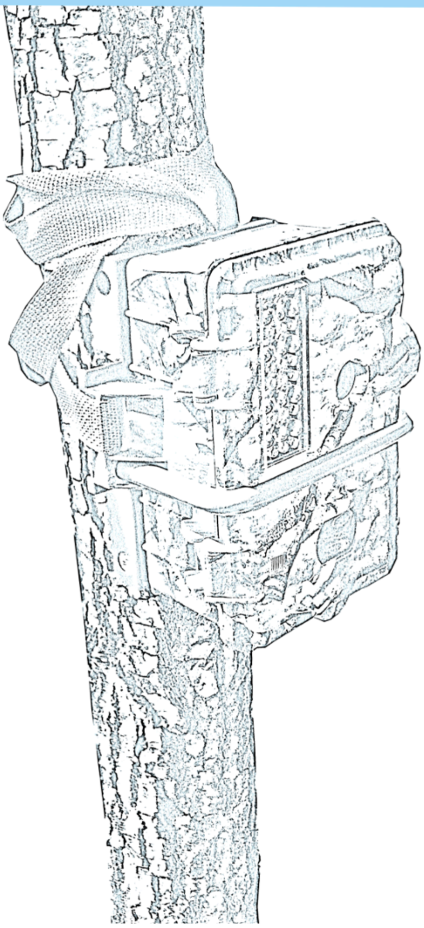
Evaluation of attractants for non-invasive studies of Iberian carnivore communities

Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South-western Europe

Efficiency of hair snares and camera traps to survey mesocarnivore populations

Methodological improvements for mesocarnivore ecological studies



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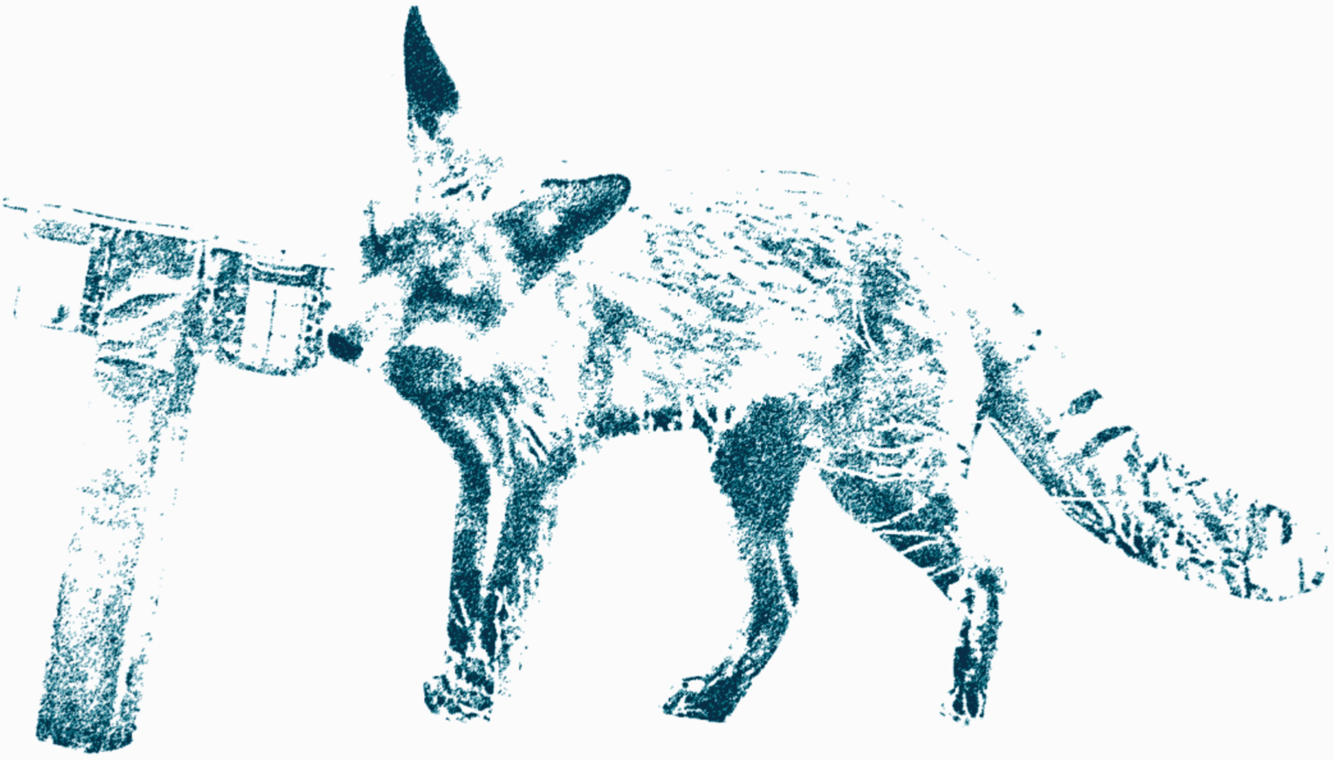

2.1 Evaluation of attractants for non-invasive studies of Iberian carnivore communities

Abstract

Context. The estimation of population parameters for mammalian carnivore species is a challenging task because of their low densities and large home ranges, which make detection probabilities very low. Several factors, such as the species abundance, habitat structure or the use of an attractant affect carnivore detection probabilities; however, attractants are the most easily manipulated. Some previous research suggests that the use of effective attractants can significantly increase detection probabilities.

Aims. To assess the effectiveness of several attractants for Iberian carnivores, and to evaluate their usefulness for noninvasive survey methods.

Methods. The responses of seven carnivore species to six potential attractants were evaluated through cafeteria-like experiments with captive specimens. A selectivity index was applied to assess the relative attractiveness of each tested substance. The enclosure tests were followed by field trials with camera-trapping, using the most promising attractants for field evaluation of their efficiency.

Key results. Enclosure trials revealed that lynx urine was the most effective and generalist attractant because it successfully attracted six of the seven species tested. Rubbing behaviour was also induced in the greatest number of species by lynx urine. Field tests using a combination of lynx urine and valerian extract solution induced investigative behaviours in over 50% of all detection events in all species, with the exception of the Eurasian badger.

Conclusions. No single attractant is effective for all species. Nevertheless, a combination of lynx urine and valerian solution should efficiently attract the majority of species present in Iberian carnivore communities. Furthermore, some species exhibit a rubbing behaviour when they come in contact with the attractants. Regardless of the generalist efficiency of the lynx urine, other tested substances revealed promising results for single-species monitoring.

Implications. Our results provide a baseline for selecting attractants in survey and monitoring programs that focus on carnivore species. The rubbing behaviours exhibited by several of the species tested suggest the use of these attractants could improve the efficiency of field studies that rely on rub-pads for the collection of biological samples.

Additional keywords: attractant effectiveness, behavioural response, efficacy, Iberian carnivores, population monitoring, species detection.

Introduction

The definition of suitable management and conservation programs for wildlife strongly depends on an accurate assessment of target-species distribution, population size and trends (Williams *et al*. 2002). In the case of carnivore species, which occur in particularly low densities and have large home ranges, these parameters are especially difficult to estimate (Wilson and Delahay 2001; Long *et al*. 2008). The inconspicuous habits along with human-phobia of many carnivore species make the use of direct and invasive field methods laborious and sometimes subject species to unnecessary disturbance (Ballenberghe 1984; Michalski *et al*. 2007). For these reasons, non-invasive methods are broadly applied to estimate carnivore distributions (Moruzzi *et al*. 2002), abundance (Mondol *et al*. 2009) and population trends (Travaini *et al*. 2010). Among these, some require an active search of the species presence, whereas others (e.g. scent stations, hair-snaring and camera-trapping) rely on natural animal movement for data collection (Wilson and Delahay 2001; Long *et al*. 2008). The use of attractants that stimulate the investigative response of the target species has been reported to significantly increase the detection probabilities of carnivores (Hunt *et al*. 2007; Schlexer 2008; Thorn *et al*. 2009). Therefore, the use of attractants should generally be incorporated into sampling methods, which will increase the reliability of resultant data and allow for more robust estimates of population parameters (Mackenzie and Royle 2005; Long *et al*. 2008).

Attractants used in carnivore studies can be clustered into the following three groups (Schlexer 2008): baits – food items or other substances that attract an animal by appealing to its sense of taste or smell, usually intended to be consumed (Roughton 1982; Zielinski *et al*. 2005); lures – substances that attract an animal via sense of smell, sight or hearing (Harrison 1997); and natural attractants – objects in the existing environment, that are regularly used by animals as a part of their behavioural repertoire. Scent marks such as anal-gland secretions, urine or faeces can be included in both of the latter attractant types, and play an important role in the communication among sympatric competitors (Ralls 1971; Schlexer 2008). Because scent marks can remain effective for long periods of time, they are used by mammals to avoid aggressive encounters between competitors by allowing for spatial or temporal segregation, the assessment of competitive ability and the establishment of dominance relationships (Ralls 1971; Gosling and McKay 1990). Previous studies assessed the effectiveness of attractants, especially in North America and Australia (e.g. Fagre *et al*. 1983; Phillips *et al*. 1990; Clapperton *et al*. 1994; Edwards *et al*. 1997; McDaniel *et al*. 2000 among others); however, nearly all (≈90%) of these evaluations focus on canid or felid species such as coyotes (*Canis latrans*; Fagre *et al*. 1983; Phillips *et al*. 1990) and red foxes (*Vulpes vulpes*; Saunders and Harris 2000; Miguel *et al*. 2005) or feral cats (Clapperton *et al*. 1994; Edwards *et al*. 1997). To our knowledge, no study has focussed on the effectiveness of attractants for entire carnivore communities, with the exception of the study of Andelt and Woolley (1996), which targeted a mammal community of urban mammals in Colorado (USA). In addition, the few scientific studies on the efficiency of attractants for carnivores have yielded conflicting results (Schlexer 2008). Hence, carnivore attractants are still selected mostly on the basis of tradition (Schlexer 2008).

The Iberian carnivore community consists of 15 native and one introduced species. Despite the importance of carnivores in Iberian natural ecosystems, there is still a lack of knowledge regarding the distributions and population trends of many carnivore species in Portugal and Spain. In fact, three species have recently been classified as ‘data deficient’ in Portugal by the latest national red book revisions (Cabral *et al*. 2005) and distribution maps of several species are incomplete (Palomo *et al*. 2007). In the present paper, we evaluate the responses of seven carnivore species present in the

Iberian ecosystems to six potential attractants. Our research objectives were to evaluate which attractants are more efficient for each species and to identify combinations of attractants that are effective for the widest range of carnivore species in the Iberian carnivore communities.

Materials and methods

Enclosure facilities, animals and attractants tested

The enclosure tests were conducted in two zoological facilities that harbour autochthonous species of Iberian vertebrate fauna. The Cañada Real Open Center (CROC) is located 48 km west of Madrid (Spain), and the Parque Biológico de Gaia (PBG) is located 10 km south of Porto (Portugal). The species tested at the CROC were red fox (1F), European wildcat (*Felis silvestris*; 1M and 2F) and Iberian wolf (*Canis lupus signatus*, 3M and 2F). Common genet (*Genetta genetta*; 1Mand 1F), stone marten (*Martes foina*, 1M), Eurasian badger (*Meles meles*, 1M and 1F) and polecat (*Mustela putorius*; 8 individuals of unknown sex) were tested in the PBG. All individuals of the same species from each facility were kept in the same enclosure. Because of logistic constraints, individual marking of the tested specimens was not possible; therefore, we were incapable of assigning behavioural responses to specific individuals. All animals included in the tests were treated in compliance with guidelines outlined by animal ethics committees in Spain and Portugal, as part of the project CGL2009-10741.

The tested attractants were selected on the basis of their traditional use in carnivore studies, and included the following: Collarum Canine Bait (Wildlife Control Supplies, East Granby, Connecticut, USA), a commercial canid-specific attractant; valerian-extract solution, containing valeric acid found in urine and anal-sac secretions of coyote and fox (Saunders and Harris 2000), and described as a felid-specific attractant (Childers-Zadah 1998; Raal *et al*. 2007); fatty acid scent (FAS), a mixture of seven volatile fatty acids found in fermented egg (Roughton 1982), commonly used as a generalist carnivore attractant in North America (Roughton and Sweeny 1982); lynx (*Lynx lynx*) urine (obtained from captive specimens (1M and 1F) kept in the CROC);

red-fox urine, obtained from captive red foxes (2M and 2F), held at Castilla La-Mancha University facilities; and a homogenized solution of stone-marten excrements (obtained from the captive specimen held at PBG). The urine and excrement solution used to test as attractants were frozen on collection, and kept frozen until the day they were used in the enclosure and field trials.

Experimental procedure

All attractants were tested simultaneously, in a cafeteria-like experiment (Rodgers 1990; Saunders and Harris 2000). The lures were included in a plastic tube (Ø = 1 cm; depth = 3 cm) filled with cotton wool, which was sprayed with 3mL of attractant. The plastic tubes were attached horizontally to wooden stakes, with the tube mouth facing outwards at a height of ~30 cm above ground. Six wooden stakes, each with a different attractant, were placed inside the enclosures, maintaining a distance of no less than 70 cm from each other. Tests were conducted between December 2008 and January 2009.

Each of the tested animals was exposed to the attractants for 3 h, during a period they were known to be active (as assessed by the facility keepers), namely during the morning for the species present at CROC and after sunset for the species present at PBG. By focusing the trials on periods of each specimen's activity, their response to the attractants was expected to be maximized. All animal movements were recorded by a video digital camera, model CAMCOLBUL2DC (Velleman, Gavere, Belgium), set so that it could include all six attractants in the frame area. Artificial illumination was used in the enclosures tested during night-time.

We considered that an animal had an investigative response whenever at least one of three behaviours, namely sniff, lick/bite and/or rub, was observed towards a specific attractant. Each individual response was adequately classified as one of the predefined behaviours and its intensity (time spent exhibiting that behaviour) was registered.

Statistical analysis

Because preference indexes are affected by individual variation, and individual identification of the tested animals was not possible because of logistic constraints, data were standardized to allow for comparisons among species and experimental treatments. The standardisation was performed by using the following equation:

$$\mathrm{SIT} = \frac{\frac{\sum \mathrm{IIT}}{\mathrm{NI}}}{\mathrm{TP}},$$

where SIT is standardized investigation time, IIT is individual investigation time (in seconds), NI is number of individuals in the captive trial and TP is trial period (in hours).

To evaluate the preference for a specific attractant in detriment of the others, we applied the modified Ivlev's selectivity index (Ivlev 1961), adapted by Jacobs (1974, hereafter JSI). This index is broadly applied in ecological studies to evaluate resource selection, whether the resources are food items (Toft 1980) or habitat types Palomares *et al*. 2000). Here, we used this index to evaluate the selection towards attractants, considering that all of them were equally available to the tested animals. The total time spent investigating the attractants was considered as the time the animal was predisposed to investigate the lures set in the enclosure; therefore, the availability for each attractant was considered to be 1/6 × Σ (time interacting with attractants). The significance of the difference between the obtained index value and zero (i.e. no selection) was evaluated by bootstrap resampling (100 replicates) (Manly 1997) and by recalculating the JSI for each bootstrap sample. We then determined the average index, standard deviation and 95% confidence intervals for each attractant and species. We considered an attractant as positively selected whenever the 95% CI of the JSI was positive and did not overlap zero. These attractants scored '+1'. Because the main purpose of the present work was to evaluate the carnivores' relative preference for attractants, and because with the applied experimental design, we could not evaluate behaviour of independent species towards each of them, we did not consider 'avoidance' as a possible outcome. For that reason, those attractants that obtained 95% CI with negative values and those that overlapped zero were aggregated into the score ‘0’. The sum of the scores of each attractant for all the tested species was considered as an overall measure of performance (OMP), and used to rank their efficiency for the Iberian carnivore community.

Field tests

After the enclosure tests, we selected a combination of attractants for field trials that promoted a significant investigative response on the maximum number of species. The field tests were performed in two distinct areas in the Iberian Peninsula, with Mediterranean pluviseasonal continental bioclimates (Rivas-Martínez *et al*. 2004). These included the Guadiana Valley Natural Park (GVNP), located in southern Portugal, and the Cabañeros National Park (CNP), located in central Spain, in the region of Castilla La-Mancha. The natural vegetation in the GVNP was dominated by the *Myrto communis–Quercetum rotundifoliae* series with other subserial stages (Costa *et al*. 1998), whereas the vegetation in the CNP was dominated by the *Pyro-Quercetum rotundifoliae* series and other subserial stages (Rivas-Martinez 1981).

The sampling design in each study area followed a gridsampling scheme, composed by 1-km2 grid squares. Camera traps, model Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA), were placed on every other vertex of the grid squares, resulting in a sampling grid of ~1.4 km (which corresponds to the distance between diagonal grid nodes). A circular area of 250-m radius surrounding each grid node was inspected for carnivore paths before placement of the camera trap. The final location of camera traps corresponded to areas of easy access and potentially good detection probability within the mentioned buffer. The distance (mean ± s.d.) between neighbouring camera stations was of 1203 ± 231matGVNP and 1220 ± 238m at CNP. Camera traps were maintained in the field for a minimum period of 28 days and were inspected for battery or card replacement every 7–10 days.

Attractants were placed in the field at a distance of 2–3m from the camera traps. The selected attractants were deployed in separated, perforated plastic tubes supported by a wooden stake, at a distance of 10–15 cm from each other and ~30 cm above the ground. A volume of 5mL of each attractant was sprayed into a cotton gaze held inside each plastic tube. Attractants were rebaited every 7–10 days.

The GVNP was sampled from 27 July to 6 September 2009 and the CNP was sampled from 24 September to 28 October 2009. We chose this season for the field trials because it corresponds to the time when the offspring of most medium sized carnivores from that year become independent (Blanco 1998). Therefore, we would expect a higher number of contacts than during the breeding season.

We considered a series of photographs of the same species within a 30-min interval as dependent events (Kelly *et al*. 2008). Therefore, only detections of the same species separated in time over 30 min were considered for this analysis, to reduce the possibility of the same animal being captured more than once in the same camera trap. Because the field trials were included in a carnivore-community research project, which required a constant and balanced effort of the entire study areas, we could not apply traditional 'control *v*. treatment' experimental protocol during field trials. Nevertheless, despite being set close to one another, the observed animal behaviours (such as sniffing, rubbing or marking) elicited by each of the attractants could be unambiguously identified from the photographs and were registered. The proportion of each observed response over the total detections for each species was calculated as an index of attractant efficiency.

Results

Captivity tests

A total of 21 h of enclosure tests revealed distinct strengths in the behavioural responses among the species and attractants evaluated. Lynx urine scored the highest of the six attractants evaluated, because it was effective for six of the carnivore species tested (OMP = +6). Only the stone marten did not spend significantly more time investigating lynx urine than what would be expected by chance.

The Collarum attractant was the second top-scored attractant (OMP = +4). This substance stimulated a significant investigative behaviour on the Iberian wolf, European wildcat, Eurasian badger and red fox. FAS effectively attracted the Iberian wolf, genet and stone marten (OMP = +3). The remaining attractants were effective for less than half of the species tested (OMP = +2, +1 and 0, for the valerian solution, red-fox urine and stone-marten excrements, respectively; Fig. 2.1.1).

As for the species responses, the Iberian wolf, European wildcat and genet revealed a significant interest for half of the substances they were exposed to (*n* = 3; Fig. 2.1.1). The Eurasian badger, the polecat and the red fox investigated two of attractants significantly more than expected by chance. The stone marten revealed a significant interest only for FAS.

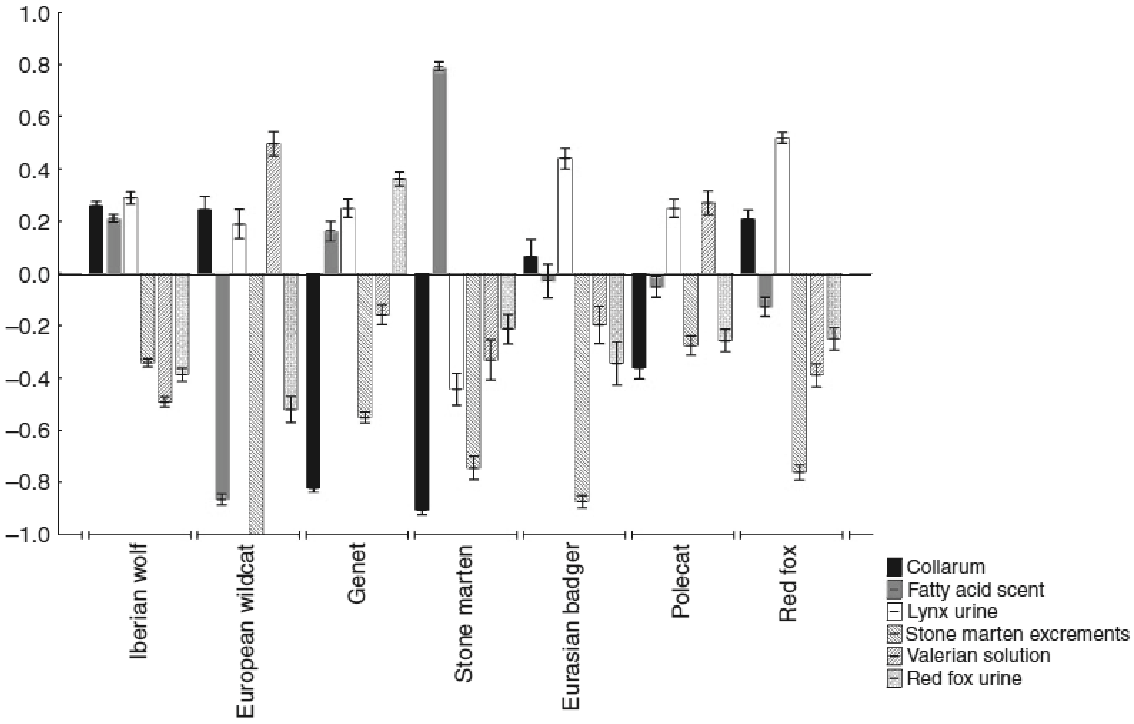

Figure 2.1.1. The average Jacobs selectivity index value with95%confidence intervals, obtained for the Iberian wolf, European wildcat, genet, stone marten, Eurasian badger, polecat and red fox towards each of the tested attractants during the enclosure tests in Cañada Real Open Center, Spain, and Parque Biológico de Gaia, Portugal, between December 2008 and January 2009.

The strength of the responses towards the elected attractants also varied among species (Table 2.1.1). Because of the high range of strength of responses observed for the different species and attractants, data were summarised with the median and the geometric mean, which reduced the effect of extreme values. The Iberian wolves and genets exhibited the strongest responses to the positively selected attractants. Each individual of these species spent, on average, between 38.0 (±3.8, s.d.) and 43.8 (±9.9) s h^{-1} (Iberian wolves) and between 69.2 (±23.6) and 92.7 (±22.8) s h^{-1} (genets) investigating them. Their overall investigation times were also the highest of all species (Table 2.1.1). The average intensity of responses by red foxes towards the positively selected attractants was 21.1 (± 7.1, s.d.) and 34.0 (±7.4) s $individual^{-1}$ h^{-1}. The summarised responses of this species revealed an intermediate response towards the attractants (Table 2.1.1). The overall strength of responses of European wildcats, stone martens, Eurasian badgers and polecats were all below 4 s $individual^{-1}$ h^{-1} (geometric mean, Table 2.1.1). However, the European wildcat did not spend any time at all investigating stone-marten excrements, but revealed intermediate investigation strengths towards the positively selected attractants (10.4±2.2 to 18.3±9.4 s $individual^{-1}$ h^{-1}; Table 2.1.1). The stone marten was only significantly more attracted towards the FAS than expected by chance, with a moderate response (22.7±5.5 s $individual^{-1}$ h^{-1}). The Eurasian badger and the polecat displayed the weakest responses, with investigative responses below 10 s $individual^{-1}$ h^{-1} towards the positively selected attractants (Table 2.1.1).

Table 2.1.1. Mean investigation time.

The mean (±s.d.) investigation time (s individual^{-1} h^{-1}) the Iberian wolf, European wildcat, genet, stone marten, Eurasian badger, polecat and red fox spent investigating attractants in enclosures in Cañada Real Open Center, Spain, and Parque Biológico de Gaia, Portugal, between December 2008 and January 2009. Zero values were replaced by the value 0.001 for the calculation of the geometric mean

Species	N	Collarum	FAS	Lynx urine	Stone marten excrements	Valerian solution	Red fox urine	Median	Geometric mean
Iberian wolf	5	41.1 (±6.0)	38 (±3.8)	43.8 (±9.9)	14.3 (±2.2)	10.3 (±2.4)	13.3 (±3.8)	26.15	22.62
European wildcat	3	11.1 (±3.8)	0.6 (±0.5)	10.4 (±4.4)	0 (±0.0)	18.3 (±9.4)	2.7 (±1.7)	6.55	1.23
Genet	2	6 (±3.2)	69.2 (±23.6)	78.8 (±24.0)	16.5 (±4.2)	39.7 (±13.1)	92.7 (±22.8)	54.45	35.46
Stone marten	1	0.4 (±0.3)	22.7 (±5.5)	2.8 (±2.0)	1.1 (±1.0)	3.8 (±2.9)	4.3 (±2.1)	3.3	2.78
Eurasian badger	2	3.1 (±1.6)	2.6 (±1.5)	5.4 (±2.0)	0.2 (±0.2)	2 (±1.3)	1.6 (±1.2)	2.6	1.77
Polecat	8	2 (±0.8)	3.5 (±1.0)	5.7 (±1.7)	2.3 (±0.8)	6.3 (±2.6)	2.5 (±1.1)	3	3.36
Red fox	1	21.1 (±7.1)	11.9 (±3.8)	34 (±7.4)	2.3 (±1.5)	7.3 (±3.6)	9.6 (±3.8)	10.75	10.55
Median		6	11.9	10.4	2.3	7.3	6.95		
Geometric mean		5.45	8.73	14	0.83	8.26	8.37		

The rubbing behaviour was rarely exhibited, except by the Iberian wolf and the genet (Table 2.1.2). For this reason, the JSI could not be applied to this behaviour. Nevertheless, some indications can be obtained from the animals' rubbing responses. Although the Iberian wolf exhibited rubbing behaviour for all attractants, this behaviour was more intense towards FAS (24.5 s individual^{-1} h^{-1}). Genets also displayed a generalist rubbing behaviour; however, the intensity of these responses was stronger towards FAS, lynx urine and red-fox urine. The red fox rubbed on Collarum, lynx urine and red-fox urine; however these responses were very weak (<2 s individual^{-1} h^{-1}). Both European wildcats and polecats displayed rubbing behaviours towards only one attractant, the valerian solution; whereas the Eurasian badger rubbed only against the lynx urine. The stone marten was the only species that did not rub on any of the tested attractants.

Table 2.1.2. Mean rubbing time**.**
The mean (±s.d.) rubbing time (s individual^{-1} h^{-1}) the Iberian wolf, European wildcat, genet, stone marten, Eurasian badger, polecat and red fox spent investigating attractants in enclosures in Cañada Real Open Center, Spain, and 0

Species	N	Collarum	FAS	Lynx urine	Stone marten excrements	Valerian solution	Red fox urine	Number of attractants with rubbing responses
Iberian wol5f	5	3.6 (±0.8)	24.5 (±3.5)	1.8 (±0.7)	5 (±1.2)	1.3 (±0.4)	3.9 (±1.3)	6
European wildcat	3	0 (±0.0)	0 (±0.0)	0 (±0.0)	0 (±0.0)	15.7 (±9.4)	0 (±0.0)	1
Genet	2	0.7 (±0.6)	57.1 (±23.0)	69.9 (±23.9)	7.6 (±3.2)	22.4 (±12.4)	74.2 (±23.4)	6
Stone marten	1	0 (±0.0)	0 (±0.0)	0 (±0.0)	0 (±0.0)	0 (±0.0)	0 (±0.0)	0
Eurasian badger	2	0 (±0.0)	0 (±0.0)	0.2 (±0.2)	0 (±0.0)	0 (±0.0)	0 (±0.0)	1
Polecat	8	0 (±0.0)	0 (±0.0)	0 (±0.0)	0 (±0.0)	3.7 (±2.5)	0 (±0.0)	1
Red fox	1	1.4 (±1.1)	0 (±0.0)	1.1 (±0.8)	0 (±0.0)	0 (±0.0)	0.3 (±0.3)	3
Number of species with rubbing responses		3	2	4	2	4	3	

Field tests

Although the combination of FAS attractant + lynx urine was effective for all species tested during the captivity trials (Fig. 2.1.1), yielding a joint OMP score of '+7', the combination of lynx urine + valerian solution induced rubbing behaviour in a greater number of species (*n* = 6; Table 2.1.2), suggesting a greater efficiency. Furthermore, previous field experience with lynx urine revealed its effectiveness for the attraction of the stone marten (Monterroso 2006). For these reasons, the combination of attractants selected for the field trials was lynx urine + valerian solution.

During field tests, we detected eight carnivore species on both study areas, six of which were evaluated during the enclosure tests, whereas the following two were not: the Egyptian mongoose (*Herpestes ichneumon*) and the least weasel (*Mustela nivalis*). Overall, 472 carnivore detections were obtained, 126 in GVNP and 346 in CNP. All species, except the Eurasian badger, displayed interactive behaviours (sniffing, biting or marking) towards some of the lure attractants on more than 50% of the detections (Table 2.1.3). The highest scores were obtained by the red fox, the wildcat, the stone marten and the Egyptian mongoose, which interacted with the attractants on at least 70% of the detection occasions.

Table 2.1.3. Field-trial carnivore responses**.**
The responses exhibited by the red fox, European wildcat, stone marten, polecat, least weasel, Eurasian badger, genet and Egyptian mongoose towards valerian extract and lynx urine during field trials in Guadiana Valley Natural Park Portugal and Cabañeros National Park, Spain, July–October 2009

Species	No. of detections			Proportion of investigative behaviors over all detections	Proportion of attractant specific investigative occasions over all occasions with investigative behavior	
	GVNP	CNP	Total		Lynx urine	Valerian solution
Red fox	41	263	304	0.75	0.69	0.25
European wildcat	22	4	26	0.81	0.67	0.14
Stone marten	16	42	58	0.72	0.52	0.17
Polecat	6	0	6	0.67	0.5	0
Least weasel	2	0	2	0.5	0	1
Eurasian badger	12	16	28	0.18	0.8	0.2
Genet	9	21	30	0.53	0.69	0.19
Egyptian mongoose	18	0	18	0.78	0.29	0.57
Mean (±s.d.)				0.62 (±0.21)	0.52 (±0.26)	0.32 (±0.32)

Of the two available attractants in the field tests, lynx urine obtained higher proportion of interactions for all species, except for the least weasel and the Egyptian mongoose, which interacted more with the valerian solution than with lynx urine.

Discussion

Despite the small sample size available for the enclosure tests, the results suggest that none of the tested attractants alone is significantly more efficient than the others for all carnivore species tested in our study. The lynx urine was the most efficient attractant for the majority of species, because only the stone marten did not spend more time than expected by chance investigating it. The Eurasian lynx does not occur naturally in the Iberian Peninsula; however, it co-occurs elsewhere with most of the carnivore species present in Iberian ecosystems (e.g. wolf, red fox, European wildcat, stone marten, Eurasian badger and polecat) (Mitchell-Jones *et al*. 1999). Where it occurs, the Eurasian lynx is a top predator, known to kill smaller carnivores (Palomares and Caro 1999). In the Iberian Peninsula, its congener, Iberian lynx (*Lynx pardinus*), is sympatric with all species tested (Palomo *et al*. 2007), being superior competitor to most of the mesocarnivores, often killing them (Palomares and Caro 1999). Several studies on carnivores suggest that individuals can identify odours from a competitor species (Erlinge and Sandell 1988; Harrington *et al*. 2009), even when it has never come in contact with them before (Harrington *et al*. 2009). The lack of avoidance and the rubbing behavior exhibited by several species in enclosure tests, and the frequent investigative behaviour towards lynx urine from most Iberian carnivores observed in field trials suggest that the predator's scent promotes investigative and scent-marking behaviours from other carnivores. This finding is in accordance with Harrington *et al*. (2009), who found little support for an avoidance of otter (*Lutra lutra*) odour by American mink (*Mustela vison*). Similarly, Howard *et al*. (2002) found that coyotes and bobcats (*Lynx rufus*) were attracted to each other's faeces. These two species are known to react negatively to each other (Wilson *et al*. 2010), and therefore this attraction to the faeces of the competing species could be the result of investigative processes that allow for the employment of adequate behavioural strategies for coexistence (Wilson *et al*. 2010). Our data suggest that the presence of lynx scent in the 'familiar' surroundings of captive and free-living Iberian carnivores must be understood by the animals as the presence of a competitor or a threat, which induces an investigative behaviour and even scent marking of their own. This was observed in red foxes, which urinated and rubbed against the scent, and in stone martens and genets that defecated on it (P. Monterroso, pers. obs.).

The attractiveness of valerian extract on cats has been referred by other authors (Raal *et al*. 2007; Klar *et al*. 2009; Jerosch *et al*. 2010), although its effectiveness has never been assessed. Our results from the enclosure tests comply with the suggestion of these previous authors because it induced not only a significant investigative response from wildcats, but it also promoted a strong rubbing behaviour. Such a response to valerian scent is traditionally known and has resulted in its use in field studies for hair snaring (Djabalameli 2005). Similar behaviour is found in other felid species towards another plant extract, the catnip (*Nepeta cataria*; Edwards *et al*. 1997; Harrison 1997;

McDaniel *et al*. 2000). Interestingly, our field tests revealed that wildcats showed more interest in lynx urine than they did in valerian solution. Edwards *et al*. (1997) suggested that the efficacy of scent-based lures may be strongly influenced by seasonal changes in reproductive behaviour, becoming particularly less effective when reproductive behaviour is relatively subdued. Our field trials were performed in late summer, when territoriality is reduced and no reproductive activity is expected to occur (Sunquist and Sunquist 2002). Therefore, it is possible that, in this season, wildcats are more interested in a potential competitor and/or predator within their home ranges than with a reproduction-appealing scent.

The Collarum Canine Bait and FAS showed significant relative efficiency for some species; however, the overall evaluation of these attractants suggests that they are not an adequate choice for the entire Iberian carnivore communities. These attractants can be better used for studies focusing on a limited number of species. Asexpected, the Collarum Canine Bait could be efficient for canid species, such as the wolf or the red fox. Our results suggest that, in Iberian carnivore assemblages, FAS should be used only in studies focused on the wolf, the genet and the stone marten, despite being broadly used in the United States in carnivore surveys (Roughton and Sweeny 1982) and being a recommended attractant for canids and temperate felids (Schlexer 2008). The homogenized solution of stone-marten excrements was ineffective for any of the species tested. The stone marten, as other mustelids, uses faeces for scent marking (Hutchings and White 2000; P. Monterroso, unpubl. data). However, scent marking does not occur all the time. Mammals tend to mark when they are both intolerant of, and dominant to, other members of the same species or when they come into contact with scent of competitor species (Ralls 1971; Miguel *et al*. 005). The captive stone marten from which excrements where collected exhibited abnormal behaviour during enclosure trials. A possible outcome of the abnormality in this specimen’s behaviour might have been non-scent marking of faeces, which could explain the lack of interest displayed by all species towards this substance. Furthermore, as excrements where presented in the form of a solution, there was no visual stimuli, which also affects the scat attractiveness to other carnivores (Howard *et al*. 2002). These two factors combined may have been responsible for the lack of interest demonstrated by all carnivores in the homogenized solution of stone-marten excrements. Red-fox urine was only effective for genets, and promoted a strong rubbing response in this species.

To our knowledge, no competitive interaction has ever been described involving these two species. We acknowledge the fact that the captive environments in which the tested animals are maintained might, to some extent, influence their behaviour towards interspecific scents. Nevertheless, genets often occur in sympatry with red foxes (Palomo *et al*. 2007) and therefore a possible subtle interaction might exist between these two species.

Rubbing behaviour in enclosure tests was exhibited by almost all species, but only towards a reduced number of attractants and very few times. This kind of behaviour is frequent across different kinds of mammals, and serves the purpose of leaving their scent in response to the scent of a stranger (Ralls 1971). This behavior has been observed in felids (Clapperton *et al*. 1994; Harrison 1997; Thomas *et al*. 2005) and canids (Harrison 2006) and serves as the basis for hair-sample collection in field surveys (McDaniel *et al*. 2000; Thomas *et al*. 2005; Weaver *et al*. 2005; Schmidt and Kowalczyk 2006). Although none of the tested attractants elicited a strong rubbing response from more than two species, the lynx urine and the valerian solution induced this type of behaviour for the largest number of species.

Most evaluations of carnivore attractants involve captive animals and their effectiveness is assessed by exposing the animals to the evaluated substances (Phillips *et al*. 1990; Harrison 1997; Saunders and Harris 2000); however, field-testing is more appropriate because it incorporates environmental factors and population density (Schlexer 2008). Because we could not apply an adequate experimental protocol for our field trials, it is not possible to unequivocally state that the use of attractants provides higher encounter rates than does not using any attractant at all. Nevertheless, our results suggest that the combination of lynx urine and valerian solution elicits investigative behaviours in nearly all target species. These results not only support those provided by the enclosure tests regarding the efficiency of lynx urine for most carnivores, but they also revealed that this attractant might also attract the stone marten and, to some extent, the Egyptian mongoose (not evaluated in captivity trials).

Our findings suggest that using lynx urine as an attractant in non-invasive survey methods would increase detection probability relative to the remaining attractants tested because this substance is actively investigated by most carnivore species present in Iberian communities. Furthermore, our results demonstrate that several of these species (e.g. the wildcat, the wolf or the red fox) exhibit rubbing behaviour in the presence of this attractant, a fact that allows for the use of rub pads to acquire hair samples that could be later used for genetic evaluation, e.g. in mark–recapture studies. Another advantage of this attractant is that lynx specimens exist in most zoological facilities, making it accessible to wildlife researchers. Indeed lynx urine fits the criteria of Fagre *et al*. (1983), who suggested that an adequate lure should be (1) uniform in quality, (2) high in availability, (3) low in cost, (4) easy to handle and (5) highly attractive to target species. Some factors, such as seasonality, might affect the composition of the urine samples collected throughout the year, thus compromising Fagres' first criteria. However, urine samples from captive animals generally fulfill these requirements because captive animals are maintained at near constant conditions, regarding feeding and environment, all year long (Howard *et al*. 2002).

The fact that the use of the same lures results in varying degrees of success (Schlexer 2008) highlights the importance of carefully replicating and evaluating attractant studies so as to obtain standardized and consistent patterns of target-species responses. To our knowledge, the present study is the first attempt to evaluate the efficiency of attractants for Iberian carnivore species. Despite the low number of captive animals tested and the seasonal characteristics of field sampling, our tests reveal patterns of relative attractant efficiency for Iberian carnivores, suggesting that for studies that focus on the assessment of carnivore assemblages similar to those present in the Iberian Peninsula, lynx urine should be a preferred lure over markings of smaller species or other commercial lures.

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References

Andelt, W. F., and Woolley, T. P. (1996). Responses of urban mammals to odor attractants and a bait-dispensing device. *Wildlife Society Bulletin* **24**, 111–118.

Ballenberghe, V. V. (1984). Injuries to wolves sustained during live-capture. *The Journal of Wildlife Management* **48**, 1425–1429. doi:10.2307/3801811

Blanco, J. C. (1998). 'Mamíferos de España, 2 Vols.' (Ed. Planeta: Barcelona, Spain.)

Cabral, M. J., Almeida, J., Almeida, P. R., Dellinger, T., Ferrand de Almeida, N., Oliveira, M. E., Palmeirim, J. M., Queiroz, A. I., Rogado, L., and Santos-Reis, M. (Eds) (2005). 'Livro Vermelho dos Vertebrados de Portugal.' 2nd edn. (Instituto da Conserva¸cão da Natureza/Assírio Alvim: Lisboa, Portugal). [In Portuguese.]

Childers-Zadah, V. (1998). Use of valerian plant and/or root as a scent attractant for stimulating canines and felines. US Patent 5,786,382.

Clapperton, B. K., Eason, T., Weston, R. J., Woolhouse, A. D., and Morgan, D. R. (1994). Development and testing of attractants for feral cats, *Felis catus* L. *Wildlife Research* **21**, 389–399. doi:10.1071/WR9940389

Costa, J. C., Aguiar, C., Capelo, J. H., Lousã, M., and Neto, C. (1998). Biogeografia de Portugal continental. *Quercetea* **0**, 5–56.

Djabalameli, J. (2005). Hair catching with the aid of the 'Lure Stick'. Proof of wildcat (*Felis silvestris*) existence by genetic analysis. A project by BUND and Bayerisches Landesamt für Umweltschutz. In 'Biology and Conservation of the European Wildcat (*Felis silvestris silvestris*)' seminar. Nienover, Germany

Edwards, G. P., Piddington, K. C., and Paltridge, R. M. (1997). Field evaluation of olfactory lures for feral cats (*Felis catus* L.) in central Australia. *Wildlife Research* **24**, 173–183. doi:10.1071/WR96013

Erlinge, S., and Sandell, M. (1988). Coexistence of stoat, *Mustela erminea*, and weasel, *M. nivalis*: social dominance, scent communication, and reciprocal distribution. *Oikos* **53**, 242–246. doi:10.2307/3566069

Fagre, D. B., Howard,W. E., Barnum, D. A., Teranishi, R., Schultz, T. H., and Stern, D. J. (1983). Criteria for the development of coyote lures. In 'Vertebrate Pest Control and Management Materials: Fourth Symposium.' ASTM STP 817. (Ed. D. E. Kaukeinen.) pp. 265–277. (American Society for Testing Materials: Philadelphia, PA.)

Gosling, L. M., and McKay, H. V. (1990). Competitor assessment by scent matching: an experimental test. *Behavioral Ecology and Sociobiology* **26**, 415–420. doi:10.1007/BF00170899

Harrington, L. A., Harrington, A. L., and Macdonald, D. W. (2009). The smell of new competitors: the response of American mink, *Mustela vison*, to the odours of otter, *Lutra lutra* and polecat, *M. putorius. Ethology* **115**, 421–428. doi:10.1111/j.1439-0310.2008.01593.x

Harrison, R. L. (1997). Chemical attractants for central American felids. *Wildlife Society Bulletin* **25**, 93–97.

Harrison, R. L. (2006).Acomparison of survey methods for detecting bobcats. *Wildlife Society Bulletin* **34**, 548–552. doi:10.2193/0091-7648(2006)34 [548:ACOSMF]2.0.CO;2

Howard, M. E., Zuercher, G. L., Gipson, P. S., and Livingston, T. R. (2002). Efficacy of feces as an attractant for mammalian carnivores. *The Southwestern Naturalist* **47**, 348–352. doi:10.2307/3672492

Hunt, R. J., Dall, D. J., and Lapidge, S. J. (2007). Effect of a synthetic lure on site visitation and bait uptake by foxes (*Vulpes vulpes*) and wild dogs (*Canis lupus dingo, Canis lupus familiaris*). *Wildlife Research* **34**, 461–466. doi:10.1071/WR05110

Hutchings,M. R., and White, P. (2000). Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review* **30**, 157–169. doi:10.1046/j.1365-2907.2000.00065.x

Ivlev, V. S. (1961) 'Experimental Ecology of the Feeding of Fishes.' (Yale University Press: New Haven, CT.)

Jacobs, J. (1974). Quantitative measurement of food selection.Amodification of the forage ratio and Ivlev's electivity index. *Oecologia* **14**, 413–417. doi:10.1007/BF00384581

Jerosch, S., Götz, M., Klar, N., and Roth, M. (2010). Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): implications for its conservation. *Journal for Nature Conservation* **18**, 45–54. oi:10.1016/j.jnc.2009.02.005

Kelly,M.J., Noss, A. J., Di Bitetti,M.S., Maffei, L., Arispe, R. L., Paviolo, A., Angelo, C. D., and Di Blanco, Y. E. (2008). Estimating puma densities from camera trapping across three study sites: Bolivia, Argentina, and Belize. *Journal ofMammalogy* **89**, 408–418. doi:10.1644/06-MAMM-A-424R.1

Klar, N., Herrmann, M., and Kramer-Schadt, S. (2009). Effects and mitigation of road impacts on individual movement behavior of wildcats. *The Journal of Wildlife Management* **73**, 631–638. doi:10.2193/2007-574

Long, R. A., MacKay, P., Ray, J., and Zielinski, W. (2008). 'Noninvasive survey methods for carnivores.' (Island Press: Washington, DC.)

Mackenzie, D. I., and Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* **42**, 1105–1114. doi:10.1111/j.1365-2664.2005.01098.x

Manly, B. (1997). 'Randomization, Bootstrap and Monte Carlo Methods in Biology.' 2nd edn. (Chapman and Hall: Boca Raton, FL.)

McDaniel, G. W., McKelvey, K. S., Squires, J. R., and Ruggiero, L. F. (2000). Efficacy of lures and hair snares to detect lynx. *Wildlife Society Bulletin* **28**, 119–123.

Michalski, F., Crawshaw, P. J. Jr, Oliveira, T. G., and Fabián, M. E. (2007). Efficiency of box-traps and leg-hold traps with several bait types for capturing small carnivores (Mammalia) in a disturbed area of southeastern Brazil. *Revista de Biologia Tropical* **55**, 315–320.

Miguel, F. J., Marques, I., and Monclús, R. (2005). Respuesta de los zorros (*Vulpes vulpes* Linnaeus, 1758) al olor de otros carnívoros. *Galemys* **17**, 113–121. [In Spanish with abstract in English]

Mitchell-Jones, A. G., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P. J. H., Spitzenberger, E., Stubbe, M., Thissen, J. B. M., Vohralik, V., and Zima, J. (1999). 'The Atlas of European Mammals.' (T and AD Poyser Natural History: London.)

Mondol, S., Karanth, K. U., Kumar, N. S., Gopalaswamy, A. M., Andheria, A., and Ramakrishnan, U. (2009). Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation* **142**, 2350–2360. doi:10.1016/j.biocon.2009.05.014

Monterroso, P. (2006). Selecção de habitat e análise dos factores que condicionam a presen¸ca e abundância de gato-bravo (*Felis silvestris*) no Parque Natural do Vale do Guadiana. M.Sc. Thesis, University of Porto, Porto, Portugal. [In Portuguese.]

Moruzzi, T. L., Fuller, T. K., DeGraaf, R. M., Brooks, R. T., and Li, W. (2002). Assessing remotely triggered cameras for surveying carnivore distribution. *Wildlife Society Bulletin* **30**, 380–386.

Palomares, F., and Caro, T.M.(1999). Interspecific killingamongmammalian carnivores. *American Naturalist* **153**, 492–508. doi:10.1086/303189

Palomares, F., Delibes, M., Ferreras, P., Fedriani, J. M., Calzada, J., and Revilla, E. (2000). Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. *Conservation Biology* **14**, 809–818. doi:10.1046/j.1523-1739.2000.98539.x

Palomo, L. J., Gisbert, J., and Blanco, J. C. (2007). 'Atlas y Libro Rojo de los Mamíferos Terrestres de España.' (Dirección General para la Biodiversidad – SECEM – SECEMU: Madrid, Spain.) [In Spanish]

Phillips, R. L., Blom, F. S., and Engeman, R. M. (1990). Responses of captive coyotes to chemical attractants. In ‘Proceedings of the Vertebrate Pest Conference’. (Eds L. R. Davis and R. E. Marsh.) pp. 285–290. (University of California: Davis.)

Raal, A., Orav, A., Arak, E., Kailas, T., and Müürisepp, M. (2007). Variation in the composition of the essential oil of *Valeriana officinalis* L. roots from Estonia. *Proceedings of Estonian Academy of Sciences Chemistry* **56**, 67–74.

Ralls, K. (1971). Mammalian scent marking. *Science* **171**, 443–449. [New Series] doi:10.1126/science.171.3970.443

Rivas-Martinez, S. (1981). Les étages bioclimatiques de la végétation de la Peninsule Iberique. *Anales del Jardin Botanico de Madrid* **37**, 251–268.

Rivas-Martínez, S., Penas, A., and Díaz, T. E. (2004). ‘Mapa Bioclimático de Europa, Bioclimas.’ (Servicio Cartográfico de la Universidad de León: Madrid, España) Available at http://www.ucm.es/info/cif/form/maps.htm [accessed January 2010]

Rodgers, A. R. (1990). Evaluating preference in laboratory studies of diet selection. *Canadian Journal of Zoology-Revue Canadienne de Zoologie* **68**, 188–190. doi:10.1139/z90-026

Roughton, R. D. (1982). A synthetic alternative to fermented egg as a canid attractant. *The Journal of Wildlife Management* **46**, 230–234. doi:10.2307/3808425

Roughton, R. D., and Sweeny, M. W. (1982). Refinements in scent-station methodology for assessing trends in carnivore populations. *The Journal of Wildlife Management* **46**, 217–229. doi:10.2307/3808424

Saunders, G., and Harris, S. (2000). Evaluation of attractants and bait preferences of captive red foxes (*Vulpes vulpes*). *Wildlife Research* **27**, 237–243. doi:10.1071/WR99052

Schlexer, F. V. (2008). Attracting animals to detection devices. In ‘Noninvasive Survey Methods for Carnivores’. (Eds R. A. Long, P. MacKay, W. J. Zielinski and J. C. Ray.) pp. 263–292. (Island Press: Washington, DC.)

Schmidt, K., and Kowalczyk, R. (2006). Using scent-marking stations to collect hair samples to monitor Eurasian lynx populations. *Wildlife Society Bulletin* **34**, 462–466. doi:10.2193/0091-7648(2006)34[462:USSTCH] 2.0.CO;2

Methodological improvements for mesocarnivore ecological studies

Evaluation of attractants for non-invasive studies of Iberian carnivore communities

Efficiency of hair snares and camera traps to survey mesocarnivore populations

Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South-western Europe

Monterroso, P., Castro, D., Silva, T.L., Ferreras, P., Godinho, R. & Alves, P.C. (2013) Journal of Zoology, 289(4): 243-250

2.2 Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South-western Europe

Abstract

Research on terrestrial carnivore ecology frequently relies on scat identification and analysis. However, species assignment is commonly based on scat morphology. Potential errors in scat identification are rarely accounted for and might contribute to substantial bias of the final results. Using molecular methods, we evaluate the accuracy of species identification based on morphological characteristics of mammalian mesocarnivore scats collected in two areas in the Iberian Peninsula. Our results revealed that error rates in species assignment of scats based on morphology were highly variable, ranging from 14%, for putative red fox *Vulpes vulpes* samples, to 88%, for putative wildcats *Felis silvestris*. The developed models revealed that putative species, season, study area and target species abundance are among the factors involved in identification accuracy. However, the low variability explained suggests that unaccounted factors also had significant effects on accuracy rates. The error rates in scat species assignment constitute a potential source of bias in ecological studies, with serious consequences for the management of threatened species, as unrealistic estimates of status and distribution are prone to occur. Our results suggest that scat identification accuracy rates are circumstance-specific and therefore should not be transferred or extrapolated. We suggest that scat-based studies should implement measures (molecular or others) that allow researchers to determine their own circumstance-specific error rates in scat identification, which should be incorporated in subsequent analyses, ensuring reliable ecological inferences.

Keywords

Mammalian mesocarnivores; scat; identification; accuracy rates; non-invasive genetics; conservation.

Introduction

Adequate and adjusted conservation planning relies on the collection, analysis and interpretation of field data. For this reason, the accuracy and reliability of data collected in the field assumes a crucial role in wildlife conservation. Data collection on mammalian carnivores is particularly challenging because they typically occur in low densities, are crepuscular and/or nocturnal, and elusive (Wilson & Delahay, 2001). As a result, knowledge on these species frequently relies on indirect methods, namely on species presence signs rather than on the observation or capture of the animals themselves (Heinemeyer, Ulizio & Harrison, 2008). Among the indirect field methods employed for carnivores, scat searching is one of the most frequently used (Davison et al., 2002). This method has been argued as being one of the most efficient methods for the detection and monitoring of European mammalian mesocarnivores (Sadlier et al., 2004; Barea-Azcón et al., 2006; Rosellini et al., 2008). Moreover, scat analysis has the potential to provide information on many other ecological aspects (e.g. Trites & Joy, 2005; Janko et al., 2011; Asa, 2012). However, all the potential information retrieved from carnivore scats can only be useful upon correct species identification. During recent years, advances in non-invasive molecular methods have allowed the extraction and amplification of fragmented and degraded DNA (Broquet, Ménard & Petit, 2007; Beja-Pereira et al., 2009) and species-specific markers have been developed (Livia et al., 2006; Oliveira et al., 2010). The application of genetic scatology has highlighted the fact that the evaluation of scat morphology alone is prone to misidentifications among sympatric carnivore species, even when evaluated by experienced field technicians (Davison et al., 2002; Janecka et al., 2008; Harrington et al., 2010). Regardless, monitoring programmes and ecological research on carnivore species are still mainly carried out based on morphologically identified scats, without acknowledging potential biases induced by misidentifications. However, morphology-based scat searching methods are often the only available alternative for conducting large-scale surveys on carnivore species because of the reduced costs and labor when compared with other methods (Wilson & Delahay, 2001; Barea-Azcón et al., 2006). Moreover, information on the diet of species as elusive as most carnivores can only be accessible through scat analysis (Janecka et al., 2008; Napolitano et al., 2008). For these reasons, scat-based methods cannot be readily discarded; however, potential biases should be acknowledged and accounted for.

The red fox *Vulpes vulpes*, the European wildcat *Felis silvestris* and the stone marten *Martes foina* are three mammalian mesocarnivores whose distribution areas overlap in Europe (Mitchell-Jones et al., 1999), occurring in sympatry in the Iberian Peninsula (Palomo, Gisbert & Blanco, 2007). These species' similar size leads to potential misidentifications of their scats, particularly when their scats dimensions and diets overlap significantly (Farrell, Roman & Sunquist, 2000; Posluszny et al., 2007).

In this work, we evaluate the accuracy of species identification of mammalian mesocarnivore scats collected in the field in two study areas during two different seasons. An evaluation of potential factors that affect scat identification accuracy is also implemented. This evaluation provides a glimpse on some factors affecting the accuracy of scat morphological identification and thus allows the implementation of measures that minimize (or at least account for) scat misidentification rates.

Methods

Study areas

Samples were collected in two Iberian Mediterranean protected areas: the Guadiana Valley Natural Park (GVNP, south-east Portugal) and the Cabañeros National Park (CNP, Central Spain). These two areas belong to the Mediterranean pluviseasonal continental bioclimate region (Rivas-Martínez, Penas & Díaz, 2004). A study area of approximately 6000 ha within each of the protected areas was selected based on the criteria of ecosystem conservation status and logistic factors.

The landscape at GVNP is highly fragmented with cereal croplands and agroforestry systems ('Montado') of stone pine *Pinus pinea* L. and holm oak *Quercus ilex* L. Scrubland patches are mainly associated with steeper slopes and elevation ridges. The red fox, stone marten, Egyptian mongoose *Herpestes ichneumon* and European wildcat are the most common mammalian mesocarnivore species present, despite the presence, in lower densities, of Eurasian badger *Meles meles* and common genet *Genetta genetta* (Monterroso et al., 2009; Monterroso, Alves & Ferreras, 2011). Predator control directed towards red fox and Egyptian mongoose is legally allowed.

The landscape at CNP is dominated by *Pyro-Quercetum rotundifoliae* series and other sub-serial stages (Rivas-Martinez, 1981), especially associated with the steeper slopes, higher elevations and main water bodies. The landscape at the central lower part of this study area constitutes a savannah-like system, with holm oak trees scattered within a grassland matrix (García-Canseco, 1997). The red fox, stone marten and common genet are the most abundant mammalian carnivore species, while wildcats and Eurasian badgers are also found but in lower densities (Guzmán, 1997; Monterroso et al., 2011). Neither hunting activity nor predator control is allowed.

Field sampling

Both study areas were sampled in two distinct seasons: summer/autumn (July-October), when the offspring of most medium-sized carnivores from that year become independent, and winter/spring (February-April), during these species breeding season (Blanco, 1998).

Within each study area, 10 transects, 3 km long each, were designed along unimproved roads or trails for active searching of carnivore signs. Each transect was sampled twice per season: once at the beginning of the sampling campaign and again after approximately 20 days (20.25 ± 3.16 days; mean ± sd). Transects were spatially distributed in order to adequately sample all existing habitats. They were surveyed on foot by trained field technicians who collected all carnivore scats within a bandwidth of 2 m to each side of the transect line. Scats were identified based on their location, morphology, dimensions, colour and odour, with the aid of specific field guides (Bang, Dahlstrom & Mears, 2007; Iglesias & España, 2010). Scats were collected, taking all precautions to prevent contamination from the collector or cross- contamination from other samples. All scats estimated to be over 1-month old, or for which species assignment was doubtful, were discarded from further procedures. Selected samples identified as belonging to the European wildcat, red fox or stone marten were preserved in plastic vials in ethanol (96%) until DNA extraction. Additional opportunistically collected scats, from the same study areas and seasons, were also included in this study.

As a measure of carnivore-relative abundance, we used data obtained from camera trapping (see details in Monterroso et al., 2011). The trap success estimated for each of the target species followed the methods described by the previous studies (Carbone et al., 2001; Kelly & Holub, 2008) and consisted of the mean number of independent detections per 100 trap days, over all camera stations.

Genetic analysis and identification

DNA extractions were performed with the Qiagen QIAamp DNA Stool Mini Kit (Qiagen, Hilden, Germany) according to manufacturer's instructions in a separate and autonomous facility, under sterile conditions. Species assignment was per- formed using two diagnostic methods described by Oliveira et al. [2010; interphotoreceptor retinoid-binding protein (IRBP) fragment] and Palomares et al. [2002; domain 1 of the control region (CR)]. Amplifications were performed in a final volume of 10µL using 5µL of Qiagen PCR MasterMix, 0.2µM of each primer and 2µL of DNA extraction (c. 10 ng of genomic DNA). Thermocycling conditions for both fragments were as follows: 95°C for 15 min, followed by 40 cycles at 95°C for 30 s, 60°C (IRBP) or 58°C (CR) for 20 s and 72°C for 20 s, with a final extension step at 72°C for 5 min (IRBP) or 60°C for 10 min (CR). Polymerase chain reaction (PCR) amplifications were carried out in a thermocycler MyCycler (Bio-Rad, Hercules, CA, USA). Successful amplifications were purified using the enzymes exonuclease I and shrimp alkaline phosphatise, and sequenced for both strands with BigDye chemistry (Applied Biosystems, Carlsbad, CA, USA). Sequencing products were separated in a 3130 XL Genetic Analyzer (Applied Biosystems). Pre- and post-PCR manipulations were conducted in physically separated rooms.

Sequence alignment was performed using Clustal W (Thompson, Higgins & Gibson, 1994) implemented in BioEdit software (Hall, 1999) and was manually checked and reassessed for any discrepancy. Species identification using IRBP followed the variants in Iberian wild carnivores reported by Oliveira et al. (2010). Aligned CR sequences were compared with the corresponding region of the mitochondrial genome from target species in the GenBank. Both markers were consistently used to increase identification confidence. Each marker has its own advantage: the IRBP nuclear marker is highly discriminative for Southern European carnivores (Oliveira et al., 2010); however, mtDNA is usually available in higher quantity in non-invasive samples, increasing the species identification success. All molecular identifications were blind, that is, information from morphologic identifications was not available to the laboratory staff.

Data analysis

For the sake of reliance, the molecular species assignment of each sample was considered the correct one. The success of the genetic procedure was assessed as the proportion of samples with species identification over the total number of samples analysed. Samples were grouped in each study area and season on the basis of their morphological identifications. The accuracy of morphological identifications was expressed as the proportion of correct identifications over the total number of samples with molecular identification. Several factors were considered to potentially influence the accuracy of morphological identifications: study area, season and mammalian community composition. These relations were tested using a binary response variable, identification accuracy, where '1' corresponds to correctly identified samples and '0' for cases where morphological and molecular identification differed. Basic variables consisted of season (summer/autumn vs. winter/spring), study area (CNP vs. GVNP) and putative species ID (i.e. morphological identification: red fox vs. stone marten vs. European wildcat). Biological variables were estimated for a buffer area of 1 km surrounding each scat- searching transects. This buffer size roughly corresponds to the radius of a hypothetical circular home range of the target species in Europe and was a criterion previously used by other authors (Barea-Azcón et al., 2006; Pita et al., 2009). Data obtained from all camera traps included in the buffer area of a particular transect were pooled to estimate biological parameters potentially related to the morphological identification accuracy. Derived variables consisted of red fox, stone marten and European wildcat camera-trap successes, as well as the interactions between these variables, and carnivore species evenness (as defined by Heip, 2009). As available prey may be related to their consumption by predator species, the camera- trap success of three prey items - European rabbit, Iberian hare Lepus granatensis and small mammals (Rodentia) - was considered. Generalized linear models were used to model the identification accuracy, assuming a binomial error distribution and logit link function (Crawley, 2007). As the ratio for global model was≈20, the corrected AIC values for small sample sizes (AIC_c) was used (Burnham & Anderson, 2002). The ∆AICc and model weights were used to compare and rank all tested models, which included all variable combinations and a null (intercept-only) model (Burnham & Anderson, 2002). We only considered the top models whose summed weights accounted for 95% of the total. Individual variable weights were estimated by summing the weights of all the selected models in which they were included. All statistical analyses were performed using R software (R Development Core Team, 2008). Models and model parameters were developed with the AICcmodavg package, version 1.21 (Mazerolle, 2011).

Results

A total of 320 putative scats from red fox, stone marten and European wildcat were submitted to genetic analysis. Approximately half of the samples were collected at each study area (44.7%, *n*=143, at CNP and 55.3%, *n*=177, at the GVNP). According to the season, 134 samples were collected in summer/autumn, while 186 were acquired in winter/spring. The majority of the collected scats (88.5%) was identified by morphological characteristics as belonging to either red fox (49.1%, *n*=157) or stone marten (39.4%, *n*=126), while potential European wildcat scats consisted only of 11.5% (*n*=37) of the total sample. Species assignment based on molecular methods was achieved in 251 samples, resulting in an overall genetic identification success of 78.4%. The genetic identification success varied slightly across seasons, areas and putative species [species G=4.501, 2 degrees of freedom (d.f.), *P*= 0.105; season G=1.049, 1 d.f., *P*= 0.306; area G=0.484, 1 d.f., *P*= 0.487], ranging from 64.0% (CNP at winter/spring) to 94.7% (GVNP at summer/autumn; Table 2.2.1). The IRBP nuclear fragment provided a lower identification success (34.3%) than the CR mitochondrial marker (97.6%). The identification success for both markers simultaneously was 31.1%.

Over a total of 251 genetically identified scats, 244 belonged to one of the target species (red fox, stone marten or wildcat), even though not always matching the morphological identification. The remaining seven samples were genetically assigned to polecat *Mustela putorius* (*n*=2) and dog *Canis lupus familiaris* (*n*=5). The morphological identification of putative red fox scats had an accuracy rate of over 82% (101 out of 117; 86.3% as average) across all seasons and study areas. Red fox misidentified scats belonged to stone marten (*n*=9, 7.7%), dog (*n*=5, 4.3%) and European wildcat (*n*=2, 1.7%; Table 2.2.1). These genetically identified stone marten scats were mostly collected at CNP (*n*=8), while most dog scats were collected at GNVP (*n*=4). European wildcat scats morphologically assigned to red fox were collected both at CNP and at GVNP.

Putative stone marten scats were accurately identified by morphological characteristics in 77.8% (84 out of 108) of the occasions. Misidentified stone marten scats were genetically assigned mostly to red fox (*n*=22, 20.4%) and, to a lesser extent, to polecat (*n*=2, 1.8%; Table 2.2.1). Misidentification of red fox scats as stone martens occurred across all seasons and study sites, while misidentification of polecat scats as stone martens only occurred in two samples collected in GVNP during summer/autumn.

The lowest overall accuracy rate corresponded to putative European wildcat scats (11.5%) and most misidentified samples were genetically assigned to red fox (84.6%; Table 2.2.1).

Data obtained from camera trapping revealed that while the three target mammalian mesocarnivores (red fox, stone marten and European wildcat) produced trap success within the same range of values in both seasons at GVNP, in the CNP study area the guild is highly biased towards the red fox (Table 2.2.1).

The models developed for scat identification accuracy hardly explained 25% of the observed variability (Table 2.2.2). The top 95% confidence model sets systematically included the season, study area and morphological species assignment, and these variables' individual weights were always higher than 0.90 (Appendix 2.2). The

European wildcat and red fox trap successes were the fourth and fifth ranked variables, with weights of 0.63 and 0.60.

Table 2.2.1 Red fox Vulpes vulpes, stone marten Martes foina and European wildcat Felis silvestris relative abundances and genetic results for the scats morphologically identified, collected at Cabañeros National Park (CNP) and Guadiana Valley Natural Park (GVNP), during the summer 2009 and winter 2010.

Putative species	Season	Study area	TS	N	SGI (%)	Proportion (%) of samples genetically identified as:				
						Red fox	Stone marten	European wildcat	Polecat	Dog
Red fox	Summer/Autumn	CNP	22.08 ± 22.04	26	64.00	**82.35**	17.65	0.00	0.00	0.00
		GVNP	4.16 ± 6.46	39	79.49	**93.55**	0.00	0.00	0.00	6.45
	Winter/Spring	CNP	34.19 ± 34.68	54	77.78	**83.33**	11.90	2.38	0.00	2.38
		GVNP	2.27 ± 4.96	38	71.05	**85.19**	3.70	3.70	0.00	7.41
	Overall		16.78 ± 25.28	157	75.52	**86.32**	7.69	1.71	0.00	4.27
Stone marten	Summer/Autumn	CNP	3.53 ± 5.72	30	90.00	7.41	**92.59**	0.00	0.00	0.00
		GVNP	1.63 ± 3.58	19	94.74	16.67	**72.22**	0.00	11.11	0.00
	Winter/Spring	CNP	2.14 ± 3.83	32	75.00	45.83	**54.17**	0.00	0.00	0.00
		GVNP	6.26 ± 7.96	45	86.67	15.38	**84.62**	0.00	0.00	0.00
	Overall		3.34 ± 5.71	126	85.71	20.37	**77.78**	0.00	1.85	0.00
European wildcat	Summer/Autumn	CNP	0.10 ± 0.30	1	100.00	100.00	0.00	**0.00**	0.00	0.00
		GVNP	0.69 ± 0.97	19	84.21	80.00	6.67	**13.33**	0.00	0.00
	Winter/Spring	CNP	0.18 ± 0.45	0	-	-	-	**-**	-	-
		GVNP	0.53 ± 1.05	17	69.23	90.00	0.00	**10.00**	0.00	0.00
	Overall		1.29 ± 2.80	37	78.78%	84.62	3.85	**11.54**	0.00	0.00

Proportion of samples genetically identified: red fox, stone marten, European wildcat, polecat *Mustela putorius* and dog scats *Canis lupus familiaris*. Correct morphological assignments are marked in bold.

n, total number of putative red fox, stone marten and European wildcat scats sent for genetic analysis; SGI, proportion of scats identified through genetic analyses; TS, trap success, that is, the number of independent red fox detection per 100 camera-trap days (mean standard deviation).

The stone marten trap success ranked next, while the remaining variables (interactions between target species trap successes) revealed a very limited influence in explaining the observed data structure (appendix 2.2).

Model parameter estimates reveal that higher morphological identification accuracy was obtained in summer/autumn season and a positive effect of the GVNP study area (Appendix 2.2). Furthermore, morphological identifications had a significantly higher probability of being accurate for samples originally classified as belonging to red fox, while samples classified as European wildcat scats had the less chance of being accurately identified. Additionally, identification accuracy was significantly higher where wildcat trap success was lower and red fox trap success was higher (Appendix 2.2). Carnivore evenness and prey availability variables had very limited influence in explaining the observed data variability.

Table 2.2.2 Models for accuracy of mammalian mesocarnivore scats morphologic identification.

Model	**k^a**	**ΔAIC_c**	**D^2**	**w_i**	**Cum.w**	**ER**	**rank**
Ssn, SA, MID, Wldct, Fox	7	0	24.70	0.31	0.31	1.00	1
Ssn, SA, MID, Wldc, Fox, Mrtn	8	1.17	25.05	0.17	0.48	1.80	2
Ssn, SA, MID, Fox:Mrtn	6	2.44	23.06	0.09	0.57	3.39	3
Ssn, SA, MID, Wldc	6	2.51	23.04	0.09	0.65	3.51	4
Ssn, SA, MID, Fox, Mrtn	7	2.81	23.69	0.07	0.73	4.07	5
Ssn, SA, MID, Wldct:Fox	6	3.59	22.65	0.05	0.78	6.03	6
Ssn, SA, MID, Wldc, Mrtn	7	3.93	23.28	0.04	0.82	7.13	7
Ssn, SA, MID, Fox	6	4.19	22.43	0.04	0.86	8.13	8
Ssn, MID, Mrtn	5	4.36	21.62	0.03	0.89	8.86	9
Ssn, SA, MID, Mrtn	6	5.66	21.91	0.02	0.91	16.13	10
SA, MID, Wldc	5	6.13	20.98	0.01	0.92	21.43	11
SA, MID, Fox	5	6.66	20.79	0.01	0.94	27.91	12
SA, MID, Wldct	5	6.89	20.71	0.01	0.95	31.41	13

ΔAIC_C, variation in Aikake's information criteria in relation to the highest ranked model; Cum.w, cumulative weight; D^2, squared deviance; ER, evidence ratio; Fox, red fox *Vulpes vulpes* trap success (detections per 100 trap days); Fox:mrtn, interaction between red fox and stone marten trap successes (detections per 100 trap days); *k*, number of model parameters; MID, morphologic identification; Mrtn, stone marten *Martes foina* trap success (detections per 100 trap days); SA, study area; Ssn, season; w_i, model weight; Wldc, European wildcat *Felis silvestris* trap success (detections per 100 trap days); Wldc:mrtn, interaction between European wildcat and stone marten trap successes detections per 100 trap days).

Discussion

Our results indicate that errors are common in the identification of mammalian mesocarnivore scats, and that its accuracy is influenced by biological, environmental and human-related factors. Morphological identification efficiency is generally assessed by comparison with alternative procedures (Barea-Azcón et al., 2006; Long et al., 2007). We used genetic identification to evaluate the accuracy of morphology-based scat identification. The technical difficulties inherent to the analysis of low quantity and quality DNA limit the efficiency of this approach (Broquet et al., 2007). However, our genetic identification success (78.4%) was in agreement with other studies: 72% in Fernandes et al. (2007), 81.1% in Oliveira et al. (2010) and 60% in Harrington et al.

(2010). Mitochondrial assays are often more efficient than nuclear ones for non-invasive samples (Broquet et al., 2007). Nevertheless, both markers provided identification data simultaneously in nearly one- third of the samples, which proves that confirming species identification using two different markers is feasible and fruitful (Beja-Pereira et al., 2009). Our study areas reach high temperatures during summer season, which leads to a fast degradation of scat DNA (Santini et al., 2007), but in both areas, the overall amplification success was high (≈80%). On the other hand, the cold weather, low atmospheric moisture and reduced precipitation during winter should help preserve DNA. Therefore, a higher extraction success would be expected during winter. However, no evident seasonal differences occur in genetic identification success, neither among putative species identification in this work. The morphological classification errors ranged between ≈14% for putative red fox and ≈88% for putative European wildcat scats. Most observed identification errors consisted of scats belonging to one of the three target species. Only seven samples (≈3%) actually belonged to other carnivores (polecat and dog). Our results are consistent with those of other authors who reported that substantial misidentifications have been perpetuated in scat-based studies on mammalian mesocarnivores in Europe. For instance, the scats of pine marten *Martes martes* were consistently misidentified in the UK, mostly with red fox (Davison et al., 2002). In another study, on American mink (*Neovison vison*), none of the genetically analysed scats belonged to the target species, rather being of pine marten or fox origin (Harrington et al., 2010).

The low variability explained by our models (25%) suggests that some important factors affecting the accuracy of morphological identification of scats were most likely not considered. Nevertheless, the accuracy of scat identification seems to be affected by the species assignment by morphological characteristics, the season and the study area. The relative abundance of target species also influenced accuracy, although to a lesser extent. Scats morphologically classified as red fox had the highest probability of being correctly identified, whereas those classified as belonging to European wildcat had the least chance of being correctly identified. The high abundances and marking behaviour may be responsible for the high detection rates of red fox scats (Cavallini, 1994; Monclús et al., 2008; Monterroso et al., 2011) and, hence, a higher probability of a given scat being from red fox.

Season also revealed a significant effect on the accuracy of scat morphological identification. Scats were more accurately identified when collected in summer/autumn than in winter/ spring. The Mediterranean area is characterized by marked seasonal climatic variations (Blondel & Aronson, 1999), causing fluctuation in the availability of food resources throughout the year. Summer and autumn are characterized by a high diversity of food items, enabling segregation in the exploitation of key resources (Barrientos & Virgós, 2006). The reduced diversity of available food resources during winter most likely leads to a high dietary niche overlap (Carvalho & Gomes, 2004) and, as a consequence, higher similarities among scats should be expected. These seasonal fluctuations in species feeding behaviours may be responsible for the varying rates of scat identification accuracy.

Overall, scats collected in the GVNP had the greatest probability of being correctly identified compared with scats collected in CNP. Feeding resources show remarkable differences in their availability among the two study areas. While the European rabbit is very abundant in the GVNP (Monterroso et al., 2009; Sarmento et al., 2009), it is nearly absent in CNP (Guzmán, 1997). Moreover, fruits are more widely available in CNP than in GVNP.

Both the European wildcat and the red fox are considered as facultative specialists in European rabbit (Lozano, Moleón & Virgós, 2006; Delibes-Mateos et al., 2008), meaning that they preferably prey on it when it is available. However, when rabbits are not available, the European wildcat switches prey, mainly towards rodents (Lozano et al., 2006), while the red fox feeds on a wider variety of alternative foods (Díaz-Ruiz et al., in press). On the other hand, the stone marten diet in Mediterranean areas is highly variable (Serafini & Lovari, 1993; Genovesi, Secchi & Boitani, 1996; Rosalino & Santos-Reis, 2009). Different availabilities of feeding resources could lead to locally adapted strategies within the carnivore community, which likely led to varying scat morphological characteristics. However, as data on the local feeding ecology of target species are not available, an adequate evaluation of how diet composition affects scat identification accuracy is not possible.

Moreover, another potential uncontrolled factor could have some influence on the observed accuracy differences among study areas, which is the human factor. The prior knowledge that field technicians have on the carnivore community structure in each area might subconsciously bias their judgment. Varying error rates were also found in other studies across different study areas surveyed (Davison et al., 2002).

The red fox and stone marten abundances showed a positive relation to classification accuracy. The same pattern has been identified by Davison et al. (2002) with pine martens and red foxes. The more abundant the target species, the more likely it is to find its scats in a given area (Sadlier et al., 2004; Webbon, Baker & Harris, 2004). Moreover, several authors have referred that scats' misidentification rates tend to increase when targeting species are rare or when scats are difficult to detect (Bulinski & McArthur, 2000; Prugh & Ritland, 2005). Thus, when target species are common, accuracy rates increase, as supported by our models. However, wildcat abundance negatively influenced identification accuracy. The European wildcat distribution in southern Iberian Peninsula is strongly influenced by the availability of the European rabbit (Monterroso et al., 2009). As a consequence, where rabbit abundances are high, so is the abundance of European wildcat, and higher dietary overlap with the red fox is expected. Scats with similar contents, combined with the increased abundance of wildcat faeces, probably lead to a decrease in the accuracy of scat classification.

The use of scats to study mammalian carnivores is common in Europe, but the use of molecular methods to assess the reliability of the identification of the collected samples is scarce. For instance, among 35 studies on ecology of mammalian mesocarnivores using scats published in the last 10 years, and performed in 13 European countries, only 8.5% assessed the reliability of the identification of the collected samples based on molecular methods (Appendix 2.2). Our results suggest that error rates in carnivore scat identifications vary between species and target species abundance, becoming more severe for scarce species or when species with similar scats occur in equivalent abundances. We suggest that some cautionary measures can be implemented to minimize potential biases, such as restricting scat collection to specific well-known sites, used exclusively by the target species. Regardless, only one-third of the reviewed literature took such cautions (Appendix 2.2). In light of our results, as well as other recent studies (Davison et al., 2002; Janecka et al., 2008; Harrington et al., 2010), mammalian mesocarnivore studies undertaken using morphology of scats should be carefully reviewed for potential biases. As bias severity is associated with species rarity, serious consequences for the management of threatened species when data led unrealistic estimates of status and distribution are prone to occur (Birks et al., 2005; Miller et al., 2011). While this study focused on a three-species complex, the applicability of our conclusions can be extended to other carnivore species complexes, where similar problems are known to occur (e.g. Hansen & Jacobsen, 1999; Pilot et al., 2007).

Our results suggest that scat identification accuracy rates are circumstance-specific, and for that reason, should not be transferred or extrapolated. We recommend that future scat- based studies should implement measures (molecular or other) that allow researchers to determine their error rates in scat identification. If financial constraints prevent all samples to be analysed, at least a subsample should be subjected to a confirmation method, and error rates should be considered for subsequent analysis, ensuring adequate results and consequent ecological inferences.

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References

Asa, C.S. (2012). Reproductive biology and endocrine studies. In Carnivore ecology and conservation: 273-293. Boitani, L. & Powell, R.A. (Eds). New York: Oxford University Press.

Bang, P., Dahlstrom, P. & Mears, R. (2007). Animal Tracks and Signs. English edn. New York: Oxford University Press.

Barea-Azcón, J.M., Virgós, E., Ballesteros-Duperón, E., Moleón, M. & Chirosa, M. (2006). Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodivers. Conserv. **16**, 1213-1230.

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

Beja-Pereira, A., Oliveira, R., Alves, P.C., Schwartz, M.K. & Luikart, G. (2009). Advancing ecological understandings through technological transformations in noninvasive genetics. Mol. Ecol. Resour. **9**, 1279-1301.

Birks, J.D.S., Messenger, J.E., Braithwaite, T., Davison, A., Brookes, R. & Strachan, C. (2005). Are scat surveys a relible method for assessing distribution and population status of pine martens? Martens and fishers (Martes) in human-altered environments: 235-252. Harrison, D.J., Fuller, A.K. & Proulx, G. (Eds). New York: Springer.

Blanco, J.C. (1998). Mamíferos De España. Barcelona: Planeta.

Blondel, J. & Aronson, J. (1999). Biology and wildlife of the Mediterranean region. New York: Oxford University Press.

Broquet, T., Ménard, N. & Petit, E. (2007). Noninvasive population genetics: a review of sample source, diet, fragment length and microsatellite motif effects on amplification success and genotyping error rates. Conserv. Genet. **8**, 249-260.

Bulinski, J. & McArthur, C. (2000). Observer error in counts of macropod scats. Wildl. Res. **27**, 277-282.

Burnham, K.P. & Anderson, D.R. (2002). Model selection and multimodel inference: a practical information-theoretic approach. 2nd edn. New York: Springer Verlag.

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**, 75-79.

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

Cavallini, P. (1994). Faeces count as an index of fox abundance. Acta Theriol. **39**, 417-424.

Crawley, M.J. (2007). The R book. Chichester: John Wiley & Sons Ltd.

Davison, A., Birks, J.D.S., Brookes, R.C., Braithwaite, T.C. & Messenger, J.E. (2002). On the origin of faeces: morpho- logical versus molecular methods for surveying rare carni- vores from their scats. J. Zool. (Lond.) **257**, 141-143.

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. Eur. J. Wildl. Res. **54**, 71-78.

Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, J.L., López-Martin, J.M., Ferreira, C. & Ferreras, P. (in press) Biogeographical patterns in the diet of an opportunistic predator: the red fox Vulpes vulpes in the Iberian Peninsula. Mammal. Rev. doi: 10.1111/j.1365-2907.2011.00206.x.

Farrell, L.E., Roman, J. & Sunquist, M.E. (2000). Dietary separation of sympatric carnivores identified by molecular analysis of scats. Mol. Ecol. **9**, 1583-1590.

Fernandes, C.A., Ginja, C., Pereira, I., Tenreiro, R., Bruford, M.W. & Santos-Reis, M. (2007). Species-specific mitochondrial DNA markers for identification of non-invasive samples from sympatric carnivores in the Iberian Peninsula. Conserv. Genet. **9**, 681-690.

García-Canseco, V. (1997). Parque Nacional de Cabañeros. 1st edn. Madrid: Ecohábitat.

Genovesi, P., Secchi, M. & Boitani, L. (1996). Diet of stone martens: an example of ecological flexibility. J. Zool. (Lond.) **238**, 545-555.

Guzmán, J.N. (1997). Mamíferos. In Parque Nacional de Cabañeros. 1st edn. 225-268. García-Canseco, V. (Ed.). Madrid: Ecohábitat.

Hall, T.A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/ NT. Nucleic Acids Symp. Ser. **41**, 95-98.

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. (Lond.) **247**, 177-181.

Harrington, L.A., Harrington, A.L., Hughes, J., Stirling, D. & Macdonald, D.W. (2010). The accuracy of scat identification in distribution surveys: American mink, Neovison vison, in the northern highlands of Scotland. Eur. J. Wildl. Res. **56**, 377-384.

Heinemeyer, K.S., Ulizio, T.J. & Harrison, R.L. (2008). Natural sign: tracks and scats. In Noninvasive survey methods for carnivores: 45-75. Long, R.A., MacKay, P., Zielinski, W.J. & Ray, J.C. (Eds). Washington: Island Press.

Heip, C. (2009). A new index measuring evenness. J. Mar. Biol. Assoc. UK **54**, 555-557.

Iglesias, A. & España, A.J. (2010). Rastros y huellas de los carnívoros ibéricos. Madrid: Ediciones Jaguar.

Janecka, J.E., Jackson, R., Yuquang, Z., Diqiang, L., Munkhtsog, B., Buckley-Beason, V. & Murphy, W.J. (2008). Population monitoring of snow leopards using noninvasive collection of scat samples: a pilot study. Anim. Conserv. **11**, 401-411.

Janko, C., Linke, S., Romig, T., Thoma, D., Schröder, W. & König, A. (2011). Infection pressure of human alveolar echinococcosis due to village and small town foxes (Vulpes vulpes) living in close proximity to residents. Eur. J. Wildl. Res. **57**, 1033-1042.

Kelly, M.J. & Holub, E.L. (2008). Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeast Nat. **15**, 249-262.

Livia, L., Francesca, V., Antonella, P., Fausto, P. & Bernardino, R. (2006). A PCR-RFLP method on faecal samples to distinguish Martes martes, Martes foina, Mustela putorius and Vulpes vulpes. Conserv. Genet. **8**, 757-759.

Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J. & Buzas, J.S. (2007). Comparing scat detection dogs, cameras, and hair snares for surveying carnivores. J. Wildl. Mgmt. **71**, 2018-2025.

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

Mazerolle, M.J. (2011). AICcmodavg: model selection and multimodel inference based on (Q)AIC(coffee). R package version 1.13. http://CRAN.Rproject.org/package= AICcmodavg

Miller, D., Nichols, J., McClintock, B., Grant, E., Bailey, L. & Weir, L. (2011). Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. Ecology **92**, 1422-1428.

Mitchell-Jones, A.G., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, E., Stubbe, M., Thissen, J.B.M., Vohralik, V. & Zima, J. (1999). The atlas of European mammals. London: T and AD Poyser Natural History.

Monclús, R., Arroyo, M., Valencia, A. & Miguel, F.J. (2008). Red foxes (Vulpes vulpes) use rabbit (Oryctolagus cuniculus) scent marks as territorial marking sites. J. Ethol. **27**, 153-156.

Monterroso, P., Alves, P.C. & Ferreras, P. (2011). Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildl. Res. **38**, 446-454.

Monterroso, P., Brito, J.C., Ferreras, P. & Alves, P.C. (2009). Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. J. Zool. (Lond.) **279**, 27-35.

Napolitano, C., Bennett, M., Johnson, W.E., O'Brien, S.J., Marquet, P.A., Barría, I., Poulin, E. & Iriarte, A. (2008). Ecological and biogeographical inferences on two sympat- ric and enigmatic Andean cat species using genetic identifi- cation of faecal samples. Mol. Ecol. **17**, 678-690.

Oliveira, R., Castro, D., Godinho, R., Luikart, G. & Alves, P.C. (2010). Species identification using a small nuclear gene fragment: application to sympatric wild carnivores from South-western Europe. Conserv. Genet. **11**, 1023-1032.

Palomares, F., Godoy, J.A., Piriz, A., O'brien, S.J. & Johnson, W.E. (2002). Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. Mol. Ecol. **11**, 2171-2182.

Palomo, L.J., Gisbert, J. & Blanco, J.C. (2007). Atlas y Libro Rojo De Los Mamíferos Terrestres De España. Madrid: Dirección General para la Biodiversidad - SECEM - SECEMU. Pilot, M., Gralak, B., Goszczynski, J. & Posłuszny, M. (2007). ´A method of genetic identification of pine marten (Martes martes) and stone marten (Martes foina) and its application to faecal samples. J. Zool. (Lond.) **271**, 140-147.

Pita, R., Mira, A., Moreira, F., Morgado, R. & Beja, P. (2009). Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. Agr. Ecosyst. Environ. 132, 57-65. Posluszny, M., Pilot, M., Goszczynski, J. & Gralak, B. (2007). ´Diet of sympatric pine marten (Martes martes) and stone marten (Martes foina) identified by genotyping of DNA from faeces. Ann. Zool. Fenn. **44**, 269-284.

Prugh, L.R. & Ritland, C.E. (2005). Molecular testing of observer identification of carnivore feces in the field. Wildl. Soc. Bull. **33**, 189-194.

R Development Core Team (2008). R: a language and environment for statistical computing.

Rivas-Martínez, S., Penas, A. & Díaz, T.E. (2004). Mapa Bioclimático de Europa, Bioclimas, http://www.ucm.es/info/cif/form/maps.htm

Rivas-Martinez, S. (1981). Les étages bioclimatiques de la végétation de la Peninsule Iberique. An. Jard. Bot. Madr. **37**, 251-268.

Rosalino, L.M. & Santos-Reis, M. (2009). Fruit consumption by carnivores in Mediterranean Europe. Mammal. Rev. **39**, 67-78.

Rosellini, S., Osorio, E., Ruiz-González, A., Piñeiro, A. & Barja, I. (2008). Monitoring the small-scale distribution of sympatric European pine martens (Martes martes) and stone martens (Martes foina): a multievidence approach using faecal DNA analysis and camera-traps. Wildl. Res. **35**, 434-440.

Sadlier, L.M.J., Webbon, C.C., Baker, P.J. & Harris, S. (2004). Methods of monitoring red foxes Vulpes vulpes and badgers Meles meles: are field signs the answer? Mammal. Rev. **34**, 75-98.

Santini, A., Lucchini, V., Fabbri, E. & Randi, E. (2007). Ageing and environmental factors affect PCR success in wolf (Canis lupus) excremental DNA samples. Mol. Ecol. Notes **7**, 955-961.

Sarmento, P., Cruz, J., Monterroso, P., Tarroso, P., Ferreira, C., Negrões, N. & Eira, C. (2009). Status survey of the critically endangered Iberian lynx Lynx pardinus in Portugal. Eur. J. Wildl. Res. **55**, 247-253.

Serafini, P. & Lovari, S. (1993). Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area. Acta Theriol. **38**, 233- 244.

Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res. **22**, 4673-4680.

Trites, A.W. & Joy, R. (2005). Dietary analysis from fecal samples: how many scats are enough? J. Mammal. **86**, 704-712.

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**, 768-779.

Wilson, G.J. & Delahay, R.J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildl. Res. **28**, 151-164.

Appendix 2.2

Table A.2.2.1. Relative contribution of each variable for the models for accuracy of morphologic identification of carnivore scats. Ssn – Season, SA – Study area, MID – Morphologic identification, Wldc – European wildcat trap success (detections/100 trap days), Fox – Red fox trap success (detections/100 trap days), Mrtn – Stone marten trap success (detections/100 trap days), Fox:mrtn – interaction between red fox and stone marten trap successes (detections/100 trap days), Wldct:mrtn – interaction between European wildcat and stone marten trap successes (detections/100 trap days).

Model	w_i [a]	Rc [b] (%)	Cc [c] (%)	rank
MID	0.94	21.08	21.08	1
Ssn	0.92	20.63	41.70	2
SA	0.90	20.18	61.88	3
Wldct	0.63	14.13	76.01	4
Fox	0.60	13.45	89.46	5
Mrtn	0.33	7.40	96.86	6
Fox:mrtn	0.09	2.02	98.88	7
Wldct:fox	0.05	1.12	100.00	8

[a] – w_i – variable weight; [b] – Rc – Relative contribution (percentage); [c] – Cc – Cumulative contribution (percentage)

Table A.2.2.2 – Model averaged coefficients of factors for accuracy of morphologic identification of carnivore scats. Ssn – Season, SA – Study area, MID – Morphologic identification, Wldct – European wildcat trap success (detections/100 trap days), Mrtn – Stone marten trap success (detections/100 trap days), Fox – Red fox trap success (detections/100 trap days).

Variable categories	Model averaged estimate	Unconditional S.E.	95% Conf. Int.	
Intercept[a]	1.56	0.73	0.13	3.00
Ssn: Winter/Spring	-1.07	0.43	-1.92	-0.22
SA: GVNP	1.65	0.76	0.15	3.15
MID: stone marten	-0.73	0.37	-1.46	0.00
MID: wildcat	-4.41	0.76	-5.91	-2.91
Wldct	-0.17	0.08	-0.32	-0.02
Mrtn	0.06	0.05	-0.04	0.17
Fox	0.04	0.02	0.00	0.07

Table A.2.2.3. Review of published literature on scat-based studies on native mammalian mesocarnivores in Europe since (2003, obtained in the Web Of Knowledge search engine using the keywords “scat”, “carnivore”, “Europe” and “ecology”.

Target species	Reference	Country	Collection	Research objective			Genetic analyses
				Spatial analysis / Habitat selection	Feeding resource selection	Other	
Martes martes	Lanszki, Heltai (2011)	Hungary	Dispersed scats		X		
Martes martes	Sidorovich, Sidorovich,, Krasko (2010)	Belarus	Dispersed scats		X		
Martes martes	Fernández, Azua (2009)	Spain	Latrines		X		
Martes martes	Skalski, Wierzbowska (2008)	Poland	Dispersed scats		X		
Martes martes	Prigioni et al. (2008)	Italy	Dispersed scats	X	X		
Martes martes	Rosellini, Barja,, Piñeiro (2008)	Spain	Dispersed scats		X		X
Martes martes	Rosellini et al. (2008)	Spain	Dispersed scats	X			X
Martes martes	Paterson, Skipper (2008)	Scotland, UK	Dispersed scats		X		
Martes martes	Posluszny et al. (2007)	Poland	Dispersed scats		X		X
Martes martes	Zalewski (2007)	Poland	Latrines		X		
Martes martes	Tosh, Preston,, McDonald (2007)	Ireland	Dispersed scats	X			
Martes martes	Barja (2005)	Spain	Dispersed scats	X			
Martes martes	Sidorovich, Krasko,, Dyman (2005)	Belarus	Dispersed scats, latrines	X	X		
Martes martes	Sklodowski, Posluszny (2005)	Poland	Dispersed scats		X		
Martes martes	Russell, Storch (2004)	Germany	Dispersed scats		X		
			n = 15	33%	80%	0%	20%
Martes foina	Lanszki, Heltai (2011)	Hungary	Dispersed scats		X		
Martes foina	Skalski, Wierzbowska (2008)	Poland	Dispersed scats		X		
Martes foina	Prigioni et al. (2008)	Italy	Dispersed scats	X	X		
Martes foina	Rosellini et al. (2008)	Spain	Dispersed scats	X			X
Martes foina	Posluszny et al. (2007)	Poland	Dispersed scats		X		X
Martes foina	Barrientos, Virgós (2006)	Spain	Dispersed scats		X		
Martes foina	Heltai et al. (2005)	Hungary	Dispersed scats	X	X		
Martes foina	Sklodowski, Posluszny (2005)	Poland	Dispersed scats		X		
			n = 8	38%	88%	0%	25%
Meles meles	Sidorovich, Rotenko,, Krasko (2011)	Belarus	Latrines		X		
Meles meles	Lanszki, Heltai (2011)	Hungary	Latrines		X		
Meles meles	Prigioni et al. (2008)	Italy	Latrines	X	X		
Meles meles	Rosalino et al. (2005)	Portugal	Latrines		X		
			n = 4	25%	100%	0%	0%

Table A.2.2.3 (cont.). Review of published literature on scat-based studies on native mammalian mesocarnivores in Europe since (2003, obtained in the Web Of Knowledge search engine using the kewords "scat", "carnivore", "Europe" and "ecology".

Target species	Reference	Country	Collection	Research objective			Genetic analyses
				Spatial analysis / Habitat selection	Feeding resource selection	Other	
Genetta genetta	Rosalino et al. (2007)	Portugal	Latrines			X	
Genetta genetta	Barrientos, Virgós (2006)	Spain	Latrines		X		
			n = 2	0%	50%	50%	0%
Felis silvestris	Lozano (2010)	Spain	Dispersed scats	X			
Felis silvestris	Malo et al. (2004)	Spain	Dispersed scats, latrines		X		
Felis silvestris	Lozano et al. (2003)	Spain	Dispersed scats, latrines	X			
			n = 3	67%	33%	0%	0%
Vulpes vulpes	D'hondt et al. (2011)	Belgium	Dispersed scats			X	
Vulpes vulpes	Sidorovich, Sidorovich,, Krasko (2010)	Belarus	Dispersed scats		X		
Vulpes vulpes	Panzacchi et al. (2008)	Norway	Dispersed scats		X		
Vulpes vulpes	Skalski, Wierzbowska (2008)	Poland	Dispersed scats		X		
Vulpes vulpes	Delibes-Mateos et al. (2008)	Spain	Dispersed scats		X		
Vulpes vulpes	Prigioni et al. (2008)	Italy	Dispersed scats	X	X		
Vulpes vulpes	Jankowiak, Antczak,, Tryjanowski (2008)	Poland	Dispersed scats		X		
Vulpes vulpes	Rosalino et al. (2007)	Portugal	Dispersed scats			X	
Vulpes vulpes	Helldin, Danielsson (2007)	Sweden	Dispersed scats		X		
Vulpes vulpes	Dell'Arte et al. (2007)	Finland	Dispersed scats		X		
Vulpes vulpes	Lanszki, Heltai,, Szabó (2006)	Hungary	Dispersed scats		X		
Vulpes vulpes	Forman (2005)	UK	Dispersed scats		X		
Vulpes vulpes	Balestrieri, Remonti,, Prigioni (2005)	Italy	Dispersed scats		X		
Vulpes vulpes	Frafjord (2005)	Norway	Dispersed scats	X			
Vulpes vulpes	Russell, Storch (2004)	Germany	Dispersed scats		X		
Vulpes vulpes	Cagnacci, Meriggi,, Lovari (2004)	Italy	Dispersed scats	X			
Vulpes vulpes	Goldyn et al. (2003)	Poland	Dispersed scats	X	X		
			n = 17	24%	76%	12%	0%
Overall	Studies*: n* = 35	Countries: *n* = 13	Dispersed scats: *n* = 24 (68.6%) Latrines: *n* = 4 (11.4%) Both: *n* = 7 (20.0%)	Spatial analysis: *n* = 4 (11.4%) Diet: *n* = 22 (62.9%) Both: *n* = 7 (20.0%) Other: *n* = 2 (5.7)			*n* = 3 (8.5%)

List 1 – List of references used in literature review presented in table A.2.2.3.

Balestrieri, A., Remonti, L. & Prigioni, C. (2005). Local feeding specialization of the red fox (*Vulpes vulpes*) in response to eastern cottontail (*Sylvilagus floridanus*) introduction (NW Italy). *Ital. J. Zool.* **16**, 113-126.

Barja, I. (2005). Winter distribution of European pine marten (*Martes martes*) scats in a protected area of Galicia, Spain. *Mammalia* **69**, 435-438.

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

Cagnacci, F., Meriggi, A. & Lovari, S. (2004). Habitat selection by the red fox *Vulpes vulpes* (L. 1758) in an Alpine area. *Ethol. Ecol. Evol.* **16**, 103-116.

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. *Eur. J. Wildl. Res.* **54**, 71-78.

Dell'Arte, G.L., Laaksonen, T., Norrdahl, K. & Korpimäki, E. (2007). Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *Acta Oecol.* **31**, 276-281.

D'hondt, B., Vansteenbrugge, L., Van Den Berge, K., Bastiaens, J. & Hoffmann, M. (2011). Scat analysis reveals a wide set of plant species to be potentially dispersed by foxes. *Plant Ecol. and Evol.* **144**, 106-110.

Fernández, J.M. & De Azua, N.R. (2009). Contribución al conocimiento de la dieta invernal de la marta (*Martes martes*) en el País Vasco. *Galemys* **21**, 47–59.

Forman, D.W. (2005). An assessment of the local impact of native predators on an established population of British water voles (*Arvicola terrestris*). *J. Zool. (Lond.)* **266**, 221-226.

Frafjord, K. (2005). Habitat use by red foxes in a northern birch forest. *Fauna* (Oslo) **58**, 2-8.

Goldyn, B., Hromada, M., Surmacki, A. & Tryjanowski, P. (2003). Habitat use and diet of the red fox Vulpes vulpes in an agricultural landscape in Poland. *Z. Jagdwiss* **49**, 191-200.

Helldin, J.-o & Danielsson, A.V. (2007). Changes in red fox *Vulpes vulpes* diet due to colonisation by lynx *Lynx lynx*. *Wildl. Biol.* **13**, 475-480.

Heltai, M., Szocs, E., Balogh, V. & Szabo, L. (2005). Study on the feeding habits and home range use of one stone marten (*Martes foina* Erxleben, 1777) specimen in an urban area. *Allattani Kozlemenyek* **90**, 75-83.

Jankowiak, L., Antczak, M. & Tryjanowski, P. (2008). Habitat Use, Food and the Importance of Poultry in the Diet of the Red Fox Vulpes vulpes in Extensive Farmland in Poland. *W. Appl. Sci. J.* **4**, 886-890.

Lanszki, J. & Heltai, M. (2011). Feeding habits of sympatric mustelids in an agricultural area of Hungary. *Acta Zool. Academiae Scientiarum Hungaricae* **57**, 291-304.

Lanszki, J., Heltai, M. & Szabó, L. (2006). Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the Pannonian ecoregion (Hungary). *Can. J. Zool.* **84**, 1647-1656.

Lozano, J. (2010). Habitat use by European wildcats (*Felis silvestris*) in central Spain : what is the relative importance of forest variables ? *Anim. Biodivers. Conserv.* **33**, 143-150.

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

Malo, A.F., Lozano, J., Huertas, D.L. & Virgós, E. (2004). Achange of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? *J. Zool. (Lond.)* **263**, 401-407.

Panzacchi, M., Linnell, J.D.C., Serrao, G., Eie, S., Odden, M., Odden, J. & Andersen, R. (2008). Evaluation of the importance of roe deer fawns in the spring–summer diet of red foxes in southeastern Norway. *Ecol. Res.* **23**, 889-896.

Paterson, W.D. & Skipper, G. (2008). The diet of pine martens (*Martes martes*) with reference to squirrel predation in Loch Lomond and The Trossachs National Park, Scotland. *Glasgow Nat.* **25**, 75-82.

Posluszny, M., Pilot, M., Goszczyński, J. & Gralak, B. (2007). Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. *Ann. Zool. Fenn.* **44**, 269-284.

Prigioni, C., Balestrieri, A., Remonti, L. & Cavada, L. (2008). Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps. *Ital. J. Zool.* **75**, 173-184.

Rosalino, L.M., Loureiro, F., Macdonald, D.W. & Santos-Reis, M. (2005). Dietary shifts of the badger (*Meles meles*) in Mediterranean woodlands: an opportunistic forager with seasonal specialisms. *Mammal. Biol.* **70**, 12-23.

Rosalino, L.M., Rodrigues, M., Santos-Silva, M. & Santos-Reis, M. (2007). Unusual findings on host-tick interactions through carnivore scat analysis. *Exp. Appl. Acarol.* **43**, 293-302.

Rosellini, S., Barja, I. & Piñeiro, A. (2008). The response of European pine marten (*Martes martes* L.) feeding to the changes of small mammal abundance. *Polish J. Ecol.* **56**, 497-503.

Rosellini, S., Osorio, E., Ruiz-González, A., Piñeiro, A. & Barja, I. (2008). Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. *Wildl. Res.* **35**, 434-440.

Russell, A.M. & Storch, I. (2004). Summer food of sympatric red fox and pine marten in the German Alps. *Eur. J. Wildl. Res.* **50**, 53-58.

Sidorovich, V., Krasko, D. & Dyman, A. (2005). Landscape-related differences in diet, food supply and distribution pattern of the pine marten, *Martes martes* in the transitional mixed forest of northern Belarus. *Folia Zool.* **54**, 39-52.

Sidorovich, V.E., Rotenko, I.I. & Krasko, D.A. (2011). Badger *Meles meles* spatial structure and diet in an area of low earthworm biomass and high predation risk. *Ann. Zool. Fenn.* **48**, 1-16.

Sidorovich, V.E., Sidorovich, A.A. & Krasko, D.A. (2010). Effect of felling on red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) diets in transitional mixed forest in Belarus. *Mammal. Biol.* **75**, 399-411.

Skalski, T. & Wierzbowska, I., (2008). Variation of insect assemblages in fox and marten faeces collected in southern Poland. *Ann. Zool. Fenn.* **45**, 308-316.

Sklodowski, J. & Posluszny, M. (2005). Beetles in the diet of the beech marten *Martes foina* and the pine marten *Martes martes*. *Baltic J. Coleopterol.* **5**, 31-36.

Tosh, D., Preston, S.J. & McDonald, R.A. (2007). The status of pine martens *Martes martes* (L.) in Northern Ireland, 1850-2004. *Irish Nat. J.* **28**, 433-439.

Zalewski, A. (2007). Does size dimorphism reduce competition between sexes? The diet of male and female pine martens at local and wider geographical scales. *Acta Theriol.* **52**, 237-250.

Efficiency of hair snares for monitoring mesocarnivores occurrence

Monterroso, P., Rich, L., Serronha, A., Ferreras, P., Alves, P.C. (2014) European Journal of Wildlife Research 60:279–28

2.3 Efficiency of hair snares and camera traps to survey mesocarnivore populations

Abstract

Mammalian carnivore communities affect entire ecosystem functioning and structure. However, their large spatial requirements, preferred habitats, low densities, and elusive behavior deems them difficult to study. In recent years, non-invasive techniques have become much more common as they can be used to monitor multiple carnivore species across large areas at a relatively modest cost. Hair snares have the potential to fulfill such requirements, but have rarely been tested in Europe. Our objective was to quantitatively assess the effectiveness of hair snares for surveying mesocarnivores in the Iberian Peninsula (Southwestern Europe), by comparison with camera trapping. We used an occupancy modeling framework to assess method-specific detectability and occupancy estimates, and hypothesized that detection probabilities would be influenced by season, sampling method, and habitat related variables.

A total of 163 hair samples were collected, of which 136 potentially belonged to mesocarnivores. Genetic identification success varied with diagnostic method: 25.2% of identification success using mitochondrial CR, and 9.9% using the IRBP nuclear gene. Naïve occupancy estimates were, in average, 5.3 ± 1.2 times higher with camera trapping than with hair snaring, and method-specific detection probabilities revealed that camera traps were, in average, 6.7 ±1.1 times more effective in detecting target species. Overall, few site-specific covariates revealed significant effects on mesocarnivore detectability.

Camera traps were a more efficient method for detecting mesocarnivores and estimating their occurrence when compared to hair snares. To improve our hair snares' low detection probabilities, we suggest increasing the number of sampling occasions and the frequency at which hair snares are checked. With some refinements to increase detection rates and the success of genetic identification, hair snaring methods may be valuable for providing deeper insights into population parameters,

attained through adequate analysis of genetic information, that is not possible with camera traps.

Keywords

Noninvasive sampling, monitoring, molecular methods, occupancy, detection probability, carnivores

Introduction

Carnivores have cascading effects on entire ecosystems despite being relative sparse across landscapes (Gompper et al. 2006). As a result, carnivores are often the target of conservation efforts and an increasing number of studies have focused on assessing their density, relative abundance, or occupancy across large geographical areas (Gompper et al. 2006, Linkie et al. 2007). However, the challenges involved with monitoring carnivores are numerous. The majority of carnivores have large spatial requirements, often live in remote and rugged habitats, occur at low densities, and are nocturnal and elusive (Long et al. 2007, Mills 1996). Invasive techniques, such as mark-recapture or radiocollaring, are impractical to apply across large spatial scales since they are time-consuming, have high costs, and involve complex logistical requirements. Non-invasive techniques are therefore becoming much more common as they can be used to monitor multiple carnivore species across large areas at a relatively modest cost (Johnson et al. 2009, Weaver et al. 2005, Zielinski et al. 2006).

Camera traps and hair snares, two non-invasive techniques, are often used to confirm the presence of a species. Camera traps have successfully documented the presence of a vast array of common and rare mammals including felids, ursids, viverrids, mustelids, and cervids (Baldwin and Bender 2008, Johnson et al. 2009, Linkie et al. 2007, Tobler et al. 2009). Camera traps generally have high detection rates (Long et al. 2007, O'Connell et al. 2006) but only permit species identification if patterns in the pelage or specific markings allow individual identification. Hair snares, conversely, permit individual and sexual identification (using genetic methods) in addition to species identification, and recently have been extensively used to detect several mammal species (Kendall et al. 2009, Mills 1996, Ruell and Crooks 2007). The complementary individual identification provided by hair snares can be used to study the spatial structure, demography and occurrence of carnivore populations (Davoli et al. 2013; Zielinski et al. 2006).

The success of camera traps and hair snares at detecting animals varies across species and habitats. Thus, quantifying the efficacy and potential biases of these techniques would help inform researchers and managers on what sampling method(s) and survey design can be used to optimally achieve their research objectives (Nichols et al. 2008). The ability to effectively and efficiently monitor carnivores is particularly critical in Southwestern (SW) Europe, since it has a diverse mammalian carnivore community, and where research studies and funding for conservation are limited in comparison to North America and other parts of Europe.

Using an occupancy modeling framework, we aimed to quantitatively assess the effectiveness of hair snares for surveying Iberian mesocarnivores, by investigating how sampling method (i.e., hair snares and camera trap surveys) affects the ability to detect and estimate species' occupancy. Occupancy modeling allows the estimation of method-specific detection probabilities, and consequently the sampling effort required to determine the occupancy status of each target species using camera traps vs. hair snares (Bailey et al. 2007). We hypothesized that site-specific covariates such as distance to water, habitat type, slope or elevation would influence target species behavior, and consequently, their detectability. Detection is also expected to be influenced by season and sampling method (O'Connell et al. 2006, Royle and Nichols 2003). Therefore, by controlling for these external factors potentially influencing detectability, we explored whether a hair snaring sampling protocol would provide adequate data for mesocarnivore population monitoring. As detection by rub stations is dependent on a behavioral response elicited by a lure or bait, we anticipated that detectability would be lower by hair snaring than by camera trapping.

Methods

This study was performed in two different protected areas within the Mediterranean bioclimatic region of the Iberian Peninsula (Rivas-Martínez et al. 2004): the Guadiana Valley Natural Park (GVNP; Portugal; N 27°40'50'', W 7°44'30''), and the Cabañeros National Park (CNP; Spain; N 39°20'10'', W 4°25'50''). A study area of approximately 6000ha within each park was selected based on the criteria of ecosystem conservation status and logistic factors. The GVNP is located in the Guadiana River basin (Southeastern Portugal), the most important ecological corridor in southern Portugal, and harbors some of the most endangered species in Europe (ICN 2006, Sarmento et al. 2004). Small game hunting is a major economic driver within GNVP, and predator control directed towards red fox (*Vulpes vulpes*) and Egyptian mongoose (*Herpestes ichneumon*) is legally allowed. The landscape is highly fragmented with cereal croplands and agroforestry systems ('Montado') of stone pine *Pinus pinea* L. and holm oak *Quercus ilex* L. Scrubland patches are mainly associated with steeper slopes and elevation ridges (Costa et al. 1998, Monterroso et al. 2009). The CNP is located in the Castilla La-Mancha Spanish community, and is dominated by *Pyro-Quercetum rotundifoliae* series and other sub-serial stages (Rivas-Martinez 1981), especially associated with the steeper slopes, higher elevations and main water bodies. The landscape at the central lower part of this study area constitutes a savannah-like system, with holm oak trees scattered within a grassland matrix (García-Canseco 1997). Neither hunting activity nor predator control is allowed.

Survey methods and design

The sampling design was based on a sampling grid composed by 1-km^2 grid cells, which was superimposed over each study area. Sampling devices were deployed at grid cell vertexes, alternating between camera traps and hair snares. As a result, all cameras and all hair snares were approximately 1.4km apart, promoting method-specific independence. Study areas were surveyed in August-October 2009 (hereafter autumn season) and in February-April 2010 (hereafter spring season) for a period ≥ 28 days, and assumed occupancy was constant during each survey period (MacKenzie et al. 2002). All procedures were performed in accordance with the guidelines for the care of mammals, as approved by the Portuguese Nature and Biodiversity Institute and the

Animal Experimentation Ethic Committee of the University of Castilla La-Mancha (process nr. PP1104.3).

Hair snares on baited rub stations consisted of hair collection structures and scent lures (Kendall and Mckelvey 2008), and were set at 38 and 29 sampling locations in CNP and GVNP, respectively. Hair collection structures included both barbed rub pads and adhesive pads. This design exploits the cheek-rubbing behavior of felids, the neck-rubbing behavior of canids, and has been found to detect other mesocarnivores (e.g., mustelids) as by-catches (Kendall and Mckelvey 2008). Rub stations comprised a 50×5×5cm wooden stake, on which four 5x3cm pieces of dog wire (one at each side of the stake) were glued at 20 to 30cm above the ground. Below the dog wire, we covered the stake with sticky-side-out tape, which functioned as an adhesive pad. The attractants were deployed in separated, perforated plastic tubes supported by the wooden stake, at a distance of 10–15cm from each other (Monterroso et al. 2011). A volume of 5mL of each attractant was sprayed into a cotton gaze held inside each plastic tube. The selected attractants were Lynx urine and Valerian, which have been described as efficient in attracting mesocarnivores (Monterroso et al. 2011, Steyer et al. 2013). Hair snares were monitored and scent lures replenished every 7 days. We collected hairs with tweezers, stored them in plastic vials with ethanol (96%) and then kept at room temperature until lab processing. Hair samples were identified under a microscope by analyzing its medular and cuticular structure with the aid of specific guides (e.g. Teerink 1991). Hair was identified as either under hair (UH), type 1 (GH1) or type 2 (GH2) guard hair. GH1 hair is usually stiff and firm, and occurs very often within pelage. It can be slightly wavy or bent. In GH2 hair the shaft is usually straight and forms an angle with the shield (Debelica and Thies 2009). Subsequently, samples were identified by molecular methods. Species assignment was performed using two diagnostic methods described by Oliveira et al. (2010; interphotoreceptor retinoid-binding protein, IRBP, fragment) and Palomares et al. (2002; domain 1 of the mitochondrial control region. CR), following the procedures described by Monterroso et al. (2012). Aligned IRBP and CR sequences were compared with the corresponding regions from the target species available in the GenBank and in CIBIO's genetic database. Both markers were consistently used to increase identification confidence. Whenever hair samples, collected from the same hair snare in the same sampling occasion, were identified as belonging to the same species from their medular and cuticular structure, they were used together for DNA extraction and molecular identification. Otherwise, single hair samples were analyzed idependently.

Leaf River IR5 infrared-triggered digital cameras (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) were deployed at 38 and 32 sampling locations in CNP and GVNP, respectively. A circular area of 250-m radius surrounding each grid-cell vertex was inspected for carnivore paths prior to camera trap placement. The final location of camera traps corresponded to areas of easy access and potentially good detection probability within the mentioned buffer. Cameras were then mounted on trees approximately 0.5 – 1.0m off the ground and set to record time and date when triggered. We programmed cameras to fire a burst of three photos when triggered, and with the minimal delay time possible (< 1min).

In order to enable adequate comparisons between sampling methods, the same attractants used in hair snares were used to attract animals to camera traps. Therefore, the same structure built for hair snares (but without the dog wire and adhesive tape) was set at a distance of 2-3m of camera traps. Scent lures at camera stations were replenished in 7 days intervals, when stations were checked for batteries and to change memory cards.

Occupancy modeling

Likelihood-based occupancy modeling was used to estimate detection probability (*P*), given presence, and the probability of occupancy (ψ; MacKenzie et al. 2002, Mackenzie et al. 2006). To account for potential heterogeneity in probabilities of occupancy and detection, and to evaluate our a priori hypotheses we assessed four site-specific covariates at the local scale: elevation, slope, distance to water and habitat type (forest, shrub or grassland). These covariates were assessed at each sampling location (camera trap or hair snare). We extracted elevation and slope data from the ASTER (Advanced Spaceborne Thermal Emission and Reflection radiometer) global digital elevation model (GDEM: www.gdem.aster.ersdac.or.jp), which has a spatial resolution of 30m; and estimated distance to water by measuring the linear distance from the sampling site to the nearest water source (i.e., river, lake, or reservoir). Habitat type was reclassified into three major structural types: forest, shrub and grassland cover from vegetation geographic information system coverages of CNP and

GVNP, with a spatial resolution of 30m, and was assigned to each sampling site (camera trap or hair snare) according to its exact location.

We divided survey periods into four 1-week sampling occasions during which the detection/non-detection data on each target species was recorded. We created species-specific detection histories, allowing us to assess factors that may affect species-specific detection. The probabilities of detecting target species given they occupy a site (i.e. P) were estimated from their detection histories. Missing values during a sampling occasion resulted from cameras malfunctioning or temporary inability to access a camera trap or hair snare.

Multi-season occupancy models were developed in PRESENCE 5.8 (Hines and Mackenzie 2013) to estimate species and method-specific occupancy and detection probabilities. A set of candidate models was built for each species-study area combination based on our *a priori* hypotheses. We modeled occupancy as constant across all sampling sites and constant *vs*. dependent on sampling season. Detection probability was modeled as constant or dependent on season, sampling occasion or site-covariates.

As we wanted to assess the effect of detection method (i.e. hair snare vs. camera trap) on detection probabilities we tested the simplest models with and without a detection method covariate: models $\psi(.)p(.)$,$\psi(.)p$(method), ψ(season)$p(.)$, ψ(season)p(method). If the effect of method was found to be significant, we developed the models further, constraining them to always include the method covariate. We used Spearman's rank correlation (r_s) to test for collinearity among the landscape variables; if variables were correlated ($r_s > 0.70$) we kept the variable with the greatest univariate effect size (β/SE) as a potential covariate for the probability of detection (Zar 2005). We estimated overall AIC weights for individual variables by summing the AIC weights of all the candidate models in which they were included (Mackenzie et al. 2006). If no single model accounted for > 90% of the total model weights, we model-averaged by extracting the top 95% model confidence set and recalculating model weights (Burnham and Anderson 2002). Model averaged estimates were calculated using the spreadsheet developed by B. Mitchell (http://www.uvm.edu/%7Ebmitchel/software.html).

Finally, we estimated the number of hair snare surveys and the number of camera trap surveys, n_i, required to achieve a specified probability of detection. We estimated n_i following Long et al. (2007): $P = 1 - (1 - p_i)^{ni}$. The effectiveness of camera traps and hair snares for mesocarnivores using 3 indicators: (1) naïve occupancy estimates (i.e. proportion of sites where the target species was detected by a single sampling method in a single season), (2) method-specific estimates of the probabilities of occupancy and detection; and (3) number of surveys required using each method to reach a designated detection probability.

Results

A total of 163 hair samples were collected in hair snare stations (Table 2.3.1). CNP accounted with 43 and 70 samples in autumn and spring seasons, respectively, while 24 and 26 samples were obtained from the same seasons at GVNP. The average number of hairs collected per sample was 5.42 ± 0.35 (mean ± SE). Hair samples that were unequivocally identified by their microscopic structure as belonging to non-target species (e.g. ungulates or lagomorphs) were not sent for genetic analysis (n=27). However, potential carnivores' or unidentified hair samples were sent for genetic analysis, and consisted of 83.4% of the total samples (n=136).

The genetic identification success varied with diagnostic method: 25.2% of identification success using mitochondrial CR, and 9.9% using the IRBP nuclear gene.

Table 2.3.1. Proportion of samples obtained of each hair type, collection structure, and results from molecular analysis obtained from hair snaring methods at Guadiana Valley Natural Park (GVNP) and Cabañeros National Park (CNP) in the autumn 2009 and spring of 2010. Proportion positive (number of samples). UH - Under hair; GH - Type I guard hair; GH2 - Type 2 guard hair.

		CNP		**GVNP**		**Total**
		Autumn	**Spring**	**Autumn**	**Spring**	
Number of samples collected		43	70	24	26	163
Presence of intact hair		0.63 (27)	0.90 (63)	0.38 (9)	0.88 (23)	0.75 (122)
Hair type	UH	0.42 (18)	0.56 (39)	0.54 (13)	0.58 (15)	0.52 (85)
	GH	0.60 (26)	0.39 (27)	0.46 (11)	0.27 (7)	0.44 (71)
	GH2	0.28 (12)	0.07 (5)	0.00 (0)	0.08 (2)	0.12 (19)
Collection device	Brush	0.86 (37)	0.81 (57)	1.00 (24)	0.85 (22)	0.86 (140)
	Tape	0.14 (6)	0.21 (15)	0.00 (0)	0.15 (4)	0.15 (25)
Samples sent for genetic ID		0.77 (33)	0.96 (67)	0.50 (12)	0.92 (24)	0.83 (136)
CR (mitochondrial)	Amplification	0.85 (28)	0.27 (18)	0.25 (3)	0.38 (9)	0.43 (58)
	Sequencing	0.85 (28)	0.21 (14)	0.25 (3)	0.38 (9)	0.40 (54)
	Identification	0.52 (17)	0.13 (9)	0.17 (2)	0.25 (6)	0.25 (34)
IRBP (nuclear)	Amplification	0.36 (12)	0.16 (11)	0.17 (2)	0.50 (12)	0.27 (37)
	Sequencing	0.27 (9)	0.10 (7)	0.08 (1)	0.50 (12)	0.21 (29)
	Identification	0.24 (8)	0.06 (4)	0.00 (0)	0.00 (0)	0.09 (12)

Hair samples were identified as belonging to red fox, stone marten, and European wildcat when employing conventional microscopic methods; no samples were identified as belonging to common genets, European badger, or Egyptian mongoose. However, employing genetic methods hair samples were identified as belonging to red fox, genet, and stone martens; no samples were identified as belonging to European wildcat, European badger, or Egyptian mongoose. 25 samples from CNP were genetically identified as red fox: 15 from autumn and 10 from spring seasons; 5 samples from GVNP were red fox: 2 from autumn and 3 from spring seasons. Genetically identified genet hair was only obtained at CNP, with one sample from each season. Only one hair sample collected at GVNP during the spring season was genetically confirmed as stone marten.

From all of the genetically confirmed red fox hair samples (n=30), 67% contained under hair (UH) while 50% and 10% contained GH2 and GH1 guard hair, respectively. Seventy-three percent of the hair samples were collected from dog wire brush and 27% from adhesive tape. Genetically confirmed common genet samples (n=2), were either UH (n=1) or GH1 (n=1). Both genet hair samples were collected from dog wire brush. The only genetically confirmed stone marten hair sample consisted of GH2 guard hair, and it was obtained from the adhesive tape.

With camera trapping methods we were able to detect red foxes, European wildcats, common genets, stone martens, Egyptian mongooses and Eurasian badgers at GVNP in both seasons (Table 2.3.2). At CNP, we were able to detect the same species during autumn using camera traps. However, the Egyptian mongoose was not detected during autumn. Although mesocarnivore species composition was similar between the two study areas, their spatial distribution differed, as supported by their naïve occupancy estimates (Table 2.3.2).

Naïve estimates, occupancy and detection probabilities

We had a greater number of detections via camera trapping than we did via hair snares. When both methods detected the target species, naïve occupancy estimates were, on average, 5.3 (± 1.2) times higher with camera trapping than with hair snaring (table 2.3.2). For the species undetected by hair snares, naïve occupancy based on camera traps were always < 10% in CNP (Table 2.3.2). Conversely, at GVNP species undetected by hair snaring displayed naïve occupancy estimates ranging from 3 to 23% (Table 2.3.2).

Table 2.3.2. Naïve occupancy estimates (# sites with detections/# sampling sites) of mesocarnivores based on camera-trapping (CT) and hair snaring (HS) at Guadiana Valley Natural Park (GVNP) and Cabañeros National Park (CNP) in the autumn 2009 and spring of 2010.

Study área	**Species**	**Overall naïve estimates**		**Partial naïve estimates**			
				Autumn		**Spring**	
		Autumn	**Spring**	**CT**	**HS**	**CT**	**HS**
GVNP	Red fox	0.23	0.20	0.41	0.03	0.25	0.14
	Stone marten	0.16	0.36	0.25	0.07	0.63	0.14
	Common genet	0.08	0.12	0.16	0.00	0.22	0.00
	European wildcat	0.26	0.13	0.44	0.07	0.25	0.00
	Eurasian badger	0.03	0.07	0.06	0.00	0.13	0.00
	Egyptian mongoose	0.11	0.18	0.22	0.00	0.34	0.00
CNP	Red fox	0.56	0.65	0.90	0.42	0.88	0.03
	Stone marten	0.26	0.22	0.46	0.05	0.28	0.16
	Common genet	0.14	0.12	0.27	0.03	0.20	0.05
	European wildcat	0.04	0.08	0.07	0.00	0.15	0.00
	Eurasian badger	0.06	0.04	0.12	0.00	0.08	0.00
	Egyptian mongoose	0.00	0.03	0.00	0.00	0.05	0.00

The limited numbers of detections prevented us from modeling common genet at GVNP and European wildcat, Eurasian badger, and Egyptian mongoose in both study areas. For the species that did have sufficient numbers of detections, our estimated probabilities of occupancy were, on average, 31.5% (± 3.7%) greater than our overall naïve estimates (Tables 2.3.2 and 2.3.3).

Method-specific detection probabilities revealed that camera traps were, on average, 6.7 (± 1.1) times more effective in detecting target species than hair snares (Table

2.3.3). Given presence, red foxes had, on average, a 49.9% (± 10.4%) and 14.2% (± 5.4%) chance of being detected by camera traps and hair snares, respectively, in a give sampling occasion (Table 2.3.3). The mean probability of detecting stone martens by camera trapping was 21.7% (± 3.2%) and 3.5% (± 0.6%) by camera trapping and hair snaring, respectively (Table 2.3.3). Common genets at CNP had mean chance of being detected of 20.1% (± 1.2%) by camera trapping and 2.1% (± 0.2%) by hair snaring (Table 2.3.3).

The top ranked models for red fox consistently included habitat type at CNP and elevation at GVNP. Distance to water was included in three, and slope in one of the top ranked models at CNP; whilst slope, elevation and distance to water were each included at a single model of the top ranked models at GVNP. The top ranked models for common genet at CNP consistently included distance to water, but elevation also appeared in 5 of these models. Slope was included in two of these models and habitat type in one.

Table 2.3.3. Model averaged occupancy ($\hat{\psi}$) and method-specific detection probabilities (*P*) of red foxes based on camera-trapping and hair snaring at Guadiana Valley Natural Park (GVNP) and Cabañeros National Park (CNP), in autumn 2009 and spring 2010. Estimates ± SE.

Study area	Parameter	Red fox		Stone marten		Common genet	
		Autumn	Spring	Autumn	Spring	Autumn	Spring
GVNP	$\hat{\psi}$	0.44 ± 0.15	0.44 ± 0.17	0.70 ± 0.19	0.71 ± 0.15	-	-
	$P_{cameras}$	0.34 ± 0.13	0.32 ± 0.14	0.16 ± 0.09	0.31 ± 0.08	-	-
	$P_{hairsnares}$	0.06 ± 0.04	0.06 ± 0.04	0.02 ± 0.02	0.05 ± 0.03	-	-
CNP	$\hat{\psi}$	0.81 ± 0.15	0.79 ± 0.15	0.67 ± 0.21	0.64 ± 0.22	0.43 ± 0.16	0.42 ± 0.17
	$P_{cameras}$	0.60 ± 0.18	0.74 ± 0.15	0.20 ± 0.09	0.20 ± 0.09	0.21 ± 0.11	0.19 ± 0.10
	$P_{hairsnares}$	0.17 ± 0.07	0.29 ± 0.14	0.04 ± 0.02	0.04 ± 0.02	0.02 ± 0.02	0.02 ± 0.02

The effect of detection method was positive and significant across species and study areas, with $\hat{\beta}$ estimates ranging from 1.75 to 2.56 (Table 2.3.4). The 95% confidence intervals of all red fox model-averaged covariates overlapped 0.0 at GVNP. However, a significant seasonal influence was detected at CNP, with the probability of detecting a red fox being significantly higher in spring than in autumn (Table 2.3.4). Elevation also showed a significant negative effect on detection probability at CNP (table 2.3.4). For stone martens at GVNP, season was the only covariate to significantly influence detectability with *P* decreasing from autumn to spring. At CNP, there were no observable covariate effects (Table 2.3.4). For genets, distance to water significantly negatively influenced detection probability (Table 2.3.4). All remaining variables' coefficients exhibited 95% confidence intervals that overlapped 0.0 (Table 2.3.4).

Table 2.3.4. Model averaged variable weights and beta estimates ($\hat{\beta}$), with 95% confidence intervals, on detection probability (*P*) at Guadiana Valley Natural Park (GVNP) and Cabañeros National Park (CNP), in autumn 2009 and spring 2010.

Study area	**Covariate**	**Red fox**		**Stone marten**		**Common genet**	
		AIC wgt	$\hat{\beta}$ [95% CI]	AIC wgt	$\hat{\beta}$ [95% CI]	AIC wgt	$\hat{\beta}$ [95% CI]
GVNP	Intercept	-	-2.97 [-4.71; -1.24]	-	-4.42 [-6-16; -2.69]	-	-
	Season	0.34	-1.09 [-4.27; 2.10]	0.32	-3.01 [-5.16; -0.87]	-	-
	Method	1.00*	2.17 [0.96; 3.38]	1.00*	2.56 [1.48; 3.64]	-	-
	Habitat: forest	0.75	0.39 [-0.64; 1.43]	0.75	-0.04 [-0.54; 0.45]	-	-
	Habitat: shrub	0.75	1.38 [-0.65; 3.41]	0.75	-0.04 [-0.61; 0.54]	-	-
	Distance to water	0.23	0.06 [-1.14; 1.25]	0.20	-0.27 [-1.79; 1.25]	-	-
	Elevation	0.27	-0.56 [-6.38; 5.26]	0.18	-1.64 [-8.14; 4.86]	-	-
	Slope	0.20	-0.02 [-0.14; 0.10]	0.25	0.10 [-0.05; 0.25]	-	-
CNP	Intercept	-	3.03 [-0.48; 6.53]	-	-4.52 [-8.88; -0.17]	-	-5.92 [-12.22; 0.38]
	Season	0.98	3.71 [0.13; 7.28]	0.27	-1.15 [-5.60; 3.31]	0.35	-2.11 [-8.83; 4.61]
	Method	1.00*	2.17 [1.23; 3.10]	0.99*	1.75 [0.70; 2.80]	1.00*	2.51 [0.90; 4.12]
	Habitat: forest	0.23	-0.17 [-1.15; 0.80]	0.18	0.07 [-0.59; 0.74]	0.29	0.02 [-1.25; 1.29]
	Habitat: shrub	0.23	-0.07 [-0.53; 0.40]	0.18	0.05 [-0.38; 0.48]	0.29	0.23 [-0.83; 1.29]
	Distance to water	0.60	-0.64 [-2.08: 0.81]	0.87	-1.98 [-4.57; 0.62]	0.93	-4.00 [-7.92; -0.09]
	Elevation	0.95	-6.42 [-11.82; -1.03]	0.46	2.31 [-3.45; 8.07]	0.62	3.83 [-4.36; 12.03]
	Slope	0.38	0.01 [-0.05; 0.07]	0.56	0.02 [-0.05; 0.09]	0.33	0.02 [-0.08; 0.11]

* - All models except models ψ(.)*p*(.) and ψ(season)*p*(.) were constrained to include the method covariate.

A greater number of 1-week sampling occasions are required to attain a given detection probability when employing hair snares than when employing camera traps (Figure 2.3.1). Based on the obtained detection probabilities, camera traps would have to be deployed, on average, for ≥ 4 1-week sampling occasions to confirm red fox occupancy, with 95% accuracy. In order to achieve the same level of accuracy, ≥ 20 1-week occasions are required when employing hair snares. Additionally, ≥ 12 and 13 camera trapping sampling occasions are required to confirm stone marten and genet occupancy, respectively, with 95% accuracy (Figure 2.3.1). It would take 6.9 and 10.8 times longer to achieve the same confidence level for stone martens and genets, respectively, if using hair snares.

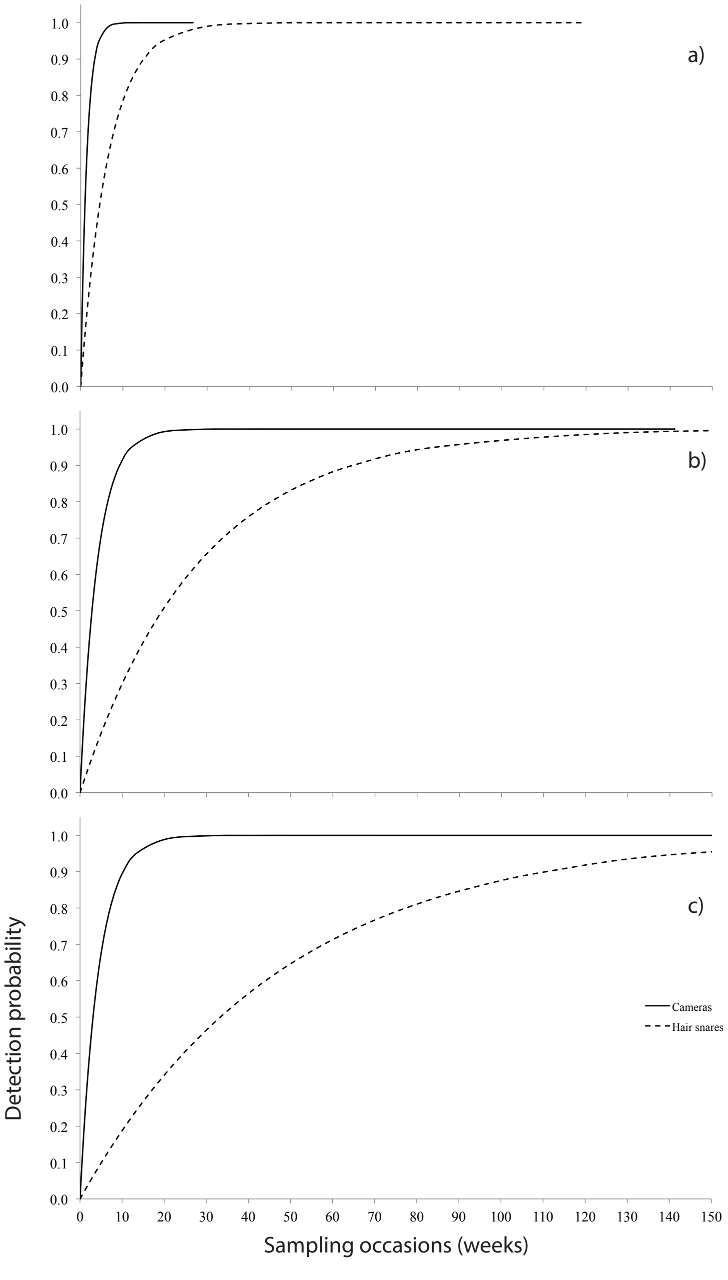

Figure 2.3.1. Mean estimated sampling occasions (weeks) required to attain a given detection probability, given species presence, for a) red foxes, b) stone martens, and c) common genets.

Discussion

Camera traps were a more efficient method for detecting mesocarnivores and estimating their occurrence when compared to hair snares. These results are consistent with previous studies done in North America (Comer et al. 2011, Long et al. 2007, O'Connell et al. 2006). We detected a total of six mesocarnivore species in each of the study areas when employing camera trapping, in comparison to only three mesocarnivore species in each of the study areas when employing hair snares. When both methods were able to detect a target species, partial naïve (raw) occupancy estimates were 7.7 ± 1.9% higher when assessed through camera trapping than through hair snaring methods. Lastly, we found that hair snares required a greater number of sampling occasions to attain a given detection probability than camera traps. This suggests that our four-week sampling period would not have provided adequate estimates of species occupancy in our study areas had we only employed hair snares.

A limited number of hairs were collected from hair snares (< 10 hairs/sample) and this number was reduced even further when considering the tufts of hair that yielded sufficient DNA for species identification. Our overall success of the molecular methods was rather low when compared to similar studies, which usually ranges from 40 to 80% (Weaver et al. 2005, Long et al. 2007, Steyer et al. 2012). Three main factors may be responsible for our low success rates in genetic identification: low DNA quantity, low DNA quality and contamination (Kendall and Mckelvey 2008). Most hair collected from rub stations, such the ones used in our study, consists of shed hair. Shed hair can provide enough DNA for genetic species assignment if mitochondrial DNA is used (Mills et al. 2000, Riddle et al. 2003). However, the DNA quantity obtained of plucked hair is usually higher because it often contains follicles, which are the main source of DNA for analysis (Goossens et al. 1998). DNA quality can also be affected by exposure to harsh environmental conditions, especially environmental temperature (Nsubuga et al. 2004, Santini et al. 2007). Both of our study areas are located in the Mediterranean Bioclimatic region of the Iberian Peninsula, where ambient temperature often rises above 35°C during the warmer seasons (Hijmans et al. 2005, Rivas-Martínez et al. 2004). These warm temperatures could have decreased DNA quality in the autumn period. Further, the spring season corresponded to a period of heavy precipitation, which could have led to sample "wash", and a consequent reduction of DNA quality.

Cross-contamination from multiple visits to the same station within a sampling occasion, can also reduce DNA identification success because mixed samples could lead to more multiple alleles at one or more diagnostic loci, preventing adequate genotyping (Mowat and Paetkau 2002). Reducing the time between station revisits could increase genetic identification success by preventing excessive exposure of hair DNA to environmental conditions and reducing the probability of multiple visits. However, a likely drawback of reducing the length of sampling occasions would be a reduction in detection probabilities and increase in survey costs (Long et al. 2007, Mowat and Paetkau 2002). Our sampling occasion length, 7 days, is similar to that used in other studies (e.g. Long et al. 2007, Stricker et al. 2012,Burki et al. 2010).

The baited hair snare model we tested (*sensu* Kendall and McKelvey 2008) required an active response from the target species in order to produce a detection (i.e. the rubbing behavior exhibited by most felid and canid species). Similar rub stations have been tested worldwide on a variety of species and yielded contrasting results. Long et al. (2007) failed to detect bobcats (*Lynx rufus*) in Vermont, USA, with rub pad hair snares, but successfully detected them with scat detection dogs and camera traps. However, they successfully detected black bears with all three methods. Comer et al. (2011) obtained low bobcat detection rates in Texas, USA, when compared to those obtained by camera traps. Using similar rub pads, Downey et al. (2007) failed to detect margays (*Leopardus wiedii*) at El Cielo Biosphere Reserve (Mexico), but obtained a 20.8% success in detecting gray foxes (*Urocyon cinereoargenteus*), whereas Castro-Arellano et al. (2008) were successful in detecting 67% of the medium and large mammals species known to be present. Steyer et al. (2012) were successful in identifying individual European wildcats with rub pad hair snares at a low-density area, in the Kellerwald-Edersee National Park,Germany. Even though cubby-like designs have been preferred for collecting hair from mustelids (Kendall and Mckelvey 2008), pine martens have been successfully detected by their hair using lure sticks at the Jura Mountains, Switzerland (Burki et al. 2010).

We used lynx urine and valerian extract solution as our scent lures because they have been found to elicit rubbing behavior in captive red foxes, European wildcats, common genets and Eurasian (Monterroso et al. 2011). We were surprised by the small number of wildcat hair samples collected in our study, especially in GVNP where a stable wildcat population is known to occur (Monterroso et al. 2009). Similar studies (with regard to hair collection structures and attractants) have proved effective for wildcat detection (Steyer et al. 2013) and estimation of population parameters (Kéry et al. 2011,). However, some studies have found valerian to be ineffective in attracting wildcats (Kilshaw & Macdonald, 2011; Anile et al. 2012), suggesting that genetic characteristics of wildcat populations could be related to their attractiveness towards valerian lure. Further field tests could help clarify the reasons for the poor performance of hair snares for detecting wildcats in our study areas.

Overall, a limited number of site-specific covariates revealed influence on the detectability of mesocarnivores. In CNP, we found the probability a red fox was detected was negatively related to elevation and the probability a genet was detected was negatively related to distance to water. We suggest that this is because the foxes' scavenging behavior at CNP is related to the abundance of Red deer (*Cervus elaphus*) and Wild boar (*Sus scrofa*) carcasses at lower elevations (García-Canseco 1997) and waterways provide abundant cover, food, and often serve as travel corridors (Rondinini and Boitani 2002, Santos et al. 2008). Given the close relationship between abundance and detectability (McCarthy et al. 2012), we would foxes were more abundant at lower elevations and genets closer to water.. In CNP, red fox were also more likely to be detected in autumn than in spring and in GVNP, stone marten were more likely to be detected in spring than in autumn. This was most likely the result of seasonal differences in the annual biological cycle of the target species. For example, the yearlings of most mesocarnivores disperse and incorporate the 'active' population in autumn. Thus, territoriality is more relaxed when compared to the spring season, which coincides with the breeding season of most species (Blanco 1998).

To our knowledge, this is the first study that evaluates the efficiency of hair snares for monitoring a mesocarnivore community in Europe. If individuals only need to be identified to the species-level, then our results suggest that camera trapping is a more efficient sampling method than hair snares. Other noninvasive methods, such as detection dogs or scat surveys, may also provide detection rates comparable to those of camera traps (Gompper et al. 2006, Long et al. 2007, O'Connell et al. 2006). However, because hair samples can be identified to the individual level through microsatellite analysis of nuclear DNA (Beja-Pereira et al. 2009), they allow for the estimation of population parameters such as density (Kéry et al. 2011), spatial organization (Davoli et al. 2012) or genetic diversity (Mullins et al. 2009).

Protected area administrations require adequate information on the status of wildlife populations through constant monitoring in order to detect population trends or sudden changes, and adjust management actions accordingly (Moriarty et al. 2011). Occupancy modeling, in combination with camera trap surveys, may be an ideal method for large-scale, long-term monitoring of wildlife populations as it provides information on the spatial distribution of species and patch-specific rates of colonization and extinction (MacKenzie et al. 2003, Moriarty et al. 2011). If management objectives, however, require deeper insights into population dynamics that can only be attained through analysis of genetic information (Kendall and Mckelvey 2008), then hair snaring may need to be employed. To improve the efficacy of hair snaring, we suggest increasing the number of sampling occasions (Bailey et al. 2007, O'Connell et al. 2006) and the frequency at which hair snares are checked. This will likely improve detection rates, minimize environmental degradation of DNA, and decrease incidence of cross-contamination. Additionally, depending on the target species, employing multiple types of hair snares (e.g., rub pads and cubby boxes) and multiple types of lures at each station may increase the number of species detected and overall detection rates. We suggest that future studies test different hair snare protocols and sampling designs, perhaps through simulation studies, to increase the efficiency of hair snare techniques; namely, determining the optimal duration of sampling occasions and the design of snares that increases both detection probabilities and the success of molecular methods.

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References

Anile S, Arrabito C, Mazzamuto MV, Scornavacca D, Ragni B (2012) A non-invasive monitoring on European wildcat (*Felis silvestris silvestris* Schreber, 1777) in Sicily using hair trapping and camera trapping: does scented lure work? Hystrix, the It J Mamm **23**:44–49. Doi: 10.1007/s10344-012-0644-0

Bailey L, Hines JE, Nichols JD, MacKenzie D (2007) Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecol Appl **17**:281–90. Doi: 10.1890/1051-0761(2007)017[0281:SDTIOS]2.0.CO;2

Baldwin RA, Bender LC (2008) Distribution, Occupancy, and Habitat Correlates of American Martens (*Martes americana*) in Rocky Mountain National Park, Colorado. J Mammal **89**:419–427. Doi: 10.1644/07-MAMM-A-053R1.1

Beja-Pereira A, Oliveira R, Alves PC, Schwartz MK, Luikart G (2009) Advancing ecological understandings through technological transformations in noninvasive genetics. Mol Ecol Resour **9**:1279–301. Doi: 10.1111/j.1755-0998.2009.02699.x

Blanco JC (1998) Mamíferos de España. Planeta, Barcelona,.

Burki S, Roth T, Robin K, Weber D (2010) Lure sticks as a method to detect pine martens *Martes martes*. Acta Theriol **55**:223–230. Doi: 10.4098/j.at.0001-7051.023.2009

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, Second edn. Springer, New York.

Castro-Arellano I, Madrid-Luna C, Lacher TE, León-Paniagua L (2008) Hair-Trap Efficacy for Detecting Mammalian Carnivores in the Tropics. J Wildlife Manage **72**:1405–1412. Doi: http://www.bioone.org/doi/abs/10.2193/2007-476

Comer CE, Symmank ME, Kroll JC (2011) Bobcats Exhibit Low Detection Rates at Hair Collection Stations in East Texas. Wildlife Biol in Practice **7**: 116–122. Doi: 10.2461/wbp.2011.7.9

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental. Quercetea 0:5–56.

Downey PJ, Hellgren EC, Caso A, Carvajal S, Frangioso K (2007) Hair Snares for Noninvasive Sampling of Felids in North America: Do Gray Foxes Affect Success? J Wildlife Manage **71**: 2090–2094. Doi: 10.2193/2006-500

Galantinho A, Mira A (2008) The influence of human, livestock, and ecological features on the occurrence of genet (*Genetta genetta*): a case study on Mediterranean farmland. Ecol Res **24**: 671–685. Doi: 10.1007/s11284-008-0538-5

García-Canseco V (1997) Parque Nacional de Cabañeros. 1st edn. Ecohábitat, Madrid.

Goldyn B, Hromada M, Surmacki A, Tryjanowski P (2003) Habitat use and diet of the red fox *Vulpes vulpes* in an agricultural landscape in Poland. Zeitschrift für Jagdwissenschaft **49**: 191–200. Doi: 10.1007/s

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. Wildlife Soc B **34**:1142–1151. Doi: 10.2193/0091-7648(2006)34[1142:ACONTT]2.0.CO;2

Goossens B, Waits LP, Taberlet P (1998) Plucked hair samples as a source of DNA: reliability of dinucleotide microsatellite genotyping. Mol Ecol **7**:1237–1241. Doi: 10.1046/j.1365-294x.1998.00407.x

Hanke PU, Dickman CR (2013) Sniffing out the stakes: hair-snares for wild cats in arid environments. Wildlife Res **40**:45–51. Doi: 10.1071/WR12210

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol **25**:1965–1978. Doi: 10.1002/joc.1276

Hines JE, Mackenzie D (2013) Presence software, v5.8.

ICN - Instituto para a Conservação da Natureza (2006) Zona de Protecção Especial Vale do Guadiana. 12. Lisboa.

ICNF (2013) www.icnf.pt. Accessed 28th May 2013.

Johnson A, Vongkhamheng C, Saithongdam T (2009) The diversity, status and conservation of small carnivores in a montane tropical forest in northern Laos. Oryx **43**: 626–633. Doi: 10.1017/S0030605309990238

Kendall KC, Mckelvey KS (2008) Hair collection. In Long RA, MacKay P, Zielinski WJ, Ray JC (eds) Noninvasive survey methods for carnivores. Island Press, Washignton DC, pp 135-176

Kendall KC., Stetz JB, Boulanger J, Macleod AC, Paetkau D, White GC (2009) Demography and Genetic Structure of a Recovering Grizzly Bear Population. J Wildlife Manage **73**:3–17. Doi: 10.2193/2008-330

Kéry M, Gardner B, Stoeckle T, Weber D, Royle JA (2011). Use of spatial capture-recapture modeling and DNA data to estimate densities of elusive animals. Conserv Biol **25**:356–364. Doi: 10.1111/j.1523-1739.2010.01616.x

Kilshaw K, Macdonald DW (2011) The use of camera trapping as a method to survey for the Scottish wildcat. Scottish Natural Heritage Commissioned Report No. 479.

Larivière S, Calzada J (2001) *Genetta genetta*. Mamm Species 680:1–6.

Larivière S, Pasitschniak-Arts M (1996) *Vulpes vulpes*. Mamm Species 537:1–11.

Linkie M, Dinata Y, Nugroho A, Haidir IA (2007) Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. Biol Conserv 137:20–27. Doi: 10.1016/j.biocon.2007.01.016

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS (2007) Comparing Scat Detection Dogs, Cameras, and Hair Snares for Surveying Carnivores. J Wildlife Manage **71**:2018–2025. Doi: 10.2193/2006-292

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecol **26**:327–340. Doi: 10.1007/s10980-010-9547-1

Mackenzie D, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006). Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, Oxford.

Mackenzie D, Nichols JD, Hines JE, Knutson M (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**:2200–2207. Doi: 10.1890/02-3090

Mackenzie D, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248–2255. Doi: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

McCarthy MA, Moore JL, Morris WK, Parris KM, Garrard GE, Vesk PA, Rumpff L, Giljohann KM, Camac JS, Bau SS, Friend T, Harrison B, Yue B (2012) The influence of abundance on detectability. Oikos.**122**: 717-726. Doi: 10.1111/j.1600-0706.2012.20781.x

Mills L, Pilgrim K, Schwartz M, McKelvey K (2000). Identifying lynx and other North American felids based on mtDNA analysis. Consev Genet 1:285–288. Doi: 10.1023/A:1011574209558

Mills MGL (1996) Methodological advances in capture, census, and food-habits studies of large African carnivores. In Gittleman JL (ed) Carnivore behavior, Ecology, and Evolution. Cornell University Press, New York,pp: 223-242.

Monterroso P, Brito JC, Ferreras P, Alves PC (2009) Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. J Zool **279**:27–35. Doi: 10.1111/j.1469-7998.2009.00585.x

Monterroso P, Castro D, Silva TL, Ferreras P, Godinho R Alves PC (2012) Factors affecting the (in)accuracy of mammalian mesocarnivore scat identification in South-western Europe. J Zool **289**: 243–250. Doi: 10.1111/jzo.12000

Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildlife Res **38**:446–454. Doi: 10.1071/WR11060

Moriarty KM, Zielinski WJ, Forsman ED (2011) Decline in American marten occupancy rates at Sagehen Experimental Forest, California. J Wildlife Manage **75**:1774–1787. Doi: 10.1002/jwmg.228

Mowat G, Paetkau D (2002) Estimating marten Martes americana population size using hair capture and genetic tagging. Wildlife Biol **8**:201–209.

Múgica M, Martínez C, Gómez-Limón J, Puertas J, Atauri JA (2012) Anuario 2011 del estado de las áreas protegidas en España. Madrid.

Mullins,J, Statham MJ, Roche T, Turner PD, O'Reilly C (2009) Remotely plucked hair genotyping: a reliable and non-invasive method for censusing pine marten (*Martes martes*, L. 1758) populations. Eur J Wildlife Res **56**:443–453. Doi: 10.1007/s10344-009-0332-x

Nichols JD, Bailey LL, O'Connell Jr. AF, Talancy NW, Grant EHC, Gilbert AT, Annand EM, Husband TP, Hines JE (2008) Multi-scale occupancy estimation and modelling using multiple detection methods. J Appl Ecol **45**:1321–1329. Doi: 10.1111/j.1365-2664.2008.01509.x

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**:2089–94. Doi: 10.1111/j.1365-294X.2004.02207.x

O'Connell AF, Talancy NW, Bailey LL, Sauer JR, Cook R, Gilbert AT (2006) Estimating Site Occupancy and Detection Probability Parameters for Meso- And Large Mammals in a Coastal Ecosystem. J Wildlife Manage **70**:1625–1633. Doi: 10.2193/0022-541X(2006)70[1625:ESOADP]2.0.CO;2

Oliveira R, Castro D, Godinho R, Luikart G, Alves PC (2010) Species identification using a small nuclear gene fragment: application to sympatric wild carnivores from

South-western Europe. Conserv Genet **11**:1023–1032. Doi: 10.1007/s10592-009-9947-4

Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical Inference from Capture Data on Closed Animal Populations. Wildlife Monographs **62**:3–135.

Palomares F, Godoy JA, Piriz A, O'brien SJ, Johnson WE (2002) Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. Mol Ecol **11**:2171–2182. Doi: 10.1046/j.1365-294X.2002.01608.x

Riddle AE, Pilgrim KL, Mills LS, McKelvey KS, Ruggiero LF (2003) Identification of mustelids using mitochondrial DNA and non-invasive sampling. Conserv Genet **4**: 241–243. Doi: 10.1023/A:1023338622905

Rivas-Martínez S. Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas. Servicio Cartográfico de la Universidad de León, Madrid.

Rivas-Martinez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique. Anales del Jardin Botanico de Madrid **37**: 251–268.

Rondinini C, Boitani L (2002) Habitat use by beech martens in a fragmented landscape. Ecography **3**:257–264. Doi: 10.1034/j.1600-0587.2002.250301.x

Rosalino LM, Sousa M, Pedroso N, Basto M, Rosario J, Santos MJ, Loureiro F (2010) The influence of food resources on red fox local distribution in a mountain area of the western mediterranean. Vie et milieu **60**:39–45.

Royle JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. Ecology **84**:777–790. Doi: 10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

Ruell EW, Crooks KR (2007) Evaluation of Noninvasive Genetic Sampling Methods for Felid and Canid Populations. J Wildlife Manage **71**:1690–1694. Doi: 10.2193/2006-061

Santini A, Lucchini V, Fabbri E, Randi E (2007) Ageing and environmental factors affect PCR success in wolf (*Canis lupus*) excremental DNA samples. Mol Ecol Notes **7**:955–961. Doi: 10.1111/j.1471-8286.2007.01829.x

Santos MJ, Pedroso N, Ferreira JP, Matos HM, Sales-Luís T, Pereira I, Baltazar C, Grilo C, Cândido AT, Sousa I, Santos-Reis M (2008) Assessing dam implementation impact on threatened carnivores: the case of Alqueva in SE Portugal. Environ Monit Assess **142**:47–64. Doi: 10.1007/s10661-007-9907-8

Sarmento P, Cruz JP, Eira CI, Fonseca C (2009) Habitat selection and abundance of common genets *Genetta genetta* using camera capture-mark-recapture data. Eur J Wildlife Res **56**:59–66. Doi: 10.1007/s10344-009-0294-z

Sarmento P, Cruz JP, Monterroso P, Tarroso P, Negrões N, Ferreira C (2004) The Iberian Lynx in Portugal: Status survey and conservation action plan. Instituto da Conservação da Natureza (ICN), Lisboa.

Schmidt K, Kowalczyk R (2006) Using Scent-Marking Stations to Collect Hair Samples to Monitor Eurasian Lynx Populations. Wildlife Soc B **34**:462–466. Doi: 10.2193/0091-7648(2006)34[462:USSTCH]2.0.CO;2

Steyer K, Simon O, Kraus RHS, Haase P, Nowak C (2013) Hair trapping with valerian-treated lure sticks as a tool for genetic wildcat monitoring in low-density habitats. Eur J Wildlife Res **59**:39–46. Doi: 10.1007/s10344-012-0644-0

Stricker HK, Belant JL, Beyer DE, Kanefsky J, Scribner KT, Etter DR, Fierke J (2012) Use of modified snares to estimate bobcat abundance. Wildlife Soc B **36**:257–263. Doi: 10.1002/wsb.137

Teerink, B. J. 1991. Hair of West-European mammals. Cambridge University Press, Cambridge; :224.

Tobler MW, Carrillo-Percastegui SE, Powell G (2009) Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. J Tropical Ecol **25**:261–270. Doi: 10.1017/S0266467409005896

Weaver JJL, Wood P,Paetkau D, Laack LL (2005) Use of Scented Hair Snares to Detect Ocelots. Wildlife Soc B **33**:1384–1391. Doi: 10.2193/0091-7648(2005)33[1384:UOSHST]2.0.CO;2

Williams BW, Etter DR, Linden DW, Millenbah KF, Winterstein SR, Scribner KT (2009) Noninvasive Hair Sampling and Genetic Tagging of Co-Distributed Fishers and American Martens. J Wildlife Manage **73**:26–34. Doi: 10.2193/2007-429

Zar JH (2005) Encyclopedia of Biostatistics. John Wiley & Sons, Ltd., Chichester.

Zielinski WJ, Schlexer FV, Pilgrim KL, Schwartz MK (2006) The Efficacy of Wire and Glue Hair Snares in Identifying Mesocarnivores. Wildlife Soc B **34**:1152–1161. Doi: 10.2193/0091-7648(2006)34[1152:TEOWAG]2.0.CO;2

Catch me if you can: diel activity patterns of mammalian prey and predators

Plasticity in activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence

Spatial interactions between sympatric mammalian mesocarnivores in Southwestern Europe

Seasonal dynamics in mesocarnivore interactions: a multidimentional analysis of niche partitioning between martens (*Martes* sp.) in Southwestern Europe

Ecological interactions in mesocarnivore communities in the Iberian Peninsula

Catch me if you can: diel activity patterns of mammalian prey and predators

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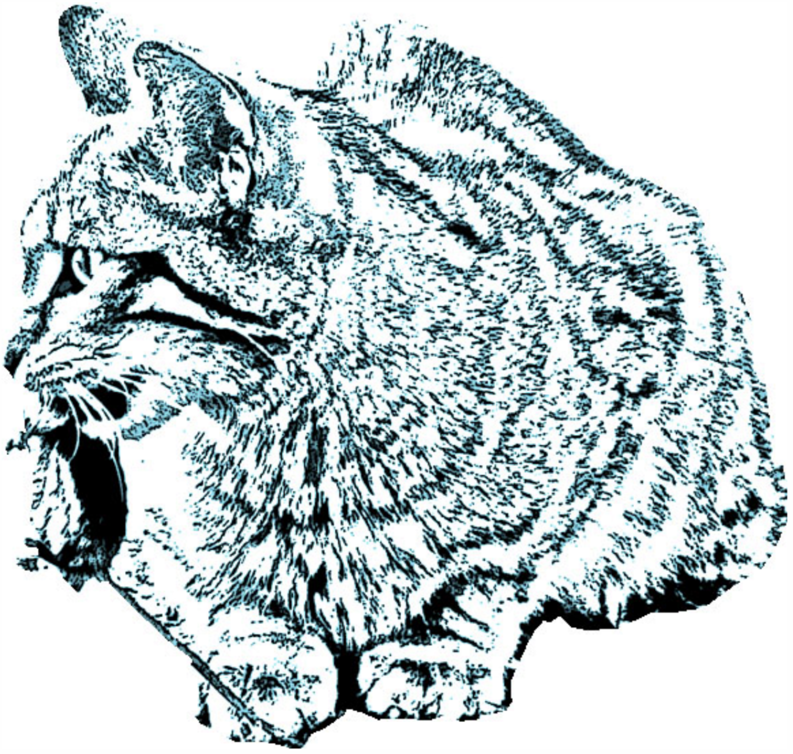

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3.1 Catch me if you can: diel activity patterns of mammalian prey and predators

Abstract

The activity patterns exhibited by animals are shaped by evolution, but additionally fine-tuned by flexible responses to the environment. Predation risk and resource availability are environmental cues which influence the behavioural decisions that make both predators and prey engage in activity bursts, and depending on their local importance, can be strong enough to override the endogenous regulation of an animals' circadian clock. In Southern Europe, wherever the European rabbit (*Oryctolagus cuniculus*) is abundant, it is the main prey of most mammalian mesopredators, and rodents are generally the alternative prey. We evaluated the bidirectional relation between the diel activity strategies of these mammalian mesopredators and prey coexisting in south-western Europe. Results revealed that even though predation risk enforced by mammalian mesocarnivores during night-time was approximately twice and five times higher than during twilight and daytime, respectively, murids consistently displayed unimodal nocturnal behaviour. Conversely, the European rabbits exhibited a bimodal pattern that peaked around sunrise and sunset. Despite the existence of some overlap between the diel rhythms of mesocarnivores and rabbits, their patterns were not synchronized. We suggest that the environmental stressors in our study areas are not severe enough to override the endogenous regulation of the circadian cycle in murids. European rabbits, however, are able to suppress their biological tendency for nocturnality by selecting a predominantly crepuscular pattern. In spite of the higher energetic input, mesocarnivores do not completely track rabbits' activity pattern. They rather track rodents' activity. We propose that these systems have probably evolved towards a situation where some degree of activity during high-risk periods benefits the overall prey population survival, while the accessibility to sufficient prey prevents predators to completely track them.

Keywords

Diel activity; Predation risk; Optimal foraging; Mesocarnivores, Southwestern Europe

Introduction

The fundamental ecological niche refers to the full range of conditions (biotic and abiotic) and resources in which an organism can survive and reproduce (Elton 2001). However, local environmental pressures such as interspecific relations act on individuals narrowing the breadth of utilization of at least one of the niche dimensions or resources, promoting coexistence (Hutchinson 1957). Apart from other biological functions, time may serve as a niche dimension over which interacting animals might segregate to reduce the effect of agonistic encounters (Carothers & Jaksić 1984). The nycthemeral or diel activity patterns are the most evident and best studied in animal ecology (Halle & Stenseth 2000) and, according to Halle (2000), consist of 'adaptative sequences of daily routines that meet the time structure of the environment, shaped by evolution, but additionally fine-tuned by flexible responses to the actual state of the environment'. This means that the daily activity of an animal is intrinsically constrained, and therefore, its plasticity for local adaptation is fairly limited (Schoener 1974; Kronfeld-Schor & Dayan 2003). For instance, nocturnal mammals have developed characteristics adapted to dim light activity (p.e. effective camouflage, large inner ears or eyes with large lens in relation to the focal length and large corneas; Ashby 1972; Bartness & Albers 2000). Therefore, each animal will try to explore the temporal niche dimension to maximize energetic gain and other biological needs, while reducing individual costs, for example mortality risk (Brown et al. 1999; Halle 2000; DeCoursey 2004). In predator–prey systems, continuous arms race take place over the spatial and temporal dimensions (Eriksen et al. 2011). While at a spatial level, prey should try to avoid using high-risk locations following what has been described as the landscape of fear (Brown et al. 1999), at the temporal level, a simplistic way of viewing this system is that prey struggles to reduce predation risk by reducing activity overlap with predators, while the latter track down prey by trying to synchronize their activity with them, in a constant and dynamic relation (Lima 2002). Consequently, we would expect that the diel activity pattern of a given prey species in a particular location to be the result of its evolutionary physiological adaptations (i.e. fundamental niche) and the selective pressures exerted locally such as predation pressure, accessibility to resources and intraguild interactions (Fenn & MacDonald 1995; Kronfeld-Schor & Dayan 2008). Predator activity should be shaped by the same evolutionary processes and local constraints, but with an additional limitation imposed by temporally available feeding resources (i.e. prey; Halle 2000; Lima 2002). However, feeding specialization and prey availability also play an important role in the structure of the daily activity pattern. A specialist predator should more avidly try to synchronize its rhythm with that of its staple prey. Conversely, a more generalist species should only track a given prey so far, especially if alternative feeding resources are available with minor costs.

In Southern Europe small mammals (mainly rodents) and the European rabbit (*Oryctolagus cunicu- lus*) are the most profitable prey for predator communities, namely mammalian mesocarnivores (Malo et al. 2004; Lozano et al. 2006; Delibes-Mateos et al. 2008b). In fact, rodents are consumed with considerable frequency by most European mesocarnivore species, especially in the Atlantic ecoregion (Lozano et al. 2006; 2006; Zhou et al. 2011; Díaz-Ruiz et al. 2013). However, the energetic trade-off between predation costs and individual prey intake favours the predation upon European rabbit wherever it reaches moderate to high abundance (Malo et al. 2004). Hence, the European rabbit assumes a particularly important role in the Mediterranean ecosystems' functioning, being the preferred prey of a variety of predators (Delibes & Hiraldo 1981; Delibes-Mateos et al. 2008a). Here, we evaluate the bidirectional temporal strategies of mammalian prey (small mammals and European rabbits) and mammalian mesocarnivore imposed predation risk. Our predictions were that where rabbits are scarce (Atlantic region), a high overlap and synchrony between rodents and mammalian mesopredators should indicate a dominant strategy within the predator community to maximize access to small mammals, whereas where European rabbits are widely available, the mammalian mesopredator community should track their activity in detriment of small mammals.

Methods

Study areas

Activity data were collected in four different study sites of the Iberian Peninsula (figure 3.1.1): two in Portugal, the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP) and two in Spain, the Cabañeros National Park (CNP) and the Muniellos Natural Reserve (MNR). Two of these study sites (GVNP and CNP) are located in the Mediterranean region of the Iberian Peninsula, and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez et al. 2004). Scrubland patches are mainly associated with steeper slopes, elevation ridges and main water bodies and are dominated by *Pyro-Quercetum rotundifoiae* and *Myrto communis–Querco rotundifoliae* series and other subserial stages (Rivas-Martínez 1981; Costa et al. 1998). Areas with gentler slopes are mainly occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*) scattered within a grassland matrix (García-Canseco 1997). The PGNP and MNR are located in the Atlantic region of the Iberian Peninsula and have a temperate oceanic sub-Mediterranean bioclimate (Rivas-Martínez et al. 2004). The landscapes consist of mountainous agricultural–forest mosaic, where mountain tops are mostly dominated by scrublands with Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially dominated by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* and *Fagus* sp.). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Prieto & Sánchez 1996; Carvalho & Gomes 2004; UNESCO). A study area of approximately 6000 ha within each of the study sites was selected, based on criteria of ecosystem conservation status and logistic factors.

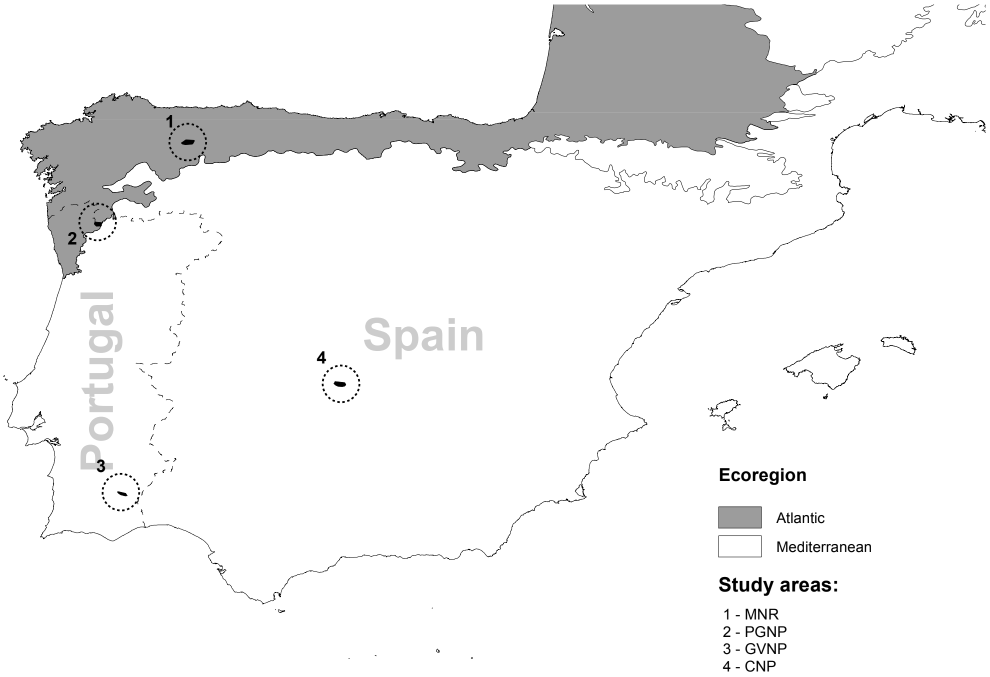

Figure 3.1.1. Location of the study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park.

Field sampling

Each study area was sampled for one year during two seasons: July–October (hereafter non-breeding season), when the offspring of most medium-sized carnivores from that year become independent; and February–April (hereafter breeding season), during these species' breeding season (Blanco 1998). Field sampling was based on camera-trapping of both carnivore mesopredators and their mammalian prey. The spatial sampling scheme and camera-trap sites' selection followed the procedures described by Monterroso et al. (2011). In summary, between 32 and 41 cameras were uniformly spaced in each study area following a grid sampling scheme. Camera traps were placed in a sampling grid, where mean distance among neighbouring cameras was ~1.4 km. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, MS, USA) and Scout- Guard (HCO OutDoor Products, Norcross, GA, USA). Cameras were mounted on trees approximately 0.5–1.0 m off the ground and set to record time and date when triggered. We programmed cameras with the minimum time delay between consecutive photos to maximize the number of photos taken per captured individual. Camera traps were maintained in the field for a minimum period of 28 days and were inspected for battery or card replacement every 7–14 d. A combination of carnivore attractants was used to incite animals' curiosity and thus increase detection probabilities. The attractants used were Lynx urine, obtained from captive specimens of Eurasian lynx (*Lynx lynx*) and Iberian lynx (*Lynx pardinus*), and Valerian extract solution, as suggested by Monterroso et al. (2011) for Iberian carnivore sampling. Attractants were placed in the field at a distance of 2–3m from the camera traps and were deployed in perforated separated plastic containers, at a distance of 10–15 cm from each other and approximately 30 cm above the ground. Five to 10 ml of each attractant was sprayed into a cotton gaze, held inside each container. Attractants were rebaited every 7–14 d. When multiple photographs of the same species were taken within a 30-min interval, we considered them as a single capture event to ensure capture independence (unless animals were clearly individually distinguishable; Kelly & Holub 2008; Davis et al. 2011).

Prey abundance

European rabbits' relative abundance was estimated using pellet counts, which has been argued as the indirect method that provides the most reliable estimates (Palomares 2001; Fernández-de-Simón et al. 2011). Fourteen to 15 (mean ± SE: 14.5 ± 0.3) grids were sampled in each study area. Each sampling grid consisted of 9–12 (mean ± SE: 10.5 ± 0.9) sampling plots, regularly spaced at 15-m intervals. Each sampling plot consisted of a circular 0.5m^2 area, which was cleared of all rabbit pellets at the beginning of each sampling campaign. Sampling plots were then recounted after 18.7 ± 0.4 (mean ± SE) days post-clearing. Rabbit relative abundance was assessed as an uncorrected daily pellet accumulation rate (UNC), which was obtained by calculating the average number of pellets per square metre divided by the number of days elapsed since the initial cleaning (Fernández-de-Simón et al. 2011). Sampling grids location in each study area followed criteria of accessibility and proportional spatial representativity of the most relevant habitats. The relative abundance of murids (*Apodemus* sp. and *Mus* sp.) was assessed by the means of live captures. Using the same sampling grids and plots' placement previously described, nine live traps (5.1 x 6.4 x 16.5 cm, SFG folding traps, H.B. Sherman traps, Tallahassee, FL, USA) were set for the capture of small mammals. In the study areas located in the Atlantic ecoregion (PGNP and MNR), an extra line of three larger sized live traps (7.6 x 8.9 x 22.9 cm, LFG folding traps, H.B. Sherman traps) was set at each sampling grid because of the expected higher abundance of voles (*Microtus* sp. and *Arvicola* sp.). A trapping campaign consisted of three consecutive trapping days. Traps were monitored after sunrise, to reduce stress in captured animals. All captured individuals were then identified to the species level, sexed, weighted and aged without the resort to any kind of chemical immobilization. Each captured animal was marked with a small hair cut in the right hind leg, to ensure that recaptures could be adequately identified. After handling, each animal was released at the capture site. A relative abundance index was calculated as the number of new individuals captured ·100 trapping-days^{-1} (Watkins et al. 2009).

Statistical analysis

Detection records for each species were regarded as a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken within any particular interval of the day (Ridout & Linkie 2009). The probability density function of this distribution (i.e. activity pattern; Linkie & Ridout 2011) was estimated nonparametrically using kernel density estimates following the procedures described by Ridout & Linkie (2009). Following the estimation of the distribution function, pairwise comparisons of activity patterns between mammalian predators and prey species were performed by estimating the coefficient of overlap Δ_1, as suggested by Ridout & Linkie (2009) and Linkie & Ridout (2011) for small sample sizes, whenever the number of records was <50 detections. The coefficient of overlap Δ_4 was used when sample size was more than 50 detections. The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap) and is obtained taking the minimum of the density functions of the two species or species complexes (e.g. all mesocarnivores) being compared at each time point. The precision of this estimator was obtained through confidence intervals, as percentile intervals from 500 bootstrap samples (Linkie & Ridout 2011). Target species consisted of all carnivore species with mean body weight between 1.0 and 7.0 kg detected in the study areas: red fox (*Vulpes vulpes*); European wildcat (*Felis silvestris*); pine marten (*Martes martes*); stone marten (*Martes foina*); Eurasian badger (*Meles meles*); common genet (*Genetta genetta*); and Egyptian mongoose (*Herpestes ichneumon*). To evaluate the potential effect of mesocarnivore-mediated predation risk on prey activity rhythm, all carnivore data were also pooled together and subjected to the same analysis. The reliability of kernel estimates was assessed using non-negative trigonometric sum distributions (Fernández-Durán 2004), which were also fitted to the same detection data. As estimates based on the trigonometric sums and kernel densities should be broadly similar (Ridout & Linkie 2009), whenever estimates' difference was more than 0.2, we assumed that they were imprecise and were therefore discarded.

Whereas the coefficient of overlap might provide useful information on the probability of two species being active at a given period of the day, alternative measures focusing on the degree of synchrony of peaks of activity may also be of ecological interest (Ridout & Linkie 2009). Therefore, Pearson's correlations were estimated to evaluate the level of synchrony between prey and predator, using kernel probability estimates for 512 equally spaced time points along the day, that is, a point at approximately each 2.8 min. All statistic analyses were performed using R software (R Development Core Team 2008). The R code used to estimate overlap coefficients was adapted from that provided by Ridout & Linkie (2009). Night-time, daytime and twilight (defined as the period enclosed between one hour prior to one hour after sunrise and sunset, Lucherini et al. 2009) durations can vary between seasons and study areas and are also different among them within the 24-h day cycle. Therefore, we calculated a 'density of detections' for both predator and prey species, where the total number of detections in each of defined periods was divided by the duration (in hours) of that period per 100 trap-days. The data on predator activity were interpreted as a predation risk proxy for each period of the day, as we assume that the density of detections relates to the probability of prey species encountering a mesocarnivore predator at a given time of the day. Data are presented as mean ± SE, unless explicitly stated.

Results

A total of 8346 trap-nights (1043 ± 47 trapping days · campaign^{-1}) were obtained from all study sites and seasons. A total of 4911 detections were obtained, of which 1309 were mesocarnivores (164 ± 52 detections · campaign^{-1}), 758 were small mammals (95 ± 20 detections · campaign^{-1}), and 2844 were European rabbits (356 ± 233 detections · campaign^{-1}) (table 3.1.1).

Small mammals activity patterns and abundance

Murid rodents were detected across all study areas and seasons (table 3.1.2). They consistently revealed nocturnal activity with a tendency for the onset to occur just after sunset and cessation just before sunrise (figure 3.1.2). Activity density functions suggest a unimodal pattern, occasionally with a slight reduction in activity between 01:00 h and 04:00 h (figure 3.1.2). The density of detections was always higher during night-time (0.84 ± 0.17 detections$\cdot$hour$^{-1}\cdot$100 trapping-days^{-1}), followed by twilight (0.13 ± 0.04 detections$\cdot$hour$^{-1}\cdot$100 trapping-days^{-1}). Daytime detections were rare (only one detection obtained during daytime, at CNP during non-breeding season). Muridae species revealed similar abundance indexes in the Atlantic (6.00 ± 1.83 new captures$\cdot$100 trapping-days^{-1}) and Mediterranean (5.18 ± 0.80 new captures$\cdot$100 trapping-days^{-1}) study areas (Kruskal–Wallis test, $H = 0.02$, $p = 0.88$). However, species compositions varied between ecoregions: in Mediterranean areas, 58% of all captured individuals were Algerian mice (*Mus spretus*), while in Atlantic areas, 97% of captures consisted of either wood or yellow- necked mouse (*Apodemus sylvaticus* and *A. flavicollis*).

Table 3.1.1. Number of camera-trap detections and relative contributions of each species for mesocarnivore and prey community data structures.

	CNP		GVNP		PGNP		MNR	
Species	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**
Small mammals	105	143	44	77	186	13	135	55
European rabbit	48	15	1705	1074	2	0	0	0
Red fox	259 (76.0%)	382 (86.2%)	40 (33.3%)	7 (5.11%)	22 (34.9%)	12 (16.4%)	6 (8.8%)	22 (34.4%)
European wildcat	4 (1.2%)	7 (1.6%)	22 (18.3%)	19 (13.9%)	1 (1.6%)	7 (9.6%)	9 (13.2%)	7 (10.9%)
Stone marten	42 (12.3%)	24 (5.4%)	16 (13.3%)	58 (42.3%)	3 (4.8%)	12 (16.4%)	1 (1.5%)	2 (3.1%)
Pine marten	0	0	0	0	13 (20.6%)	27 (37.0%)	40 (58.8%)	27 (42.2%)
Marten spp.*	0	0	0	0	12 (19.1%)	6 (8.2%)	4 (5.9%)	2 (3.1%)
Eurasian badger	15 (4.4%)	8 (1.8%)	12 (10.0%)	5 (3.6%)	0	1 (1.4%)	1 (1.5%)	2 (3.1%)
Common genet	21 (6.16%)	16 (3.6%)	8 (6.7%)	30 (21.9%)	12 (19.1%)	8 (11.0%)	7 (10.3%)	2 (3.1%)
Egyptian mongoose	0	6 (1.4%)	22 (18.3%)	18 (13.1%)	0	0	0	0
Mesocarnivore community	**341**	**443**	**120**	**137**	**63**	**73**	**68**	**64**

* - Photographs in which it was impossible to distinguish between pine marten and stone marten.

CNP, Cabañeros National Park; GVNP, Guadiana Valley Natural Park; PGNP, Peneda-Gerês National Park; MNR, Muniellos Natural Reserve.

European rabbit activity patterns and abundance

European rabbits were mostly detected in the Mediterranean study areas. Only two rabbit detections were obtained from the Atlantic region, both from the PGNP in non-breeding season (table 3.1.1). Activity was recorded at all hours of the day, but activity density functions revealed a strong bimodal activity pattern, with a major activity peak occurring at sunrise and throughout the morning. A second activity peak took place in late afternoon, dropping after sunset (figure 3.1.3). Activity was more intense during twilight hours (3.23 ± 2.22 detections$\cdot$hour$^{-1}\cdot$100 trapping-days^{-1}). The intensity of activity recorded during night-time and daytime was of 1.29 ± 0.91 and 1.40 ± 0.93 detections $\cdot$ hour^{-1} $\cdot$ 100 trapping-days^{-1}, respectively. However, no statistically significant differences were detected (Kruskal–Wallis test, $H = 0.55$, p =0.76). The European rabbit, when detected, revealed only residual abundances in the study areas from the Atlantic region (table 3.1.2). In the Mediterranean study areas, this lagomorph was over 10 times more abundant at GVNP (174.9 ± 31.5 pellets$\cdot$100 d$^{-1}\cdot$m^{-2}) than in CNP (11.5 ± 5.1 5 pellets$\cdot$100 d$^{-1}\cdot$m^{-2}).

Table 3.1.2. Prey species relative abundance in the study areas. European rabbit - pellet production$\cdot$100 days$^{-1}\cdot$m^{-2}; Murinae spp. - *Apodemus* sp. and *Mus* sp. new captures$\cdot$100 trapping days^{-1}. Results presented as average ± standard error. Note that units are different for both prey types.

	CNP		**GVNP**		**PGNP**		**MNR**	
Species	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**	**Non-breeding**	**Breeding**
European rabbit	6.7 ± 3.4	16.2 ± 6.8	179.5 ± 31.6	170.2 ± 31.4	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Murinae spp.	3.07 ± 0.95	5.15 ± 2.18	6.97 ± 1.97	5.52 ± 2.52	10.82 ± 2.35	2.23 ± 1.44	6.52 ± 2.23	4.42 ± 0.24

CNP, Cabañeros National Park; GVNP, Guadiana Valley Natural Park; PGNP, Peneda-Gerês National Park; MNR, Muniellos Natural Reserve.

Activity rhythm of mesocarnivores and temporal structure of predation risk

Carnivore detections were obtained in 1309 occasions across all study areas and seasons, 58.4% of which belonged to red fox (N = 750, table 3.1.1, figure 3.1.4). The pine marten, stone marten and common genet were detected in 158 (12.3%), 107

(8.3%) and 104 (8.1%) occasions. The European wildcat accounted for 76 detections (5.9%) and the Eurasian badger and Egyptian mongoose for 44 (3.4%) and 46 (3.7%) detections, respectively. The proportional contribution of each species to the mesocarnivore detection data varied across sites and seasons (figure 3.1.4). The pine marten was only detected in study areas in the Atlantic region, while the Egyptian mongoose was only detected in the Mediterranean ones (figure 3.1.4, appendix 3.1). The remaining species had variable individual contributions across study areas and seasons. Predation risk imposed by mammalian mesocarnivores revealed a consistent tendency to be higher during night-time, although with variable degrees of diurnal intensity (figures 3.1.2 and 3.1.3). Concordantly, night-time was the period that accounted for more density of detections (1.06 ± 0.27 $\text{detections}\cdot\text{hour}^{-1}\cdot 100\ \text{trapping-days}^{-1}$), followed by twilight (0.61 ± 0.19 $\text{detections}\cdot\text{hour}^{-1}\cdot 100\ \text{trapping-days}^{-1}$) and daytime (0.26 ± 0.12 $\text{detections}\cdot\text{hour}^{-1}\cdot 100\ \text{trapping-days}^{-1}$). Daytime activity in the Mediterranean areas was mostly due to red fox and Egyptian mongoose activities, which accounted for 71% and 25% of all diurnal detections in this region, respectively. The high proportion of red fox detections was responsible for the observed daytime activity of mesocarnivore community at CNP (appendix 3.1), while at GVNP, daytime activity was mainly due to the activity of Egyptian mongooses, which contributed with 80% of all daytime detections. In the Atlantic ecoregion, daytime activity was only detected in three species: the red fox, the European wildcat and the pine marten. Considering detection rates, the chances of a prey species encountering a mesocarnivore during the night would be, on average, 1.9 ± 0.2 greater than during twilight and 5.2 ± 0.8 times greater than during daytime. Likewise, the chances of encounters with these predators during the twilight are, on average, 2.9 ± 0.4 times greater than during daytime. The rank of predation risk during these periods of the daily cycle was consistent across all study areas and seasons.

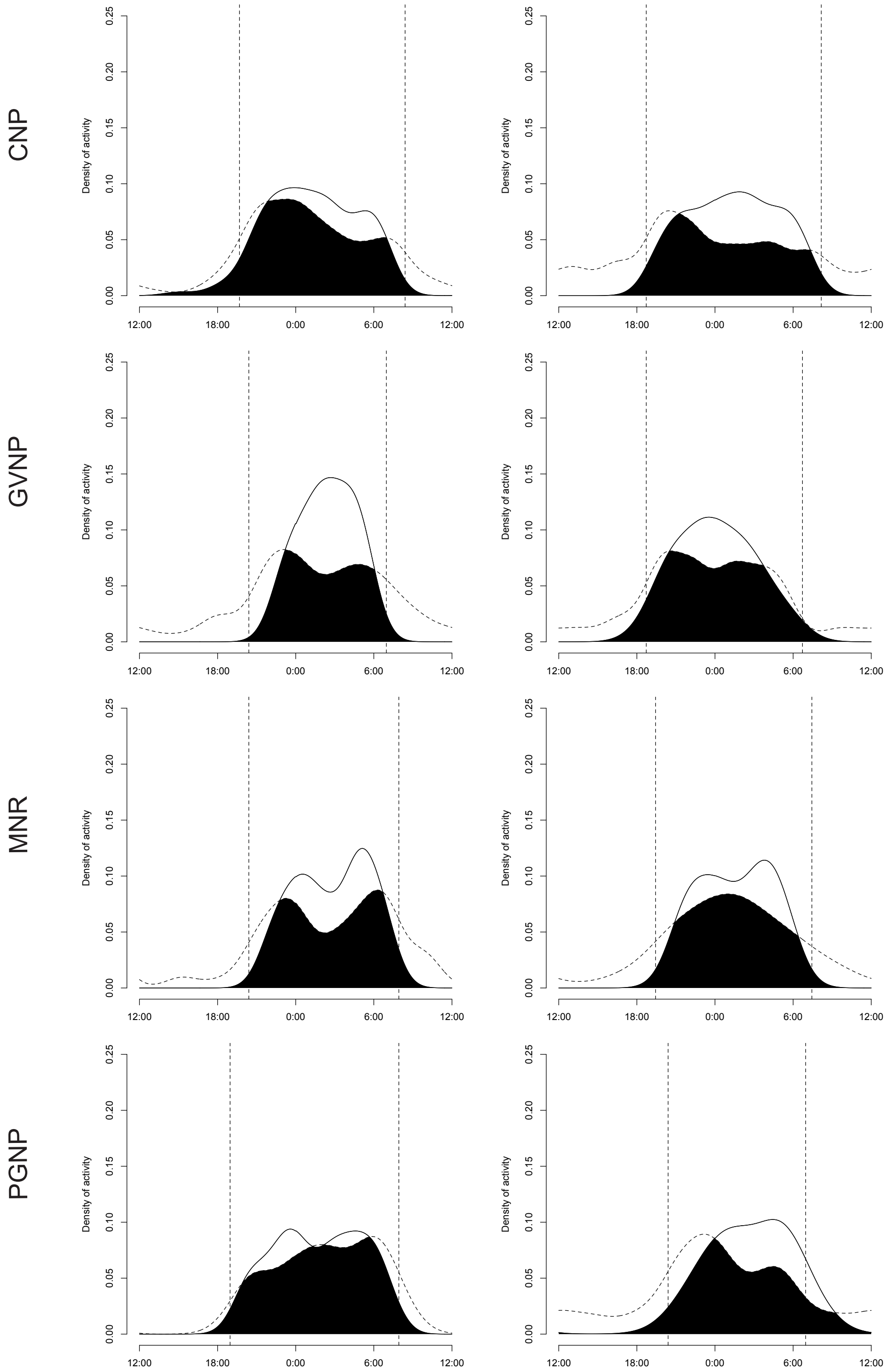

Figure 3.1.2. - Activity overlap between the mesocarnivore community (dashed line) and murid species (full line) in all study areas - Cabañeros National Park (CNP), Guadiana Valley Natural Park (GVNP), Muniellos Natural Reserve (MNR) and Peneda-Gerês National Park (PGNP) - during non-breeding and breeding sampling campaigns, as determined by camera-trapping. Vertical dashed lines represent sunset and sunrise times, respectively.

Predator and prey activity overlap and synchrony

The coefficient of overlap estimates obtained from Δ_1 and Δ_4 produced very similar results for study areas and seasons (mean difference = 0.017 ± 0.002). Therefore, the results will be reported only for $\Delta 4$. The mesocarnivore community revealed a diel activity pattern, which widely overlaps with the one observed for small mammals in all study areas and seasons. Mean coefficient of overlap ranged from 0.60 to 0.89 (appendix 3.1). High synchrony was also observed between mesocarnivore species and small mammals' activities, as mean Pearson's correlation ranged from 0.74 to 0.94 (appendix 3.1). The coefficient of overlap between mesocarnivore activity and small mammals was similar in Mediterranean and Atlantic areas (0.73 ± 0.05 vs. 0.78 ± 0.04; Kruskal–Wallis test, $H = 0.53$, $p = 0.47$). Activity synchrony values revealed the same pattern (0.85 ± 0.05 vs. 0.87 ± 0.04; Kruskal–Wallis test, $H = 0.00$, $p = 1.00$). Concordantly, in Mediterranean areas, where enough data on European rabbits allowed for an adequate evaluation of activity patterns, the overlap between the mesocarnivore community activity was higher with that of small mammals than with that of lagomorphs, with differences being almost significant (0.73 ± 0.05 vs. 0.52 ± 0.08; Kruskal–Wallis test, $H = 3.00$, $p = 0.08$). Moreover, significant differences exist between the same pairs with respect to synchrony of activity (0.85 ± 0.05 vs. -0.20 ± 0.23; Kruskal–Wallis test, $H = 5.30$, $p = 0.02$), suggesting that despite the existence of some overlap in the diel rhythms of rabbits and their mammalian predators, the former tend to intensify their activity at dawn and dusk (figure 3.1.3), when predation risk is lower (appendix 3.1).

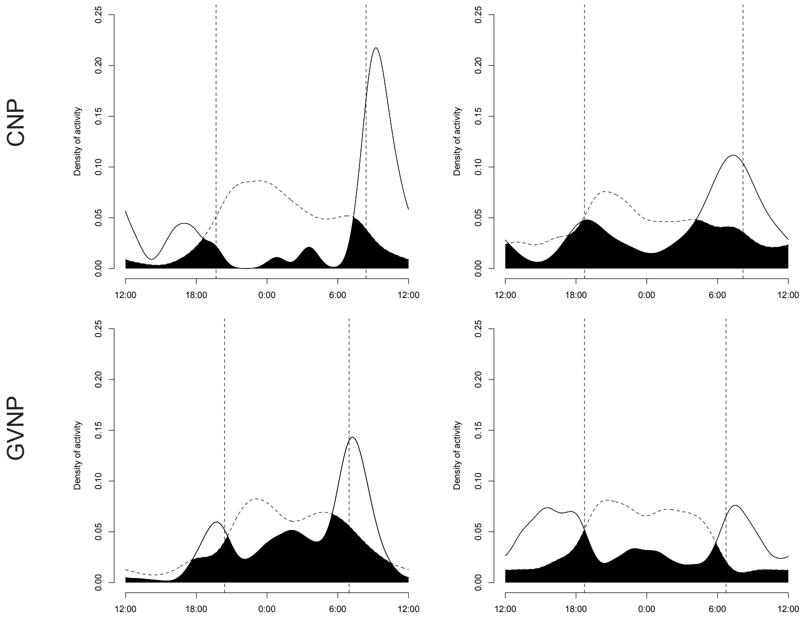

Figure 3.1.3. Activity overlap between the mesocarnivore community (dashed line) and European rabbits (full line) in Mediterranean study areas - Cabañeros National Park (CNP) and Guadiana Valley Natural Park (GVNP) - during non-breeding and breeding sampling campaigns, as determined by camera-trapping. Vertical dashed lines represent sunset and sunrise times, respectively.

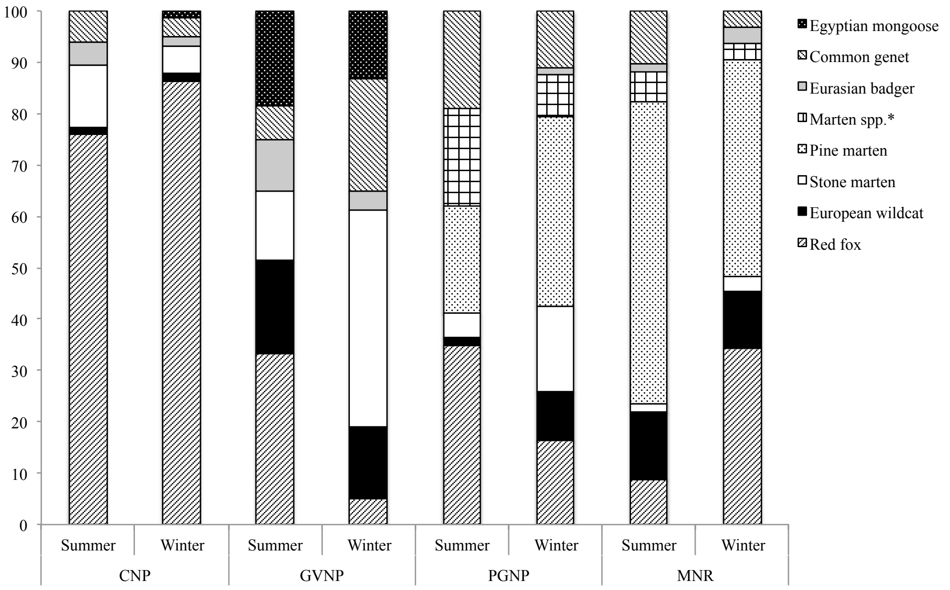

Figure 3.1.4. Relative contributions (percentage of total number of detections during a sampling campaign) of each species for mesocarnivore community data structures. (* - Photographs in which it was impossible to distinguish between pine marten and stone marten).

Discussion

Activity rhythms of small mammals

The rodent communities present in our study areas appear to be mostly composed by wood, yellow- necked and Algerian mice, which revealed to be nearly exclusively nocturnal. Generally, the onset of activity followed sunset, whereas offset preceded sunrise. Very few records of small mammal activity were collected after sunrise and before sunset, and only three (≈0.4%) were obtained in plain daytime. These results are consistent with findings of Roll et al. (2006) who, after a revision of the activity patterns of 1150 species of rodents, concluded that phylogeny constrains species' activity patterns, and muridae are nocturnal species. However, the rigidness of the underlying endogenous circadian clock may be masked on an ecological timescale through the effect of adaptations to local environmental challenges, such as predation risk (Jedrzejewska & Jedrzejewski 1990; Halle 2000; Kronfeld-Schor & Dayan 2008). The Algerian mouse in the Iberian Peninsula has been described as mainly nocturnal except in winter, when it is multiphasic (Palomo et al. 2009). Similarly, the wood mouse has been described as predominantly nocturnal (Wolton 1983), even though some diurnal activity has also occasionally been registered (Flowerdew 2000). The diel pattern of predation risk imposed by mammalian mesocarnivores varies between the different ecoregions and study areas (appendix 3.1). However, predation risk does not come from only one group of predators (mammalian carnivores, considered in this work), but rather from a joint effect of several predator assemblages (e.g. including diurnal and nocturnal raptors; Halle 2000), which also vary between areas. In spite of these differences, the nocturnality of murid rodents in the Iberian Peninsula was consistent through study areas, suggesting that the environmental stressors found there are not severe enough to override the endogenous regulation of the circadian cycle.

Activity rhythm of European rabbits

The diel activity pattern of European rabbits revealed consistent crepuscular activity peaks in both Mediterranean study areas, with higher activity density at sunrise than at dusk (Villafuerte et al. 1993; Díez et al. 2005), especially in the non-breeding season. Despite possessing the general characteristics of nocturnal animals (Jilge & Hudson 2001), the European rabbit possesses high plasticity, which allows it to display a variety of activity patterns (Moreno et al. 1996; Lombardi et al. 2003; Moseby et al.

2005). Under field conditions, rabbits have been found to respond to perceived nocturnal predation risk by increasing daytime foraging (Bakker et al. 2005) or to vary from crepuscular to nocturnal activity as a response to relative abundance of nocturnal vs. diurnal predators (Fernández-de-Simón et al. 2009). The plasticity in the diel pattern of European rabbits grants them adaptative advantages by being able to choose the activity period that reduces the probability of being predated. Predominant crepuscular activity has been suggested as a strategy of prey species to avoid both diurnal and nocturnal predators (Halle 2000), and the twilight period probably provides the best survival probabilities for European rabbits where predation pressure is high both by diurnal predators, such as avian raptors, and nocturnal mammalian carnivores. Our results revealed that predation risk by mesocarnivores is nearly twice during night-time than during twilight. In spite of the lower predation risk by mammalian predators during daytime, diurnal raptors will most likely make this period of the day highly risky as both Mediterranean study areas harbour healthy populations of raptor predators (García-Canseco 1997; ICN 2006).

A downside of our analysis is that it evaluates the activity patterns of rabbits as if it was similar across the entire landscape (irrespective to habitat structure). Previous work has suggested both rabbits and rodents can locally adapt their spatial and temporal strategies as a response to perceived predation risk (Moreno et al. 1996; Villafuerte & Moreno 1997; Fernández-de-Simón et al. 2009) in what has been described as ‘the ecology of fear’ (Brown et al. 1999; Ripple & Beschta 2004). Therefore, within each study area, both rabbits’ and murids’ behavioural responses could change at a micro scale as an adjusted response to locally implemented predation risk. However, even though we did not perform microhabitat analyses to detect these fine scale nuances of prey behaviour, we were able to characterize the circadian activity cycles that reflect the behavioural strategies of the studied populations.

Predator and prey activity overlap and synchrony

Optimal foraging theory predicts that an animal will display a foraging pattern that maximizes its caloric intake per time unit (MacArthur & Pianka 1966; Pyke et al. 1977). Therefore, taking into account that most species found in European mesocarnivore communities require prey to be active in order to detect and capture them, we would expect mesocarnivore activity patterns to be close to that of the most profitable available prey. Small mammals are the most preferred prey by European mesocarnivores in the Atlantic region (Virgós et al. 1999; Lozano et al. 2006; Zhou et al. 2011; Díaz-Ruiz et al. 2013), while in the Mediterranean region, the European rabbit takes place as the most profitable prey because of its high energetic value (Malo et al. 2004). However, our results reveal a high consistency in the synchrony and overlap between small mammals' and mesocarnivores' activity patterns, even in the Mediterranean study areas. In this region, where the European rabbit should emerge as preferred prey, only moderate values of activity overlap and low values of synchrony were found with mesocarnivores. The predation risk allocation hypothesis proposed by Lima & Bednekoff (1999) advocates that through a reasonably accurate perception of predation risk, prey species adapt their activity strategies to avoid being active in high-risk periods. By allocating strong antipredator behaviours to such periods, they then compensate by focusing its feeding effort in low-risk situations. This theory is supported by Fenn & MacDonald (1995) who found that brown rats (*Rattus norvegicus*) shift their diel activity patterns when perceived predation risk by red foxes was removed. Low-risk feeding efforts may be particularly intense when high-risk periods are long or frequent (Lima & Bednekoff 1999; Sih & McCarthy 2002). This situation seems to apply to the case of the European rabbit in the Mediterranean region. The strong bimodal pattern of the rabbits diel activity is coherent with a strategy of antipredator behaviour during long periods of high predation risk, while an intensification of the feeding efforts is concentrated in periods when predation pressure relaxes. However, if we look at this system from the predators' point of view, if the European rabbit is such an energetically profitable prey, why don't predators completely overlap European rabbits' daily rhythms? The predator–prey temporal relations vary between two extremes: first, the prey species completely manages to avoid predators by being active when they are not. This situation would obviously be disadvantageous for the predators, which would lose important energetic intake and probably reduce their populations up to the level of local extinction (specialist predator species; Ferrer & Negro 2004) or to a point where predation risk would stop being significant for the prey population (Halle 2000). In the other extreme, predators perfectly track prey in the temporal scale. In this case, predation success would probably be excessively high, leading to the depletion of the feeding resource (Sinclair et al. 1998) or driving prey into a predator pit (Trout & Tittensor 1989; Pech et al. 1992; Sinclair et al. 1998). Neither of these antagonist cases is beneficial for any of the species in the long run. Therefore, and assuming that unaccounted factors are not significantly influencing our results, we suggest that predators only track prey activity so far, reaching a point when the trade-off between predation success and the energetic intake is sufficient to fulfil its biological needs, especially in the case when prey availability is not a limiting factor. This situation should hold for species that, like the European rabbit, have a wide option of temporal selection (i.e. are able to forage at different periods of the day) and that suffer from intensive stalking from predator species. Such a pattern was reported by Arias-Del Razo et al. (2011) with coyotes (*Canis latrans*) and lagomorphs in Mexico. They found that both predator and prey species exhibited bimodal diel activity, but only one of the activity peaks was synchronized between them, meaning that there was a part of the day when prey chose to be active when the predator was not. Similarly, Roth & Lima (2007) found that sharp-shinned hawks (*Accipiter striatus*) and their preferred prey activities only partially overlapped, contradicting predator–prey game theory (Kotler et al. 2002). The strong evolutionary imprint that binds the murid species to nocturnal activity (Roll et al. 2006) constrains their activity to the periods of the day with dim light conditions. According to the predation risk allocation hypothesis (Lima & Bednekoff 1999), if high-risk periods are frequent or lengthy, then an animal has little choice but to feed under high risk. This means that murid rodents have no choice but to venture during the periods of high predation risk imposed by mesocarnivore activity. In this case, the probability of an individual of the prey species being killed by predation is lower when activity is synchronized among its community and span for a longer period of the day, instead of being concentrated in time (Halle 2000). This favours the observed unimodal and continuous pattern activity observed throughout the night-time of murid rodents in all studied areas.

Conclusions

The constant arms race that takes place between predators and prey, and how it shapes community structure and behaviour has been matter of intense study and controversy (e.g. Blumstein 2008; Dickman 2008; Gompper & Vanak 2008; Shanas et al. 2008; Shapira et al. 2008). It is, however, widely accepted that adaptations are bidirectional and take place over at least two dimensions: spatial and temporal (Lima & Bednekoff 1999; Lima 2002). Our work focuses on the temporal component, and provides some interesting insights into the structure of predator and prey adaptations. Contrary to our predictions, we found that in spite of the higher energetic input provided by preying on European rabbits (when compared to rodents), mesocarnivores do not completely track its activity pattern. This observation is irrespective to European rabbit's abundance. We found however, that mesocarnivores, as a community, tend to track small mammals activity irrespective to the ecoregion, and even though a preferred or more profitable prey is available. The somewhat constant and long period of activity of rodent prey may allow predators to explore this resource sequentially, thus avoiding agonistic encounters among intraguild competitors. Conversely, concentrating in the short period of time when European rabbits peak their activity would probably potentiate these encounters and consequently enhance competition stress. Further research should focus on the evaluation of the spatial variation of these temporal strategies in relation to microhabitat, as predation risk and prey vulnerability may differ over a small spatial scale, thus leading to an adjustment of the behaviours of both predator and prey species (Fenn & MacDonald 1995; Lima & Bednekoff 1999; Quinn & Cresswell 2004).

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References

Arias-Del Razo I, Hernández L, Laundré JW, Myers O (2011) Do predator and prey foraging activity patterns match? A study of coyotes (*Canis latrans*), and lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*). J Arid Environ **75**: 112-118. DOI: 10.1016/j.jaridenv.2010.09.008

Ashby K (1972) Patterns of daily activity in mammals. Mamm Rev **1**: 171–185. DOI: 10.1111/j.1365-2907.1972.tb00088.x

Bakker ES, Reiffers RC, Olff H, Gleichman JM (2005) Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. Oecologia **146**: 157–67. DOI: 10.1007/s00442-005-0180-7.

Bartness TJ, Albers HE (2000) Activity Patterns and the Biological Clock in Mammals. In Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York, pp. 23–47.

Blanco JC (1998) Mamíferos de España. Planeta, Barcelona.

Blumstein DT (2008) Does agriculture drive predator-mediated behavioral effects on prey? Anim Conserv **11**: 9-10. DOI: 10.1111/j.1469-1795.2008.00158.x

Brown JS, Laundre JW, Mahesh G (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal **80**: 385–399. DOI: 10.2307/1383287

Carothers JH, Jaksić FM (1984) Time as a Niche Difference: The Role of Interference Competition. Oikos **42**: 403–406.

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool **263**: 275–283. DOI: 10.1017/S0952836904005266

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental. Quercetea **0**: 5–56.

Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Anim Conserv **14**: 56–65. DOI: 10.1111/j.1469-1795.2010.00389.x

DeCoursey PJ (2004) Diversity of Function of SCN Pacemakers in Behavior and Ecology of Three Species of Sciurid Rodents. Biol Rhythm Res **35**: 13–33. DOI: 10.1080/09291010412331313214

Delibes M, Aymerich M, Cuesta L (1984) Feeding habits of the Herpestes ichneumon or Egyptian mongoose in Spain. Acta Theriol **29**: 205-218.

Delibes M, Hiraldo F (1981) The rabbit as prey in the Iberian Mediterranean ecosystem. In Myers K, MacInnes CD (eds) Proceedings of the World Lagomorph Conference, University of Guelph, Ontario, pp. 614–622.

Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte, R. (2008a) Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot. Conserv Biol **22**: 1106–17. DOI: 10.1111/j.1523-1739.2008.00993.x

Delibes-Mateos M, Fernández-de-Simón J, Villafuerte R, Ferreras P (2008b) Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. Eur J Wildl Res **54**: 71–78. DOI: 10.1007/s10344-007-0111-5

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martin JM, Ferreira C, Ferreras P (2013) Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. Mamm Rev **43**: 59-70. DOI: 10.1111/j.1365-2907.2011.00206.x

Dickman CR (2008) Indirect interactions and conservation in human-modified environments. Anim Conserv **11**: 11-12. DOI: 10.1111/j.1469-1795.2008.00159.x

Díez C, Pérez JA, Prieto R, Alonso ME, Olmedo JA (2005) Activity patterns of wild rabbit (*Oryctolagus cuniculus*, L. 1758), under semi-freedom conditions, during Autumn and Winter. Wildl Biol Pract **1**: 41-46. DOI: 10.2461/wbp.2005.1.6

Ebensperger L, Wallem P (2002) Grouping increases the ability of the social rodent, *Octodon degus*, to detect predators when using exposed microhabitats. Oikos **98**: 490-496. DOI: 10.1034/j.1600-0706.2002.980313.x

Elton CS (2001) Animal Ecology. University of Chicago Press, Chicago.

Eriksen A, Wabakken P, Zimmermann B, Andreassen HP, Arnemo JM, Gundersen H, Liberg O, Linnell J, Milner JM, Pedersen HC, Sand H, Solberg EJ, Storaas T (2011) Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. Anim Behav **81**: 423–431. DOI: 10.1016/j.anbehav.2010.11.011

Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric Mediterranean carnivores. Oecologia **121**: 138-148. DOI: 10.1007/s004420050915.

Fenn MGP, MacDonald DW (1995) Use of middensby red foxes: risk reverses rhythms of rats. J Mammal **76**:130-136.

Fernández-de-Simón J, Díaz-Ruiz F, Cirilli F, Tortosa FS, Villafuerte R, Delibes-Mateos M, Ferreras P (2011) Towards a standardized index of European rabbit abundance in Iberian Mediterranean habitats. Eur J Wildl Res **57**: 1091–1100. DOI: 10.1007/s10344-011-0524-z

Fernández-de-Simón J, Díaz-Ruiz F, Cirilli F, Tortosa FS, Villafuerte R, Ferreras P (2009) Relación entre la presión de depredación y los ritmos de actividad del conejo de monte: aplicación a las estimas de densidad. IX SECEM Conference, Bilbao. [in spanish]

Fernández-Durán JJ (2004) Circular Distributions Based on Nonnegative Trigonometric Sums. Biometrics **60**: 499–503. DOI: 10.1111/j.0006-341X.2004.00195.x

Ferrer M, Negro JJ (2004) The Near Extinction of Two Large European Predators: Super Specialists Pay a Price. Conserv Biol **18**: 344-349. DOI: 10.1111/j.1523-1739.2004.00096.x

Flowerdew JR (2000) Wood Mice - Small Granivores/Insectivores with Seasonally Variable Patterns. In Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York, pp. 177–189.

García-Canseco V (1997) Parque Nacional de Cabañeros, 1st edn. Ecohábitat, Madrid.

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

Gompper ME, Vanak AT (2008) Subsidized predators, landscapes of fear and disarticulated carnivore communities. Anim Conserv **11**: 13-14. DOI: 10.1111/j.1469-1795.2008.00160.x

Halle S (2000) Ecological Relevance of Daily Activity Patterns. In Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York, pp. 67–90.

Halle S, Stenseth NC (2000) Introduction. In Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York, pp. 4–17.

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol **22**: 415–427.

ICN - Instituto para a Conservação da Natureza (2006) Zona de Protecção Especial Vale do Guadiana. , **12**. [in portuguese]

Jacob J, Brown JS (2000) Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. Oikos **91**: 131–138. DOI: 10.1034/j.1600-0706.2000.910112.x

Jedrzejewska B, Jedrzejewski W (1990) Antipredatory behaviour of bank voles and prey choice of weasels - enclosure experiments. Ann Zool Fenn **27**: 321–328.

Jilge B, Hudson R (2001) Diversity and development of circadian rhythms in the European rabbit. Chronobiol Int **18**: 1–26. DOI: 10.1081/CBI-100001275

Kavanau JL and Ramos J (1975) Influences of Light on Activity and Phasing of Carnivores. Am Nat **109**: 391-418. DOI: 10.1086/283009

Kelly MJ, Holub EL (2008) Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond

Mountain, Giles County, Virginia. Northeast Nat **15**: 249–262. DOI: 10.1656/1092-6194(2008)15[249:CTOCTS]2.0.CO;2

Kotler BP, Brown JS, Dall SRX, Gresser S, Ganey D, Bouskila A (2002) Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. Evol Ecol Res **4**: 495–518.

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu. Rev. Ecol. Syst **34**: 153–181. DOI: 10.1146/annurev.ecolsys.34.011802.132435

Kronfeld-Schor N, Dayan T (2008) Activity patterns of rodents: the physiological ecology of biological rhythms. Biol Rhythm Res **39**: 193–211. DOI: 10.1080/09291010701683268

Lima SL (2002) Putting predators back into behavioral predator–prey interactions. Trends Ecol Evol **17**: 70–75. DOI: 10.1016/S0169-5347(01)02393-X

Lima SL, Bednekoff PA (1999) Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. Am Nat **153**: 649-659.

Linkie M, Ridout MS (2011) Assessing tiger-prey interactions in Sumatran rainforests. J Zool **284**: 224–229. DOI: 10.1111/j.1469-7998.2011.00801.x

Lombardi L, Fernández N, Moreno S, Villafuerte R (2003) habitat-related differences in rabbit (*Oryctolagus cuniculus*) abundance, distribution, and activity. J Mammal **84**: 26–36. DOI: 10.1644/1545-1542(2003)084<0026:HRDIRO>2.0.CO;2

Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. J Biogeogr **33**: 1076–1085. DOI: 10.1111/j.1365-2699.2006.01474.x

Lucherini M, Reppucci J, Walker R., Villalba M, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal **90**: 1404–1409. DOI: 10.1644/09-MAMM-A-002R.1

MacArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. Am Nat **100**: 603-609.

Malo AF, Lozano J, Huertas DL, Virgós E (2004) A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? J Zool **263**: 401–407. DOI: 10.1017/S0952836904005448

Marinis A, Masseti M (1995) Feeding habits of the pine marten *Martes martes* L., 1758, in Europe: a review. Hystrix **7**: 143-150. DOI: 10.4404/hystrix-7.1-2-4063

Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildl Res **38**: 446–454. DOI: 10.1071/WR11060

Moreno S, Delibes M, Villafuerte R (1996) Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Can J Zool **74**: 1656–1660. DOI: 10.1139/z96-183

Moseby KE, De Jong S, Munro N, Pieck A (2005) Home range, activity and habitat use of European rabbits (*Oryctolagus cuniculus*) in arid Australia: implications for control. Wildl Res **32**: 305–311. DOI: 10.1071/WR04013

Palomares F, Delibes M (2000) Mongooses, Civets and Genets - Carnivores in Southern Latitudes. In Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York, Pp: 119-130.

Palomares F, Gaona P, Ferreras P, Delibes M (1995) Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits. Conserv Biol **9**: 295-305. DOI: 10.1046/j.1523-1739.1995.9020295.x

Palomares, F. (2001) Comparison of 3 methods to estimate rabbit abundance in a Mediterranean environment. Wildl Soc Bull **29**: 578–585.

Palomo LJ, Justo ER, Vargas JM (2009) *Mus spretus* (Rodentia: Muridae). Mammal Species **840**: 1–10. DOI: 10.1644/840.1

Pech RP, Sinclair ARE, Newsome AE, Catling PC (1992) Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. Oecologia **89**: 102-112. DOI: 10.1007/BF00319021

Pierce B, Longland W, Jenkins S (1992) Rattlesnake Predation on Desert Rodents: Microhabitat and Species-Specific Effects on Risk. J Mammal **73**: 859-865.

Prieto JAF, Sánchez ÁB (1996) La Reserva Integral de Muniellos: Flora y Vegetación. Servicio central de publicaciones del Principado de Asturias, Oviedo. [in spanish]

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and Tests. Q Rev Biol **52**: 137-154.

Quinn JL, Cresswell W (2004) Predator hunting behaviour and prey vulnerability. J Anim Ecol **73**: 143–154. DOI: 10.1046/j.0021-8790.2004.00787.x

R Development Core Team. 2008. R: A language and environment for statistical computing.

Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat **14**: 322–337. DOI: 10.1198/jabes.2009.08038

Ripple WJ, Beschta RL (2004) Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? BioScience **54**: 755-766. DOI: 10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2

Rivas-Martínez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique. Anales Jard. Bot. Madrid **37**: 251–268.

Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas, http://www.ucm.es/info/cif/form/maps.htm

Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining activity patterns of rodents. Evol Ecol **20**. 479–490. DOI: 10.1007/s10682-006-0015-y

Roth II TC, Lima SL (2007) The predatory behavior of wintering Accipiter hawks: temporal patterns in activity of predators and prey. Oecologia, **152**: 169-178. DOI: 10.1007/s00442-006-0638-2

Schoener, T.W. (1974) Resource partitioning in ecological communities. Science **185**: 27–39. DOI: 10.1126/science.185.4145.27

Shanas U, Shapira I and Sultan H (2008) Behavioural alterations as part of an agricultural edge effect. Anim Conserv **11**: 15-16. DOI: 10.1111/j.1469-1795.2008.00161.x

Shapira I, Sultan H and Shanas U (2008) Agricultural farming alters predator–prey interactions in nearby natural habitats. Anim Conserv **11**: 1-8. DOI: 10.1111/j.1469-1795.2007.00145.x

Sih A, McCarthy T (2002) Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Anim Behav **63**: 437-443. DOI: 10.1006/anbe.2001.1921

Sinclair ARE, Pech RP, Dickman CR, Hik D, Mahon P, Newsome AE (1998) Predicting Effects of Predation on Conservation of Endangered Prey. Conserv Biol **12**: 564-575. DOI: 10.1111/j.1523-1739.1998.97030.x

Trout RC, Tittensor AM (1989) Can predators regulate wild Rabbit *Oryctolagus cuniculus* population density in England and Wales. Mammal Rev **19**: 153-173. DOI: 10.1111/j.1365-2907.1989.tb00409.x

UNESCO. UNESCO - MAB Biosphere Reserve Directory, http://www.unesco.org/mabdb/br/brdir/directory/database.asp

Villafuerte R, Kufner,MB, Delibes M, Moreno (1993) Environmental factors influencing the seasonal daily activity of the European rabbit (*Oryctolagus cuniculus*) in a Mediterranean area. Mammalia **57**: 341-347. DOI: 10.1515/mamm.1993.57.3.341

Villafuerte, R. and Moreno, S. (1997) Predation risk, cover type, and group size in European rabbits in Doñana (SW Spain). Acta Theriol **42**: 225-230. DOI: oai:rcin.org.pl:12688

Virgós E, Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. Mammal Rev **29**: 119-128. DOI: 10.1046/j.1365-2907.1999.00041.x

Virgós E, Revilla E, Mangas JG, Barea-Azcón JM, Rosalino, ML, Marinis A (2005) Revisión de la dieta del Téjon (*Meles meles*) en la Península Ibérica: comparación con otras localidades de su área de distribución natural. In Virgós E, Mangas JG, Revilla E, Roura X-D (eds) Ecología, distribución y estatus de conservación del tejón Ibérico. Sociedad Española para la Conservación y Estudio de los Mamíferos, Málaga. Pp 67-80.

Watkins AF, McWhirter JL, King CM (2009) Variable detectability in long-term population surveys of small mammals. Eur J Wildl Res **56**: 261–274. DOI: 10.1007/s10344-009-0308-x

Weckel M, Giuliano W, Silver S (2006) Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. J Zool **270**: 25-30. DOI:10.1111/j.1469-7998.2006.00106.x.

Wolton,BYRJ (1983) The Activity of Free-Ranging Wood Mice *Apodemus sylvaticus*. J Anim Ecol 52: 781–794.

Zalewski A (2000) Factors affecting the duration of activity by pine martens (Martes martes) in the Bialowieza National Park, Poland. J Zool **251**: 439-447. DOI: 10.1111/j.1469-7998.2000.tb00799.x

Zhou Y, Newman C, Xu W, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie Z-Q (2011) Biogeographical variation in the diet of Holarctic martens (genus Martes, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr **38**: 137–147. DOI: 10.1111/j.1365-2699.2010.02396.

Supporting information: Appendix 3.1

Table 1 - Density of activity of each species and mesocarnivore community, for each period considered of day.

Table 2 - Coefficient of overlap and Pearson correlation (activity synchrony) between terrestrial carnivores, small mammals and European rabbits.

Appendix 3.1

Table A.3.1.1. Density of activity (number of detections·hour^{-1}·100 trap-days^{-1}) of each species and mesocarnivore community, for each period considered of day: N - Nighttime, C - Crepuscular, D - Daytime.

Species	CNP						GVNP						PGNP						MNR					
	Non-breeding			Breeding			Non-breeding			Breeding			Non-breeding			Breeding			Non-breeding			Breeding		
	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D
European rabbit	0.02	0.42	0.23	0.05	0.17	0.02	7.07	17.20	4.09	3.18	8.00	6.90	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Small mammals	0.75	0.15	0.03	1.14	0.19	0.00	0.53	0.00	0.00	0.89	0.19	0.00	1.62	0.31	0.00	0.13	0.05	0.00	1.20	0.18	0.00	0.48	0.00	0.00
Red fox	1.38	1.16	0.26	1.89	1.64	1.02	0.26	0.36	0.04	0.21	0.00	0.00	0.18	0.08	0.00	0.09	0.05	0.02	0.05	0.02	0.00	0.18	0.04	0.00
European wildcat	0.02	0.00	0.01	0.06	0.00	0.00	0.22	0.08	0.01	0.12	0.15	0.05	0.01	0.00	0.00	0.00	0.02	0.05	0.05	0.02	0.03	0.04	0.02	0.01
Stone marten	0.32	0.02	0.00	0.20	0.00	0.00	0.19	0.00	0.00	0.64	0.19	0.00	0.02	0.03	0.00	0.12	0.02	0.00	0.00	0.02	0.00	0.02	0.00	0.00
Pine marten	-	-	-	-	-	-	-	-	-	-	-	-	0.09	0.08	0.00	0.15	0.15	0.06	0.24	0.20	0.05	0.15	0.15	0.04
Eurasian badger	0.13	0.08	0.00	0.14	0.00	0.00	0.08	0.03	0.00	0.33	0.09	0.00	0.11	0.00	0.00	0.09	0.00	0.00	0.07	0.00	0.00	0.02	0.00	0.00
Common genet	0.12	0.00	0.00	0.06	0.00	0.01	0.14	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00
Egyptian mongoose	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.05	0.18	0.00	0.03	0.21	-	-	-	-	-	-	-	-	-	-	-	-
Mesocarnivore community	1.98	1.27	0.27	2.35	1.64	1.09	0.90	0.51	0.23	1.37	0.46	0.26	0.50	0.23	0.00	0.53	0.30	0.13	0.43	0.29	0.08	0.43	0.20	0.05

Table A.3.1.2. Coefficient of overlap (Δ_4) and Pearson correlation (activity synchrony) between terrestrial carnivores, small mammals (SM)and European rabbits (ER) (estimate and [95% confidence interval]).

Study area	**Season**	**Prey species**	**Metric**	**Red fox**	**European wildcat**	**Stone marten**	**Pine marten**	**Eurasian badger**	**Common genet**	**Egyptian mongoose**	**Mesocarnivore community**
CNP	Non-breeding	SM	Δ_4	0.77 [0.67-0.81]	-	0.79 [0.61-0.86]	-	-	0.92 [0.60-0.90]	-	**0.83 [0.76-0.87]**
			Pearson	0.80** [0.60-0.89]	-	0.85** [0.57-0.94]	-	0.72** [0.32-0.89]	0.97** [0.59-0.97]	-	**0.93** [0.79-0.96]**
		ER	Δ_4	0.33 [0.21-0.41]	-	0.12 [0.04-0.19]	-	-	0.17 [0.05-0.26]	-	**0.29 [0.19-0.37]**
			Pearson	-0.31** [-0.47--0.12]	-	-0.40** [-0.55--0.23]	-	-	-0.42** [-0.57--0.14]	-	**-0.39** [-0.53--0.23]**
	Breeding	SM	Δ_4	0.65 [0.58-0.70]	-	0.77 [0.52-0.84]	-	-	0.78 [0.51-0.83]	-	**0.69 [0.62-0.73]**
			Pearson	0.58** [0.28-0.78]	-	0.82** [0.53-0.92]	-	-	0.84** [0.49-0.91]	-	**0.74** [0.49-0.88]**
		ER	Δ_4	0.65 [0.34-0.75]	-	0.38 [0.13-0.52]	-	-	0.38 [0.12-0.54]	-	**0.64 [0.35-0.75]**
			Pearson	-0.01 [-0.42-0.58]	-	-0.07 [-0.42-0.39]	-	-	-0.13** [-0.48-0.40]	-	**-0.06 [-0.46-0.48]**
GVNP	Non-breeding	SM	Δ_4	0.54 [0.37-0.67]	0.71 [0.47-0.82]	0.74 [0.46-0.90]	-	0.61 [0.28-0.82]	0.88 [0.46-0.89]	0.02 [0.00-0.04]	**0.60 [0.48-0.67]**
			Pearson	0.40** [0.09-0.66]	0.83** [0.36-0.94]	0.77** [0.35-0.96]	-	0.66** [0.24-0.91]	0.97** [0.47-0.97]	-0.68** [-0.80--0.40]	**0.78** [0.49-0.89]**
		ER	Δ_4	0.64 [0.47-0.68]	0.46 [0.28-0.56]	0.33 [0.17-0.35]	-	0.24 [0.11-0.26]	-	0.30 [0.16-0.40]	**0.65 [0.54-0.70]**
			Pearson	0.66** [0.32-0.79]	0.17** [-0.06-0.43]	-0.03 [-0.12-0.09]	-	0.08 [-0.14-0.11]	-	-0.15** [-0.37-0.11]	**0.36** [0.11-0.55]**
	Breeding	SM	Δ_4	0.80 [0.48-0.85]	0.62 [0.34-0.73]	0.85 [0.68-0.91]	-	-	0.59 [0.40-0.75]	0.04 [0.00-0.08]	**0.80 [0.67-0.85]**
			Pearson	0.88** [0.48-0.94]	0.49** [-0.13-0.79]	0.92** [0.68-0.97]	-	-	0.53** [0.26-0.78]	-0.81** [-0.84--0.57]	**0.94** [0.72-0.98]**
		ER	Δ_4	0.23 [0.14-0.25]	0.60 [0.35-0.61]	0.28 [0.23-0.32]	-	-	0.25 [0.16-0.28]	0.53 [0.35-0.55]	**0.47 [0.41-0.54]**
			Pearson	-0.52** [-0.61--0.26]	-0.04 [-0.43-0.38]	-0.66** [-0.72--0.50]	-	-	-0.44** [-0.51--0.29]	0.46** [0.11-0.59]	**-0.69** [-0.75--0.51]**
PGNP	Non-breeding	SM	Δ_4	0.82 [0.52-0.86]	-	-	0.77 [0.39-0.84]	-	0.80 [0.44-0.81]	-	**0.89 [0.73-0.91]**
			Pearson	0.86** [0.46-0.93]	-	-	0.81** [0.26-0.90]	-	0.84** [0.43-0.86]	-	**0.93** [0.68-0.96]**
	Breeding		Δ_4	0.67 [0.25-0.82]	0.09 [0.00-0.16]	-	0.58 [0.30-0.72]	-	0.73 [0.28-0.85]	-	**0.70 [0.43-0.79]**
			Pearson	0.66** [0.02-0.92]	-0.94** [-0.88--0.30]	-	0.41** [-0.22-0.86]	-	0.86** [0.25-0.95]	-	**0.77** [0.24-0.95]**
MNR	Non-breeding	SM	Δ_4	-	0.58 [0.20-0.69]	-	0.69 [0.52-0.76]	-	0.64 [0.52-0.76]	-	**0.74 [0.62-0.82]**
			Pearson	-	0.43** [-0.32-0.74]	-	0.69** [0.32-0.84]	-	0.69** [0.32-0.84]	-	**0.85** [0.57-0.93]**
	Breeding		Δ_4	0.62 [0.55-0.87]	0.67 [0.21-0.72]	-	0.70 [0.50-0.81]	-	-	-	**0.80 [0.64-0.85]**
			Pearson	0.91** [0.50-0.95]	0.64** [-0.13-0.80]	-	0.82** [0.22-0.93]	-	-	-	**0.93** [0.67-0.95]**

* - significant correlation (p<0.05); ** - highly significant correlation (p<0.01).

Plasticity in activity patterns of mesocarnivores in Southwestern Europe

Monterroso, P., Alves, P.C., Ferreras, P. (in press) Behavioral Ecology and Sociobiology

3.2 Plasticity in activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence

Abstract

Limiting similarity theory predicts that competing species must segregate along one or more dimensions of their ecological niche in order to coexist. In predator communities, interspecific interactions are influenced by a diversity of factors; therefore the behavioural patterns of composing species will differ due to locally adapted interactions.

We deployed 32 - 41 camera-traps in five study areas across the Iberian Peninsula to investigate the temporal relations between mesocarnivores in SW Europe. The selection for a period of the diel cycle and plasticity in activity patterns was evaluated using the Jacobs selection index (JSI) and the coefficient of activity overlap (Δ_1). Furthermore, we investigated whether temporal shifts can facilitate coexistence by reducing activity overlap.

Seven species of mesocarnivores were detected and were assigned into one of three behaviourally distinct groups: diurnal ($JSI_{day} \geq 0.8$), strictly nocturnal ($JSI_{night} \geq 0.8$) or facultative nocturnal species ($0.4 \geq JSI_{night} > 0.8$). Most species exhibited substantial flexibility, which allowed them to locally adapt their foraging strategies (intraspecific $\Delta_1 = 0.70 - 0.77$). Mean Δ_1 from all interspecific pairwise comparisons was negatively correlated with the number of carnivore species with ≥ 10 detections ($r = -0.76$, $p = 0.02$). Our results suggest that temporal segregation is likely to play an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity, where most species' activity peaks were asynchronous. These results contribute for understanding the dynamics and behavioural strategies of coexisting mesocarnivores, crucial for forecasting the possible outcomes of conservation or management actions.

Introduction

A population of a given species can be ecologically described by its position along a set of dimensions ordering environmental variables (Schoener 1974), thus occupying a specific ecological niche (Hutchinson 1957). MacArthur and Levins' (1967) limiting similarity theory predicts that there is a threshold of niche similarity between sympatric species under which stable coexistence is allowed. This means that competing species must segregate, at least partially, along one or more dimensions of their ecological niche (Hardin 1960; MacArthur and Levins 1967; Szabó and Meszeéna 2006). Alternatively to this kind of displacement, limiting theory predicts that depending on the competitive abilities of the species involved, competition would be reflected in their population numbers (Abrams 1983). Schoener (1974) found that the separation among species niches is generally multidimensional, and two is the most common number of dimensions separating species. Despite being regarded as the least important of the three main niche axes - spatial, temporal and resource exploitation - , the temporal niche axis is particularly relevant in the case of predator species as they often segregate across the diel cycle, promoting coexistence (e.g. Di Bitetti et al. 2009; Harrington et al. 2009; Wang and Fisher 2012). Further, the presence of competitors frequently influences activity patterns through interference competition, which is expected to be stronger whenever similarity in other niche dimensions and body mass are high (Schoener 1974; Linnell and Strand 2000; Donadio and Buskirk 2006; Ritchie and Johnson 2009). However, a species activity pattern along the diel cycle is not only regulated by competition. It is internally regulated by each specie's endogenous clock (Kronfeld-Schor and Dayan 2003) and by external abiotic and biotic factors which, in the case of predator species, are strongly constrained by the accessibility to preys, that often have their own well defined activity patterns (Halle 2000; Arias-Del Razo et al. 2011). Biological and ecological similitudes bind mesocarnivore species, making this group particularly interesting for addressing community functioning studies (Roemer et al. 2009). The ecological interactions within a carnivore community should vary as a result of several factors such as community structure, species plasticity and bottom-up and top-down control effects (Linnell and Strand 2000; Elmhagen and Rushton 2007; Ritchie and Johnson 2009; Elmhagen et al. 2010). A consequence of such complexity is that mesocarnivore communities with similar species composition may differ in their internal organization, niche relations and behavioural patterns relative to species interactions. Different guild compositions and structures should result into different interspecific relations among its composing species, and potentially drive their positions along specific niche axes to change from one area to another. In the presence of competition for a position in a specific niche axis, a subordinate competitor is either plastic enough to displace its position along that axis or will change along some other axis to further reduce niche overlap. However, resource partitioning is a community wide phenomenon and the interactions involved are complex. Therefore, the analysis and interpretation of such interspecific relations require a holistic approach (Schoener 1974; Ritchie and Johnson 2009).

Southwestern (SW) European mesocarnivore communities include a total of seven species, which not all occur in sympatry or coexist spatially within their distribution areas by result of ecosystem disruption, habitat fragmentation, direct persecution or other historical factors (Cabral et al. 2005; Palomo et al. 2007). For example, the pine marten (*Martes martes*) distribution is restricted to the northern fringe of the Iberian Peninsula (López-Martin 2007), and the Egyptian mongoose (*Herpestes ichneumon*) to the Mediterranean bioclimatic region (Palomares 2007). In SW European mesocarnivore communities, the potential for exploitation and/or interference competition exists among several species pairs along various niche dimensions due to above-mentioned high diversity of mesocarnivore community structures' that can be found.

Here, we analyze data on the diel activity of mesocarnivores of several areas and bioclimatic regions in SW Europe. We aimed to evaluate the level of plasticity of the species that compose these mesocarnivore communities in their activity patterns and whether ecological shifts along the temporal axis could promote coexistence by reducing the overlap in activity periods with competitors.

Methods

Study areas

The Iberian Peninsula (IP) is included in two biogeographical regions: the Mediterranean region, which occupies roughly 2/3 of the southwestern IP; and the

Atlantic region, which is restricted to the northern fringe and extends towards the Pyrenees (European Environmental Agency 2012). In order to obtain data from the mesocarnivore communities of both bioclimatic regions, five study sites were selected, distributed across the IP (Fig. 3.2.1): the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP), located in Portugal; and the Cabañeros National Park (CNP), the Sierra de Andújar Natural Park (SANP) and the Muniellos Natural Reserve (MNR), located in Spain. GVNP, CNP and SANP are located in the Mediterranean region, and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez, Penas, and Díaz 2004). Scrublands are mainly associated with steeper slopes, elevation ridges and main water bodies, and are dominated by Pyro-Quercetum rotundifoliae and *Myrto communis*–*Querco rotundifoliae* series and other subserial stages (Rivas-Martinez 1981; Costa et al. 1998). At CNP and GVNP, areas with gentler slopes are mainly occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*) scattered within a grassland matrix (García-Canseco 1997). At the SANP, areas with gentler slopes are rather dominated by Stone pine (*Pinus pinea*) and Maritime pine (*Pinus pinaster*) forests with and without understorey (Gil-Sánchez et al. 2006). Human access is highly restricted at CNP and SANP, for conservation purposes. However, at GVNP hunting activity is extremely important in this region and about 86% of the land is included in hunting estates.

The PGNP and MNR are located in the Atlantic region, and have a temperate oceanic submediterranean bioclimate (Rivas-Martínez et al. 2004). The landscapes consist of mountainous agricultural–forest mosaic, where mountain tops are mostly dominated by scrublands with Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially dominated by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* sp. and *Fagus* sp.). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Prieto and Sánchez 1996; Carvalho and Gomes 2004). High levels of tourist visitation (namely hikers) also characterize the PGNP study area, which are mainly focused in the warmer months and in the main valley. Human access is limited inside the integral reserve of MNR, and is restricted to 20 persons per day along a specific trail. The neighboring areas also included in the study area have relatively low disturbance (mainly hikers), which is mainly concentrated in the summer months.

A study area of approximately 6000ha within each of the study sites was selected, based on criteria of ecosystem conservation status and logistic factors. The only exception was the SANP study area, where we were only allowed to work in an area of 2700ha.

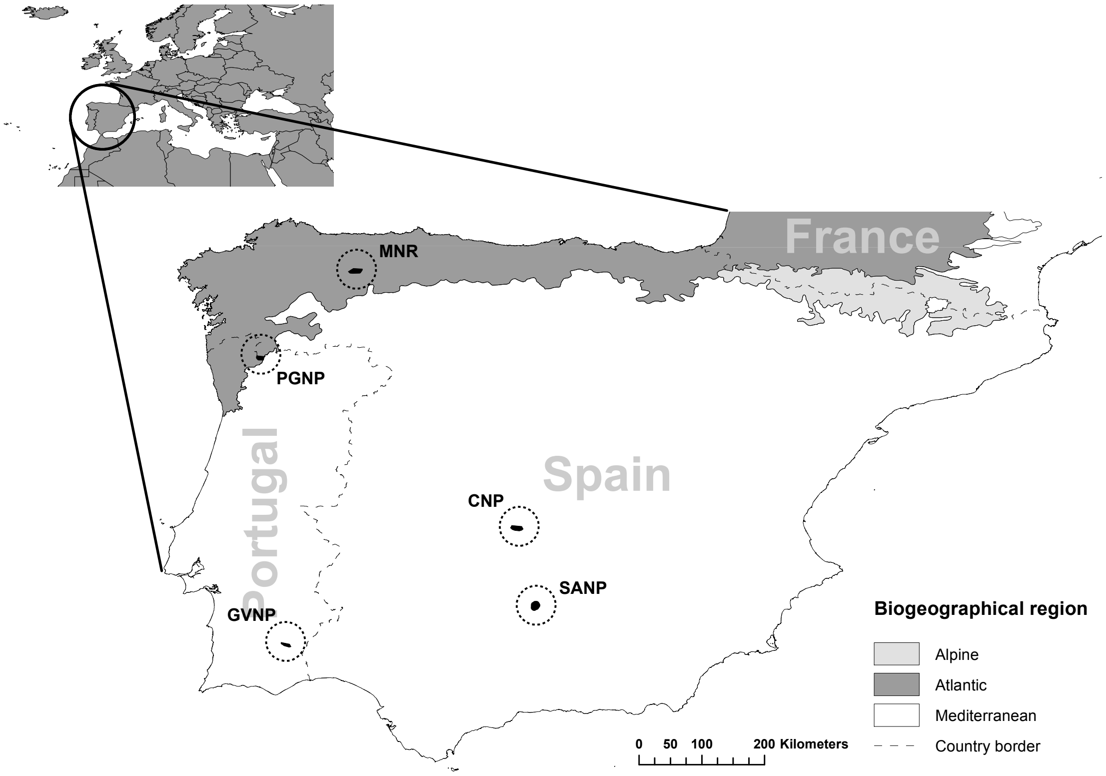

Figure 3.2.1 Location of the study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park; SANP - Sierra de Andújar Natural Park.

Field sampling

All study areas were sampled in two seasons: non-breeding (Jul-Oct), when the offspring of most medium-sized carnivores from that year become independent; and breeding season (Feb-Apr), during these species' breeding season (Blanco 1998). CNP and GVNP were sampled in 2009/2010, PGNP and MNR in 2010/2011, and SANP in 2012.

Data collection was obtained by camera-trapping methods, and followed the sampling scheme and trap sites selection described by Monterroso, Alves, and Ferreras (2011). Briefly, 32 to 41 cameras were uniformly spaced in each study area following a grid-sampling scheme, where distance between camera traps was approximately 1.4 km apart, promoting spatial independence. The exception was SANP, where only 20 cameras were placed due the smaller size of this area. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) and ScoutGuard SG550V (HCO OutDoor Products, Norcross, Georgia, USA), which have trigger times of 0.9 and 1.3 seconds, respectively. Cameras were mounted on trees approximately 0.5 – 1.0m off the ground and set to record time and date when triggered. We programmed cameras with the most sensitive sensor setting, to fire a burst of three photos when triggered and with the minimal delay time possible (<1 min), to maximize the number of photos taken per captured individual. Camera-traps were maintained in the field for a minimum period of 28 days and were inspected for battery and memory card replacement every 7 to 14 days. If there was evidence that a camera trap was not working during the entire sampling period, we considered the effective sampling period as the time frame between camera setting (or the previous inspection) and the date of the last photograph taken. A combination of carnivore attractants was used in order to incite animals' curiosity and thus increase detection probabilities. The attractants used were Lynx urine, obtained from captive specimens of Eurasian lynx (*Lynx lynx*) and Iberian lynx (*Lynx pardinus*), and Valerian extract solution, as suggested by Monterroso et al. (2011) for Iberian carnivore sampling. Attractants were placed in the field at a distance of 2-3 m from the camera-traps, and were deployed in perforated separated containers (plastic or PVC), at a distance of 10-15 cm from each other and approximately 30 cm above the ground. Five to 10 mL of each attractant were sprayed into a cotton gaze, held inside each container. Attractants were re-baited every 7 to 14 days. When multiple photographs of the same species were taken within a 30-minute interval we considered them as a single capture event to ensure capture independence (unless animals were clearly individually distinguishable; Davis et al. 2011).

Target species consisted of all mammalian carnivore species with mean body weight between 1.0 and 7.0kg (i.e. all mesocarnivore species): the red fox (*Vulpes vulpes*), the European wildcat (*Felis silvestris*), the stone marten (*Martes foina*), the pine marten (*Martes martes*), the Eurasian badger (*Meles meles*), the common genet (G*enetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*). We also included the Iberian lynx because of its reported physical and spatial interactions with several species of mesocarnivores (Palomares et al. 1996, 1998; Palomares and Caro 1999) (Table 1).

Cats detected by camera trapping were identified as wildcats (*F. s. silvestris*) or domestic cats (*F. s. catus*) by the most diagnostic phenotypic traits, particularly tail shape and colour pattern, and lateral coat pattern (Ragni and Possenti 1996; Spassov et al. 1997; Kitchener et al. 2005). Whenever it was visible, the extent of the dorsal stripe was also used. Individuals that did not display these characteristics, considered diagnostic of wildcats, were considered domestic cats. Domestic cats were only detected in GVNP study area at only few sites, and with few detections. Furthermore the levels of admixture found in putative wildcats were low in GVNP (Oliveira et al. 2007) providing further confidence in the genetic integrity of the detected wildcats. In areas of co-occurrence, the distinction between pine and stone martens was also assessed by evaluating several (not always all) morphological traits and coat patterns, namely leg size; over and undercoat color; bib shape, color and contour; ear size, color and shape (Blanco 1998, López-Martin 2007, Reig 2007, Wilson and

Mittermeier, 2009). All photos of martens were subjected to a blind identification procedure by three experienced researchers (PM, PF and PCA). Identification to the species level was only considered when consensus was achieved. All remaining photos were only identified to the genus level.

Assessment of diel activity patterns and species plasticity

The independent detection records for each target species were regarded as a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken within any particular interval of the day (Ridout and Linkie 2009). The probability density function of this distribution (i.e. activity pattern; Linkie and Ridout 2011) was estimated nonparametrically using kernel density (Ridout and Linkie, 2009) considering only cases with ≥10 detections.

In order to evaluate the plasticity of the diel distribution function for each species, pairwise comparisons of activity patterns for all study areas and seasons combinations were performed by estimating the coefficient of overlap Δ_1, as suggested by Ridout and

Linkie (2009) and Linkie and Ridout (2011) for small sample sizes. The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap), and is obtained taking the minimum of the density functions of the two cycles being compared at each time point. The precision of this estimator was obtained by computing a standard deviation from 500 bootstrap samples. These analyses were performed using R software (R Development Core Team 2008). The R code used to estimate overlap coefficients was that provided by Ridout and Linkie (2009). As we sampled all study areas around the equinoxes (autumn and spring), we assumed that daylight length would not change significantly and therefore no standardizations were performed with respect to sunrise and sunset times. The evaluation of Δ_1 values, and consequent definition of “high” or “low” overlap between two distinct activity patterns is largely subjective. For that reason, within the scope of our analysis, we defined “low”, ”moderate” or “high” activity overlap values with respect to the overall pairwise comparisons performed. Hence, compared activity patterns with Δ_1 values ≤ 50th percentile of our sample were considered as “low overlap values”. Activity patterns with 50th percentile < Δ_1 ≤ 75th percentile were considered “moderate overlap values”, and Δ_1 > 75th were defined as “high overlap values”.

Because the coefficient of overlap is purely descriptive, i.e. does not provide a threshold value below which two activity patterns might be significantly different, we used the Mardia-Watson-Wheeler test (MWW test; Batschelet 1981) to compare the distribution of detections across the diel cycle for all sampling campaign pairs (Brook et al. 2012; Gerber et al. 2012). This test pools the samples together and sorts them into increasing angles. They are then evenly distributed around the diel cycle by calculating a uniform score (or circular rank). If the distributions of the samples are identical then the new uniform scores for the samples should be evenly interspersed around the diel cycle, and their resultant vector lengths R should be short and similar. Any significant difference between the Rs will lead to a large W test statistic and rejection of the null hypothesis of identical distributions (Kovach 2011). Only distributions with ≥10 detections were considered (Gerber et al. 2012). These analyses were performed using the software Oriana v. 4.01 (Kovach 2011).

In order to evaluate each species strength of selection for diel period, four periods of the diel cycle where considered: Day - defined as the period enclosed between 1h after sunrise and 1h before sunset; Night - between 1h after sunset and 1h before sunrise; Dawn - between 1h prior and 1h after sunrise, and Dusk - between 1h prior and 1h after sunset (Lucherini et al. 2009; Gerber et al. 2012; Foster et al. 2013). Species selection for each period of the diel cycle was evaluated using the modified Ivlev's selectivity index (Ivlev 1961), adapted by Jacobs (1974), hereafter JSI. This index is broadly applied in ecological studies to evaluate selection for various types of resources (e.g. Palomares et al. 2000; Blanco-Garrido et al. 2007; Monterroso et al. 2011). Using bootstrap resampling (500 replicates) (Manly 1997) and recalculating the JSI for each bootstrap sample, we determined the average JSI index and 95% confidence intervals for each period and species. We then considered each diel period as positively (or negatively) selected whenever the 95% CI of the JSI was positive (or negative) and did not overlap zero (i.e. used as expected by chance).

Temporal segregation among species

For each sampling campaign (study area x season) the temporal segregation between coexisting mammalian carnivores was evaluated by comparing the distribution of their activity records along the diel cycle. This comparison was performed using the coefficient of overlap Δ_1 (Ridout and Linkie 2009) between pairs of species, as described above. The significance of the differences in the diel activity patterns between coexisting pairs of mesocarnivores was evaluated using multiple comparison MWW tests (Batschelet 1981). Multiple comparison MWW tests were controlled for type I errors using the Bonferroni correction by adjusting the significance level (alpha): dividing the type I error (0.05) by the number of tests (McDonald 2009). Data are presented as mean ± SE, unless explicitly stated otherwise.

Results

Camera-trapping results and species detected

A total of 1514 independent detections allowed species level identification of mammalian carnivores from 9955 effective trap-days (905 ± 75 trapping days/campaign). Overall, we obtained 99 detections (24.8 ± 14.9 detections/campaign) of unidentified taxonomic origin, corresponding to 1.2% of all animal records. The range of target species detected in each study area and season did not vary greatly, especially within bioclimactic region. European wildcats, Eurasian badgers, stone martens and common genets were detected in all study areas. The Egyptian mongoose was only detected at CNP and GVNP, the Iberian lynx was only detected at SANP and the pine marten was only detected as PGNP and MNR. Reliable discrimination between stone and pine martens was not possible in nine (19.6%) and three (9.4%) of the detections in MNR, during nonbreeding and breeding seasons, respectively. Neither was it possible in 14 (46.7%) and eight (17.8%) marten detections for the same seasons at PGNP. In spite of some consistency in composition, community structure varied across sampling campaigns (Table 3.2.3, Appendix 3.2). Several target species were detected in the distinct sampling campaigns, but with insuficcient data for estimating their activity patterns: the red fox in MNR during nonbreeding season; the European wildcat in CNP, MNR, PGNP in both seasons and SANP during nonbreeding season; the stone marten in MNR in both season, in PGNP during nonbreeding season and in SANP during breeding season; the common genet in MNR and SANP in both seasons, in GVNP during nonbreeding season, and in PGNP during breeding season; the Eurasian badger in MNR in both seasons, in GVNP and PGNP during breeding season, and in SANP during nonbreeding season; the Egyptian mongoose at CNP during breeding season. The European wildcat was detected in all sampling campaigns except at SANP during breeding season, however sufficient number of records was only obtained at GVNP for both seasons.

Domestic carnivores were rarely detected over the course of the sampling campaigns, and the low number of detections prevented the estimation of these species' activity patterns.

In total, dogs (*Canis familiaris*) were detected six times. They were detected in all study areas, except in CNP, and only at one camera-trapping station per study area. Domestic cats were only detected at GVNP at three camera-trapping stations out of 32 (9.4%) in only seven occasions out of 41: three during the non-breeding and four during the breeding season.

Species plasticity and selection for diel period

Mean coefficients of overlap were similar across species: $0.70 \leq \Delta_1 \leq 0.77$ (Table 3.2.1, Appendix 3.2). However, MWW tests revealed that the red fox was the only species that showed statistically different use of the diel cycle between several pairs of sampling campaigns (Table 3.2.1, Appendix 3.2). The Egyptian mongoose was only detected during daytime. Regardless, significant differences were detected in their patterns of activity between both seasons (Table 3.2.1). The remaining species revealed some consistency in their use of the diel periods between sampling campaigns, but displayed some plasticity in the way they used their preferred activity periods, as suggested by asynchronous peaks between sampling campaigns and some MWW tests, despite lack of statistical significance (Figs. 3.2.2 and 3.2.3; Appendix 3.2).

Table 3.2.1. Description of target species, average bodymass (kg), described distribution and feeding specialization, and mean coefficient of overlap (Δ_1; mean ± SD) and Mardia-Watson-Wheeler (MWW) test between the activity patterns of each species across all sampling areas and seasons (only for cases when the number of detections was ≥10). N - Number of pairwise comparisons.

Species	**Mean body mass (kg)**	**European distribution**	**Feeding specialization**	**N**	Δ_1	**MWW test**	
						W	***p***
Vulpes vulpes	6.0[1]	Pan-European	Generalist[9]	36	0.73 ± 0.08	86.72**	<0.01
Felis silvestris	4.7[3]	Pan-European	Facultative specialist[11]	1	0.70	5.06	0.08
Lynx pardinus	10.5[2]	South Iberian Peninsula	Specialist[10]	1	0.73	0.59	0.74
Martes foina	1.5[4]	Pan-European, except Scandinavia and UK	Generalist[12]	10	0.71 ± 0.10	13.15	0.11
Martes martes	1.1[5]	Pan-European, except South Iberian Peninsula	Generalist[12,13]	6	0.77 ± 0.08	6.66	0.35
Meles meles	7.3[6]	Pan-European	Generalist[14]	6	0.73 ± 0.08	13.07	0.04
Genetta genetta	1.9[7]	Iberian Peninsula and SW France	Facultative specialist[15]	6	0.75 ± 0.11	11.08	0.09
Herpestes ichneumon	2.8[8]	South Iberian Peninsula	Generalist[16]	1	0.75	6.04*	<0.05

[1] - Gortázar (2007); [2] - Rodríguez (2007); [3] - García-Perea (2007); [4] - Reig (2007); [5] - López-Martin (2007); [6] - Revilla et al. (2007); [7] - Calzada (2007); [8] - Palomares (2007); [9] - Díaz-Ruiz et al. (2013); [10] - Gil-Sánchez et al. (2006); [11] - Lozano et al. (2006); [12] - Zhou et al. (2011); [13] - Marinis and Masseti (1995); [14] - Virgós et al. (2005); [15] - Virgós et al. (1999); [16] - Delibes et al. (1984). ** - Highly significant ($p < 0.01$); * - Significant ($p < 0.05$)

Most carnivore species detected in Iberian communities revealed strong signals of preference for the nighttime period (Table 3.2.2, Appendix 3.2). Stone martens, genets and Eurasian badgers, revealed a particularly strong selection for the nighttime, with mean JSInight values ≥ 0.80 (Appendix 3.2). However, their preferred period at night varied between study areas and seasons, as suggested by the mean Δ_1 values ≤ 0.75 (Table 3.2.1). The activity of stone martens varied from bimodal (during breeding season) to unimodal pattern, with peaks at different periods of the nighttime (mainly during non-breeding season; Figs. 3.2.2 and 3.2.3). Similarly, the activity patterns of common genets varied from nearly constant during nighttime, to unimodal or bimodal pattern. The Eurasian badger varied from marked bimodal to a unimodal pattern with an activity peak occuring between 22h00 and 24h00 (at CNP, during breeding season). These species consistently avoided daytime (mean JSI_{day} values ≤ -0.95), but their activity could be extended towards the periods of dim light, although with less intensity. Although preferring the nighttime, red foxes, European wildcats, pine martens and Iberian lynx, may also be active in the remaining periods of the diel cycle (Table 3.2.2, Appendix 3.2). A common pattern detected in red foxes, European wildcats and pine martens was an overall tendency for diurnal activity to be less pronounced in the non-breeding season, as supported by and average strength of selection for daytime of -0.85 ± 0.06 and -0.53 ± 0.08 for the non-breeding and the breeding season, respectively. However, Iberian lynx did not exhibit such a tendency (Table 3.2.1, Appendix 3.2).

The Egyptian mongoose is the only species with marked diurnal behaviour (JSI_{day} values ≥ 0.80), however its activity pattern differed between the non-breeding and breeding periods, as supported by the $\Delta_1 \approx 0.75$ and significant MWW test (Appendix 3.2). A detailed description of the temporal plasticity of each species can be found in the Appendix 3.2.

Table 3.2.2. Mean Jacobs Selectivity Index (JSI), for each of the defined periods of the diel cycle: Night, Dawn, Day and Dusk. Estimate [95% confidence interval].

Species	JSI_{night}	JSI_{Dawn}	JSI_{Day}	JSI_{Dusk}
Vulpes vulpes	0.59 [0.41; 0.77]*	-0.34 [-0.71; 0.04]	-0.74 [-0.92; -0.56]*	-0.14 [-0.43; 0.15]
Felis silvestris	0.50 [-0.05; 1.00]	-0.25 [-0.51; 0.02]	-0.70[-1.00; -0.29]*	0.04 [-0.84; 0.92]
Lynx pardinus	0.53 [0.44; 0.61]*	-0.12 [-0.54; 0.31]	-0.67 [-0.67; -0.66]*	-0.44 [-1.00; 0.66]
Martes foina	0.88 [0.79; 0.96]*	-0.75 [-1.00; -0.27]*	-1.00 [-1.00; -1.00]*	-0.48 [-0.98; 0.02]
Martes martes	0.46 [0.28; 0.63]*	0.09 [-0.11; 0.28]	-0.65 [-0.89; -0.41]*	-0.24 [-0.75; 0.28]
Meles meles	0.94 [0.82; 1.00]*	-1.00 []-1.00; -1.00]*	-0.95 [-1.00; -0.84]*	-0.82 [-1.00; -0.47]*
Genetta genetta	0.83 [0.74; 0.91]*	-0.38 [-0.79; 0.03]	-1.00 [-1.00; -1.00]*	-0.47 [-0.87; 0.06]
Herpestes ichneumon	-1.00 [-1.00; -1.00]*	-0.73 [-1.00; -0.19]*	0.88 [0.79; 0.96]*	-0.42 [-0.50; -0.33]*

* - Significant ($p < 0.05$)

Temporal segregation among species

Mean Δ_1 values obtained in interspecific pairwise comparisons were of 0.61 ± 0.03 (mean ± SE), and the 50 and 75 percentiles of that distribution were 0.66 and 0.76, respectively, being therefore considered as the thresholds between “low”, “moderate” and “high activity overlap.

Several species pairs revealed significant segregation in their use of the diel cycle (Table 3.2.3). However, the degree of segregation of each species’ pair was not constant across study areas or seasons. The mean Δ_1 values obtained from all pairwise comparisons in each sampling campaign was negatively correlated with the number of carnivore species with ≥ 10 detections (Spearman rank correlation: s=-0.76, n=9, p = 0.018), suggesting that the level of circadian segregation increases with community diversity. Excluding the strictly diurnal Egyptian mongoose, mean Δ_1 values between coexisting mesocarnivores were significantly higher (Wilcoxon test: V=112, n=32, p=0.02) in non-breeding season ($\Delta_{1\text{Non-breeding}}$ = 0.76 ± 0.02) than in breeding season ($\Delta_{1breeding}$ = 0.66 ± 0.02). However, no significant differences were found between the mean Δ_1 values between mesocarnivores' diel activity in the Mediterranean vs. Atlantic region (Kruskal-Wallis test: W=88.5, n=34, p=0.86).

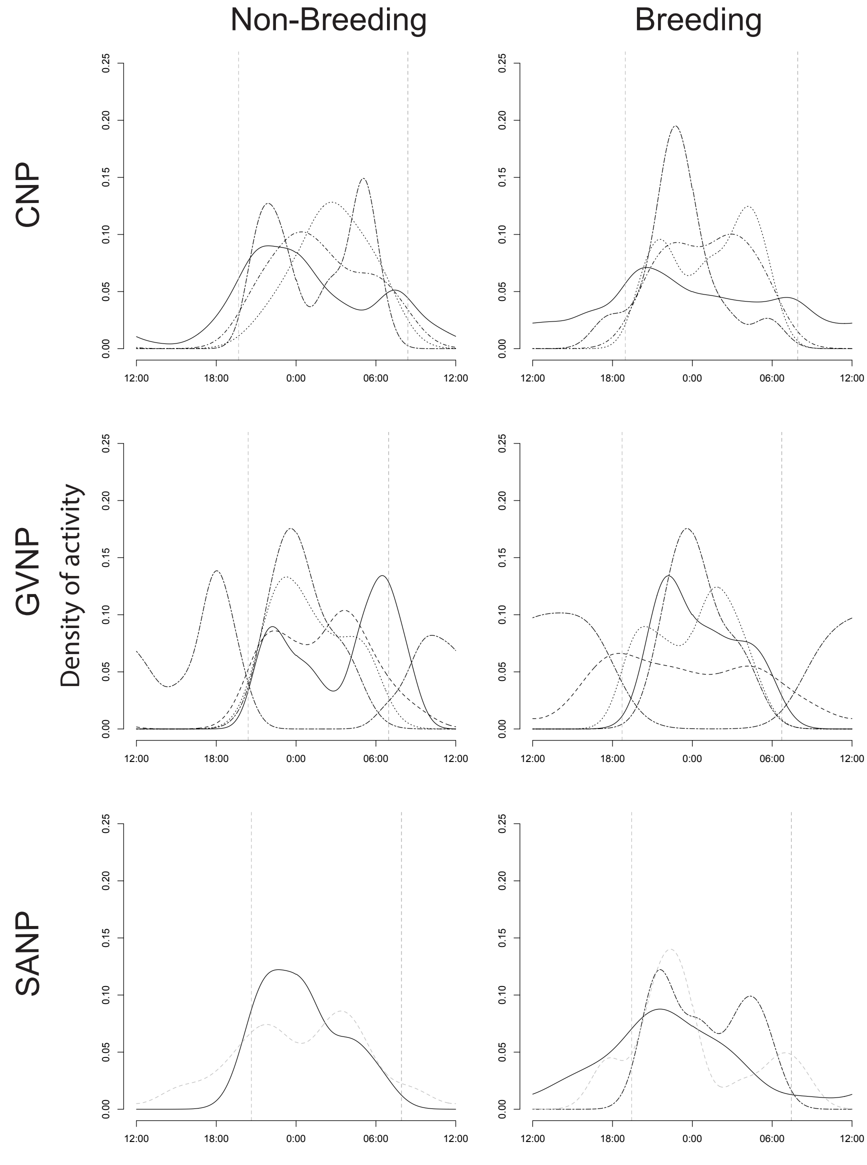

Figure 3.2.2. Diel activity patterns of target mammalian carnivores in the Mediterranean region study areas: CNP - Cabañeros National Park; GVNP - Guadiana Valley Natural Park; SANP - Sierra de Andújar Natural Park. Red fox (solid line), European wildcat (dashed line), stone marten (dotted line), common genet (dotdash line), Eurasian badger (long dash line), Egyptian mongoose (long dotdash line) and Iberian lynx (grey dashed line). Vertical dashed lines represent sunrise and sunset times, respectively.

The level of segregation between each species pairs was not constant across study areas. For instance, the diel activity patterns of red foxes and stone martens revealed significant differences in 3 out of 5 (60%) pairwise comparisons, and mean Δ_1 values were low: 0.65 ± 0.03 (Table 3.2.3). The mean activity overlap between red foxes and common genets was moderate (Δ_1 = 0.75 ± 0.06), and their patterns were only statistically different during breeding season, at CNP and GVNP (W_{CNP} = 16.01, $p<0.05$; W_{GVNP} = 7.77, $p<0.05$; Table 3.2.3). Despite the activity patterns of red foxes and badgers were significantly different during the non breeding season at CNP and GVNP, their activity was largely asynchronic, as supported by a mean Δ_1 of 0.63 ± 0.03.

As expected from its diurnal behaviour, the activity pattern of the Egyptian mongoose was significantly different from that of all other carnivore species in both seasons (Table 3.2.3), and Δ_1 values were very low (range $\Delta_{1Non\text{-}breeding}$ = 0.07 - 0.20; range $\Delta_{1Breeding}$ = 0.09 - 0.41). Several other statistically different activity patterns were detected in other species pairs, although less consistently (see Table 3.2.3).

Iberian lynx were only detected at SANP, and their activity patterns were not statistically different from that of red foxes in any of the seasons (WNon-breeding season=3.12, n=40, p=0.21; WBreeding season=0.56, n=37 ,p=0.76; Table 3). Similarly, no circadian segregation was detected between the Eurasian badger and neither of the other coexisting carnivores in breeding season (Table 3). Coefficients of activity overlap were always above or close to 0.70. The only species which provided enough detections for activity pattern analysis in MNR study area were the pine marten in both seasons and the red fox in spring. During spring season, the unimodal nocturnal pattern of red foxes contrasted with the slightly bimodal pattern of pine martens (Fig. 3). Regardless, no significant differences were detected by MWW test (WBreeding season =4.87, n=49, p=0.09) and the activity overlap Δ1 was 0.79 ± 0.09.

Despite the preference of most species for the nightime period, a sequential use of the diel cycle was observed in several study areas and both seasons, as suggested by the observed asynchrony between the activity peaks of different coexisting mesocarnivores (Fig. 2). An area-by-area detailed description of the temporal segregation among species can be found in the Electronic Supplementary Information Text 2.

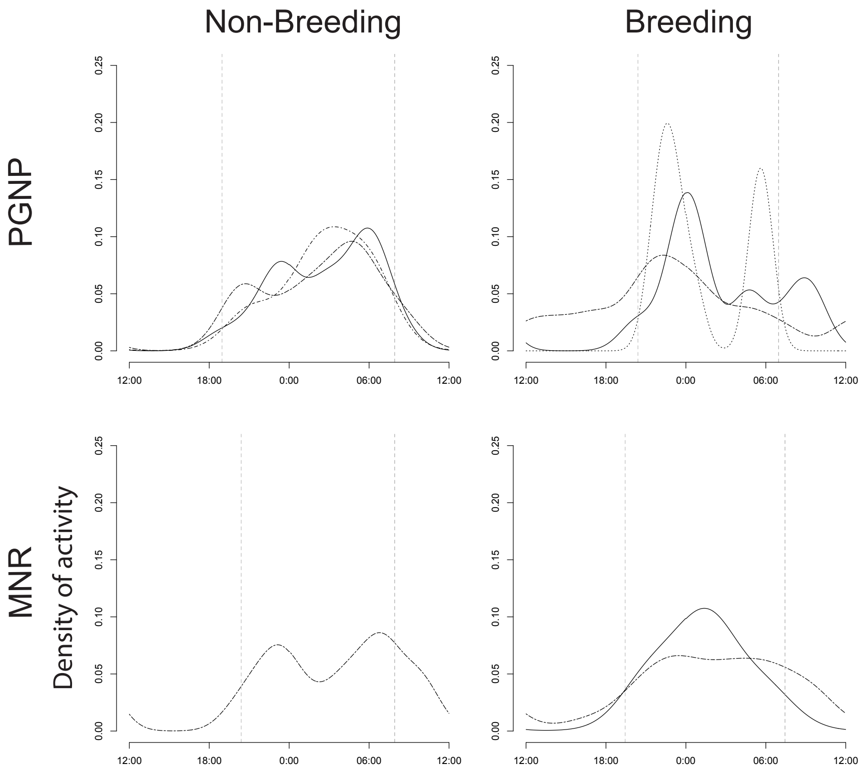

Figure 3.2.3. Diel activity patterns of target mammalian carnivores in the Atlantic region study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês Natural Park. Red fox (solid line), stone marten (dotted line), common genet (dotdash line), pine marten (long dotdash line). Vertical dashed lines represent sunrise and sunset times, respectively.

Table 3.2.3. Coefficient of overlap (Δ_1; mean ± SD, in bold) and Mardia-Watson-Wheeler test (W) between the activity patterns of coexisting carnivore species at all study areas, during non-breeding season sampling campaign (only for species with ≥10 detections). n - Number of detections; Δ_1 - Coefficient of overlap. MNR data is not presented due to the low functional mesocarnivore diversity found at this study area.

Study area	Season	Δ_1 W statistic	*Lynx pardinus*	*Felis silvestris*	*Vulpes vulpes*	*Martes foina*	*Martes martes*	*Meles meles*	*Genetta genetta*	*Herpestes ichneumon*
CNP	**Non-breeding**	*Vulpes vulpes (n=259)*	-	-	-	**0.63 ±**	-	**0.65 ±**	**0.79 ±**	-
		Martes foina (n=42)	-	-	34.42**	-	-	**0.70 ±**	**0.83 ±**	-
		Meles meles (n=15)	-	-	2.08	3.28	-	-	**0.72 ±**	-
		Genetta genetta (n=21)	-	-	5.71^{+}	4.52	-	0.33	-	-
	Breeding	*Vulpes vulpes (n=481)*	-	-	-	**0.61 ±**	-	**0.59 ±**	**0.64 ±**	-
		Martes foina (n=39)	-	-	23.65**	-	-	**0.64 ±**	**0.91 ±**	-
		Meles meles (n=13)	-	-	11.47**	7.84*	-	-	**0.67 ±**	-
		Genetta genetta (n=21)	-	-	16.01**	1.03	-	4.01		-
GVNP	**Non-breeding**	*Felis silvestris (n=22)*	-	-	**0.76 ±**	**0.84 ±**	-	**0.71 ±**	-	**0.20 ±**
		Vulpes vulpes (n=40)	-	4.11	-	**0.68 ±**	-	**0.57 ±**	-	**0.20 ±**
		Martes foina (n=16)	-	2.78	7.87*	-	-	**0.86 ±**	-	**0.11 ±**
		Meles meles (n=12)	-	6.88*	12.86**	0.96	-	-	-	**0.07 ±**
		Herpestes ichneumon	-	34.29**	40.50**	29.75**	-	24.24**	-	-
	Breeding	*Felis silvestris (n=19)*	-	-	**0.62 ±**	**0.65 ±**	-	-	**0.64 ±**	**0.41 ±**
		Vulpes vulpes (n=17)	-	4.91^{+}	-	**0.77 ±**	-	-	**0.66 ±**	**0.09 ±**
		Martes foina (n=58)	-	9.7**	1.6	-	-	-	**0.69 ±**	**0.14 ±**
		Genetta genetta (n=30)	-	3.05	7.77*	10.78**	-	-	-	**0.14 ±**
		Herpestes ichneumon	-	21.73**	28.41**	39.11**	-	-	35.47**	-
SANP	**Non-season**	*Lynx pardinus (n=14)*		-	**0.78 ±**	-	-	-	-	-
		Vulpes vulpes (n=26)	3.12	-	-	-	-	-	-	-
	Breeding	*Lynx pardinus (n=15)*		-	**0.75 ±**	-	-	**0.71 ±**	-	-
		Vulpes vulpes (n=22)	0.56	-	-	-	-	**0.69 ±**	-	-
		Meles meles (n=15)	1.64	-	1.19	-	-	-	-	-
PGNP	**Non-breedin**	*Vulpes vulpes (n=22)*	-	-	-	-	**0.89 ±**	-	**0.89 ±**	-
		Martes martes (n=13)	-	-	0.02	-	-	-	**0.88 ±**	-
		Genetta genetta (n=12)	-	-	0.80	-	0.31	-	-	-
	Breeding	*Vulpes vulpes (n=12)*	-	-	-	**0.58 ±**	**0.64 ±**	-	-	-
		Martes foina (n=11)	-	-	1.22	-	**0.49 ±**	-	-	-
		Martes martes (n=26)	-	-	3.42	2.12	-	-	-	-

** - Highly significant ($p < 0.01$); * - Significant ($p < 0.05$); $^{+}$ - $0.05 \leq p < 0.1$.

Discussion

Species plasticity

With the exception of the Egyptian mongoose, which strongly selected daytime, all studied mammalian carnivore species revealed preference for the nighttime period. However, in spite of this preference we could clearly define two groups of species from a behavioural point of view: strictly and facultative nocturnal species. The first group includes species that reveal particularly strong selection indices towards nighttime (JSI_{night} > 0.80), with little activity during the twilight periods, and strong avoidance of daytime. The stone marten, common genet and Eurasian badger exhibited such activity patterns, irrespective of study area, season or bioclimatic region. Despite being described as mainly nocturnal (Posillico et al. 1995; Herr 2008; López-Martín et al. 2008; Wilson and Mittermeier 2009), the stone marten has been reported to have occasional activity bouts during daytime or twilight (Posillico et al. 1995; Herr 2008; López-Martín et al. 2008). Similarly, common genets and Eurasian badgers have been reported to be predominantely (Camps 2008) or exclusively (Palomares and Delibes 2000; Kowalczyk et al. 2003; Wilson and Mittermeier 2009) nocturnal, although some occasional exceptions can be found in the literature (e.g. Rodríguez et al., 1996). However, while strongly bound to the nighttime, stone martens, common genets and Eurasian badgers exhibited some plasticity within this preferred period. Neither of these species showed a uniform activity pattern at night, nor was the activity pattern constant across study areas, seasons or bioclimatic regions. Other studies have found Eurasian badgers to uniformly use the nighttime period (Kowalczyk et al. 2003) or varying between continous and intermittent (Zabala et al. 2002; Goszczynski et al. 2003). Common genets have been found to have more intense activity in the first half of the night (Palomares and Delibes 2000; Camps 2008). The activity peak of stone martens occurred later in the night in Luxembourg (Herr 2008), while the activity of a radiotracked individual in NE Spain peaked between 18h00 and 24h00, during non-breeding season (López-Martín et al. 2008). Our results suggest that, in spite of the rigidness of the endogenous regulation of the nighttime/daytime activity, stone martens, common genets and Eurasian badgers can locally adapt their strategies in response to environmental cues, possibly to maximize foraging efficiency and reduce the chances for agonistic encounters.

The facultative nocturnal group included the red fox, European wildcat, pine marten and Iberian lynx. These species positively selected nighttime, but also use, in average, the twilight periods as expected by chance. Furthermore, while exploring daytime less than expected by chance these species do not strictly avoid it. Previous studies on red foxes have reported significant daytime activity (Sunquist 1989; Cavallini and Lovari 1991, 1994; Travaini et al. 1993), suggesting some flexibility in their activity patterns, facilitating access to their their main prey (Ables 1969; Cavallini and Lovari 1991) or avoidance of the most risky periods of the day (Doncaster and Macdonald 1997; Adkins and Stott 1998). The European wildcat and the pine marten exhibit comparable plasticity in their diel activity structure. Overall, 21% of all our wildcat detections were diurnal. This is in accordance with previous studies which found that European wildcats can be active over 20% of the daytime (Urra 2003; Monterroso 2006; Germain et al. 2008). Equivalent activity patterns have been described for both pine martens and Iberian lynx (Zielinski et al. 1983; Clevenger 1993; Beltrán and Delibes 1994; Fedriani et al. 1999; Zalewski 2000).

No seasonal differences were detected in the pattern of daytime activity of Iberian lynx. This is in accordance with what has been observed in the Doñana population (Fedriani et al. 1999). However red foxes, European wildcats and pine martens revealed a tendency for diurnal activity to be less pronounced in the non-breeding season. This observation contrasts with previous studies which suggest that mesocarnivores are active for less time and are more nocturnal during the breeding season (Posillico et al. 1995; Zalewski 2000; Zielinski 2000; Kowalczyk et al. 2003). Behavioural strategies are influenced by a combination of intrinsic and extrinsic factors, including ambient temperature (Liberek 1999; Zalewski 2000; Weir and Corbould 2007). The climate in the IP is charaterized by mild winters, even in the Atlantic region, where the average temperature ranges from 0.8 ± 3.5^{o}C to 23.9 ± 2.5^{o}C (Hijmans et al. 2005). However, the ambient temperature often rises above 35oC in the Mediterranean region during the warmer seasons (Rivas-Martínez et al. 2004; Hijmans et al. 2005). This could lead to thermoregulatory stress, inhibiting activity during midday. This could help explain the reduction in activity at midday by Egyptian mongooses (at GVNP) and during daylight hours by most other mesocarnivores at the Mediterranean study sites in non-breeding season (Fig. 3.2.2).

The pine marten, which only occurs in the Atlantic region of Iberian Peninsula (López-Martin 2007), is not affected by the severe summers of the continental Mediterranean climate. Therefore, it should be able to explore the daytime period during non-breeding season. However, this pattern was not observed (Fig. 3.2.3). The increased accessibility to small mammals could be related to the observed levels of nocturnal activity (Monterroso et al. 2013). An analysis of the pine martens' feeding ecology in PGNP and MNR has shown that they prey frequently on small mammals, especially during non-breeding season (FO = 90.80 ± 2.11; Rebelo 2013). Human disturbance also affects animals activity, and other studies have shown that predators exhibit behavioural responses to the patterns of human disturbance (Kitchen et al. 2000; Muhly et al. 2011; Kight and Swaddle 2011). Although we could not test its effect, it is possible that seasonal differences in tourism-related human presence (namely by hikers, supported by park visitation rates), could also contribute to the more nocturnal pattern during non-breeding season.

Temporal segregation

According to the competitive exclusion principle (Hardin 1960) we would expect that segregation along the temporal axis would be an effective behavioural response favouring coexistence among mammalian carnivores, especially when they are forced to overlap in other niche dimension (Lucherini et al. 2009; Di Bitetti et al. 2009; Gerber et al. 2012).

Our results suggest that competition among mesocarnivores might be minimized by segregation along the diel cycle. At GVNP and CNP, where mesocarnivore communities appeared to be more complex, mean activity overlap was low (mean Δ_1 = 0.57±0.04) when compared to the results obtained in other studies using similar methods (Ridout and Linkie 2009; Linkie and Ridout 2011; Wang and Fisher 2012; Foster et al. 2013), even when excluding the strictly diurnal Egyptian mongoose (mean Δ_1 = 0.63±0.04). Moreover, nearly 60% of all possible pairwise comparisons revealed significant differences in activity patterns (Table 3.2.3). Additionally, the activity peaks of most coexisting mesocarnivores in these study areas were, at least partially asynchronous. In Southwestern Europe European rabbits, which are more abundant in the Mediterranean region, are among the most profitable prey for mammalian mesocarnivores (Malo et al. 2004; Díaz-Ruiz et al. 2013). Whenever rabbit abundance is low (mainly in the Atlantic region), rodents take its place as the preferred prey of many mammalian mesocarnivores (Lozano et al. 2006; Zhou et al. 2011). In our study areas, European rabbits exhibit peaks of activity on the twilight periods while rodents were mainly nocturnal (Monterroso et al. 2013). The combined activity patterns of rodents and rabbits provide continuous mammalian prey availability from before sunset to after sunrise, potentially allowing mesocarnivores to segregate within a relatively long period while maintaining access to prey (Monterroso et al. 2013).

In cases when asymmetrical competition occurs, the subordinate species adjusts its behaviour to minimize agonistic encounters with the superior competitor (Palomares et al. 1996; Azlan and Sharma 2006; Harrington et al. 2009). Where Iberian lynx occur, they have the ability to structure mesocarnivore communities through top-down regulation of subordinate competitors (Palomares et al. 1996; Fedriani et al. 1999), which often takes the form of intraguild predation (Palomares and Caro 1999). Historically Iberian lynx was widespread in SW Iberia, but it is currently absent from most of its historical range, which includes GVNP and CNP (Sarmento et al. 2009; Gil-Sánchez and McCain 2011). However, it is the dominant competitor within the carnivore community at SANP. There, in spite of the high risks that encounters with Iberian lynx pose to the integrity of red foxes, no significant differences were observed between the activity patterns of these two species. This could be related to a spatial avoidance of red foxes of those areas with higher probability of lynx encounter, as seems to be supported by camera-trapping results (Monterroso 2013). Similar findings were described by Fedriani et al. (1999) who suggested that red foxes avoided lynx predation by habitat segregation during activity periods. In other systems, coexistence between a superior and subordinate competitors have been sustained by spatio-temporal adjustments in the behaviour of the latter (Azlan and Sharma 2006; Harrington et al. 2009; Brook et al. 2012).

The outcome of agonistic encounters in mutual reciprocal interactions is less certain (Donadio and Buskirk 2006). In those cases, the most flexible species should more easily shift their behavioural patterns promoting coexistence (Di Bitetti et al. 2010). Along the temporal dimension, cathemerality could provide enough plasticity for the adjustment of a species activity patterns to local conditions to increase its fitness and reduce competition (Di Bitetti et al. 2009; Lucherini et al. 2009; Gerber et al. 2012). Our results support that the Iberian lynx, red fox, pine marten and European wildcat exhibit such characteristics, and suggest that temporal segregation plays an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity.

Overall, we obtained low detection rates in both Atlantic study areas, especially at MNR where meaningful activity was only recorded for pine martens and red foxes. In these areas, European rabbits are very scarce (Monterroso et al. 2013), therefore mammalian prey is mostly restricted to rodent species, which are phylogenetically bound to nocturnal activity (Roll et al. 2006). However, in these study areas a variety of alternative food resources, such as fruits and invertebrates are seasonally widely available (Prieto and Sánchez 1996; Carvalho and Gomes 2004). It has been suggested that the strength of the interactions between competing species is linked to the availability of a shared resource (Valeix et al. 2007). Most mesocarnivores with significant activity detected by camera-trapping in this ecoregion are feeding generalists (Table 3.2.1), but with significant consumption of rodents (Marinis and Masseti 1995; Virgós et al. 1999; Zhou et al. 2011; Díaz-Ruiz et al. 2013), which is reflected by the high synchrony between their activity and that of rodents (Monterroso et al. 2013). However, the activity strategies of each mesocarnivore species varied between sampling campaigns, especially at PGNP where activity overlap decreased from the non-breeding (mean Δ_1 = 0.89±0.00) to the breeding season (mean Δ_1 = 0.57±0.04). This could be related with access to feeding resources, which are highly available during the non-breeding season, and of limited access during the breeding season (Humphries et al. 1996; Fedriani and Delibes 2009; Monterroso et al. 2013).

Conclusions

Interspecific relations between mesopredators are not constant, resulting in non-equilibrium, where changing resource availability might cause shifts in the relative fortunes of the species concerned (Linnell and Strand 2000). With this work we provide an insight into the temporal functioning of mesocarnivore communities in SW European ecosystems. We identified three clear groups of species among Iberian mesocarnivores: strictly norturnal, facultative nocturnal and diurnal animals, with the latter group consisting of only one species, the Egyptian mongoose. In spite of the constraints imposed by their endogenous regulation on when to be active, all species exhibited substantial flexibility within their preferred activity periods. This fact facilitates segregation within their own endogenous boundaries enabling them to concentrate activity bouts on the most beneficial periods, maximizing resource acquisition (Monterroso et al. 2013, Rebelo 2013). Spatial interference as well as exploitative competition for shared resources, have been already advocated in several species pairs in southern European mesocarnivore communities (Palomares et al. 1996; Fedriani et al. 1999; Barrientos and Virgós 2006; Zabala et al. 2009). Our results suggest that temporal partitioning is likely to play an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity. However, and given that interspecific interactions between species and within guilds are multidimensional, further work simultaneously evaluating the interspecific relations along several niche axes among Iberian mesocarnivores could provide vital information for conservation planning and for the undestanding of the full implications of predators interspecific interactions.

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References

Ables ED (1969) Activity Studies of Red Foxes in Southern Wisconsin. J Wildlife Manage 33:145–153

Abrams P (1983) The theory of limiting similarity. Annu Rev Ecol Syst 14:359–376

Adkins CA, Stott P (1998) Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. J Zool 244:335–346

Arias-Del Razo I, Hernández L, Laundré JW, Myers O (2011) Do predator and prey foraging activity patterns match? A study of coyotes (*Canis latrans*), and lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*)

Azlan JM, Sharma DSK (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40:36-41

Barrientos R, Virgós E (2006) Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. Acta Oecol 30:107–116

Batschelet E (1981) Circular Statistics in Ecology. Academic Press, London

Beltrán JF, Delibes M (1994) Environmental determinants of circadian activity of free-ranging Iberian lynxes. J Mammal 75:382–393

Di Bitetti MS, De Angelo CD, Di Blanco YE, Paviolo A (2010) Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecol 36:403–412

Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pérez IJ (2009) Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and Pampas foxes (*Lycalopex gymnocercus*). J Mammal 90:479–490

Blanco JC (1998) Mamíferos de España. Planeta, Barcelona

Blanco-Garrido F, Prenda J, Narvaez M, (2007) Eurasian otter (*Lutra lutra*) diet and prey selection in Mediterranean streams invaded by centrarchid fishes. Biol Invasions 10:641–648

Brook LA, Johnson CN, Ritchie EG (2012) Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. J Appl Ecol 49:1278-1286

Cabral MJ, Almeida J, Almeida PR, Dellinger T, Ferrand de Almeida N et al. (2005) Livro Vermelho dos Vertebrados de Portugal, 2nd ed. Instituto da Conservação da Natureza/Assírio Alvim, Lisbon

Calzada J (2007) *Genetta genetta*. In:Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 330–332

Camps D (2008) Activity patterns of adult common genets *Genetta genetta* (Linnaeus, 1758) in northeastern Spain. Galemys 20:47–60

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool 263:275–283

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 39:279–287.

Clevenger AP (1993) Pine marten (*Martes martes* L.) home ranges and activity patterns of the island of Minorca, Spain. Z Säugetierkd 58:137–143

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental. Quercetea 0:5–56

Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Anim Conserv 14:56–65

Delibes M, Aymerich M, Cuesta L (1984) Feeding habits of the *Herpestes ichneumon* or Egyptian mongoose in Spain. Acta Theriol 29:205–218

Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in the conservation of the Western Mediterranean basin hotspot. Conserv Biol 22:1106–1117

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martín JM, Ferreira C, Ferreras P (2013) Biogeographical patterns in the diet of an opportunistic predator:the red fox *Vulpes vulpes* in the Iberian Peninsula. Mammal Rev 43:59–70

Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat 167:524–36

Doncaster CP, Macdonald DW (1997) Activity patterns and interactions of red foxes (*Vulpes vulpes*) in Oxford city. J Zool 241:73–87

Elmhagen B, Ludwig G, Rushton SP, Helle P, Lindén H (2010) Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. J Anim Ecol 79:785–794

Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? Ecol Lett 10:197–206

European Environmental Agency (2012) Biogeographic regions in Europe, http://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe

Fedriani JM, Delibes M (2009) Seed Dispersal in the Iberian Pear, Pyrus bourgaeana: A Role for Infrequent Mutualists. Ecoscience 16:311–321

Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric Mediterranean carnivores. Oecologia 121:138–148

Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácomo ATA, Negrões N, Fonseca C, Silveira L (2013) Jaguar and puma activity patterns and predator-prey interactions in four brazilian biomes. Biotropica 45:373-379

García-Canseco V (1997) Parque Nacional De Cabañeros, 1st edition. Ecohábitat, Madrid

García-Perea R (2007) *Felis silvestris*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 333–338

Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. J Mammal 93:667–676

Germain E, Benhamou S, Poulle M-L (2008) Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. J Zool 276:195–203

Gil-Sánchez JM, Ballesteros-Duperón E, Bueno-Segura J (2006) Feeding ecology of the Iberian lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). Acta Theriol 51:1–6

Gil-Sánchez JM, McCain EB (2011) Former range and decline of the Iberian lynx (*Lynx pardinus*) reconstructed using verified records. J Mammal 92:1081–1090

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. Behav Ecol Sociobiol 10:57–63

Gortázar C (2007) *Vulpes vulpes*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 277–279.

Goszczynski J, Juszko S, Pacia A, Skoczynska J (2003) Activity of badgers (*Meles meles*) in Central Poland. Mamm Biol 70:1–11

Halle S (2000) Ecological relevance of daily activity patterns. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer, New York, pp 67–90

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297

Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald DW (2009) The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216

Herr J (2008) Ecology and behaviour of urban Stone Martens (*Martes Foina*) in Luxembourg. University of Sussex, Brighton

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Humphries CJ, Press JR, Sutton DA (1996) Árvores de Portugal e da Europa. FAPAS, Fundo para a Protecção dos Animais Selvagens & Camara Municipal do Porto, Porto

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Sym on Quantitative Biology 22:415–427

Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven

Jacobs J (1974) Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417

Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an integrative, mechanistic review. Ecol Lett 14:1052–1061

Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. Can J Zool 78:853–857

Kitchener AC, Yamaguchi N, Ward JM, Macdonald DW (2005) A diagnosis for the Scottish wildcat (*Felis silvestris*): a tool for conservation action for a critically-endangered felid. Anim Conserv 8:223-237

Kovach WL (2011) Oriana – Circular Statistics for Windows. Kovach Computing Services, Pentraeth, UK

Kowalczyk R, Jedrzejewska B, Zalewski A (2003) Annual and circadian activity patterns of badgers (*Meles meles*) in Białowieza Primeval Forest (Eastern Poland) compared with other Palaearctic populations. J Biogeogr 30:463–472

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu Rev Ecol Evol S 34:153–181

Liberek M (1999) Eco-ethologie du chat sauvage *Felis s. silvestris*, Schreber 1777 dans le Jura Vaudois (Suisse): Influence de la couverture neigeuse. Université de Neuchatel, Neuchatel

Linkie M, Ridout MS (2011) Assessing tiger-prey interactions in Sumatran rainforests. J Zool 284:224–229

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

López-Martin JM (2007) *Martes martes*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 302–304

López-Martin JM, Ruiz-Olmo J, Cahill S (2008) Autumn home range and activity of a stone marten (*Martes foina* Erxleben, 1777) in Northeastern Spain. Miscellan Zool 16:258–260

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

Lucherini M, Reppucci J, Walker R, Villalba M, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal 90:1404–1409

MacArthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat 101:377–385

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

Manly BFJ (1997) Randomization, bootstrap and monte carlo methods in biology, 2nd edn. Chapman and Hall, Boca Raton

Marinis AM, Masseti M (1995) Feeding habits of the pine marten *Martes martes* L., 1758, in Europe: a review. Hystrix 7:143–150

McDonald JH (2009) Handbook of biological statistics, 2nd edn. Sparky House Publishing, Baltimore

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

Monterroso P (2006) Distribuição, selecção de habitat e actividade do Gato-bravo (*Felis silvestris*) no Parque Natural do Vale Do Guadiana. MSc thesis, University of Porto, Porto

Monterroso P (2013) Ecological interactions and species coexistence in Iberian mesocarnivore communities. PhD thesis, University of Porto, Porto

Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildlife Res 38:446–454

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

Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M (2011) Human activity helps prey win the predator-prey space race. PloS ONE 6:e17050

Oliveira R, Godinho R, Randi E, Ferrand N, Alves PC (2007) Molecular analysis of hybridisation between wild and domestic cats (*Felis silvestris*) in Portugal: implications for conservation. Conserv Genet 9:1-11

Palomares F (2007) *Herpestes ichneumon*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 327–329.

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508

Palomares F, Delibes M (2000) Mongooses, civets and genets - carnivores in southern latitudes. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer, New York, pp 119–130

Palomares F, Delibes M, Ferreras P, Fedriani JM, Calzada J, Revilla E (2000) Iberian lynx in a fragmented landscape: predispersal, dispersal, and postdispersal habitats. Conserv Biol 14:809–818

Palomares F, Ferreras P, Fedriani JM, Delibes M (1996) Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. J Appl Ecol 33:5–13

Palomares F, Ferreras P, Travaini A, Delibes M (1998) Co-existence between Iberian lynx and Egyptian mongooses: estimating interaction strength by structural equation modelling and testing by an observational study. J Anim Ecol 67:967–978

Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y libro rojo de los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid

Posillico M, Serafini P, Lovari S (1995) Activity patterns of the stone marten *Martes foina* Erxleben, 1777, in relation to some environmental factors. Hystrix 7:79–97

Prieto JAF, Sánchez ÁB (1996) La reserva integral de muniellos: flora y vegetación. Servicio central de publicaciones del Principado de Asturias, Oviedo

R Development Core Team (2008) R: A language and environment for statistical computing.

Ragni B, Possenti M (1996) Variability of coat-colour and markings system in *Felis silvestris*. Ital J Zool 63:285-292

Rebelo P (2013) An insight into the trophic ecology of the pine marten (*Martes martes*) in Northwestern Iberian Peninsula. MSc thesis, University of Porto, Porto

Reig S (2007) *Martes foina*. Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 305–307

Revilla E, Casanovas JG, Virgós E (2007) *Meles meles*. Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 308–311

Ridout M, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Envir S 14:322–337

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998

Rivas-Martinez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique. An Jard Bot Madr 37:251–268

Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas. http://www.ucm.es/info/cif/form/maps.htm

Rodríguez A (2007) *Lynx pardinus*. Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los mamíferos terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, pp 342–347

Rodríguez A, Franquelo RM, Delibes M (1996) Space use and activity in a Mediterranean population of badgers *Meles meles*. Acta Theriol 41:59–72

Roemer GW, Gompper ME, Valkenburgh BV (2009) The ecological role of the mammalian mesocarnivore. Bioscience 59:165–173

Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining activity patterns of rodents. Evol Ecol 20:479–490

Rosalino L, Macdonald D, Santos-Reis M (2005) Activity rhythms, movements and patterns of sett use by badgers, *Meles meles*, in a Mediterranean woodland. Mammalia 69:395–408

Sarmento P, Cruz J, Monterroso P, Tarroso P, Ferreira C, Negrões N, Eira C (2009) Status survey of the critically endangered Iberian lynx *Lynx pardinus* in Portugal. Euro J Wildlife Res 55:247–253

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39

Spassov N, Simeonovski V, Spiridonov G (1997) The wild cat (*Felis silvestris* Schr.) and the feral domestic cat: problems of the morphology, taxonomy, identification of the hybrids and purity of the wild population. Hist Nat Bulg 8:101–120

Sunquist M (1989) Comparison of spatial and temporal activity of red foxes and gray foxes in North-Central Florida. Fla Field Nat 17:11–18

Szabó P, Meszeéna G (2006) Limiting similarity revisited. Oikos 112:612–619

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

Urra F (2003) El gato montés en Navarra: Distribución, ecología y conservación. Universidad Autónoma de Madrid, Madrid

Valeix M, Chamaillé-Jammes S, Fritz H, (2007) Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. Oecologia 153:739–748

Virgós E., Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. Mammal Rev 29:119–128

Virgós E, Revilla E, Mangas JG, Barea-Azcón JM, Miguel L, Marinis A (2005) Revisión de la dieta del Téjon (*Meles meles*) en la Península Ibérica: comparación con otras localidades de su área de distribución natural. In: Virgós E, Mangas JG, Revilla E, Roura X-D (eds) Ecología, distribución y estatus de conservación del tejón Ibérico. Sociedad Española para la Conservación y Estudio de los Mamíferos, Málaga, pp 67–80

Wang Y, Fisher D (2012) Dingoes affect activity of feral cats, but do not exclude them from the habitat of an endangered macropod. Wildlife Res 39:611–620

Weir RD, Corbould FB (2007) Factors affecting diurnal activity of fishers in north-central British Columbia. J Mammal 88:1508–1514

Wilson DE, Mittermeier RA (2009) Handbook of the Carnivores of the World. Vol. I - Carnivores. Lynx editions, Barcelona

Zabala J, Zuberogoitia I, Garín I, Aihartza JR (2002) Seasonal activity patterns of badgers (*Meles meles*) related to food availability and requirements. Estud Mus Cienc Nat Álava 17:201–207

Zabala J, Zuberogoitia I, Martínez-climent JA (2009) Testing for niche segregation between two abundant carnivores using presence-only data. Folia Zool 58:385–395

Zalewski A (2000) Factors affecting the duration of activity by pine martens (*Martes martes*) in the Bialowieza National Park, Poland. J Zool 251:439–447

Zhou Y, Newman C, Xu W, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie, Z-Q (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr 38:137–147

Zielinski WJ (2000) Weasels and martens - carnivores in northern latitudes. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals: an ecological approach. Springer, New York, pp 95–118

Zielinski WJ, Spencer WD, Barrett RH (1983) Relationship between food habits and activity patterns of pine martens. J Mammal 64:387–396

Supporting information: Appendix 3.2

Table 1 - Coefficient of overlap (Δ_1) and Mardia-Watson-Wheeler test (W) of diel activity data on mesocarnivores in all sampling campaigns.

Table 2 - Mean Jacobs Selectivity Index (JSI), based on 500 bootstrap replicates, for each of the defined periods of the diel cycle: Night, Dawn, Day and Dusk.

Text 1 - Detailed description of diel period selection and species plasticity results.

Text 2 - Detailed description of temporal segregation among species results.

Appendix 3.2

Table A.3.2.1. Coefficient of overlap (Δ_1, in bold) and Mardia-Watson-Wheeler test (W) of diel activity data on mesocarnivores in all sampling campaigns.

		Δ_1	CNP		GVNP		SANP		MNR		PGNP	
W statistic			**Non-Breeding**	**Breeding**	**Non-Breeding**	**Breeding**	**Non-Breeding**	**Breeding**	**Non-Breeding**	**Breeding**	**Non-Breeding**	**Breeding**
Vulpes vulpes	*CNP*	*Non-breeding (n=259)*	-	**0.83 ± 0.03**	**0.70 ± 0.06**	**0.72 ± 0.06**	**0.75 ± 0.04**	**0.84 ± 0.07**	-	**0.79 ± 0.07**	**0.74 ± 0.08**	**0.76 ± 0.13**
		Breeding (n=481)	23.13**	-	**0.62 ± 0.04**	**0.59 ± 0.05**	**0.62 ± 0.04**	**0.83 ± 0.07**	-	**0.68 ± 0.06**	**0.66 ± 0.07**	**0.68 ± 0.11**
	GVNP	*Non-breeding (n=41)*	8.95*	17.91**	-	**0.65 ± 0.09**	**0.64 ± 0.08**	**0.58 ± 0.08**	-	**0.69 ± 0.09**	**0.85 ± 0.07**	**0.72 ± 0.12**
		Breeding (n=17)	5.06^{+}	14.71**	5.99^{+}	-	**0.92 ± 0.09**	**0.67 ± 0.08**	-	**0.84 ± 0.11**	**0.72 ± 0.11**	**0.73 ± 0.12**
	SANP	*Non-breeding (n=26)*	7.36*	21.44**	7.36*	0.08	-	**0.71 ± 0.08**	-	**0.85 ± 0.08**	**0.71 ± 0.10**	**0.76 ± 0.12**
		Breeding (n=22)	1.59	4.49	7.98*	4.26	4.27	-	-	**0.70 ± 0.10**	**0.62 ± 0.10**	**0.62 ± 0.12**
	MNR	*Breeding (n=22)*	7.90*	16.94**	5.60^{+}	1.48	3.29	5.04^{+}	-	-	**0.80 ± 0.10**	**0.78 ± 0.12**
	PGNP	*Non-breeding (n=22)*	7.40*	12.29**	1.34	1.92	3.05	7.63*	-	3.26	-	**0.75 ± 0.13**
		Breeding (n=22)	1.86	4.60	3.39	0.09	0.10	3.76	-	1.77	1.63	-
Felis silvestris	*GVNP*	*Non-breeding (n=22)*	-	-	-	-	-	**0.70 ± 0.10**	-	-	-	-
		Breeding (n=19)	-	-	-	-	5.06^{+}	-	-	-	-	-
Martens foina	*CNP*	*Non-breeding (n=42)*	-	**0.80 ± 0.07**	**0.76 ± 0.11**	**0.72 ± 0.07**	-	-	-	-	-	**0.57 ± 0.11**
		Breeding (n=39)	2.38	-	**0.83 ± 0.09**	**0.79 ± 0.07**	-	-	-	-	-	**0.62 ± 0.11**
	GVNP	*Non-breeding (n=16)*	3.26	3.02	-	**0.73 ± 0.09**	-	-	-	-	-	**0.69 ± 0.12**
		Breeding (n=58)	4.70^{+}	1.49	1.35	-	-	-	-	-	-	**0.54 ± 0.10**
	PGNP	*Breeding (n=11)*	8.51*	3.05	3.35	2.94	-	-	-	-	-	-
Martes martes	*MNR*	*Non-breeding (n=40)*	-	-	-	-	-	-	-	**0.86 ± 0.07**	**0.81 ± 0.10**	**0.67 ± 0.08**
		Breeding (n=27)	-	-	-	-	-	-	0.28	-	**0.85 ± 0.10**	**0.76 ± 0.08**
	PGNP	*Non-breeding (n=13)*	-	-	-	-	-	-	0.92	0.59	-	**0.68 ± 0.11**
		Breeding (n=26)	-	-	-	-	-	-	5.75^{+}	2.71	2.99	-
Genetta genetta	*CNP*	*Non-breeding (n=21)*	-	**0.88 ± 0.08**	-	**0.64 ± 0.09**	-	-	-	-	**0.84 ± 0.10**	-
		Breeding (n=21)	0.07	-	-	**0.69 ± 0.09**	-	-	-	-	**0.82 ± 0.10**	-
	GVNP	*Breeding (n=30)*	4.63^{+}	8.46*	-	-	-	-	-	-	**0.62 ± 0.11**	-
	PGNP	*Non-breeding (n=12)*	2.14	0.89	-	3.99	-	-	-	-	-	-
Meles meles	*CNP*	*Non-breeding (n=15)*	-	**0.65 ± 0.13**	**0.66 ± 0.13**	-	-	**0.87 ± 0.12**	-	-	-	-
		Breeding (n=13)	3.23	-	**0.75 ± 0.11**	-	-	**0.71 ± 0.12**	-	-	-	-
	GVNP	*Non-breeding (n=12)*	7.30*	2.17	-	-	-	**0.72 ± 0.14**	-	-	-	-
	SANP	*Breeding (n=15)*	0.32	4.65*	7.15*	-	-	-	-	-	-	-
Herpestes ichneumon	*GVNP*	*Non-breeding (n=22)*	-	-	-	**0.75 ± 0.09**	-	-	-	-	-	-
		Breeding (n=18)	-	-	6.04*	-	-	-	-	-	-	-
Lynx pardinus	*SANP*	*Non-breeding (n=14)*	-	-	-	-	-	**0.73 ± 0.11**	-	-	-	-
		Breeding (n=15)	-	-	-	-	0.59	-	-	-	-	-

** - Highly significant ($p < 0.01$); * - Significant ($p < 0.05$); $^{+}$ - $0.05 < p \leq 0.1$

Table A.3.2.2. Mean Jacobs Selectivity Index (JSI), based on 500 bootstrap replicates, for each of the defined periods of the diel cycle: Night, Dawn, Day and Dusk. (mean ± SD).

Species	***Study area***	***Season***	**JSI$_{night}$**	**JSI$_{Dawn}$**	**JSI$_{Day}$**	**JSI$_{Dusk}$**
Vulpes vulpes	*CNP*	*Non-breeding*	0.45 ± 0.05*	0.08 ± 0.11	-0.65 ± 0.06*	0.15 ± 0.10^{+}
		Breeding	0.14 ± 0.04*	0.09 ± 0.08^{+}	-0.33 ± 0.04*	0.31 ± 0.06*
	GVNP	*Non-breeding*	0.38 ± 0.13*	0.59 ± 0.12*	-0.79 ± 0.10*	-0.12 ± 0.33
		Breeding	1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**
	SANP	*Non-breeding*	0.74 ± 0.11*	-1.00 ± 0.00**	-1.00 ± 0.00**	0.39 ± 0.26
		Breeding	0.41 ± 0.19*	-1.00 + 0.00**	-0.42 ± 0.21*	0.16 ± 0.37
	MNR	*Breeding*	0.87 ± 0.09*	-0.45 ± 0.44	-1.00 ± 0.00**	-0.45 ± 0.47
	PGNP	*Non-breeding*	0.77 ± 0.13*	-0.09 ± 0.46	-1.00 ± 0.00**	-0.47 ± 0.45
		Breeding	0.56 ± 0.22*	-0.24 ± 0.59	-0.49 ± 0.22*	-0.24 ± 0.58
		Average	**0.59 ± 0.27**	**-0.34 ± 0.57**	**-0.74 ± 0.28**	**-0.14 ± 0.45**
Felis silvestris	*GVNP*	*Non-breeding*	0.78 ± 0.11*	-0.11 ± 0.44	-0.90 ± 0.10*	-0.41 ± 0.47
		Breeding	0.22 ± 0.21	-0.38 ± 0.49	-0.49 ± 0.21*	0.49 ± 0.25^{+}
		Average	**0.50 ± 0.40**	**-0.24 ± 0.19**	**-0.70 ± 0.29**	**-0.04 ± 0.64**
Martes foina	*CNP*	*Non-breeding*	0.96 ± 0.04*	-1.00 ± 0.00**	-1.00 ± 0.00**	-0.64 ± 0.31*
		Breeding	0.83 ± 0.08*	-1.00 ± 0.00**	-1.00 ± 0.00**	0.07 ± 0.28
	GVNP	*Non-breeding*	1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**
		Breeding	0.82 ± 0.06*	-1.00 ± 0.00**	-1.00 ± 0.00**	0.17 ± 0.19
	PGNP	*Breeding*	0.77 ± 0.16*	0.23 ± 0.52	-1.00 ± 0.00**	-1.00 ± 0.00**
		Average	**0.88 ± 0.10**	**-0.75 ± 0.55**	**-1.00 ± 0.00**	**-0.48 ± 0.57**
Martes martes	*MNR*	*Non-breeding*	0.36 ± 0.15*	0.27 ± 0.22	-0.64 ± 0.13*	0.15 ± 0.16
		Breeding	0.41 ± 0.17*	0.05 ± 0.38	-0.53 ± 0.18*	-0.16 ± 0.39
	PGNP	*Non-breeding*	0.72 ± 0.18*	0.20 ± 0.46	-1.00 ± 0.00**	-1.00 ± 0.00**
		Breeding	0.34 ± 0.16*	-0.18 ± 0.42	-0.43 ± 0.18*	0.07 ± 0.35
		Average	**0.46 ± 0.18**	**0.08 ± 0.20**	**-0.65 ± 0.25**	**-0.24 ± 0.53**
Genetta genetta	*CNP*	*Non-breeding*	0.76 ± 0.14*	-0.05 ± 0.44	-1.00 ± 0.00**	-0.43 ± 0.48
		Breeding	0.93 ± 0.07*	-1.00 ± 0.00**	-1.00 ± 0.00**	-0.43 ± 0.46
	GVNP	*Breeding*	0.76 ± 0.10*	-0.23 ± 0.39	-1.00 ± 0.00**	0.00 ± 0.36
	PGNP	*Non-breeding*	0.85 ± 0.14*	-0.24 ± 0.59	-1.00 ± 0.00**	-1.00 ± 0.00**
		Average	**0.82 ± 0.08**	**-0.38 ± 0.42**	**-1.00 ± 0.00**	**-0.46 ± 0.41**
Meles meles	*CNP*	*Non-breeding*	1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**
		Breeding	0.76 ± 0.16*	-1.00 ± 0.00**	-0.79 ± 0.19*	-0.29 ± 0.57
	GVNP	*Non-breeding*	1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**
	SANP	*Breeding*	1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**	-1.00 ± 0.00**
		Average	**0.94 ± 0.12**	**-1.00 ± 0.00**	**-0.95 ± 0.10**	**-0.82 ± 0.36**
Herpestes ichneumon	*GVNP*	*Non-breeding*	-1.00 ± 0.00**	-0.45 ± 0.45	0.83 ± 0.12*	-0.46 ± 0.45
		Breeding	-1.00 ± 0.00**	-1.00 ± 0.00**	0.92 ± 0.08*	-0.37 ± 0.50
		Average	**-1.00 ± 0.00**	**-0.72 ± 0.32**	**0.88 ± 0.06**	**-0.42 ± 0.06**
Lynx pardinus	*SANP*	*Non-breeding*	0.48 ± 0.22*	-0.33 ± 0.58	-0.67 ± 0.21*	0.12 ± 0.49
		Breeding	0.57 ± 0.20*	0.10 ± 0.48	-0.66 ± 0.21*	-1.00 ± 0.00**
		Average	**0.52 ± 0.06**	**-0.12 ± 0.30**	**-0.67 ± 0.01**	**-0.44 ± 0.79**

Text 1 - Detailed description of diel period selection and species plasticity results

The red fox consistentely displayed a predominantly nocturnal behaviour (mean $JSI_{night} = 0.59 \pm 0.27$). Nonetheless, in spite of generaly avoiding daytime (mean $JSI_{day} = -0.74 \pm 0.28$; table 3.2.2), daytime activity was consistently detected (Figure 3.2.2 and 3.2.3, Appendix 3.2 Table 2). The distribution of red fox detections across the diel cycle was statistically different between several pairs of sampling campaigns (MWW tests, table 3.2.1; Appendix 3.2. Table 2), and an overall tendency to use dawn and dusk in lesser proportion than expected by chance, suggests some degree of plasticity in its activity pattern selection.

Only at GVNP enough data (≥10 detections) was collected on the European wildcats to allow a proper analysis of activity patterns and diel period selection. They significantly avoided being active during daytime, and used both twilight periods as expected by chance in both seasons (Appendix 3.2 Table 2). Nightime was only significantly selected in the non-breeding season ($JSI_{night} = 0.78 \pm 0.11$). Although not significant, signals of differencial use of the diel cycle between both seasons were detected ($W = 5.06$, $p = 0.08$; Appendix 3.2 Table 2). These results, and the record of several detections during daytime in other study areas (CNP, MNR and PGNP), suggest that wildcats can be plastic in the selection of activity patterns.

The stone marten revealed a strictly nocturnal and crepuscular activity pattern (table 3.2.2; Appendix 3.2 Table 2). No significant differences were detected across study areas and seasons (MWW test, table 3.2.1). The nighttime period was significantly selected (mean $JSI_{night} = 0.88 \pm 0.10$) and daytime avoided ($JSI_{day} = -1.00 \pm 0.00$). Although not significant, the stone marten revealed a tendency towards negative selection of the dawn and dusk periods (table 3.2.2; Appendix 3.2 Table 2).

Despite being detected only at four sampling seasons (2 seasons * 2 study areas), pine martens showed the most consistent activity patterns among all studied species (mean $\Delta_1 = 0.77 \pm 0.08$, table 3.2.1; Appendix 3.2 Table 1), and activity records across the diel cycle were not significantly different between study areas and seasons ($W = 6.66$, $p = 0.35$; Appendix 3.2 Table 1). Significant positive and negative selections were detected for the nightime and daytime periods, respectively (mean $JSI_{night} = 0.46 \pm 0.18$; mean

JSI_{day} = -0.65 ± 0.25), showing a clear nocturnal behaviour. Both twilight periods were generally used as would be expected by chance (Appendix 3.2 Table 2).

The common genet also showed high consistency in its activity patterns (mean Δ_1 = 0.75 ± 0.11, multiple comparison tests W = 11.09, p = 0.09; table 3.2.1). The positive selection for nighttime and avoidance of daytime reveals a nocturnal behaviour (table 3.3.2). In general, a negative selection of the twilight periods was detected, although not statistically significant (table 3.2.2; Appendix 3.2 Table 2). Pairwise comparisons revealed differences between the GVNP and CNP during breeding season (Appendix 3.2 Table 1) and a tendency for differencial use of the diel cycle between CNP in non-breeding season and GVNP in breeding season (Appendix 3.2 Table 1).

Similarly, the Eurasian badger consistentely revealed nocturnal behaviour (mean JSI_{night} = 0.94 ± 0.12), with only one daytime detection obtained amongst all study areas. All the periods of the diel cycle other than nighttime were significantly avoided (table 3.2.2; Appendix 3.2 Table 2). Despite the strong selection for the nighttime period, the Eurasian badger is still able to use different phases within the period, as suggested by a mean Δ_1 of 0.73 ± 0.08, and significant differences detected in MWW tests in several pairwise comparions (table 3.2.1; Appendix 3.2 Table 1).

The Egyptian mongoose revealed highy consistent activity pattern (Δ_1 = 0.75), being the only target species that was preferentialy active during daytime (JSI_{day} = 0.88 ± 0.06) and avoided nightime (JSI_{night} = -1.00 ± 0.00), although the former was explored differencially in both seasons (W=6.04; p = 0.05; Appendix 3.2 Table 2). Although generally not significant, the Egyptian mongoose revealed a tendency towards negative selection of the dawn and dusk periods (table 3.2.2; Appendix 3.2 Table 2).

The Iberian lynx was only present at SANP where no statistically significant differences were detected between periods of study (W=0.59; p = 0.74, table 3.2.1; Appendix 3.2 Table 1). This species exhibited significant selection and avoidance for the nighttime and daytime periods, respectively (mean JSI_{night} = 0.52 ± 0.06; mean JSI_{day} = -0.67 ± 0.01; table 3.3.2). In general, no statistically significant selection was detected for any of the twilight periods, however, the tendency was towards a negative usage of these periods (table 3.2.2; Appendix 3.2 Table 2).

Text 2 - Detailed description of temporal segregation among species results

At CNP, during non-breeding season campaign, the use of the diel cycle by red foxes and stone martens was significantly different (W=34.42, P<0.01). This asynchrony in activity patterns was supported by a Δ_1 of 0.63 ± 0.05. The red fox displayed stronger intensity of activity in the early night while the activity of the stone marten peaked after the decrease of the former (Figure 3.2.2). Altought not significant, marked differences between the activity patterns of the red fox and common genet were detected (W=5.71; p=0.06). The common genet increased activity early in the night, partially overlapping the period of intense activity with that of the red fox (Figure 3.2.2), as supported by a Δ_1 of 0.79 ± 0.06. Despite some sequential use of the nighttime period between the stone marten, common genet and Eurasian badger, suported by moderate Δ_1 values (table 3.3.3), MWW tests did not reveal significant differences.

Breeding season provided clearer evidences of diel activity segregation between mesocarnivores at CNP. Highly significant differences in activiy patterns were observed between red fox and all coexisting carnivore species (table 3.3.3). In spite of the presence of a small peak of intensity after sunset, the red fox displayed a cathemeral pattern of activity, which contrasted with the strictly nocturnal patterns of the remaing evaluated mesocarnivores, as supported Δ_1 values always under 0.66 (table 3.3.3). MWW tests also produced significant differences between stone marten and Eurasian badger activity patterns (W=7.84, p=0.02). While the former displayed a nocturnal bimodal pattern of activity with higher use of the late night, the Eurasian badger had a major peak in the early night (around 23h), after which activity decreased for the remainder of the night (Figure 3.2.2). As for the non-breeding period, the nighttime period was sequentially used by the stone marten, common genet and Eurasian badger, as supported by dominating low Δ_1 values (table 3.3.3, Figure 3.2.2).

Several cases of temporal segregation were observed at GVNP (table 3.3.3). The diurnal activity pattern of the Egyptian mongoose was significantly different from that of all other carnivores species in both seasons (table 3.3.3), and Δ_1 values were very low (0.07 - 0.20 in autum and 0.09 - 0.41 in breeding season). In non-breeding season the red fox displayed an activity pattern that differed significantly from that of the stone marten (Δ_1=0.68 ± 0.08; W=7.87, p=0.02) and of the Eurasian badger (Δ_1=0.57 ± 0.10; W=12.86; p<0.01). These differences were mainly related to differential intensity of activity of these species pairs during the nighttime and dawn period: while the activity of the stone marten and Eurasian badger peaked during nighttime and diminished towards dawn, the red fox displayed an inverse pattern (Figure 3.2.2). Significant differences were also detected between the activity patterns of European wildcats and Eurasian badgers (Δ_1=0.71 ± 0.13; W=6.88; p=0.03), which should be related with the strong unimodal pattern exhibited by the latter, which contrasted with a slight bimodal pattern of the wildcat, that peaked after sunset and before sunrise (Figure 3.2.2).

In breeding season the activity pattern of the red fox significantly differed from that of the common genet (Δ_1=0.66 ± 0.08; W=7.77; p=0.02) and, although not significant, revealed a tendency towards temporal segregation with the European wildcat (Δ_1=0.62 ± 0.09; W=4.91; p=0.09). Other species pairs that displayed statistically different activity patterns were the European wildcat *vs.* stone marten (Δ_1=0.65 ± 0.09), and the stone marten *vs.* common genet (Δ_1=0.64 ± 0.08; table 3.3.3). In this season, the common genet displayed a nocturnal, but strongly marked bimodal pattern (Figure 3.2.2), with activity peaks just after sunset and before sunset. This strategy contrasted with that of the red fox and stone marten, which intensified their activity in the middle of the night. The European wildcat displayed a smoother activity pattern, with a tendency for cathemerality, which contrasted with the marked nocturnal behavior of the stone marten and red fox (Figure 3.2.2).

The SANP was the only study area with confirmed presence of the Iberian lynx. Despite the presence of several carnivore species such as the European wildcat, stone marten and common genet, their relative abundances were very low (authors, unpublished data). As a result, activity pattern analyses were only possible for the Iberian lynx, red fox in both seasons and additionaly for the Eurasian badger in breeding season. The activity patterns of Iberian lynxes and red foxes were not statistically different in any of the seasons ($W_{\text{Non-Breeding}}$=3.12; p=0.21; W_{Spring}=0.56; p=0.76). Similarly, no circadian segregation was detected between the Eurasian badger and neither of the other coexisting carnivores in breeding season (table 3.3.3). Coefficients of activity overlap were always above or close to 0.70. Regardless of being active through the entire diel cycle, the Iberian lynx displayed a predominant bimodal activity pattern in both seasons, with peaks around sunrise and sunset (Figure 3.2.2).

The sunset activity peak was synchronous with that o the red fox in non-breeding season which, in turn, only displayed crespuscular and nocturnal activity. During breeding season, the red fox had smoother and more continuous activity during the diel cycle, but the sunset peak was consistent with that displayed in non-breeding season, and synchronous with that of the Iberian lynx (Figure 3.2.2). The Eurasian badger displayed an exclusively nocturnal bimodal pattern, somewhat consistent whith that of the other target species.

The only species which provided enough detections for activity pattern analysis in MNR study area were the pine marten in both seasons and the red fox in breeding season. During spring season, the red fox displayed a mainly unimodal nocturnal activity pattern, which contrasted with slightly bimodal pattern of the pine marten, intenser during the early night and dawn (Figure 3.2.3). Altough no significant differences were detected by MWW test (W=4.87; p=0.09), these contrasts resulted in a Δ_1, of 0.79 ± 0.09.

The red fox, pine marten and common genet were the mesocarnivores with higher detection rates at PGNP during the non-breeding season. These three species displayed highly overlaped activity patterns, as sustained by Δ_1 values above 0.85, and no significant differences by MWW tests in any of the pairwise comparisons (table 3.3.3). The unimodal pattern of the common genet actvity contrasted with the slightly bimodal one exhibited by the pine marten and the red fox (Figure 3.2.3). However, all patterns were tipically nocturnal and broadly synchronous. In the spring season, only the red fox, pine marten and stone marten produced enough data for analysis. The coefficients of activity overlap between all species were lower than those observed in non-breeding season, ranging from 0.49 ± 0.09 to 0.64 ± 0.12 (table 3.3.3). Despite the low values of actvity overlap, MWW tests failed to detect significant differences between their activity patterns in all pairwise comparisons. The pine marten displayed a smooth pattern of activity across the diel cycle, with a peak around sunset (Figure 3.2.3). This pattern contrasted with the strong bimodal nocturnal pattern of the stone marten, which displayed activity peaks after sunset and before sunrise (Figure 3.2.3). The red fox, also displayed a nocturnal pattern, but with peak of activity around 0:00 h, after which its intensity decreased until the morning (Figure 3.2.3).

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Monterroso, P., Alves, P.C., Ferreras, P. (in prep)

3.3 Spatial interactions in mesocarnivore communities in Southwestern Europe

Introduction

Ecological integrity is maintained by a complex web of inter and intra-specific relations upheld by coexisting species. Typically, in a predator community, mesopredators' biomass largely exceeds that of apex predators. Moreover, community structure of mesopredators is complex and results from a multidimensional web of interactions such a top-down regulation employed from apex predators, bottom-up regulation imposed by accessibility to feeding resources (prey), intraguild interactions by coexisting competitors or habitat quality. Further, the entanglement of interactions should increase with system complexity, as each of the species involved must adjust its position along possible positions in each niche axis so as to optimize survival and reproductive chances, and maximize resource acquisition following optimal foraging theory. Several cases of ecosystem deregulation (e.g. demographic explosion of predation-released prey species; or predation driven predator-pit control of prey populations) have been reported worldwide as a result of changes in mesocarnivore communities. Interspecific relations between mesopredators are not constant, resulting in non-equilibrium, where changing resource availability might cause shifts in the relative fortunes of the species concerned (Linnell and Strand 2000). Temporal partitioning and exploitative competition for shared resources, have been advocated as playing an important role in sustaining mesocarnivore coexistence and diversity, especially with increasing community complexity between several species pairs in Southern European mesocarnivore communities (e.g. Barrientos and Virgós, 2006; Fedriani et al., 1999, Monterroso et al., submitted). However, (Schoener 1974)found that the separation among species niches is generally multidimensional, and two is the most common number of dimensions separating species. Furthermore, the two niche axis over which segregation between species occurs consist of spatial use and resource selection (Schoener 1974). Spatial interference has been described as an important factor shaping mesocarnivore communities (Palomares et al. 1996; Zabala et al. 2009; Rauset et al. 2012). When clear asymmetrical competition occurs, the subordinate species adjusts its behaviour to minimize agonistic encounters with the superior competitor (Palomares et al. 1996; Azlan and Sharma 2006; Harrington et al. 2009). However, when asymmetry is not so clear (as in the case of mesocarnivore communities), the outcome of agonistic encounters is less certain (Donadio and Buskirk 2006), and the dominant-subordinate relation may not be so clear.

Southwestern (SW) European mesocarnivore communities include a total of seven species (six native and one introduced) which, due to historical and antropogenic causes not always occur in sympatry or coexist spatially within their distribution areas (Cabral et al. 2005; Palomo et al. 2007). While most species are widespread, others have restricted ranges. The pine marten (*Martes martes*) distribution is restricted to the northern fringe of the Iberian Peninsula (López-Martin 2007), the Egyptian mongoose (*Herpestes ichneumon*) to the SW Iberian Peninsula (Palomares 2007; Balmori and Carbonell 2012), and the Iberian lynx (*Lynx pardinus*) to two unconnected populations in the south of Spain (Sarmento et al. 2009; Gil-Sánchez and McCain 2011). As a consequence mesocarnivore communities vary in composition and structure across the SW Europe, potentially compelling interspecific relations between the same species pairs to change from one area to another. Within the SW European mesocarnivore communities, the potential for exploitation and/or interference competition exists among several species pairs along various niche dimensions (table 1). However, resource partitioning is a community wide phenomenon and the interactions involved are complex. Therefore, the analysis and interpretation of such interspecific relations require a holistic approach (Schoener 1974; Ritchie and Johnson 2009).

In this work, we analyse camera trapping data on mesocarnivores across several areas in SW Europe to investigate their co-occurrence patterns. We aimed to address three main biological questions: a) Are there relations of spatial avoidance or association among species in SW mesocarnivore communities?; b) Is the occurrence of subordinate species conditional on the presence of superior competitors?; c) Does the presence of a superior competitor influence subordinate species detectability?

Methods

Study areas

The Iberian Peninsula (IP) is mostly included in two biogeographical regions: the Mediterranean region, which occupies roughly 2/3 of the IP; and the Atlantic region, which is restricted to the northern fringe and extends towards the Pyrenees (European Environmental Agency 2012). In order to obtain data from the mesocarnivore communities of both biogeographical regions, five study sites distributed across the IP were selected (figure 3.3.1): the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP), located in Portugal; and the Cabañeros National Park (CNP), the Sierra de Andújar Natural Park (SANP) and the Muniellos Natural Reserve (MNR), located in Spain. GVNP, CNP and SANP are located in the Mediterranean region, and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez et al. 2004). Scrublands are mainly associated with steeper slopes, elevation ridges and main water bodies, and are dominated by *Pyro-Quercetum rotundifoliae* and *Myrto communis–Querco rotundifoliae* series and other subserial stages (Costa et al. 1998; Rivas-Martinez 1981). In CNP and GVNP, areas with gentler slopes are mainly occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*) scattered within a grassland matrix (García-Canseco 1997). In SANP, areas with gentler slopes are rather dominated by Stone pine (*Pinus pinea*) and Maritime pine (*Pinus pinaster*) forests with and without understorey (Gil-Sánchez et al. 2006).

The PGNP and MNR are located in the Atlantic region, and have a temperate oceanic submediterranean bioclimate (Rivas-Martínez et al. 2004). The landscapes consist of mountainous agricultural–forest mosaic, where mountaintops are mostly dominated by scrublands with Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially covered by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* sp. and *Fagus* sp.). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Carvalho and Gomes 2004; Prieto and Sánchez 1996).

A study area of approximately 6000ha within each of the study sites was selected, based on criteria of ecosystem conservation status and logistic factors. The only exception was the SANP study area, where we were only allowed to work in an area of 2700ha.

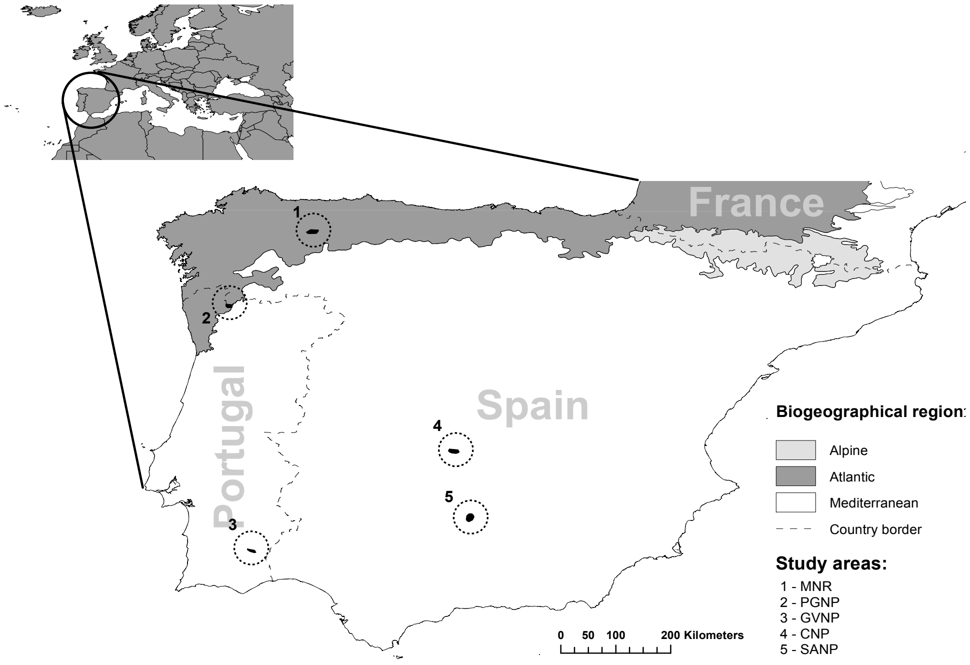

Figure 3.3.1 Location of the study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park; SANP - Sierra de Andújar Natural Park.

Field sampling

All study areas were sampled in two seasons: *Non-breeding* (July-October), when the offspring of most medium-sized carnivores from that year become independent; and *Breeding* (February-April), during these species' breeding season (Blanco 1998).

Data collection was obtained by camera-trapping methods, and followed the sampling scheme and trap sites selection described by Monterroso et al. (2011; 2013). Briefly, 32 to 41 cameras were uniformly spaced in each study area following a grid-sampling scheme in approximately 1.4km intervals. However, at SANP only 20 cameras were placed due to the smaller size of this study area. Overall, our sampling consisted of 173 camera-trapping stations. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) and ScoutGuard (HCO OutDoor Products, Norcross, Georgia, USA). Cameras were mounted on trees approximately 0.5 – 1.0m off the ground and set to record time and date when triggered. We programmed cameras with the minimum time delay between consecutive photos to maximize the number of photos taken per captured individual. Camera-traps were maintained in the field for a minimum period of 28 days and were inspected for battery or card replacement every 7 to 14 days. A combination of Lynx urine and Valerian extract solution were used as attractants to incite animals' curiosity and thus increase detection probabilities (Monterroso et al. 2011). Five to 10 mL of each attractant were sprayed into a cotton gaze, held inside perforated separated containers (plastic or PVC), at a distance of 10-15 cm from each other ~30 cm off the ground. Attractants were re-baited every 7 to 14 days. Target species consisted of three of the most common mesocarnivore species present in Iberian communities: the red fox (*Vulpes vulpes*), the stone marten (*Martes foina*) and the common genet (*Genetta genetta*).

Statistical analysis

Spatial co-occurrence patterns between each of the species pairs were evaluated by likelihood-based occupancy modeling, developed in the software PRESENCE 6.0 (Hines and Mackenzie 2013; Mackenzie et al. 2006; MacKenzie et al. 2002). We divided our survey periods into 1-week sampling occasions during which the detection/non-detection data on each target species was recorded. Then, we created species-specific detection histories, allowing us to assess factors that may affect occupancy and detection probabilities, as well as species co-occurrence and detectability patterns. As co-occurrence models can easily become very complex due to the increase of model parameters (Fauteux et al. 2013), we assumed that mesocarnivore occupancy remained unchanged across seasons, but allowed detection probabilities to vary.

To account for potential heterogeneity in the probabilities of occupancy, detection (*p*) and interspecific interactions we assessed several covariates: distance to water, the proportion of each habitat in home range (HR), European rabbit (*Oryctolagus cuniculus*) abundance, rodents (order Rodentia) abundance (both potential prey for mesocarnivores), season and study area (table 3.3.1). Study area was included as a proxy covariate for unaccounted local effects (e.g. level of human protection/disturbance). We estimated distance to water by measuring the linear distance from the sampling site to the nearest water source. We reclassified original vegetation maps of each of the study areas into five dominant habitat types: oak autochthonous woodlands, coniferous woodlands, mixed woodlands, scrublands and open areas. We then estimated the proportion of each habitat type in an 800m radius circular buffer (≈ 2.0 km^2) around camera trapping sites. This buffer size was selected because it approximately represents the home range size for mesocarnivores species in Europe (Monterroso et al. 2009; Santos-Reis et al. 2005; Travaini et al. 1993; Zalewski and Jędrzejewski 2006). Rodent and European rabbit (*Oryctolagus cuniculus*) abundance was assessed for each camera station and period by calculating their trapping success (TS). TS estimation followed the methods described by the previous studies, and consisted of the number of independent detections per 100 trap days (Davis et al. 2011; Kelly and Holub 2008). Independence among carnivore records was assumed when photographs of the same species were taken at least 30-min apart, unless animals were clearly individually distinguishable (Davis et al. 2011; Kelly and Holub 2008). Regional effects of habitat type and prey availability were evaluated by considering the interaction between these covariates and the bioclimatic region (Atlantic *vs.* Mediterranean). All continuous covariates were transformed to z-scores (Mackenzie et al. 2006).

Table 3.3.1. Covariates used to model target species occupancy, co-occurrence and detection probabilities.

Type	Covariate	Scale	Values	Model which included covariate
Season [SS]	Non-breeding	-	Reference	p
	Breeding	-	Bin	p
Global [RGN]	Atlantic [Atl]	-	Reference	p
	Mediterranean [Mdt]	-	Bin	
Study area [SA]	Cabañeros National Park [CNP]	-	Reference	ψ
	Guadiana Valley Natural Park [GVNP]	-	Bin	ψ
	Peneda-Gerês National Park [PGNP]	-	Bin	ψ
Habitat	Oak Woodlands [BRL]	Local / HR	Bin / Cont	p / ψ
	Coniferous Woodlands [CNF]	Local / HR	Bin / Cont	p / ψ
	Mixed Woodlands [MXD]	Local / HR	Bin / Cont	p / ψ
	Scrublands [SCR]	Local / HR	Bin / Cont	p / ψ
	Open areas [OPN]	Local / HR	Reference / Cont	p / ψ
	Distance to water [WTR]	HR	Continuous	ψ
Prey	Rodent abundance [ROD]	Local	Continuous	ψ
	Rabbit abundance [RBT]	Local	Continuous	ψ

Local - habitat or prey abundance where camera station was located; HR - Proportion occupied by a given habitat at the home-range scale (800m buffer surrounding camera station); Bin - Binary variable (presence/absence); Cont. - Continuous variable; Reference - covariate used as reference in the occupancy models.

The evaluation of the spatial interactions of each of the species pairs followed a two-step procedure. First, we used single season singles species occupancy models to evaluate the best detection models and the informative covariates for each species individually (Richmond et al. 2010; Steen et al. 2013). Then, we modeled first order spatial interactions between target species by using the psiBa parameterization (Richmond et al. 2010), where the probability of detection and occupancy of the subordinate species is modeled as conditional on the occupancy of the dominant species.

We assumed the red fox competitive dominance over stone martens and common genets based on average bodyweight differences (Blanco 1998). The close body sizes of stone martens and common genets precluded us from defining an unambiguous dominant species (López-Martin 2003). Therefore we used a criterion of 'indigenously', where we assumed that, as stone martens are indigenous of the Iberian Peninsula and common genets are an introduced species from Africa (Gaubert et al. 2011), the former is expected to have some competitive advantages as it should be better adapted to the Iberian ecosystems. Hence, we defined stone martens as the dominant species in the stone marten *vs*. common genets co-occurrence models.

For each target species, we developed single season occupancy models. We first held occupancy constant and proceeded to find the best detection model (Richmond et al. 2010; Sarmento et al. 2010). Following the recommendations of Arnold (2010) for exploratory approaches that involve many variables, we used a sequential modeling approach to find the best detection model set and discard uninformative variables. Therefore, we started by building a full effects detection model and performed a backward-stepwise model selection to sequentially eliminate the covariate with the weaker effect size (β/SE). This process was kept until the deletion of an additional covariate led to an increase in AICc (Pagano and Arnold 2009). After finding the best detection model, we held it constant and evaluated the individual effect of all covariates and covariate interactions in the occupancy probabilities by building single covariates' models. We selected as informative covariates for inference if 85% confidence intervals did not include zero (Arnold 2010). Then we built a full effects occupancy model using only informative covariates. The final step of single species models consisted in a backward-stepwise procedure, similar to that above described for the detection model. For each of the species' final model set, we selected as informative covariates for inference those that were in models within 2 AICc units of the top-supported model and whose 85% confidence intervals did not include zero (Arnold 2010).

The best detection models encountered for each of the target species were used, and held them constant in across our entire co-occurrence model panel. Then, we built the most complete occupancy models for each of the target species (defined in the singles species occupancy modeling step) and performed a backward-stepwise model selection to sequentially eliminate the covariate with the weaker effect size (β/SE), in a similar fashion as that described for single species model selection.

Co-occurrence models followed the following parameterization (adapted from Richmond et al., 2010): ψ^{A} denotes the unconditional probability of occupancy of species A (dominant), ψ^{BA} denotes the conditional probability of occupancy for species B (subordinate), given species A is present; ψ^{Ba} denotes the conditional probability of occupancy for species B, given species A is absent; p^{A} denotes the unconditional detection probability of species A; p^{B} denotes the unconditional detection probability of species B; r^{A} denotes the conditional detection probability of species A, given that both species are present; r^{B} denotes the conditional detection probability of species B, given that both species are present. As we wanted to assess the effect of a dominant species (species A) occupancy in the occupancy and detection probabilities of the subordinate species (species B), we started from the same (full effects) models considering conditional ($\psi^{BA} \neq \psi^{Ba}$) and unconditional ($\psi^{BA} = \psi^{Ba}$) occupancy probabilities, and subordinate species detection probabilities as conditional ($p^{B} \neq r^{B}$) or unconditional ($p^{B} = r^{B}$) on the presence of the dominant species.

A species interaction factor (φ) was calculated (Richmond et al. 2010). If φ <1, suggests that there is evidence of avoidance, whereas φ > 1 reflects species aggregation (i.e. species A and species B tend to co-occur). Only species/study area combinations where the combined proportion of positive sampling occasions was ≥ 5% were included in the analysis.

We used Spearman's rank correlation (r_s) to test for collinearity among the landscape variables; if variables were correlated (r_s > 0.70) we kept the variable with the greatest univariate effect size (β/SE) as a potential covariate for the probability of detection (Zar 2005). We evaluated the candidate models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). Because no goodness-of-fit test exists for co-occurrence models (Steen et al. 2013), we could not correct them for overdispersion. If no single model accounted for >90% of the total model weights, then we used model averaging. We model averaged by extracting the top 95% model confidence set and recalculating model weights (Burnham and Anderson 2002). We calculated model-averaged estimates using the spreadsheet developed by B. Mitchell (http://www.uvm.edu/%7Ebmitchel/software.html).

Results

Camera-trapping results

Red foxes, stone martens and common genets were the most common species detected in all study areas over a total of 1296 sampling occasions (259.2 ± 33.7 sampling occasions/study area). Red foxes were detected in 300 sampling occasions (60.0 ± 35.4 sampling occasions/area), while stone martens and common genets were detected in 111 (22.2 ± 9.6 sampling occasions/area) and 75 (15.0 ± 4.4 sampling occasions/area), respectively (table 3.3.2). European wildcats and Eurasian badgers were detected in all study areas in 62 (12.2 ± 5.1 sampling occasions/area) and 58 (11.6 ± 4.2 sampling occasions/area) sampling occasions, respectively. Pine martens were only detected at MNR and PGNP, in 43 and 27 sampling occasion, respectively. Egyptian mongooses were detected in 5 sampling occasions at CNP and in 33 sampling occasions at GVNP. The Iberian lynx was only detected at SANP, in 20 sampling occasions. The high variability in the proportions of positive occasions for each species across study areas prevents broad evaluations of all species pairs. For this reason, further analyses of co-occurrence patterns were assessed only for the three most common species: the red fox, stone marten and common genet. The proportions of stone marten and common genet positive sampling occasions at SANP and MNR were always below 3.0% of all valid occasions. For this reason, these study areas were discarded from further analysis. The joint proportion of positive sampling occasions for the red fox/stone marten, red fox/common genet and stone marten/common genet complexes at the CNP, GVNP and PGNP study areas was always superior to 10.0%, and were therefore considered.

Table 3.3.2. Number of positive 1-week sampling occasions and respective proportion (in brackets) over all sampling occasions for mesocarnivores in each of the study areas.

	Red fox	Stone marten	Common genet	European wildcat	Pine marten	Eurasian badger	Egyptian mongoose	Iberian lynx
CNP	201 (65.0%)	47 (15.1%)	29 (9.3%)	11 (3.4%)	0 (0.0%)	23 (7.0%)	5 (1.5%)	0 (0.0%)
GVNP	36 (15.3%)	44 (18.6%)	16 (6.8%)	31 (12.1%)	0 (0.0%)	15 (5.9%)	33 (12.9%)	0 (0.0%)
SANP	23 (16.5%)	2 (1.4%)	3 (2.2%)	1 (0.1%)	0 (0.0%)	16 (10.0%)	0 (0.0%)	20 (12.5%)
MNR	17 (5.2%)	7 (2.2%)	9 (2.8%)	13 (3.8%)	43 (12.6%)	3 (0.1%)	0 (0.0%)	0 (0.0%)
PNGP	23 (8.1%)	11 (3.9%)	18 (6.3%)	6 (2.1%)	27 (9.4%)	1 (0.0%)	0 (0.0%)	0 (0.0%)

CNP - Cabañeros National Park; GVNP - Guadiana Valley Natural Park; SANP - Sierra de Andújar Natural Park; Peneda-Gerês National Park; MNR - Muniellos Natural Reserve.

Single species occupancy models and informative covariates

The best detection model for the red fox included regional and habitat effects. Red fox detectability was higher in the Mediterranean region ($\beta = 2.61 \pm 0.37$). Regarding habitat type, detectability was higher at oak ($\beta = 0.82 \pm 0.27$) and lowest at coniferous woodlands ($\beta = -1.65 \pm 0.44$).

The proportions of open areas, coniferous and oak woodlands at the home range scale, as well as the abundance of rodents influenced red fox occupancy probability. The proportion of open areas had a positive effect on occupancy probability ($\beta = 1.07 \pm 0.60;\ \omega = 0.06$) and exhibited regional effects, as it was more informative at the Mediterranean region ($\beta = 1.07 \pm 0.60;\ \omega = 0.15$) than in the Atlantic region ($\beta = -0.09 \pm 0.42;\ \omega = 0.02$). Coniferous woodlands had a negative effect ($\beta = -0.60 \pm 0.33;\ \omega = 0.14$), which was stronger in the Mediterranean region ($\beta = -0.57 \pm 0.32;\ \omega = 0.14$). Although with lower weight of evidence ($\omega = 0.04$), oak woodlands negatively affected the probability of red fox occupancy in the Mediterranean region ($\beta = -1.02 \pm 0.89$). Distance to water revealed positive effect ($\beta = 0.40 \pm 0.38$), but also with small weight of evidence ($\omega = 0.04$). We found no evidence supporting that mammalian prey abundance influences the probability of red fox occupancy.

We identified seasonal effects on stone marten, with detection probabilities being slightly higher in non-breeding season. In the Mediterranean region stone marten detectability was 1.43 ± 0.62 higher than in the Atlantic study area. Habitat type also influenced detection probability, and was higher in oak woodlands ($\beta = 1.23 \pm 0.40$) and lowest in open areas (reference habitat). Univariate contributions revealed that probability of stone marten occupancy was positively affected by the proportion of oak woodlands ($\beta = 1.61 \pm 1.02;\ \omega = 0.13$), especially in the Mediterranean region ($\beta = 1.65 \pm 1.03;\ \omega = 0.16$), and negatively affected by the proportion of scrublands ($\beta = -1.28 \pm 1.00;\ \omega = 0.07$) and distance to water ($\beta = -0.70 \pm 0.37;\ \omega = 0.12$). Stone marten occupancy also exhibited regional differences in the responses to these covariates, which were stronger in Mediterranean. Interestingly, rodent abundance exhibited a negative influence on the probability of stone marten occupancy. However, while it was informative, this covariate's strength was small and had little weight of evidence ($\beta = -0.03 \pm 0.02;\ \omega = 0.05$).

The detectability of common genets was not influenced by biogeographical region nor season. However, it was significantly affected by habitat type, and detectability was higher at oak woodlands ($\beta = 1.79 \pm 0.46$), mixed woodlands ($\beta = 2.54 \pm 0.65$) and scrublands ($\beta = 1.56 \pm 0.43$) than at open habitat (reference habitat). Informative covariates in common genets occupancy models were the proportion of open areas, scrublands, oak and coniferous woodlands in the home range. While the proportion of open areas had a negative relation with the probability of genets' occupancy ($\beta = -0.75 \pm 0.31;\ \omega = 0.47$), scrubland coverage showed the inverse pattern, although with a less precise estimate ($\beta = 2.67 \pm 2.48;\ \omega = 0.28$). Oak woodlands were positively associated with common genets' occupancy ($\beta = 0.89 \pm 0.73;\ \omega = 0.02$), especially in the Atlantic study area ($\beta = 0.85 \pm 0.70;\ \omega = 0.03$), and coniferous woodlands in the Mediterranean areas were negatively associated with it ($\beta = -0.53 \pm 0.47;\ \omega = 0.02$). However, these latter had little influence, as reflected by their low weight of evidence ($\omega < 0.05$).

Table 3.3.3. Single species single season occupancy models for the red fox, stone marten and common genet, within the top ranked < 2 Δ AIC units.

Species	Detection model	Occupancy model	AICc	Δ AICc	K	ω
Red fox	p(RGN,BRL,CNF,SCR)	ψ (SA,OPN*Mdt)	767.68	0	9	0.120
		ψ (SA,CNF)	767.77	0.09	9	0.114
		ψ (SA,CNF,WTR)	767.96	0.28	10	0.104
		ψ (SA,CNF*Mdt)	768.09	0.41	9	0.098
		ψ (SA,OPN*Mdt,CNF,WTR)	769.39	1.71	11	0.051
		ψ (SA)	769.48	1.80	8	0.049
		ψ (SA,OPN)	769.60	1.92	9	0.046
Stone marten	p(SS,RGN,BRL,CNF,MXD,SCR)	ψ (SA,BRL*Mdt,WTR,ROD)	573.39	0	13	0.134
		ψ (SA,BRL*Mdt,ROD)	573.40	0.01	12	0.134
		ψ (SA,BRL*Mdt)	573.91	0.52	11	0.104
		ψ (SA,BRL)	574.23	0.84	11	0.088
		ψ (SA,WTR)	574.41	1.02	11	0.081
		ψ (SA,WTR*Mdt)	574.70	1.31	11	0.70
		ψ (SA,BRL*Mdt,WTR,SCR,ROD)	574.79	1.4	14	0.067
Common genet	*p*(BRL,CNF,MXD)	ψ (SA,OPN,SCR)	419.10	0	9	0.263
		ψ (SA,OPN)	420.13	1.03	8	0.160
		ψ (SA,OPN,CNF*Mdt)	420.30	1.20	9	0.140
		ψ (SA,SCR)	420.99	1.89	8	0.102

SS - Season; SA - Study areas; OPN - Open areas; BRL - Oak woodlands; CNF - Coniferous woodlands; SCR - Scrublands; WTR - Distance to water; ROD - Rodent abundance; 'X'*Mdt - A given 'X' habitat in the Mediterranean region; RGN - Biogeographical region.

Spatial relations among coexisting mesocarnivores

Our models of co-occurrence suggest that the detection patterns of stone martens is most likely conditional on the presence of red foxes, as supported by cumulative Aikaike weights: $\omega_{conditional} = 0.87$ *vs.* $\omega_{unconditional} = 0.13$ (tables 4 and 5).

Although with low precision, model averaged estimates revealed that stone marten detectability is lower when red foxes occur, especially during breeding season: $p_B = 0.05\ [0.02 - 0.15]$ *vs.* $r_{BA} = 0.04\ [0.00 - 0.33]$. However, we found no evidence of spatial interaction between these species, as models considering stone martens' occupancy unconditional of the presence of red foxes have greater support: $\omega_{unconditional} = 0.74$ *vs.* $\omega_{conditional} = 0.26$ (table 3.3.4).

Our models provided stronger support for unconditional detection ($\omega_{unconditional} = 0.71$ *vs.* $\omega_{conditional} = 0.29$) and occupancy probabilities ($\omega_{unconditional} = 0.71$ *vs.* $\omega_{conditional} = 0.29$) between red foxes and common genets (tables 4 and 5). This suggests that common genets do not exhibit any spatially explicit behavioural response to the presence of red foxes in our study areas.

Table 3.3.4. Relative support for the different formulations of two-species interaction models, given by the summed Aikaike weights for all models sharing a given model structure. Occupancy (ψ) and detection (*p*) of the subordinate species is either conditional or unconditional on the dominant species.

Species pair	**Occupancy**	**Detection**		
		Conditional	*Unconditional*	Total
Red fox / Stone marten	*Conditional*	0.129	0.128	**0.257**
	Unconditional	0.743	0.001	**0.744**
	Total	**0.872**	**0.128**	-
Red fox / Common genet	*Conditional*	0.112	0.182	**0.294**
	Unconditional	0.174	0.531	**0.705**
	Total	**0.286**	**0.713**	-
Stone marten / Common genet	*Conditional*	0.462	0.300	**0.762**
	Unconditional	0.230	0.008	**0.238**
	Total	**0.692**	**0.308**	-

The stone marten *vs.* common genet models provided stronger support for conditional detection ($\omega_{conditional} = 0.69$ *vs.* $\omega_{unconditional} = 0.31$) and occupancy probabilities ($\omega_{conditional} = 0.76$ *vs.* $\omega_{unconditional} = 0.24$; table 3.3.4). These species basal interaction factor (φ) was 1.30, suggesting that they tend to co-occur. However, this co-occurrence pattern is minor at GVNP, where these species tend to occur independently ($\varphi = 1.08$). The proportion of scrublands in their home range mediates the strength of the interaction between stone martens and common genets, as they strongly co-occur in landscapes with lower scrubland coverage and tend to be distributed independently at higher scrubland coverage values (table 3.3.2). Also, common genets detection probability is higher when they co-occur with stone martens: $p_B = 0.04\ [0.00 - 0.99]$ *vs.* $r_{BA} = 0.34\ [0.05 - 0.79]$. However, given the strong association between these to species, both the estimates of occupancy (ψ^{Ba}) and detection (pB) probabilities in the absence of stone martens were largely imprecise: $\psi^{Ba} = 0.04\ [0.00 - 1.00]$; p_B= 0.01 [0.00 - 1.00].

Table 3.3.5. Co-occurrence single season occupancy models within the top ranked < 2 Δ AIC units.

Species pair	Occupancy model	Detection model	AICc	Δ AICc	*K*	ω
Red fox / Common genet	ψ^{A} (CNF), $\psi^{BA} = \psi^{Ba}$ (OPN)	*p*A*p*B	1189.78	0	11	0.239
	ψ^{A} (CNF,WTR), $\psi^{BA} = \psi^{Ba}$ (OPN)	*p*A*p*B	1190.44	0.66	12	0.172
	ψ^{A} (CNF), $\psi^{BA} \neq \psi^{Ba}$ (OPN)	*p*A*p*B	1191.75	1.97	12	0.089
Red fox / Stone marten	ψ^{A} (SA), $\psi^{BA} = \psi^{Ba}$ (GVNP)	*p*A*p*B*r*B	1358.01	0	14	0.212
	ψ^{A} (SA), $\psi^{BA} = \psi^{Ba}$ (SA)	*p*A*p*B*r*B	1358.20	0.19	14	0.192
	ψ^{A} (SA,CNF), $\psi^{BA} = \psi^{Ba}$ (SA)	*p*A*p*B*r*B	1358.82	0.81	15	0.141
	ψ^{A} (SA,CNF), $\psi^{BA} = \psi^{Ba}$ (SA,ROD)	*p*A*p*B*r*B	1359.07	1.06	16	0.125
Stone marten / Common genet	ψ^{A} (GVNP,BRL*Mdt), $\psi^{BA} \neq \psi^{Ba}$ (GVNP)	*p*A*p*B*r*B	968.29	0	14	0.2364
	ψ^{A} (GVNP,BRL*Mdt,WTR), $\psi^{BA} \neq \psi^{Ba}$ (GVNP,SCR)	*p*A*p*B	968.56	0.27	15	0.2066
	ψ^{A} (GVNP,BRL*Mdt,WTR), $\psi^{BA} = \psi^{Ba}$ (GVNP,OPN)	*p*A*p*B*r*B	969.24	0.95	15	0.147
	ψ^{A} (GVNP,BRL*Mdt), $\psi^{BA} \neq \psi^{Ba}$ (GVNP,OPN)	*p*A*p*B*r*B	969.62	1.33	15	0.1216

SA - Study areas; GVNP - Guadiana Valley Natural Park; OPN - Open areas; BRL - Oak woodlands; CNF - Coniferous woodlands; SCR - Scrublands; WTR - Distance to water; ROD - Rodent abundance; ‘X’*Mdt - A given ‘X’ habitat in the Mediterranean region; Rgn - Bioclimatic region.

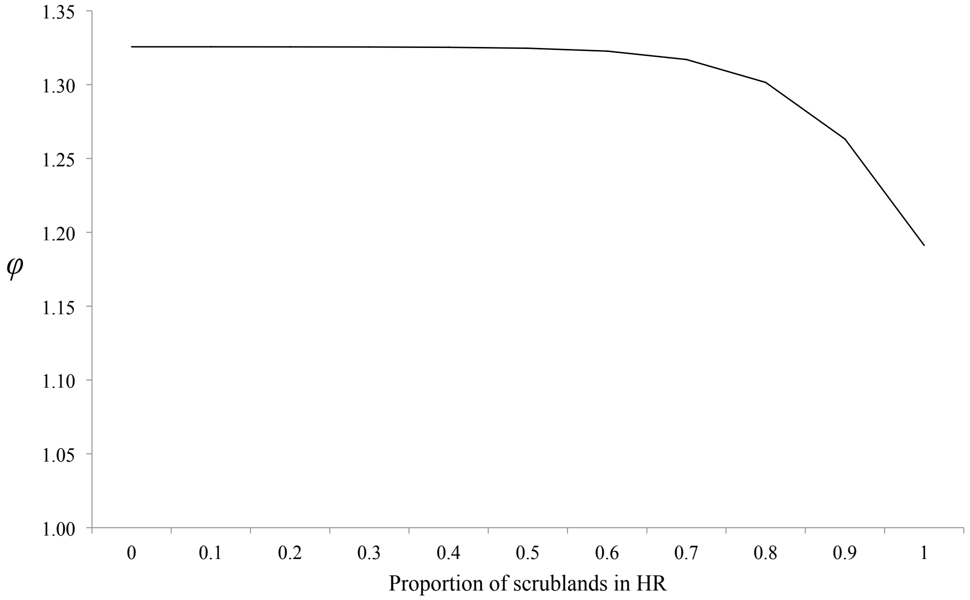

Figure 3.3.2. Species interaction factor (φ) for stone martens and common genets as a function of the proportion of scrublands in their home-range.

Discussion

In several instances, competitive exclusion has been advocated as the main reason explaining of the unexpected distributional or habitat usage patterns in mesocarnivore communities, even in the absence of apex predators (Pereira et al. 2012; Zabala et al. 2009). However, we found no evidence of competitive exclusion in neither of the analized species pairs. Moreover, we found no evidence supporting that the presence of a potentially dominant competitor would have any kind of negative influence in the probability of the subordinate species' occupancy.

All covariates tested in our single species models for red fox occupancy had low weight of evidence. This is in accordance with tred foxes' generalistic behavior (Larivière and Pasitschniak-arts 1996). Singles species models for stone martens revealed a positive association with the proportion of oak woodlands in their home range and a negative effect of the distance to water sources, especially in the Mediterranean region. This is concurrent with previous findings of other authors, who suggest that stone martens are drawn to areas with vegetative cover of high structural complexity, where they can find shelter as well as benefit from a diversity of feeding resources such as fruits and berries, rodents and birds (Mortelliti and Boitani 2008; Sarmento et al. 2010; Virgós et al. 2010; Virgós and García 2002). The negative effect of the abundance of rodents was an unexpected result, even though this effect was small. Despite the generalistic feeding behaviour of stone martens, (Genovesi et al. 1996; Rödel and Stubbe 2006), rodents are always an important food item (López-martín 2006; Zhou et al. 2011). In spite of the low rodent consumption at GVNP (0.7% of ingested biomass; unpublished data), probably due to the high abundance of European rabbits (*Oryctolagus cuniculus*) at CNP and PGNP (Monterroso et al. 2013), rodents consisted of 9.2 and 30.3% of the overall ingested biomass, respectively (Monterroso et al., in prep; unpublished data). Therefore, we believe that the avoidance of areas with high rodent density might be an artefact that results from the interference of confounding effects of unaccounted covariates. At GVNP, European rabbits constitute 86.2% of all ingested biomass, whereas at CNP and PGNP fruits provide the greatest contribution for stone martens diet, consisting of 53.6 and 60.5% of ingested biomass (unpublished data). Its is possible that stone martens are mainly attracted to feeding hotspots, where the energy expenditure employed to acquire food is minimized, which might not coincide with the spatial distribution of rodents' abundance.

We assumed the red fox to be a dominant competitor over the other studied species (Pereira et al. 2012). However, the only interaction supported by our models between red foxes and any of the other target species was the lower detectability of stone martens in the areas occupied by red foxes. This suggests that, while not being able to competitively exclude stone martens, red foxes may impose a landscape of fear (Brown et al. 1999; Laundré et al. 2001), compelling stone martens to adjust their behaviour in the areas of co-occurrence, becoming less conspicuous. However, given the close relationship between abundance and detectability (McCarthy et al. 2013), it is also possible that the lower detection detection rates of stone martens in areas of co-occurrence could be the reflection of localized lower abundances. If this is the case, then a suppressive effect of red foxes over stone martens occurs, even if its not "captured" by occupancy probabilities. The trophic ecology of these two species may be involved in the observed patterns. Both species are feeding generalists, which exhibit preferencial consumption of the most available feeding resources (Díaz-Ruiz et al. 2013; Genovesi et al. 1996; Larivière and Pasitschniak-arts 1996; López-martín 2006). In our study areas, as in much of their Iberian range, the red fox and the stone marten feed mainly on fruits during autumn, complementing it with other feeding resources, such as rodents, lagomorphs and arthropods (Guzmán 1997; Rosalino and Santos-Reis 2009). In winter and spring, their diets tend to converge due to the lower availability of feeding resources (Carvalho and Gomes 2004; Díaz-Ruiz et al. 2013; Guzmán 1997). The exception would be GVNP, where both prey heavily on European rabbits (Monterroso et al. 2006; unplublished data). This suggest that, in these areas of sympatry, they are most likely drawn to feeding resources' hotspots, which will increase the chances of direct encounters. Ecological theory suggests that, if a shared resource is not limiting, the competitive stress between co-existing species relaxes enabling long term co-existence (Linnell and Strand 2000; Ritchie and Johnson 2009). However, this coexistence might be facilittated by the avoidance of direct encounters (Fedriani et al. 1999; Linnell and Strand 2000), which may be dangerous given that the body weight ratio between red foxes and stone martens (4.0; Blanco 1998) falls within the interval where intraguild predation events are most frequent: 2.0 - 5.4 (Donadio and Buskirk 2006).

Our common genets' singles species occupancy models supported that occupancy rates were negatively affected by the amount of open habitats (i.e. pastures, agricultural fields or meadows) in their home range. The common genet has been described as habitat generalist, but always requiring vegetative cover and benefiting from habitats with a developed vertical component (i.e. woodlands and forests) (Camps 2011; Matos et al. 2008; Santos-Reis et al. 2005; Sarmento et al. 2010; Sarmento et al. 2009). Regarding their trophic ecology, common genets are mainly rodent consumers (López-Martín 2006; Virgós et al. 1999). Our results are coherent with these assertions as this species exploited woodlands and scrublands in our study areas, where vegetation cover can provide shelter and denning places, as well as their staple prey, i.e. rodents (Calzada 2007; Pereira et al. 2012; Virgós et al. 1999; Zabala et al. 2009). Foxes, however, may explore all kinds of habitats, namely areas with scarce vegetation, as it was observed in our study areas. This hability for the exploitation of distinct habitats and prey, may be sufficient to allow them to co-occur with an alleviated competitive stress. In fact, several studies in SW Europe have reported the co-existence of red foxes and common genets with no suggestion of any kind of competitive stress (Matos et al. 2008; Sarmento et al. 2010). Further, the arboreal behaviour of common genets allows them to thoroughly explore the vertical component of forested habitats, fact that has been suggested as a behavioural trait that aids their co-existence with red foxes (Pereira et al. 2012).

The stone marten and common genet have very similar ecological requirements, which means that they often overlap extensively their ecological niches when in sympatry (López-martín 2006; Ruiz-Olmo and López-Martín 2001; Sarmento et al. 2010; Zabala et al. 2009). They are habitat generalists that rarely venture into open areas (Mangas et al. 2007; Virgós et al. 2002); although genets are more strictly dependent on rodents, both significantly consume these prey (López-martín 2006; Santos-Reis et al. 2005); and both species have strictly nocturnal activity (Monterroso et al., accepted). Previous work focusing on the spatial patterns of these species simultaneously provide contrasting results. Zabala et al. (2009) invoke the competitive exclusion principle (Hardin 1960) to explain these species spatial segregation in the Bask country (N Spain). These authors suggest that common genets drive stone martens to sub-optimal habitats. Pereira et al. (2012) found contrasting results in central Portugal. These authors found that stone martens occupy the most densely vegetated authotonous woodland, which had a greater abundance of rodents, whereas common genets used a sub-optimal habitat (Eucaliptus forests), presumably to avoid competition with red foxes. However, Sarmento et al. (2010) failed to detect any effect of competitior abundance in the probability of mesocarnivores' occupancy in Serra da Malcata Natural Reserve (central Portugal), and detected high degrees of overlap in the spatial distributions of stone martens and common genets. Our results do not support any kind of spatially segregated distribution between stone martens and common genets. In fact, we found common genets be more conspicuous in the areas of co-occurrence. We suggest two potential explanations for this pattern, which may act alone or simultaneously. First, areas of co-occurrence are likely to be areas with good conditions (i.e. good habitat and feeding resources availability) for both species, where genets can reach higher densities, consequently increasing detection probabilities (McCarthy et al. 2013). Secondly, given the ecological similarity between stone martens and genets, it is possible that they coincide in prey hotspots, especially if prey is spatially clustered. López-Martin (2003) suggested that behavioural adjustments in these two species along other niche axes (eg. temporal niche) or at finer scales could facilitate coexistence. Indeed, Monterroso et al. (accepted) found nocturnal mesocarnivores to exhibit asynchronous activity peaks in the diel cycle. Barrientos and

Virgós (2006), found stone martens and genets to reduce their exploitative competition by sequentially using the available feeding resources. Moreover, some indications of fine scale spatial avoidance between these two mesocarnivores have been proposed (Pereira et al. 2012; Santos-Reis et al. 2005). We found the strength of association between these species to be mediated by the amount of scrublands in their home-range. Given their preference for this habitat type, especially in Mediterranean ecosystems (Mangas et al. 2007), its reduction in availability would force them to coincide in the existing patches (Virgós et al. 2002; Virgós and García 2002), especially if feeding resources are locally abundant (Mortelliti and Boitani 2008).

Conclusions

The competitive stress between sympatric carnivores is largely mediated by the availability of a shared resource (Donadio and Buskirk 2006; Linnell and Strand 2000), and coexistence may be promoted through behavioural adjustments that reduce the probability of agonistic encounters (Carothers and Jaksić 1984; Ritchie and Johnson 2009; Wilson et al. 2010). In SW European carnivore communities, as in much of the rest of the world, apex predators have been largely extirpated releasing mesocarnivores from top-down regulation and unbalancing interspecific relations (Estes et al. 2011; Prugh et al. 2009). Our results do not support the existence of competitive exclusion among the three studie mesocarnivores (red fox, stone marten and common genet) , at least along the spatial niche axis. However some evidence of interference between red foxes and stone martens was observed, translated by reduced conspicuity of the latter species in areas of co-occurrence, suggesting a landscape of fear effect. No evidence of spatial avoidance exists between the ecologically similar stone martens and common genets, but rather a tendency for co-occurrence mediated by the availabilty of favorable habitat. We suggest that further research on mesocarnivores' community-wide ecological relations should be carried out to allow a better understanding of how habitat structure and prey availability affects fine-scale interactions and what mechanisms act in promoting their co-existence.

References

Adkins CA, Stott P (1998) Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. J Zool 244:335–346.

Arnold TW (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J Wildl Manage 74:1175–1178.

Azlan JM, Sharma DSK (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40:36.

Balestrieri A, Remonti L, Ruiz-González A, et al. (2010) Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mamm Biol 75:412–419.

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

Blanco (1998) Mamíferos de España. Planeta, Barcelona, Spain

Brown JS, Laundre JW, Mahesh G (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399.

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, Second ed. Springer Verlag

Cabral MJ, Almeida J, Almeida PR, Dellinger T, Ferrand N, Oliveira M, Palmeirim JM, Queiroz A, Rogado L, Santos-Reis M (2005) Livro Vermelho dos Vertebrados de Portugal, 2nd ed. Instituto da Conservação da Natureza/Assírio Alvim, Lisboa.

Calzada J (2007) *Genetta genetta*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 330–332.

Camps D (2011) Resting site selection, characteristics and use by the common genet *Genetta genetta* (Linnaeus 1758). Mammalia 75:23–29.

Carbone C, Gittleman JL (2002) A common rule for the scaling of carnivore density. Science 295:2273–2276.

Carothers JH, Jaksić FM (1984) Time as a Niche Difference: The Role of Interference Competition. Oikos 42:403–406.

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool 263:275–283.

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

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental. Quercetea 0:5–56.

Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Anim Conserv 14:56–65.

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martín JM, Ferreira C, Ferreras P (2013) Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. Mamm Rev 43:59–70.

Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat 167:524–36.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond Wj, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. Science 333:301–306.

Fauteux D, Mazerolle MJ, Imbeau L, Drapeau P (2013) Site occupancy and spatial co-occurrence of boreal small mammals are favoured by late-decay woody debris. Can J For Res 43:419–427.

Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric Mediterranean carnivores. Oecologia 121:138–148.

García-Canseco V (1997) Parque Nacional de Cabañeros, 1st editio. Ecohábitat, Madrid.

Gaubert P, Machordom A, Morales A, et al. (2011) Comparative phylogeography of two African carnivorans presumably introduced into Europe: disentangling natural versus human-mediated dispersal across the Strait of Gibraltar. J Biogeogr 38:341–358.

Genovesi P, Secchi M, Boitani L (1996) Diet of stone martens: an example of ecological flexibility. J Zool 238:545–555.

Gil-Sánchez JM, Ballesteros-Duperón E, Bueno-Segura J (2006) Feeding ecology of the Iberian lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). Acta Theriol 51:1–6.

Guzmán JN (1997) Mamíferos. In: García-Canseco V (ed) Parq. Nac. Cabañeros, 1st editio. Ecohábitat, Madrid, Spain, pp 225–268.

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297.

Harrington L a., Harrington AL, Macdonald DW (2009) The Smell of New Competitors: The Response of American Mink, *Mustela vison*, to the Odours of Otter, *Lutra lutra* and Polecat, *M. putorius*. Ethology 115:421–428.

Hines JE, Mackenzie DJ (2013) Presence.

Kelly MJ, Holub EL (2008) Camera Trapping of Carnivores: Trap Success Among Camera Types and Across Species, and Habitat Selection by Species, on Salt Pond Mountain, Giles County, Virginia. Northeast Nat 15:249–262.

Larivière S, Calzada J (2001) *Genetta genetta*. Mamm Species 680:1–6.

Larivière S, Pasitschniak-arts M (1996) *Vulpes vulpes*. Mamm Species 537:1–11.

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the “landscape of fear” in Yellowstone National Park, U.S.A. Can J Zool 79:1401–1409.

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

López-Martin JM (2003) Comparación de la ecología de la Marta (*Martes martes* L. 1758) y la Garduña (*M. foina* Erx.1777) en el N.E. Ibérico, e interacciones con la Gineta. PhD, Universitat de Bracelona, Barcelona.

López-martín JM (2006) Comparison of feeding behaviour between stone marten and common genet: living in coexistence. In: Santos-Reis M, Birks JDS, O’Doherty EC, Proulx G (eds) Martes Carniv. Communities. Alpha Wildlife Publications, Alberta, Canada, pp 137–155.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle AR, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

Mackenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press.

Mangas JG, Lozano J, Cabezas-Díaz S, Virgós E (2007) The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. Biodivers Conserv 17:43–51.

Matos HM, Santos MJ, Palomares F, Santos-Reis M (2008) Does riparian habitat condition influence mammalian carnivore abundance in Mediterranean ecosystems? Biodivers Conserv 18:373–386.

McCarthy MA, Moore JL, Morris WK, et al. (2013) The influence of abundance on detectability. Oikos 122:717–726.

Monterroso P, Alves PC, Ferreras P (2013) Catch Me If You Can: Diel Activity Patterns of Mammalian Prey and Predators. Ethology 119:1044–1056.

Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildl Res 38:446–454.

Monterroso P, Alves PC, Ferreras P (accepted) Plasticity in activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav. Ecol. Sociobiol.

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

Monterroso P, Moreira P, Castro D, et al. (2006) Predação sobre o coelho-bravo (*Oryctolagus cuniculus*) em ecossistemas mediterrâneos. In: Ferreira C, Alves PC (eds) Gestão Popul. coelho-bravo (Oryctolagus cuniculus algirus). Federação alentejana de caçadores, pp 51–79.

Mortelliti A, Boitani L (2008) Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. Landsc Ecol 23:285–298.

Pagano AM, Arnold TW (2009) Detection Probabilities for Ground-Based Breeding Waterfowl Surveys. J Wildl Manage 73:392–398.

Palomares F, Ferreras P, Fedriani JM, Delibes M (1996) Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. J Appl Ecol 33:5–13.

Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain.

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

Prieto JAF, Sánchez ÁB (1996) La reserva integral de Muniellos: Flora y vegetación. Servicio central de publicaciones del Principado de Asturias, Oviedo

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

Rauset GR, Mattisson J, Andrén H, Chapron G, Persson J (2012) When species' ranges meet: assessing differences in habitat selection between sympatric large carnivores. Oecologia 172: 701-711.

Richmond OMW, Hines JE, Beissinger SR (2010) Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecol Appl 20:2036–2046.

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998.

Rivas-Martinez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique. An del Jard Bot Madrid 37:251–268.

Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas. In: Serv. Cart. la Univ. León Madrid, Spain. http://www.ucm.es/info/cif/form/maps.htm.

Rödel HG, Stubbe M (2006) Shifts in food availability and associated shifts in space use and diet in stone marten. 49:67–72.

Roemer GW, Gompper ME, Van Valkenburgh B (2009) The Ecological Role of the Mammalian Mesocarnivore. Bioscience 59:165–173.

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. Mamm Rev 39:67–78.

Rosellini S, Osorio E, Ruiz-González A, Piñeiro A, Barja I (2008) Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. Wildl Res 35:434–440.

Ruiz-Olmo J, López-Martín J (2001) Relaciones y estrategias ecológicas de los pequeños y medianos carnívoros forestales. In: Camprodon J, Plana E (eds) Conserv. la Biodivers. y gestión For. Edicions de la Universitat de Barcelona, pp 397–414.

Santos-Reis M, Santos MJ, Lourenco S, Marques JT, Pereira I, Pinto B (2005) Relationships between stone martens, genets and cork oak woodlands in Portugal. In: Harrison DJ, Fuller AK, Proulx G (eds) Martens Fish. human-altered Environ. Springer, pp 147–172.

Sarmento PB, Cruz J, Eira C, Fonseca C (2010) Modeling the occupancy of sympatric carnivorans in a Mediterranean ecosystem. Eur J Wildl Res 57:119–131.

Sarmento PB, Cruz JP, Eira CI, Fonseca C (2009) Habitat selection and abundance of common genets *Genetta genetta* using camera capture-mark-recapture data. Eur J Wildl Res 56:59–66.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39.

Steen DA, McClure CJW, Brock JC, Rudolph DC, Pierce JB, Lee JR, Humphries WJ, Gregory BB, Sutton WB, Smith LL, Baxley DL, Stevenson DJ, Guyer C (2013) Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. J Anim Ecol. (*in press*).

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

Virgós E, Cabezas-Díaz S, Mangas JG, Lozano J (2010) Spatial distribution models in a frugivorous carnivore, the stone marten (*Martes foina*): is the fleshy-fruit availability a useful predictor? Anim Biol 60:423–436.

Virgós E, García FJ (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 23:231–237.

Virgós E, Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. Mamm Rev 29:119–128.

Virgós E, Tellería J, Santos T (2002) A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. Biodivers Conserv 11:1063–1079.

Wilson RR, Blankenship TL, Hooten MB, Shivik JA (2010) Prey-mediated avoidance of an intraguild predator by its intraguild prey. Oecologia 164:921–929.

Zabala J, Zuberogoitia I, Martínez-climent JA (2009) Testing for niche segregation between two abundant carnivores using presence-only data. Folia Zool 58:385–395.

Zalewski A, Jędrzejewski W (2006) Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieza Forest (E Poland) compared with other European woodlands. Ecography (Cop) 29:31–43.

Zar JH (2005) Encyclopedia of Biostatistics. John Wiley & Sons, Chichester .

Zhou Y, Newman C, Xu W, et al. (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr 38:137–147.

General Introduction

Methodological improvements for mesocarnivore ecological studies

Evaluation of attractants for non-invasive studies of Iberian carnivore communities

Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South-western Europe

Efficiency of hair snares for monitoring mesocarnivores occurrence

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General discussion

Plasticity and niche relations between to sympatric competitors

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3.4 Niche partitioning at the edge of the range: a multidimensional analysis with sympatric martens

Abstract

The structure of mesopredators' communities is complex and results from a multidimensional web of interactions. The pine marten (*Martes martes*) and the stone marten (*Martes foina*) have overlapping ecological traits and distributions over their European range. The absence of stone martens from potentially adequate areas has been advocated as the result of competitive exclusion by pine martens. However, their elusive behavior and the morphological similarity of their scats often precluded the evaluation of their ecological traits in areas of co-occurrence.

Using camera trapping and genetically identified scats, we evaluated the ecological relations between pine and stone martens in the South-western limit of their range along three main ecological niches: spatial, trophic and temporal; under a hypothesis of competitive dominance of pine martens.

We found no spatial segregation and that coexistence was facilitated by seasonally adjusted shifts along the trophic and temporal axes. While both species often co-occurred spatially, during the season of low food resources pine martens exploited the less profitable feeding resource, and displayed an activity pattern that while reducing the probabilities of encounters with stone martens, constrained their access to rodents.

We suggest that the relative dominance position has changed in favor of the stone marten in our study area, probably as a result of factors such as habitat quality, human disturbance and range edge effects. These findings support the relative instability of interspecific interactions among similar sized species, which should be evaluated using multidimensional approaches in order to provide adequate baseline information in conservation and management actions.

Introduction

According to the concept of limiting similarity, "complete competitors cannot coexist" (Hardin 1960). This idea seems appealing and reasonably straightforward, however the patterns found in nature indicate that coexistence rather than exclusion of closely related species is the rule (den Boer 1986), because sympatric organisms must adapt to the same environment (Grant 1972). The limiting similarity theory (MacArthur and Levins 1967) attempts to incorporate the effects of these simultaneous forces, suggesting a threshold of niche similarity under which stable coexistence is allowed. Hence, competing species must segregate, at least partially, along one or more dimensions of their ecological niche (Hardin 1960, MacArthur and Levins 1967, Szabó and Meszeéna 2006).

In recent years, particularly boosted by modern technological advances in field techniques and noninvasive sampling (Long et al. 2008), several studies have focused on the coexistence patterns and competition between sympatric carnivore species. Carnivores provide particularly interesting organisms to study such patterns because of their disproportional impact in the ecosystems. Futhermore, carnivores are particularly prone to aggressive interspecific interactions, which are largely mediated by the availability of a shared resource and by their relative body sizes (Palomares and Caro 1999, Arim and Marquet 2004, Donadio and Buskirk 2006, Ritchie and Johnson 2009).

Among carnivores, the greater range overlap is observed between sister species that differ in morphological traits related to resource use and that occupy similar ecological niches (Davies et al. 2007). However, cases of sister species with overlapping ecological requirements are frequently found among carnivores in several terrestrial ecosystems (Wilson and Mittermeier 2009). The pine marten (*Martes martes*) and the stone marten (*Martes foina*) are two closely related medium-sized mustelids that have extensively overlapping distributions, particularly in their European ranges (Figure 3.4.1) (Proulx et al. 2005, Kranz et al. 2008, Tikhonov et al. 2008). Although displaying a high distributional overlap and having similar body sizes (Blanco 1998), some morphometric traits allow the discrimination of these species (Loy et al. 2004, Gasilin and Kosintsev 2013). Particularly, their cranial morphology suggests that the stone marten should be better adapted to hypercarnivory, while the pine marten's skull is suggestive of more diverse feeding habits (Loy et al. 2004).

In spite of this apparent divergence in chewing apparatus, the pine and stone marten often have overlapping diets (López-Martin 2003, Posluszny et al. 2007, Zhou et al. 2011) and habitat requirements (Ruiz-Olmo and López-Martín 2001, Proulx et al. 2005, Wilson and Mittermeier 2009), fact that should potentiate the competitive stress between them. Accordingly, the competitive exclusion principle has been invoqued to justify the absence of stone martens from otherwise adequate areas within their distribution range (Balestrieri et al. 2010a; Rosellini et al. 2008b). Therefore, whenever they co-occur a high potential for competitive interactions is expected. However, given their secretive behaviour and the impossibility to distinguish their scats based on morphological characteristics (Rosellini et al. 2008b), there is a considerable lack of studies where both species' ecological traits are simultaneously addressed (Balestrieri et al. 2010b; Goszczyński 1976; Posluszny et al. 2007). Non-invasive molecular methods provide a valuable tool for determining the species presence using scats collected in the field, allowing for unambiguous studies on these two closely related co-occurring mesocarnivores (Broquet et al. 2006, Ruiz-González et al. 2007, Beja-Pereira et al. 2009).

In the Iberian Peninsula (Southwest Europe), the stone marten is widespread (Reig 2007, Tikhonov et al. 2008) while the pine marten is restricted to the northern fringe, comprising the South-western limit of its European range (Proulx et al. 2005, López-Martin 2007). In this region, stone and pine martens potentially coexist, therefore providing a good opportunity to study the strategies of these two sympatric species in the South-western most limit of their distribution range.

In this study we evaluated the three main niche dimensions - spatial, trophic and temporal - of pine and stone martens. Particularly we wanted to evaluate if the previously reported competitive dominance of pine martens over stone martens would hold in the limit of the former's range. If pine martens outcompete stone martens, we expected this dominance to be expressed over one or more of the main ecological niche dimensions: (1) spatially, by excluding or reducing the probability of stone martens occurrence in the most beneficial habitats; (2) trophically, by reducing stone martens' access to the most beneficial feeding resources; or (3) temporally, by forcing stone martens to adjust their activity patterns so that they reduce the probability of interspecific encounters. Therefore we predicted that pine martens would be present in their preferred habitats (mature oak woodlands) and stone martens would be present only in sub-optimal habitats, such as scrublands and fragmented areas. Further, we predicted that pine martens would preferably explore rodents as their main prey, and that stone martens would shift prey towards other feeding resources (such as fruits, arthopods or carrion). Finally, we anticipated that if these species do not segregate over these dimensions (spatial and trophic), temporal partitioining should play a particularly significant role in separating their ecological niches.

Methods

Study area

This work was conducted at Peneda-Gerês National Park (PGNP, Portugal; Figure 3.4.1), which is a part of the Cantabrian-Atlantic subprovince, Juresian-Queixensean Sector and Amarela-Gerês district, and is included in the montane bioclimatic level with a hyper-humid and ultra-hyper-humid ombroclimate (Costa et al. 1998; Honrado 2003; Rivas-Martínez et al. 2002). Diverse types of granitic soils and a great topographic complexity result in a diversification of ecological conditions, which are reflected in the presence of several climacic forests, particularly, mature forests of European oak (*Quercus robur*) (Honrado 2003). The vegetation is dominated by *Luzula henriquesii-Quercus robur, Betula celtibérica-Sorbus aucuparia, Quercus pyrenaica- Q. x andegavensis, Myrtillo-Quercetum roboris and Rusco-Quercetum roboris subas. prunetosum lusitanicae* series. At higher altitudes, there is a prevalence of *Cytiso striati-Genistetum polygaliphyllae, Carici asturicae-Ericetum aragonensis* and *Juniperus communis* subsp. *alpina* e *Erica australis* subsp. *aragonensis* series (Honrado 2003). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Carvalho and Gomes 2004). A study area of approximately 6000ha was selected, based on criteria of ecosystem conservation status and logistic factors.

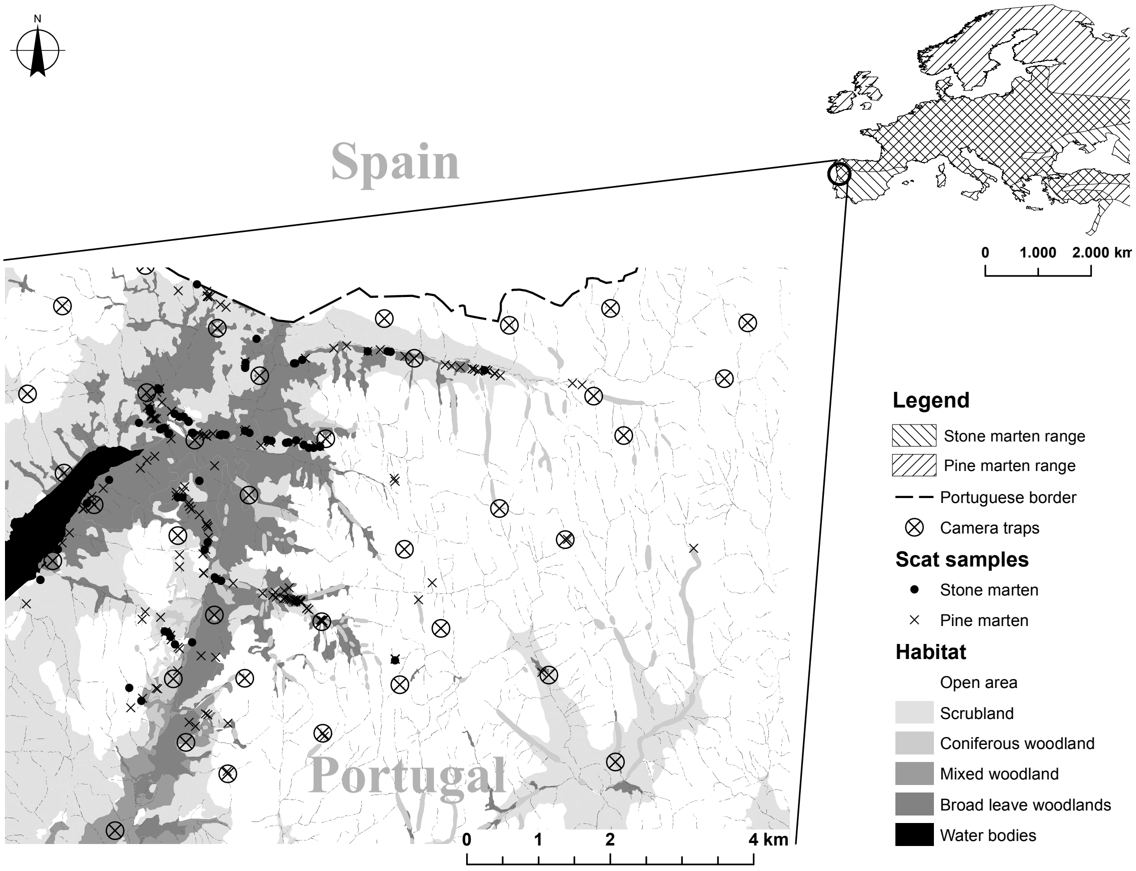

Figure 3.4.1 Small inset: European range of pine and stone martens, adapted from IUCN Red List of Threatened Species, Version 2013.2. (www.iucnredlist.org). Large inset: Spatial representation of habitat composition, camera-trap placement and genetically confirmed marten scats at Peneda-Gerês National Park (PGNP, Portugal).

Field sampling

The study area was sampled in two seasons: non-breeding (Oct-Nov), when the offspring of most medium-sized carnivores from that year become independent; and breeding (Apr-May), during most mesocarnivores' breeding season (Blanco 1998).

Data were obtained using exclusively non-invasive methods, including camera trapping and diet analysis based on genetically identified scats. The camera trapping sampling design and trap sites selection were those described in Monterroso et al. (2011; 2013). Briefly, 36 cameras were uniformly spaced in the study area following a grid-sampling scheme, with an inter-camera distance of ≈1.4km. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) and ScoutGuard SG550V (HCO OutDoor Products, Norcross, Georgia, USA), which have triggering times of 0.9 and 1.3 seconds, respectively. Cameras were mounted on trees approximately 0.5 – 1.0m off the ground and set to record time and date when triggered. We programmed cameras to fire a burst of three photos when triggered, with the minimal delay time possible (< 1min). Camera-traps were maintained in the field for a period of 28 to 31 days and were inspected for battery or card replacement every two weeks. We used a combination of Lynx urine and Valerian extract solution as lures to incite target species' curiosity and thus increase detection probabilities (Monterroso et al. 2011, Garrote et al. 2012). Attractants were placed in the field at a distance of 2-3 m from the camera-traps, and were deployed in perforated separated PVC containers, at a distance of 10-15 cm from each other and approximately 30 cm above the ground. Five to 10 mL of each attractant were sprayed into a cotton gaze, held inside each container. Attractants were re-baited every two weeks.

Ten 3-km long transects, were defined along unimproved roads or trails for active searching of marten scats. Each transect was sampled twice per season: at the beginning of the sampling campaign and after approximately 20 days. Transects were spatially distributed in order to adequately sample all main habitats. Transects were surveyed on foot by trained field technicians who collected all carnivore scats within a bandwidth of 2 m to each side of the transect line. Scats were initially identified in the field based on their location, morphology, dimensions, color and odor, with the aid of specific field guides (Bang et al. 2007, Iglesias and España 2010) and were collected taking all precautions to prevent contamination from the collector or cross-contamination from other samples. All scats not exhibiting external characteristics of being fresh (wetness, shine, dark color) were discarded. Selected samples pre-identified as belonging to marten species were preserved in plastic vials in ethanol (96%) until DNA extraction. Additional opportunistically collected scats (for instance, at camera-trap locations) were also included in this study.

Genetic Analysis

All scats collected during fieldwork were submitted for genetic analysis. DNA extractions were performed with the Qiagen QIAamp DNAStool Mini Kit (Qiagen, Hilden, Germany) according to manufacturer's instructions in a separate and autonomous facility, under sterile conditions. Species assignment was performed using two diagnostic methods: the interphotoreceptor retinoid-binding protein (IRBP) fragment (Oliveira et al. 2010); and the domain 1 of the control region (CR) (Palomares et al. 2002). Amplifications were performed in a final volume of 10 µL using 5 µL of Qiagen PCR MasterMix, 0.2 µM of each primer and 2 µL of DNA extraction (c. 10 ng of genomic DNA). Thermocycling conditions for both frag- ments were as follows: 95°C for 15 min, followed by 40 cycles at 95°C for 30 s, 60°C (IRBP) or 58°C (CR) for 20 s and 72°C for 20 s, with a final extension step at 72°C for 5 min (IRBP) or 60°C for 10 min (CR). Polymerase chain reaction (PCR) amplifications were carried out in a thermocycler MyCycler (Bio-Rad, Hercules, CA, USA). Successful amplifications were purified using the enzymes exonuclease I and shrimp alkaline phosphatise, and sequenced for both strands with BigDye chemistry (Applied Biosystems, Carlsbad, CA, USA). Sequencing products were separated in a 3130 XL Genetic Analyzer (Applied Biosystems). Pre- and post-PCR manipulations were conducted in physically separated rooms. Sequence alignment was performed using Clustal W (Thompson et al. 1994) implemented in BioEdit software (Hall 1999) and was manually checked and reassessed for any discrepancy. Aligned CR sequences were compared with the corresponding region of the mitochondrial genome from target species in the GenBank. Both markers were consistently used to increase identification confidence.

Diet Analysis

All samples genetically confirmed as belonging to either pine or stone martens were used for diet analysis. Scats were dried at 60ºC for a 48h, weighted with a digital scale (precision of 0,001g) and soaked in water with some drops of lye during 24h before analysis to facilitate the separation of its components. The soaked material was then rinsed in 0.5mm and 0.25mm sieves under a slight stream of tap water. All the undigested food remains where then carefully inspected and separated by food items and type of remains.

The undigested contents were identified using a magnifier (Zeiss Stemi 2000-C 10x/27-5x). Mammalian prey were identified by their teeth, mandibles and hair structure. Hair samples were identified under an optic microscopic (Leitz HM-LUX 3 10x100), using the cross-section technique (Teerink 1991), and species identification was assessed using hair identification manuals (Debrot et al. 1982, Teerink 1991). Teeth and mandibles were identified with the aid of reference keys (Gállego Castejón and López 1982, Dueñas Santero and Peris Alvarez 1985). Birds were classified to the Order level according to the feathers with the aid of reference keys (Day 1966). After triage, all food remains were dried at 60ºC for 48 hours. Their dry weight was then assessed, using a digital scale (precision of 0.001g).

Statistical analysis: spatial partitioning

Spatial co-occurrence patterns between pine and stone martens were evaluated by likelihood-based occupancy modeling (MacKenzie et al. 2002, Mackenzie et al. 2006) using single-season occupancy models in the software PRESENCE 6.0 (Hines and Mackenzie 2013). We divided our survey periods into 1-week sampling occasions during which the detection/non-detection data of each target species was recorded. Then, we created species-specific detection histories, allowing us to assess factors that may affect species-specific occupancy and detection.

Mackenzie et al. (2004) proposed an occupancy model for estimating species co-occurrence patterns. However, they reported problems in the numerical convergence of model parameters when covariates were included (Mackenzie et al. 2004, 2006). To deal with this problem, Richmond et al. (2010) proposed the psiBa parameterization, where the probability of occupancy of the subordinate species is conditional on the occupancy of the dominant species. Despite the robustness of this parameterization, convergence problems can also arise (Steen et al. 2013). We also found convergence problems with co-occurrence occupancy models for our pine and stone marten dataset using both the above mentioned parameterizations. Therefore, by assuming pine marten to be the dominant species (López-Martin 2003, Balestrieri et al. 2010a), we estimated its occupancy (ψ^A) unconditional of stone martens' presence. To account for potential heterogeneity in the probabilities of occupancy (ψ) and detection (p) we tested the effect of covariates: distance to water, habitat availability, prey (rodents, order Rodentia) abundance, and season. We estimated distance to water by measuring the linear distance from the sampling site to the nearest water source. Rodent availability was assessed for each camera station and period by calculating trap success (TS). TS estimation followed the methods described by previous studies (Kelly and Holub 2008, Davis et al. 2011) and consisted of the mean number of detections of a given species per 100 trap days. When multiple photographs of the same species were taken within a 30-minute interval we considered them to be dependent, and therefore regarded them as a single capture event to ensure capture independence (unless animals were clearly individually distinguishable) (Davis et al. 2011). We reclassified original vegetation maps obtained for PGNP into four dominant habitat types: broadleaf autochthonous woodlands, coniferous woodlands, scrublands and open areas. Then, following Long et al. (2011) we assessed the proportion of each habitat type around each camera at two different scales using two analysis windows: 0.0079km2 and 2.01km2. These areas respectively corresponded with 50m and 800m radius circles centered on the camera trap locations (hereafter referred to as local and home range scales). This home range buffer size was selected because it approximately represents the home range size for marten species in Europe (Santos-Reis et al. 2004, Zalewski and Jędrzejewski 2006). All continuous covariates (proportion of habitat in HR, Distance to water and rodent TS) were transformed to z-scores (Mackenzie et al. 2006).

Our final covariate set was defined following a Spearman’s rank correlation (rs) to test for collinearity among variables; if variables were correlated (rs>0.70) we kept the variable with the greatest univariate effect size (β/SE) (Zar 2005).

Following the recommendations of Arnold (2010) for exploratory approaches that involve many variables, we used a sequential modeling approach to find the best model set and discard uninformative variables. We started by building a main-effects model, including all variables. We then used a backward-stepwise selection to sequentially eliminate the covariate with the weaker effect size (β/SE). This process was kept until the deletion of an additional covariate led to an increase in AIC (Pagano and Arnold 2009). We considered as informative covariates those that were in models within 2 AIC units of the top-supported model and whose 85% confidence intervals did not include zero (Arnold 2010).

We then modeled the probability of stone martens’ occupancy by including the conditional probability of pine marten occupancy (ψ^A), given its detection history, as a potential covariate. We evaluated species interactions by comparing models with and without ψ^A, using habitat and prey variables as covariates of occupancy (Steen et al. 2013). We also investigated the effect of pine martens’ presence on stone martens’ detectability by evaluating models with and without ψ^A as a covariate for detection (Steen et al. 2013).

We evaluated the candidate models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002), and model fit was assessed through the calculation of the overdispersion parameter ($\hat{c}$) using the most parameterized model (Burnham and Anderson 2002). We then used $\hat{c}$ to correct AIC for small sample size (AICc) and for overdispersion (QIACc) (Burnham and Anderson 2002).

While a species' trap success may be a biased proxy of its abundance (Sollmann et al. 2013), it provides information regarding the intensity of use of a given area. Therefore, we calculated the Spearman rank correlation between pine and stone martens' TS to evaluate if areas intensively used by one species would be less used by the other.

To further evaluate the spatial relations between the two congeneric species, we evaluated the spatial patterns of the detected scats. Hence, for each season, we evaluated if the mean distance between nearest scats of the same species was significantly different from the mean distance between nearest scats of different species using the paired Wilcoxon test. We then used the Fisher's exact test to compare the number of scats of each species collected in each habitat type.

Statistical analysis: trophic ecology

We assessed the martens' diet by estimating the frequency of occurrence (FO; # of scats containing a particular item/ total analyzed scats) and ingested biomass (g) of each considered food item (Nilsen et al. 2012). The ingested biomass was estimated by measuring the dry mass of each food item (Reynolds and Aebischer 1991), and then the ingested biomass of that food item (Klare et al. 2011) was estimated using correction factors developed for pine martens (Lockie 1961, Balharry 1993) and for polecat, Mustela putorius (Roger et al. 1991), in order to cover all the dietary spectrum of the target species. The seasonal trophic niche overlap between pine and stone martens was assessed using Pianka's index (α) (Pianka 1974). Interspecific differences in the frequency of occurrence of each food item were evaluated using chi-square tests on built contingency tables. Differences in the mean ingested biomass per scat were assessed using a one-way analysis of variance (ANOVA) on log-transformed ingested biomass values (Loveridge and Macdonald 2003). These analyses were performed in R (R Development Core Team 2008) using the SPecies Association Analysis package (Zhang 2013).

Statistical analysis: temporal partitioning

Temporal segregation between the two marten species was assessed using camera-trapping data. The independent detection records were regarded as a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken within any particular interval of the day (Ridout and Linkie 2009). The probability density function of this distribution (i.e. activity pattern) was estimated nonparametrically using kernel density (Ridout and Linkie 2009, Linkie and Ridout 2011).

The temporal segregation between pine and stone martens in each sampling season was evaluated by pairwise comparisons of their activity patterns, performed by estimating the coefficient of overlap Δ_1, as suggested for small sample sizes (Ridout and Linkie 2009, Linkie and Ridout 2011). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap), and is obtained taking the minimum of the density functions of the two cycles being compared at each time point. The precision of this estimator was obtained by computing a standard deviation from 500 bootstrap samples in the software R (R Development Core Team 2008). The R code used to estimate overlap coefficients was that provided by (Ridout and Linkie 2009). Additionally, we used the Mardia-Watson-Wheeler test (Batschelet 1981) to compare the distribution of detections across the diel cycle between both species. This test pools the samples together and sorts them into increasing angles. They are then evenly distributed around the diel cycle by calculating a uniform score (or circular rank). If the distributions of the samples are identical then the new uniform scores should be evenly interspersed around the diel cycle, and their resultant vector lengths (R) should be short and similar. Any significant difference between the R's will lead to a large W test statistic and rejection of the null hypothesis of identical distributions (Kovach 2011). These analyses were performed using the software Oriana v. 4.01 (Kovach 2011). Only distributions with ≥10 detections were considered (Gerber et al. 2012).

Because martens are active rodent predators (Zalewski 2005, Zhou et al. 2011), the coefficient of activity overlap between the pine and stone marten with rodents was also assessed. Rodent data were obtained from the same camera traps, and following the same procedures as data from martens. However, to evaluate the synchrony between prey and predator activities we estimated a Pearson's correlation using kernel probability estimates for 512 equally spaced time points along the day, that is, a point at approximately each 2.8 min (Monterroso et al. 2013).

Results

Spatial interactions

We recorded 13 and 26 independent pine marten detections in camera-traps during the non-breeding and breeding seasons, respectivey. Stone martens accounted for three and 11 independent detections in the same seasons.

All of the best models for pine marten included the effect of season (table 3.4.1), revealing a higher probability of site occupancy during breeding than during non-breeding season (85% conf. interval excluded zero). Rodent trap success and the presence of authoctonous broadleaf woodlands also exhibited positive effects on pine marten occupancy probabilities and were included in two and one of the top supported models, respectively (table 3.4.1). Although being included in one of the top supported models, the distance to roads was considered uninformative given the low precision of its estimate (85% confidence interval overlapped zero).

Four models had substancial level of empirical support of being the best models for stone marten occupancy. Three of these models included the conditional probability of pine marten presence, which had a significant positive effect on the probability of stone marten occupancy (table 3.4.1). Although being included in some of the top-supported models, rodent trap success and the proportion of open areas at the home range scale were uninformative in the estimation of the probability of stone martens' occupancy (table 3.3.1).

The seasonal evaluation of pine and stone marten traps successes revealed a positive but not significant correlation ($r_{nonbreeding} = 0.23$; $p = 0.19$; $r_{breeding} = 0.49$; $p = 0.20$). However, the correlation between these two species trap success for the pooled data was positive and highly significant ($r = 0.42$; $p < 0.01$).

The spatial patterns of the target species' scats were coherent with those obtained from the camera-trapping data. The mean distance between a given stone marten scat to the nearest pine marten scat was 474.3 ± 167.7m and 114.9 ± 20.3m in the non-breeding and breeding seasons, respectively, and differences between the interspecific and intraspecific nearest neighbor distances were not statistically different for any of the seasons evaluated ($W_{nonbreeding}$ = 174; p = 0.98; $W_{breeding}$ = 610; p = 0.40).

Table 3.4.1. Top-supported models (ΔQAICc ≤ 2.0) and covariate estimates (β) used to evaluate occupancy patterns and interspecific interactions between pine martens (Martes martes) and stone martens (Martes foina) in Peneda Gerês National Park (PGNP), during the non-breeding season of 2010 and breeding season of 2011.

Pine marten	**QAIC$_c$**	**ΔQAIC$_c$**	ω_i	***k***	**Covariate estimates ($\hat{\beta}$)**			
					Season	***Rodent***	***Brd***	***Distance to roads***
$\psi(season + rdt), \mathrm{p}(.)$	122.52	0	0.240	4	2.17 ± 1.13*	2.20 ± 2.03*	-	-
$\psi(season), \mathrm{p}(.)$	123.34	0.82	0.160	3	1.62 ± 1.20*	-	-	-
$\psi(.), \mathrm{p}(.)$	123.42	0.90	0.153	2	-	-	-	-
$\psi(season + \mathrm{brd}), \mathrm{p}(.)$	123.90	1.38	0.120	4	1.56 ± 0.97*	-	1.70 ± 1.38*	-
$\psi(season + Distance\ to\ roads + rdt), \mathrm{p}(.)$	124.25	1.73	0.101	5	2.43 ± 1.51*	1.90 ± 1.62*	-	-0.58 ± 0.73
Stone marten	**QAIC$_c$**	**ΔQAIC$_c$**	ω_i	***k***	***Pmarten***	***Rodent***	***Opn_HR***	
$\psi(Pmarten), \mathrm{p}(Brd + Mxd)$	62.90	0	0.338	5	3.88 ± 2.33*	-	-	-
$\psi(Pmarten + rdt), \mathrm{p}(Brd + Mxd)$	63.07	0.17	0.310	6	4.93 ± 2.63*	-1.71 ± 1.76	-	-
$\psi(.), \mathrm{p}(Brd + Mxd)$	64.84	1.94	0.128	4	-	-	-	-
$\psi(Pmarten + rdt + Opn_{HR}), \mathrm{p}(Brd + Mxd)$	64.86	1.96	0.127	7	5.92 ± 3.36*	-2.22 ± 2.29	-0.56 ± 1.10	-

Model parameters: 'ψ' - Occupancy probability; '*p*' - Detection probability;

Model covariates: '.' - Constant (i.e. no covariates); 'Season' - Seasonal effects (non-breeding *vs*. breeding season); 'Rodent' - Rodent trap-success (detections/100 trapping-nights); 'Brd' - Broadleaf woodland; 'Mxd' - Mixed woodland; 'Opn_HR' - Proportion of open areas at the home-range scale; 'Distance to roads' - Linear distance to nearest road (meters); 'Pmarten' - Conditional probability of pine marten occupancy, given the detection history.

'*' - Informative covariate (i.e. 85% confidence interval not overlapping zero)

Significant differences in the proportion of scats collected per habitat type were detected during the non-breeding season (Fisher's exact test: p = 0.02). During this season, most pine marten scats were collected on broadleaf woodlands (50%), coniferous woodlands (26%) and scrublands (19%), while stone martens' were mostly detected on broadleaf woodlands (69%), scrublands (12%) and open areas (8%). Such significant differences were not detected during breeding season (Fisher's exact test: p

= 0.07). During this season scats were collected in the same habitats in comparable proportions: 47% and 48% in broadleaf woodlands, 24% and 33% in scrublands, and 20% and 13% in open areas for pine and stone martens, respectively.

Trophic ecology

A total of 97 scats were genetically identified as pine martens' scats, with 67 from non-breeding season and 30 from breeding season. The sample of stone marten scats consisted of 27 from non-breeding season and 46 from breeding season. Rodents and fruits dominated the diet of both species (table 3.4.2), ≥ 70% of all ingested biomass in each season.

Overall, no significant differences were observed in the frequency of occurrence of food items during the non-breeding season (table 3.4.2). However, there was a tendency for stone martens to ingest fruits more frequently than did pine martens, and for pine martens to consume rodents, insectivores and birds more frequently than stone martens during this season (table 3.4.2). The estimates of ingested biomass per food item were coherent with frequency of occurrence results, revealing a higher intake of fruits by stone martens, and of small mammals and birds by pine martens, although without significant differences during non-breeding season (table 3.4.2). During this season the diets of pine and stone marten were very similar, as supported by a Pianka's index (α) of 0.92 and 0.97 for the occurrence and ingested biomass, respectively (Table 3). However, while the pine marten maintained fairly constant diet across seasons ($\alpha_{FO} = 0.89$; $\alpha_{Biomass} = 0.97$), stone martens' dietary niche changed ($\alpha_{FO} = 0.65$; $\alpha_{Biomass} = 0.42$). During breeding season, stone martens reduced the use of fruits, which were significanlty less consumed than by pine martens both in terms of frequency and biomass (table 3.4.2). During this season, stone martens also explored carrion (artiodactyla) significantly more frequently than pine martens. While the frequency of occurrence and mean ingested biomass per scat of rodents was not significantly different between stone and pine martens, the overall contribution of this food resource (percent ingested biomass) indicates higher intake by stone martens during breeding season (table 3.4.2). This component consisted of 20 and 60% of the ingested biomass by pine and stone martes, respectively. An analogous situation was found in the consumption of arthropods, however, their contribution for the total ingested biomass was smaller (table 3.4.2). This dietary shift of the stone marten between seasons resulted in a lower niche overlap during breeding season: $\alpha_{FO} = 0.80$; $\alpha_{Biomass} = 0.51$ (table 3.4.3).

During the non-breeding season, both species displayed a high consumption of fruits, especially Iberian pears (*Pyrus bourgaeana*). During this season, rodents (especially the wood mouse, *Apodemus sylvaticus*) consisted the second most consumed resource type, with a contribution of 21.98% and 31.97% of all ingested biomass by stone martens and pine martens, respectively (table 3.4.2). During the breeding season, stone martens drastically reduced the consumption of fruits, and rodents took place as the main feeding resource, accouting for nearly 60% of all ingested biomass (table 3.4.2). Pine martens, however, continued to rely mainly on fruits, particularly common ivy (*Helix hedera*), primarely complemented by rodents and insectivores (Table 3.4.2).

During the non-breeding season, both martens species displayed a high consumption of fruits, especially Iberian pears (*Pyrus bourgaeana*). During this season, rodents (especially the wood mouse, *Apodemus sylvaticus*) consisted the second most consumed resource type, with a contribution of 16.44 and 23.42% of all ingested biomass by stone martens and pine martens, respectively (table 3.4.2). During the breeding season, stone martens drastically reduced the consumption of fruits, and rodents took place as the main feeding resource, accouting for nearly 60% of all ingested biomass (table 3.4.2). During this season, pine martens continued to rely mainly on fruits, particularly common ivy (*Helix hedera*), primarely complemented by rodents and insectivores (table 3.4.2). The feeding strategies of these congeneric species are reflected by an almost complete overlap of feeding niches during the non-breeding season, supported by a Pianka's index $\alpha = 0.99$; and a substantial segregation during the breeding season ($\alpha = 0.35$).

Table 3.4.2. Frequency of occurrence and ingested biomass of each considered food item of pine martens (Martes martes) and stone martens (Martes foina) in Peneda Gerês National Park (PGNP), during the non-breeding season 2010 and the breeding season 2011.

Season	Food item	Frequency of occurrence (%)				Ingested biomass (g)				Ingested biomass (%)	
		Martes martes	***Martes foina***	χ^2	***p***	***Martes martes***	***Martes foina***	**F**	***p***	***Martes martes***	***Martes foina***
Non-breeding	**Rodentia**	0.85	0.67	2.98	0.084	7.71 ± 1.16	5.77 ± 1.83	1.764	0.187	0.32	0.22
	Insectivora	0.15	0.00	3.08	0.079	0.91 ± 0.45	0.00 ± 0.00			0.04	0.00
	Artiodactyla (Carrion)	0.09	0.07	0.03	0.869	0.04 ± 0.02	0.03 ± 0.02	0.001	0.979	<0.01	0.00
	Aves	0.27	0.07	3.27	0.071	1.02 ± 0.52	0.01 ± 0.01	3.535	0.063	0.04	<0.01
	Reptilia	0.04	0.00	0.22	0.639	0.00 ± 0.00	0.00 ± 0.00			<0.01	0.00
	Amphibia	0.01	0.04	0.01	0.906	0.01 ± 0.01	0.00 ± 0.00	0.342	0.560	<0.01	<0.01
	Arthropoda	0.46	0.26	2.52	0.113	0.51 ± 0.39	0.11 ±0.06	0.198	0.657	0.02	<0.01
	Gastropoda	0.01	0.04	0.01	0.906	0.00 ± 0.00	0.00 ± 0.00	0.070	0.792	<0.01	<0.01
	Fruits/Seeds	0.64	0.93	6.41	0.011	13.42 ± 2.22	20.26 ± 3.85	4.488	0.036	0.56	0.77
	Vegetal matter	0.36	0.19	1.95	0.163	0.33 ± 0.14	0.06 ± 0.04	1.796	0.184	0.01	<0.01
	Honey	0.01	0.00			0.15 ± 0.15	0.00 ± 0.00			0.01	<0.01
Breeding	**Rodentia**	0.40	0.61	2.39	0.122	3.72 ± 1.55	5.87 ± 1.28	3.946	0.051	0.20	0.60
	Insectivora	0.13	0.11	0.03	0.869	2.06 ± 1.77	0.19 ± 0.12	1.054	0.308	0.11	0.02
	Artiodactyla (Carrion)	0.07	0.22	9.23	0.002*	1.66 ± 1.65	0.22 ± 0.12	0.045	0.832	0.09	0.02
	Aves	0.20	0.22	0.01	0.916	0.50 ± 0.44	0.58 ± 0.40	0.018	0.892	0.03	0.06
	Reptilia	0.27	0.13	1.43	0.232	0.22 ± 0.12	0.13 ± 0.09	0.957	0.331	0.01	0.01
	Amphibia	0.00	0.04	0.18	0.671	0.00 ± 0.00	0.01 ± 0.01			0.00	<0.01
	Arthropoda	0.53	0.70	1.42	0.232	0.49 ± 0.42	0.86 ± 0.34	2.827	0.097	0.03	0.09
	Gastropoda	0.00	0.07	0.68	0.410	0.00 ± 0.00	0.01 ± 0.01			0.00	<0.01
	Fruits/Seeds	0.80	0.15	28.93	<0.001*	9.47 ± 1.39	0.96 ± 0.54	65.440	<0.001**	0.52	0.10
	Vegetal matter	0.57	0.41	1.16	0.282	0.24 ± 0.10	0.88 ± 0.41	1.305	0.257	0.01	0.09
	Honey	0.00	0.00			0.00 ± 0.00	0.00 ± 0.00			0.00	0.00

Table 3.4.3. Overlap in the diets of pine martens (*Martes martes*) and stone martens (*Martes foina*) in Peneda Gerês National Park (PGNP), during the non-breeding season 2010 and the breeding season 2011, calculated using the Piankas' index for both the relative frequency of occurrence and percent ingested biomass.

Species	**Season**	**Frequency of occurrence**	**Percent ingested biomass**
M. martes / *M foina*	Non-Breeding	0.92	0.97
	Breeding	0.80	0.51
M. martes	Non-breeding / Breeding	0.89	0.97
M. foina		0.65	0.42

Temporal partitioning

The pine marten revealed a mainly nocturnal activity pattern, with a tendency for bimodality in the non-breeding season (figure 3.4.2). It displayed a first activity peak around sunset and a second and higher peak between 04h00 and 06h00. During this season, pine martens' activity overlapped with rodents' (Δ_1 = 0.83 ± 0.10), and was highly synchronized with these prey (Pearson correlation = 0.91; p <0.001). We only obtained three stone marten detections during the non-breeding season, which prevented an adequated analysis of its activity pattern.

During the breeding season, the pine marten displayed a smooth pattern of activity across the diel cycle, with a peak around sunset (figure 3.4.2). This pattern contrasted with the strong bimodal nocturnal pattern of the stone marten, which displayed activity peaks after sunset and before sunrise (figure 3.4.2). These differences were supported by a low coefficient of overlap: Δ_1 = 0.49 ± 0.09 However, the Mardia-Watson-Wheeler test failed to detect significant differences between the structures of the activity patterns of the two marten species (W = 2.12; p = 0.35).

During this season the activity overlap between pine martens and rodents dropped by 22% (Δ_1 = 0.61 ± 0.09), and their activity patterns also reduced in synchrony (Pearson correlation = 0.40; p <0.001). While exhibiting little time overlap with the pine martens', the stone marten revealed an akin pattern of overlap and synchrony with rodents (Δ_1 = 0.60 ± 0.11; Pearson correlation = 0.57; p <0.001).

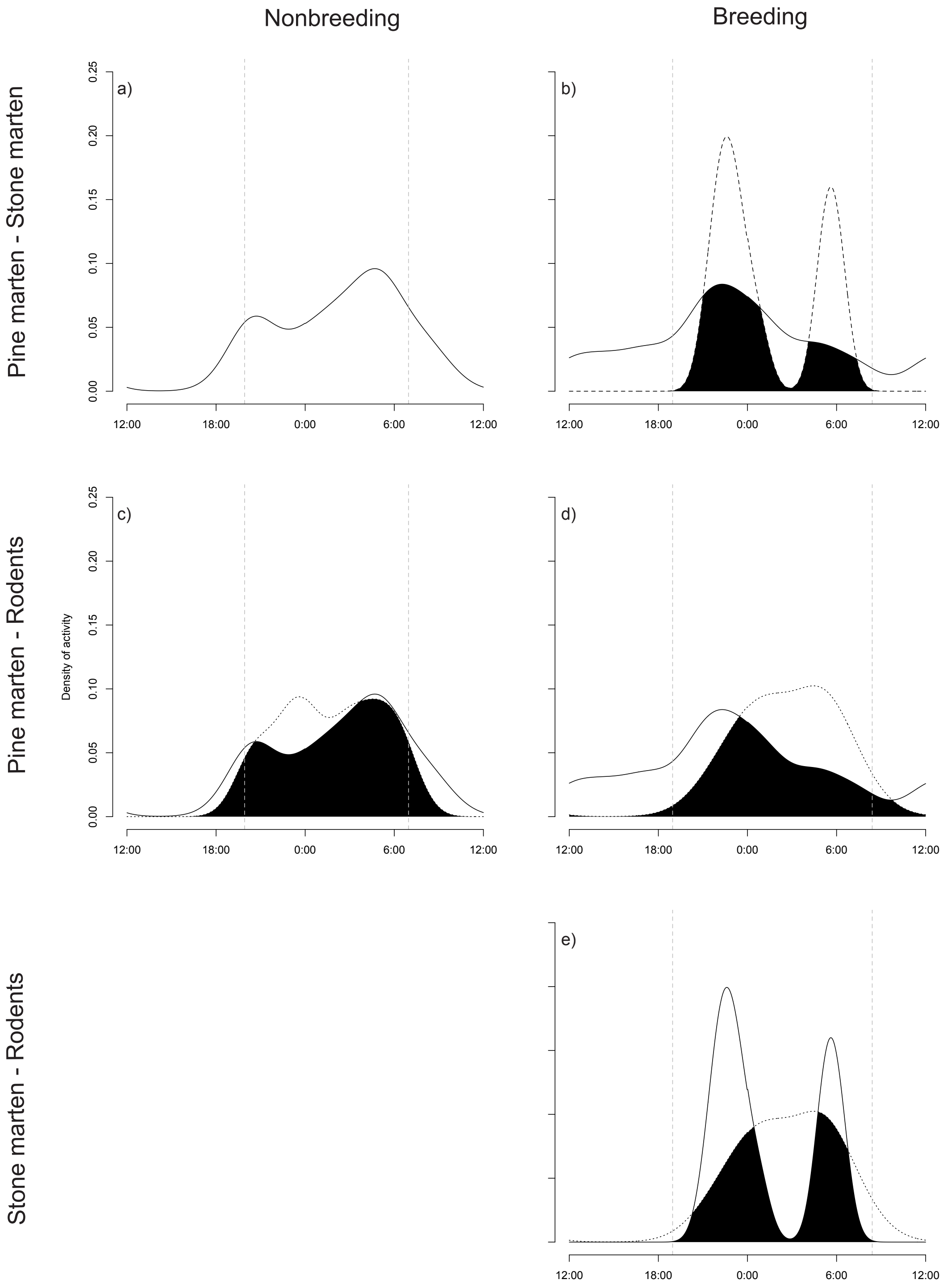

Figure 3.4.2. Diel activity patterns of pine martens (solid line) and stone martens (dashed line) at Peneda-Gerês Natural Park (PGNP), in: a) non-breeding season 2010; and b) breeding season 2011. Vertical dashed lines represent sunset and sunrise times, respectively. A low detection sample (n=3) for the stone marten prevented the analysis of its activity pattern during the non-breeding season.

Discussion

Spatial interactions

Our results do not support the hypothesis of stone martens' competitive exclusion from the most beneficial habitats, observed elsewhere (Ruiz-Olmo and López-Martín 2001, Rosellini et al. 2008a, Balestrieri et al. 2010a). In fact, the occupancy models suggest that the two congeneric species tend to co-occur in our study area.

The only covariate that significantly affected stone martens' occupancy probability was the unconditional probability of pine marten occupancy, which had a positive effect. This was a surprising result given the widely reported dominance of pine martens over stone martens, often driving the latter to sub-optimal areas, or even to the complete exclusion from a given area (Ruiz-Olmo and López-Martín 2001, Rosellini et al. 2008a, Balestrieri et al. 2010a). This absence of spatial segregation is not only supported by our occupancy modelling approaches, but also by the correlation between both species trap success and the high proximity of sites where scats from both species were collected (Figure 3.4.1). Our results diverge from the prediction of spatial segregation between pine and stone martens, or avoidance of the latter of sites occupied by pine martens in our study area. In fact, we found the opposite pattern, where both species tend to co-occur.

These findings are coherent with the widely held assumption that fitness decreases towards the edge of a species distribution range (Sexton et al. 2009). Although this assumption cannot be generalized, Sexton et al. (2009) found support that at least one of the fitness components was lower at the range edge when compared to its centre in 67% of the examined studies. Our study was performed at the Southwestern edge of the pine martens' distribution range (Proulx et al. 2005, Kranz et al. 2008), which is coincident with the transition from the Atlantic to the Mediterranean biogeographic region, whereas the core of its distribution is located in Atlantic to Continental regions (European Environmental Agency 2011). Although our data does not allow testing of the 'abundant centre hypothesis' (Sagarin and Gaines 2002), it is possible that, at this edge of its range, a reduction in pine martens' fitness could result in a downgrading from its competitive superiority over the stone marten. Alongside, according to the limiting similarity principle (MacArthur and Levins 1967), if pine and stone martens are able to segregate along other niche axes, their competitive stress along the spatial axis may be alleviated, allowing them to co-occur. The trophic niche is particularly important in mediating the strength of interactions between coexisting carnivores (Donadio and Buskirk 2006, Ritchie and Johnson 2009). Therefore, the trophic relations between the pine and stone martens in our study area could be involved in the observed pattern of co-occurrence.

The limited influence of other landscape covariates on stone martens' occupancy is in accordance with the reported ecological flexibility (Rondinini and Boitani 2002, López-Martin 2003, Tikhonov et al. 2008, Herr et al. 2009, 2010, Virgós et al. 2010). The spatial patterns of pine martens however, were mostly linked to the availability of feeding resources while habitat structure appears to have little effect. The close relation between pine marten occupancy and rodent availability is not surprising, as these prey are always noticeably consumed by pine marten in Europe (Marinis and Masseti 1995, Helldin 2000, Zalewski 2005, Posluszny et al. 2007, Rosellini et al. 2008b, Balestrieri et al. 2010b). The inclusion of rodent availability in the best-supported models suggests that rodents are also of high importance for pine martens in our study area. The seasonal pattern, nevertheless, appears to be counterintuitive as warmer temperatures and the recruitment of yearly cubs should increase the spatial patterns of land use during the non-breeding season. However, this season provides a period of higher food availability (Humphries et al. 1996, Rosellini et al. 2008b, Fedriani and Delibes 2009, Monterroso et al. 2013). Conversely, the reduced abundance of rodents and other alternative feeding resources during breeding season may impel martens to forage through wider areas in order to fulfil their energetic demands (Gittleman and Harvey 1982). Our study was conducted in the wider continuous potential area for pine martens regionally, and presents an overall adequacy for its presence (Álvares and Brito 2006). However, we found no effect of habitat composition in the probability of pine marten occurrence. While it has been widely described as a species dependent on mature woodlands (López-Martin 2003, Álvares and Brito 2006, Zalewski and Jędrzejewski 2006, Larivière and Jennings 2009), some authors have reported an independence of forest cover (Pereboom et al. 2008, Balestrieri et al. 2010a).

Feeding ecology

The feeding ecology of pine and stone martens highly overlaped during the non-breeding season, but diverged during the breeding season in our study area. Given the similar morphology of pine and stone marten scats, its identification is deemed impossible without the resort to molecular techniques (Pilot et al. 2007, Ruiz-González et al. 2007). Consequently, very little information exists regarding their feeding ecology in areas of co-occurrence. In central Poland, Posluszny et al. (2007) found that small rodents and birds were more often consumed by pine martens, whereas the stone marten fed more frequently on fruits and insects, and that the similarity between their diets was the highest in summer. In the same protected area where we performed this study, Carvalho and Gomes (2004) found that mesocarnivore trophic niche converges in the breeding season, due to lower resource availability. We found the opposite pattern between congeneric martens, which diverge in their trophic niche axis in the presence of limiting resource availability - breeding season - congruently with a hypothesis of competition (MacArthur and Levins 1967, Schoener 1983). In spite of presenting the overall general feeding patterns of the genus Martes (Zhou et al. 2011), the stone martens generally appear to be highly flexible in the selection of their feeding resources (Genovesi et al. 1996, López-Martín 2006). This flexibility should provide a higher adaptation capacity to local conditions and hence, under competitive stress, allow stone martens to explore different feeding resources, and reduce exploitative competition with co-occurring pine martens (López-Martin 2003). However, and coherently with our findings from the spatial analysis, our results conflict with our prediction of the pine martens' competitive dominance over stone martens. If there was a clear competitive dominance of pine martens in our study area, as reported elsewhere, stone martens should shift to less profitable resources under exploitative stress (Ruiz-Olmo and López-Martín 2001, Posluszny et al. 2007, Rosellini et al. 2008a, Balestrieri et al. 2010a). However, we found that pine martens reduced the consumption of their staple prey (rodents) in the period of least availability. Although our data on the seasonality of trophic niche similarity concurs with that obtained by Posluszny et al. (2007), it contradicts theirs regarding the trophic niche composition in the season of least similarity, suggesting a competitive superiority of the stone marten in our study area.

Activity patterns

We found pine martens to be mostly nocturnal, with a more pronounced daytime activity during the breeding than during the non-breeding season. During breeding season, stone martens exhibited a strongly bimodal nocturnal pattern, coherent with its strictly nocturnal behaviour described in the Iberian Peninsula (Monterroso et al. in press). Still, by concentrating their activity in two short periods of the night, they manage to maintain access to rodent prey (60% frequency of occurrence in scats; Table 3.4.2), while reducing the activity overlap with pine martens, as supported by the low Δ_1 values obtained for this season ($\Delta_1 = 0.49 \pm 0.09$), when compared to other studies on coexisting carnivores using this metric: 0.63 ± 0.04 (Ridout and Linkie 2009); 0.64 ± 0.05 (Lynam et al. 2013); 0.61 ± 0.03 (Monterroso et al. in press).

Given a likely increase in competitive stress between these twin species in the breeding season promoted by food shortage, and that temporal avoidance is a mechanism that promotes mesocarnivore coexistence by alleviating the likelihood of direct agonistic encounters (Halle 2000, Lucherini et al. 2009, Di Bitetti et al. 2009), it is plausible to consider pine and stone martens may relieve interspecific competition by expanding their activity periods to daytime hours. However, if our predictions of pine martens' competitive superiority held in our study area, they would benefit the most by tracking the circadian patterns of activity of rodents, maximizing accessibility to this prey (Zalewski 2005, Monterroso et al. 2013). However, we found a reduced activity overlap between pine and stone martens during the period of limiting resource availability, where none of this species maximized access to this shared resource.

Apart from interspecific relations, other factors could also influence the observed activity patterns. Although our study area is located in the South-western edge of pine martens range (Figure 3.4.1), were environmental temperature is not likely to be a limiting factor for adults, it may be for young cubs. A shift in the main activity peak from dawn to earlier in the night has also been registered by Zalewski (2001), which attributed the decrease in activity in female activity during the coldest part of the night (04h00-08h00) to care for their young. Furthermore, mice of the genus Apodemus constitute the main rodent prey of pine martens in the Mediterranean region (Zalewski 2005), as they are in our study area. However, following the reduction in the consumption of this prey in the breeding season, martens also reduce their activity pattern overlap and synchrony with that of their rodent prey. The more pronounced daytime activity during the breeding could also be related to overall feeding resources availability or anthropogenic disturbance. During the breeding season, feeding resources become scarcer (Carvalho and Gomes 2004, Monterroso et al. 2013). Therefore, martens may have to venture for longer distances and for longer periods to fulfil their metabolic demands (Gittleman and Harvey 1982). Additionally, pine martens appear to react cautiously to signs of human activity in forests (Goszczyński et al. 2007), developing high levels of physiological stress associated with human presence (Barja et al. 2007, Piñeiro et al. 2012). Although we could not test its effect, it is possible that seasonal differences in tourism-related human presence could also act by limiting pine martens' ability to explore most of the daytime period.

Regardless of the potential effect of other factors in the observed activity patterns of martens in our study area, we observed an abnormally low overlap and synchrony in their activity patterns during the breeding season. Therefore, we suggest that in the food shortage period of our study area, both pine and stone martens may use the temporal axis of their ecological niche to reduce their competitive stress.

Integrating the spatial, temporal and trophic niche dimensions

Three main dimensions of the ecological niche are usually involved in interspecific competitive relations - spatial, trophic and temporal (Schoener 1974). We evaluated these three dimensions, and demonstrate that the coexistence between two ecologically similar species may be mediated by adjustments over more than one of these axes. Furthermore, we found that these adjustments may vary seasonally, suggesting that the relationships among coexisting species are not static, but rather a dynamic process. The well-developed complexity of temperate forests could facilitate the coexistence between the pine and stone marten in northern Europe, as pine martens make more intense use of the three-dimensional space than stone martens (Jedrzejewski et al. 1993, Goszczyński et al. 2007). A higher diversity of rodents in this region (Mitchell-Jones et al. 1999) could also be involved in facilitating coexistence, by allowing both species to explore different prey (Posluszny et al. 2007). Furthermore, the stone martens' synanthropic behaviour (Reig 2007, Goszczyński et al. 2007, Herr et al. 2009, 2010) and their plasticity in habitat selection (Rödel and Stubbe 2006, Reig 2007, Pereira et al. 2012) may further support their coexistence.

In Southern Europe, the competitive exclusion principle has been advocated as the main reason for the absence stone martens in areas of sympatry with pine martens (López-Martin 2003, Rosellini et al. 2008a, Balestrieri et al. 2010a). However, our results do not support such pattern in our study area. Although we did not observe segregation along the spatial niche axis, we found that under unfavourable conditions (i.e., limiting resources), pine martens adjusted their position along the trophic axis by exploring less profitable resources, leading to niche divergence with stone martens. Further divergence was obtained by mutual adjustments along the temporal niche axis.

Among carnivore species, habitat composition and the availability of feeding resources may influence the relative dominance position in mutual reciprocal relations (Donadio and Buskirk 2006, Ritchie and Johnson 2009). Furthermore, if the abundant centre hypothesis (Sagarin and Gaines 2002) holds, species abundance and fitness should decline towards the edge of its range (Sexton et al. 2009). Although having a generalist diet, rodents are the staple prey of pine martens all over its European range (Jedrzejewski et al. 1993, Marinis and Masseti 1995, Zalewski 2005). Moreover, pine martens exhibit numerical responses to the abundance of forest rodents (Zalewski and Jędrzejewski 2006), which is inversely related to latitude in the Palearctic region following a gradient of net productivity of ground vegetation (Jędrzejewski and Jędrzejewska 1996). However, their preferred rodent prey consists of bank voles, and a functional response by pine martens is exhibited following the abundance of this species (Jedrzejewski et al. 1993, Helldin 2000, Zalewski 2005). Mice (Apodemus spp.) however, consist of alternative prey, as they are preyed upon less than could be expected by its proportion in the biomass of forest rodents (Jedrzejewski et al. 1993). However, mice are roughly the only available rodent prey available in our study area (Monterroso et al. 2013), suggesting that the Peneda-Gerês National Park may not provide optimum feeding resources for the pine marten. Furthermore, from a biogeographical standpoint, our study area is affected by Mediterranean influence (Rivas-Martínez et al. 2004, European Environmental Agency 2011), a bioclimatic transition which roughly coincides with the southern distribution range of the pine marten in the Iberian Peninsula (López-Martin 2007, Kranz et al. 2008). This fact also suggests a suboptimal suitability of this rim for the pine marten. Recent studies have shown that although requiring a certain level of forest cover, pine martens are not strictly dependent on mature woodlands as previously thought (Pereboom et al. 2008, Balestrieri et al. 2010a). However the coexistence and relative abundance of both marten species may depend on woodland complexity and management (Goszczyński et al. 2007). Despite the reasonable fragmentation of the landscape in our study area, the well-developed patches of deciduous woodlands (Álvares and Brito 2006) may facilitate the spatial coexistence of the two marten species, while providing hotspots of rodent and fruit availability. Being spatially clustered, there are higher chances for interspecific encounters, which appear to be minimized by some degree of mutual segregation across the diel cycle, at least during the breeding season. Because stone martens are bound to dim light periods, only exceptionally foraging under daylight conditions (Posillico et al. 1995, López-Martín et al. 2008, Monterroso et al. in press), this segregation may be facilitated by the nycthemeral abilities of the pine marten (Clevenger 1993, Zielinski 2000, Zalewski 2001, Monterroso et al. in press).

We suggest that in the Southwestern edge of pine martens range, their ecological interactions with stone martens need not to involve spatial exclusion, as reported over some other areas of its southern range (Rosellini et al. 2008a, Balestrieri et al. 2010a), but rather by seasonally adjusted changes in feeding resource consumption (trophic axis) and circadian activity patterns (temporal axis). We found that at the edge of its range and under food shortage conditions, the pine marten changes to alternative and less profitable feeding resources, contradicting its natural preference of rodent predation (Jedrzejewski et al. 1993, Zalewski 2005), suggesting a local competitive dominance of stone martens.

Our study is an example of how further research on the interspecific relations among coexisting mesocarnivores should be evaluated using multidimensional approaches and across wider scales, encompassing the core and edges of their respective ranges, in order to provide a more comprehensive understanding of how these species adjust their ecological niches to facilitate coexistence, and thus produce reliable information for adequate conservation and management plans.

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References

Álvares F, Brito JC (2006) Habitat requirements and potential areas of occurrence for the pine marten in North-Western Portugal: Conservation implications. In: Santos-Reis M, Birks JDS, O'Doherty EC, Proulx G (eds) Martes Carniv. Communities. Alpha Wildlife Publications, Alberta, Canada, pp 27–43

Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. Ecol Lett 7:557–564. doi: 10.1111/j.1461-0248.2004.00613.x

Arnold TW (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. J Wildl Manage 74:1175–1178. doi: 10.2193/2009-367

Balestrieri A, Remonti L, Ruiz-González A, Gómez-Moliner BJ, Vergara M, Prigioni C (2010a) Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mamm Biol 75:412–419. doi: 10.1016/j.mambio.2009.05.003

Balestrieri A, Remonti L, Ruiz-González A, Vergara M, Capelli E, Gómez-Moliner BJ, Prigioni C (2010b) Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). Acta Theriol 56:199–207. doi: 10.1007/s13364-010-0015-8

Balharry D (1993) Factors affecting the distribution and population density of pine martens (*Martes martes*) in Scotland. University of Aberdeen

Bang P, Dahlstrom P, Mears R (2007) Animal signs and tracks. Oxford University Press, Oxford.

Barja I, Silván G, Rosellini S, Piñeiro A, González-Gil A, Camacho L, Illera JC (2007) Stress physiological responses to tourist pressure in a wild population of European pine marten. J Steroid Biochem Mol Biol 104:136–142. doi: 10.1016/j.jsbmb.2007.03.008

Batschelet E (1981) Circular statistics in ecology. Academic Press, London

Beja-Pereira A, Oliveira R, Alves PC, Schwartz MK, Luikart G (2009) Advancing ecological understandings through technological transformations in noninvasive genetics. Mol Ecol Resour 9:1279–301. doi: 10.1111/j.1755-0998.2009.02699.x

Blanco (1998) Mamíferos de España. Planeta, Barcelona

Broquet T, Ménard N, Petit E (2006) Noninvasive population genetics: a review of sample source, diet, fragment length and microsatellite motif effects on amplification success and genotyping error rates. Conserv Genet 8:249–260. doi: 10.1007/s10592-006-9146-5

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, Second edi. Springer Verlag

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool 263:275–283. doi: 10.1017/S0952836904005266

Clevenger AP (1993) Pine marten (*Martes martes* L.) home ranges and activity patterns of the island of Minorca, Spain. Zeitschrift für Säugetierkd 58:137–143.

Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental. Quercetea 1:5–56.

Davies TJ, Meiri S, Barraclough TG, Gittleman JL (2007) Species co-existence and character divergence across carnivores. Ecol Lett 10:146–152. doi: 10.1111/j.1461-0248.2006.01005.x

Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Anim Conserv 14:56–65. doi: 10.1111/j.1469-1795.2010.00389.x

Day MG (1966) Identification of hair and feather remains in the gut and faeces of stoats and weasels. J Zool 148:305–320.

Debrot S, Fivaz G, Mermod C, Weber JM (1982) Atlas de poils dês Mammifères d’Europe. Institut de Zoologie, Université de Neuchâtel, Neuchâtel

Den Boer PJ (1986) The present status of the competitive exclusion principle. Trends Ecol Evol 1:25–28. doi: 10.1016/0169-5347(86)90064-9

Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pérez IJ (2009) Time Partitioning Favors the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes (*Lycalopex gymnocercus*). J Mammal 90:479–490. doi: 10.1644/08-MAMM-A-113.1

Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat 167:524–36. doi: 10.1086/501033

Dueñas Santero ME, Peris Alvarez SJ (1985) Clave para los Mamíferos (Insectivora y Rodentia) del Centro y Sur de la Península Ibérica. Ediciones Universidad de Salamanca, Salamanca

European Environmental Agency (2012) Biogeographic regions in Europe. http://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe. Accessed 25 Jan 2013

Fedriani JM, Delibes M (2009) Seed Dispersal in the Iberian Pear, *Pyrus bourgaeana*: A Role for Infrequent Mutualists. Ecoscience 16:311–321. doi: 10.2980/16-3-3253

Gállego Castejón L, López S (1982) Mamíferos Insectívoros. Vertebrados Ibericos (Claves para su determinación). Imprenta Sevillana, Sevilla

Garrote G, Gil-Sánchez JM, McCain EB, Lillo S, Tellería JL, Simón MÁ (2012) The effect of attractant lures in camera trapping: a case study of population estimates for the Iberian lynx (*Lynx pardinus*). Eur J Wildl Res 58:881–884. doi: 10.1007/s10344-012-0658-7

Gasilin V V., Kosintsev PA (2013) Identification of the subgenus *Martes* str. species (*Martes zibellina*, *M. martes*, *M. foina*, and *M. melampus*; Carnivora, Mustelidae) according to the mandibular metric characteristics. Biol Bull 40:708–717. doi: 10.1134/S1062359013080050

Genovesi P, Secchi M, Boitani L (1996) Diet of stone martens: an example of ecological flexibility. J Zool 238:545–555. doi: 10.1111/j.1469-7998.1996.tb05412.x

Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. J Mammal 93:667–676. doi: 10.1644/11-MAMM-A-265.1

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. Behav Ecol Sociobiol 10:57–63. doi: 10.1007/BF00296396

Goszczyński J, Posłuszny M, Pilot M, Gralak B (2007) Patterns of winter locomotion and foraging in two sympatric marten species: *Martes martes* and *Martes foina*. Can J Zool 85:239–249. doi: 10.1139/Z06-212

Grant PR (1972) Convergent and divergent character displacement. Biol J Linn Soc 4:39–68.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/ NT. Nucleic Acids Symp Ser 41:95–98.

Halle S (2000) Ecological Relevance of Daily Activity Patterns. In: Halle S, Stenseth NC (eds) Act. Patterns Small Mamm. An Ecol. Approach. Springer, New York, pp 67–90

Hardin G (1960) The competitive exclusion principle. Science (80) 131:1292–1297.

Helldin J (2000) Seasonal diet of pine marten *Martes martes* in southern boreal Sweden. Acta Theriol 45:409–420.

Herr J, Schley L, Engel E, Roper TJ (2010) Den preferences and denning behaviour in urban stone martens (*Martes foina*). Mamm Biol 75:138–145. doi: 10.1016/j.mambio.2008.12.002

Herr J, Schley L, Roper TJ (2009) Socio-spatial organization of urban stone martens. J Zool 277:54–62. doi: 10.1111/j.1469-7998.2008.00510.x

ines JE, Mackenzie DJ (2013) Presence V5.8.

Honrado J (2003) Flora e Vegetação do Parque Nacional da Peneda-Gerês. Universidade do Porto, Porto

Humphries CJ, Press JR, Sutton DA (1996) Árvores de Portugal e da Europa. FAPAS, Fundo para a Protecção dos Animais Selvagens & Camara Municipal do Porto, Porto

Iglesias A, España AJ (2010) Rastros y huellas de carnívoros ibéricos. Jaguar eds, Madrid

Jędrzejewski W, Jędrzejewska B (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. Acta Theriol 41:1–34.

Jedrzejewski W, Zalewski A, Jedrzejewska B (1993) Foraging by pine marten *Martes martes* in relation to food resources in Bialowieza National Park, Poland. Acta Theriol 38:405–426.

Kelly MJ, Holub EL (2008) Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. Northeast Nat 15:249–262. doi: 10.1656/1092-6194(2008)15[249:CTOCTS]2.0.CO;2

Klare U, Kamler JF, MacDonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. Mamm Rev 41:294–312. doi: 10.1111/j.1365-2907.2011.00183.x

Kovach WL (2011) Oriana – Circular Statistics for Windows. Kovach

Computing Services, Pentraeth

Kranz A, Tikhonov A, Conroy J, Cavallini P, Herrero J, Stubbe M, Maran T, Abramov A (2008) *Martes martes*. In: IUCN Red List Threat. Species. Version 2013.2. www.iucnredlist.org. Accessed 24 Mar 2014

Larivière S, Jennings AP (2009) Family MUSTELIDAE (weasels and relatives). Handb. Mamm. world. Vol. I - Carniv. Lynx editions, Barcelona, pp 564–656

Linkie M, Ridout MS (2011) Assessing tiger-prey interactions in Sumatran rainforests. J Zool 284:224–229. doi: 10.1111/j.1469-7998.2011.00801.x

Lockie JD (1961) The food of the pine marten *Martes martes* in West Ross-Shire, Scotland. Proc Zool Soc London 136:187–195. doi: 10.1111/j.1469-7998.1961.tb06171.x

Long R, Donovan TM, MacKay P, Zielinski WJ, Buzas JS (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landsc Ecol 26:327–340. doi: 10.1007/s10980-010-9547-1

Long RA, Mackay, Zielinski WJ, Ray J (2008) Noninvasive survey methods for carnivores. Island Press, Washington DC

López-Martin JM (2003) Comparación de la ecología de la Marta (*Martes martes* L. 1758) y la Garduña (*M. foina* Erx.1777) en el N.E. Ibérico, e interacciones con la Gineta. Facultat de Biologia de la Universitat de Barcelona, Bracelona

López-Martin JM (2007) *Martes martes*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 302–304

López-Martín JM (2006) Comparison of feeding behaviour between stone marten and common genet: living in coexistence. In: Santos-Reis M, Birks JDS, O'Doherty EC, Proulx G (eds) Martes Carniv. Communities. Alpha Wildlife Publications, Alberta, Canada, pp 137–155

López-Martín J, Ruiz-Olmo J, Cahill S (2008) Autumn home range and activity of a stone marten (*Martes foina* Erxleben, 1777) in Northeastern Spain. Miscellània Zoològica 16:258–260.

Loveridge AJ, Macdonald DW (2003) Niche separation in sympatric jackals (*Canis mesomelas* and *Canis adustus*). J Zool 259:143–153. doi: 10.1017/S0952836902003114

Loy A, Spinosi O, Carlini R (2004) Cranial morphology of *Martes foina* and *M. martes* (Mammalia, Carnivora, Mustelidae): The role of size and shape in sexual dimorphism and interspecific differentiation. Ital J Zool 71:27–34. doi: 10.1080/11250000409356547

Lucherini M, Reppucci JI, Walker RS, Villalba ML, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal 90:1404–1409. doi: 10.1644/09-MAMM-A-002R.1

Lynam AJ, Jenks KE, Tantipisanuh N, et al. (2013) Terrestrial activity patterns of wild cats from camera-trapping. RAFFLES Bull Zool 61:407–415.

MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385. doi: 10.1086/282505

Mackenzie DI, Bailey LL, Nichols JD (2004) Investigating species co-occurrence patterns when species are detected imperfectly. J Anim Ecol 73:546–555. doi: 10.1111/j.0021-8790.2004.00828.x

MacKenzie DI, Nichols JD, Lachman GB, et al. (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255. doi: 10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Mackenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (2006) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press

Marinis AM de, Masseti M (1995) Feeding habits of the pine marten *Martes martes* L., 1758, in Europe: a review. Hystrix 7:143–150.

Mitchell-Jones AG, Amori G, Bogdanowicz W, Krystufek B, Reijnders PJH, Spitzenberger E, Stubbe M, Thissen JBM, Vohralik V, Zima J (1999) The Atlas of European Mammals. T and AD Poyser Natural History, London,

Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of Iberian carnivore communities. Wildl Res 38:446–454. doi: 10.1071/WR11060

Monterroso P, Alves PC, Ferreras P (2013) Catch Me If You Can: Diel Activity Patterns of Mammalian Prey and Predators. Ethology 119:1044–1056. doi: 10.1111/eth.12156

Monterroso P, Alves PC, Ferreras P (in press) Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behavioral Ecology and Sociobiology. doi: 10.1007/s00265-014-1748-1

Nilsen EB, Christianson D, Gaillard J-M, Halley D, Linnell JDC, Odden M, Panzacchi M, Toigo C, Zimmermann B (2012) Describing food habits and predation: field methods and statistical considerations. In: Boitani L, Powell RA (eds) Carnivore Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford, pp. 256–272

Oliveira R, Castro D, Godinho R, et al. (2010) Species identification using a small nuclear gene fragment: application to sympatric wild carnivores from South-western Europe. Conserv Genet 11:1023–1032. doi: 10.1007/s10592-009-9947-4

Pagano AM, Arnold TW (2009) Detection Probabilities for Ground-Based Breeding Waterfowl Surveys. J Wildl Manage 73:392–398. doi: 10.2193/2007-411

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508. doi: 10.1086/303189

Palomares F, Godoy JA, Piriz A, O'Brien SJ (2002) Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. Mol Ecol 11:2171–2182. doi: 10.1046/j.1365-294X.2002.01608.x

Pereboom V, Mergey M, Villerette N, Helder R, Gerard J-F, Lodé T (2008) Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. Can J Zool 86:983–991. doi: 10.1139/Z08-076

Pereira P, Alves da Silva A, Alves J, Matos M, Fonseca C (2012) Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. Ecol Res 27:745–753. doi: 10.1007/s11284-012-0949-1

Pianka E (1974) Niche Overlap and Diffuse Competition. Proc Natl Acad 71:2141–2145.

Pilot M, Gralak B, Goszczyński J, Posłuszny M (2007) A method of genetic identification of pine marten (*Martes martes*) and stone marten (*Martes foina*) and its application to faecal samples. J Zool 271:140–147. doi: 10.1111/j.1469-7998.2006.00179.x

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

Posillico M, Serafini P, Lovari S (1995) Activity patterns of the stone marten *Martes foina* Erxleben, 1777, in relation to some environmental factors. Hystrix 7:79–97.

Posluszny M, Pilot M, Goszczyński J, Gralak B (2007) Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. Ann Zool Fennici 44:269–284.

Proulx G, Aubry K, Birks J, Buskirk S, Fortin C, Frost H, Krohn W, Mayo L, Monakhov V, Payer D, Saeki M, Santos-Reis M, Weir R, Zielinski W (2005) World distribution and status of the genus *Martes* in 2000. In: Harrison DJ, Fuller AK, Proulx G (eds) Martens Fish. human-altered Environ. Kluwer Academic Publishers, pp 21–76

Reig S (2007) *Martes foina*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 305–307

Reynolds JC, Aebischer NJ (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. Mamm Rev 21:97–122. doi: 10.1111/j.1365-2907.1991.tb00113.x

Richmond OMW, Hines JE, Beissinger SR (2010) Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. Ecol Appl 20:2036–2046. doi: 10.1890/09-0470.1

Ridout M, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J Agric Biol Environ Stat 14:322–337. doi: 10.1198/jabes.2009.08038

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998. doi: 10.1111/j.1461-0248.2009.01347.x

Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas. In: Serv. Cart. la Univ. León Madrid, Spain. http://www.ucm.es/info/cif/form/maps.htm.

Rivas-Martínez S, Díaz TE, Fernández-González F, Izco J, Loidi J, Lousã M, Penas Á (2002) Vascular plant communities of Spain and Portugal. Addenda to the Syntaxonomical checklist of 2001. Itinera Geobot 15:5–922.

Rödel HG, Stubbe M (2006) Shifts in food availability and associated shifts in space use and diet in stone marten. Lutra 49:67–72.

Roger M, Pascal M, Pruniére P (1991) Facteurs correctifs de quantification du régime alimentaire du putois (*Mustela putorius* L.). Gibier Faune Sauvag 7:343–357.

Rondinini C, Boitani L (2002) Habitat use by beech martens in a fragmented landscape. Ecography 25:257–264. doi: 10.1034/j.1600-0587.2002.250301.x

Rosellini S, Barja I, Piñeiro A (2008a) The response of European pine marten (*Martes martes* L.) feeding to the changes of small mammal abundance. Polish J Ecol 56:497–503.

Rosellini S, Osorio E, Ruiz-González A, Piñeiro A, Barja I (2008b) Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. Wildl Res 35:434–440. doi: 10.1071/WR07030

Ruiz-González A, Rubines J, Berdión O, Gómez-Moliner BJ (2007) A non-invasive genetic method to identify the sympatric mustelids pine marten (*Martes martes*) and stone marten (*Martes foina*): preliminary distribution survey on the northern Iberian Peninsula. Eur J Wildl Res 54:253–261. doi: 10.1007/s10344-007-0138-7

Ruiz-Olmo J, López-Martín J (2001) Relaciones y estrategias ecológicas de los pequeños y medianos carnívoros forestales. In: Camprodon J, Plana E (eds) Conserv. la Biodivers. y gestión For. Edicions de la Universitat de Barcelona, pp 397–414

Sagarin RD, Gaines SD (2002) The “abundant centre” distribution: to what extent is it a biogeographical rule? Ecol Lett 5:137–147. doi: 10.1046/j.1461-0248.2002.00297.x

Santos-Reis M, Santos MJ, Lourenco S, Marques JT, Pereira I, Pinto B (2004) Relationships between stone martens, genets and cork oak woodlands in Portugal. In: Harrison DJ, Fuller AK, Proulx G (eds) Martens Fish. human-altered Environ. Springer, pp 147–172

Schoener T (1974) Resource partitioning in ecological communities. Science (80) 185:27–39.

Schoener T (1983) Field experiments on interspecific competition. Am Nat 122:240–285.

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annu Rev Ecol Evol Syst 40:415–436. doi: 10.1146/annurev.ecolsys.110308.120317

Sollmann R, Mohamed A, Samejima H, Wilting A (2013) Risky business or simple solution – Relative abundance indices from camera-trapping. Biol Conserv 159:405–412. doi: 10.1016/j.biocon.2012.12.025

Steen DA, McClure CJW, Brock JC, Rudolph D, Pierce JB, Lee JR, Humphries W, Gregory BB, Sutton WB, Smith LL, Baxley DL, Stevenson DJ, Guyer C (2014) Snake co-occurrence patterns are best explained by habitat and hypothesized effects of interspecific interactions. J Anim Ecol 83:286–95. doi: 10.1111/1365-2656.12121

Szabó P, Meszeéna G (2006) Limiting similarity revisited. Oikos 112:612–619. doi: 10.1111/j.0030-1299.2006.14128.x

Teerink BJ (1991) Hair of West-European mammals. Cambridge University Press, Cambridge

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res 22:4673–4680. doi: 10.1093/nar/22.22.4673

Tikhonov A, Cavallini P, Maran T, Krantz A, Herrero J, Giannatos G, Stubbe M, Libois R, Fernandes M, Yonzon P, Choudhury A, Abramov A, Wozencraft C (2008) *Martes foina*. In: IUCN Red List Threat. Species. Version 2013.2. www.iucnredlist.org. Accessed 24 Mar 2014

Virgós E, Cabezas-Díaz S, Mangas JG, Lozano J (2010) Spatial distribution models in a frugivorous carnivore, the stone marten (*Martes foina*): is the fleshy-fruit availability a useful predictor? Anim Biol 60:423–436. doi: 10.1163/157075610X523297

Wilson DE, Mittermeier RA (2009) Handbook of the mammals of the world. Vol. I - Carnivores. Lynx editions, Barcelona

Zalewski A (2005) Geographical and seasonal variation in food habits and prey size of European pine martens. In: Harrison DJ, Fuller AK, Proulx G (eds) Martens Fish. human-altered Environ. Kluwer Academic Publishers, pp 77–98

Zalewski A (2001) Seasonal and sexual variation in diel activity rhythms of pine marten Martes martes in the Bialowieza National Park (Poland). Acta Theriol 46:295–304.

Zalewski A, Jędrzejewski W (2006) Spatial organisation and dynamics of the pine marten *Martes martes* population in Białowieza Forest (E Poland) compared with other European woodlands. Ecography 29:31–43. doi: 10.1111/j.2005.0906-7590.04313.x

Zar JH (2005) Encyclopedia of Biostatistics. John Wiley & Sons, Ltd. doi: 10.1002/0470011815

Zhang J (2013) Package “spaa”: SPecies Association Analysis.

Zhou Y, Newman C, Xu W, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie Z-Q (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr 38:137–147. doi: 10.1111/j.1365-2699.2010.02396.x

Zielinski WJ (2000) Weasels and Martens - Carnivores in Northern Latitudes. In: Halle S, Stenseth NC (eds) Act. Patterns Small Mamm. An Ecol. Approach. Springer, New York, pp 95–118

General Introduction

Methodological improvements for mesocarnivore ecological studies

Evaluation of attractants for non-invasive studies of Iberian carnivore communities

Factors affecting the (in) accuracy of mammalian mesocarnivore scat identification in South-western Europe

Efficiency of hair snares for monitoring mesocarnivores occurrence

Ecological interactions in mesocarnivore communities in the Iberian Peninsula

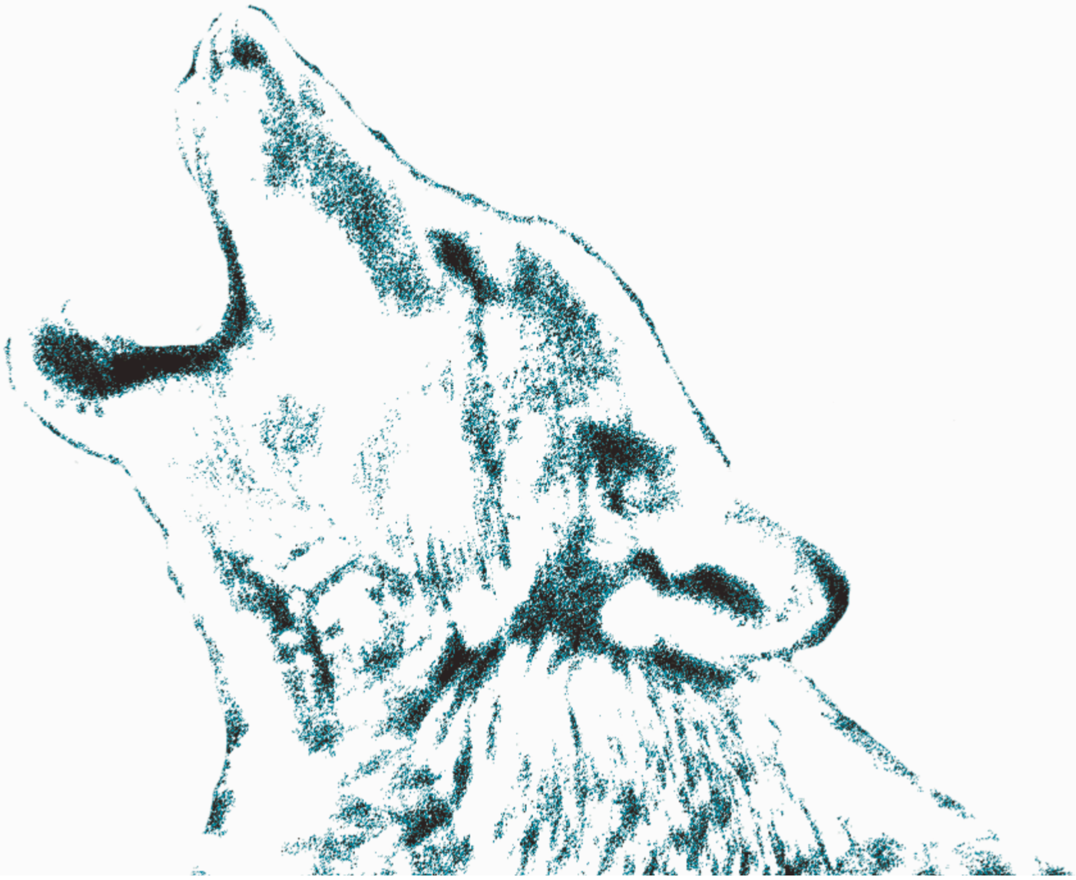
Catch me if you can: diel activity patterns of mammalian prey and predators

Plasticity in activity patterns of mesocarnivores in Southwestern Europe

Spatial interactions in mesocarnivore communities in Southwestern Europe

Plasticity and niche relations between to sympatric competitors

General discussion



4 General Discussion

Predators, namely mammalian carnivores play a crucial role in structured ecosystems, namely by enforcing top-down regulation, increasing resilience against introduced species, controlling the impact of diseases and promoting seed dispersal (Carlsson et al. 2009; Estes et al. 2011; Prugh et al. 2009; Rosalino and Santos-Reis 2009; Salo et al. 2008). Interactions among mammalian carnivores are complex and it has been suggested that lasting coexistence can only be sustained through ecological divergence (Hardin 1960; MacArthur and Levins 1967; Schoener 1974). However, current knowledge regarding the mechanisms that promote and sustain carnivore coexistence in terrestrial systems is still largely deficient. The coexistence of terrestrial carnivores appears to be often promoted by behavioral adjustments in intervening species. The behavioral effects most frequently reported consist in the limitation of accessibility for the most favorable habitats, prey and period of the day (Di Bitetti et al. 2009; Cupples et al. 2011; Harrington and Macdonald 2008; Moreno et al. 2006; Palomares et al. 1996). We predicted that, in Iberian carnivore communities, spatial segregation would be frequent in asymmetrical interactions. However, it would be less frequent between similar sized species, and that the trophic and temporal dimensions should be more important in the ecological separation of these coexisting species. Particularly, when coexisting carnivores share a specific prey, they should segregate spatially when prey availability is widely distributed in the landscape, or segregate temporally when prey distribution is clustered. However, if at least one of the species is not specialized in a particular prey, and alternative feeding resources are available, then trophic niche segregation could be preferred to reduce competitive stress.

In this work we develop non-invasive methods for surveying mammalian carnivores in southwestern Europe, and use these methods for assessing the interactions among the carnivore community in the two main Iberian bioclimatic regions. Overall, our results were in agreement with our predictions. Where clear asymmetrical relations existed, in SANP, spatial segregation was detected between the Iberian lynx (apex predator) and subordinate species. In this case, there was no evidence of segregation in the activity patterns (chapter 3.2). However, among similar sized mesocarnivores, we found no support of ecological separation along the spatial dimension (chapters 3.3 and 3.4). Our results also suggest that circadian segregation may facilitate carnivores' coexistence (chapter 3.3), while allowing access to preferred prey (chapter 3.1). Furthermore, trophic segregation may also be involved in the reduction of competitive stress when feeding resources become limiting (chapter 3.4).

In the following sections, the results obtained in the distinct chapters are integrated and discussed in light of our initial predictions.

4.1 Refinements in noninvasive methods for surveying European mesocarnivores

The extensive use of noninvasive sampling methods in the study of mammalian carnivores arises from recent revolutionary advances in technology, statistics and modeling approaches (Kelly et al. 2012; Long et al. 2008). Advantages of noninvasive methods include the possibility of producing large sample sizes, with consequent reduction in bias and increase in precision, while expanding the spectrum of research topics (Kelly et al. 2012). However, the novelty of such methods requires testing and comparative analysis. The contemporary noninvasive field sampling methods most commonly employed for surveying carnivore populations are scat-searching methods, hair collection and camera trapping (Kelly et al. 2012; Long et al. 2008; McCallum 2013). While the current employment of the two former methods are nearly exclusively in combination with molecular genetics (Heinemeyer et al. 2008; Kendall and Mckelvey 2008), the two latter require animals to encounter the detections stations (hair collection of camera-trapping) (Kays and Slauson 2008; Kelly et al. 2012; Kendall and Mckelvey 2008; O’Connell et al. 2011).

The use of attractants have been reported to increase detection probabilities in mammalian carnivore studies (Hunt et al. 2007; Schlexer 2008; Thorn et al. 2009). While attracting animals to the detection stations may overestimate abundance, several authors report consistent results produced by baited and unbaited stations, although with increased accuracy of the former (Garrote et al. 2012; Mccoy et al. 2011). Regardless, if the research objectives are species, for example, inventories or analysis of occupancy patterns, enhancing detectability will ameliorate the quality of the obtained results (Bailey et al. 2007).

Our results suggest that, no single attractant among those tested provides a high performance in eliciting investigative response for all carnivore species. However, the combination of two of them, the lynx urine and the valerian extract solution, provided good results in attracting most mesocarnivores present in SW European communities. Although lynxes (Eurasian and Iberian lynxes) have been reported to reduce fox populations and kill other smaller mammalian carnivores (Palomares et al. 1996; Palomares and Caro 1999; Pasanen-Mortensen et al. 2013), our results show that their urine does not inhibit the investigative or even rubbing response of mesocarnivores in our study areas. In fact, even in the study area where Iberian lynxes coexist with red foxes, Eurasian badgers, stone martens and genets (chapter 3.2), and intraguild predation has been observed (Gil-Sánchez, personal communication), all detected mesocarnivores showed curiosity towards the lynx scent at camera stations. Whether this response is motivated by territoriality or by fear, allowing for the employment of adequate behavioral strategies for coexistence as a response to a landscape of fear effect (Laundré et al. 2010; Wilson et al. 2010), the fact remains that the animals are attracted to the devices, most likely enhancing detection probabilities and providing the possibility to recover hair samples. Valerian extract complemented the effect of the lynx urine for the species that exhibited less strong attraction behaviors towards the stations, facilitating community-wide surveys.

When combined, lynx urine and valerian extract elicited rubbing behavior in European wildcats, red foxes, common genets and Eurasian badgers in our enclosure tests, and elicited interactive responses in all mesocarnivores during our field trials. However, these behaviors were not reflected in the detection probabilities of mesocarnivores by hair snaring stations. Where the hair snares' were tested (CNP and GVNP), they detected only half (N=3) of the mesocarnivore species than did camera traps (N=6), and detection probabilities were 6.7 ± 1.1 lower. Hair snares detection probabilities were always lower than 0.10 per week, except for the red foxes at CNP. Although red fox density, assessed by distance sampling, at CNP was estimated to be 0.65 ± 0.16 individuals/km^2, which is in within the average for most Spanish territory (0.11 to 3.7 individuals/km^2) (Ferreras et al. 2011), its relative abundance based on camera-trapping rates was much higher than all other mesocarnivore species (chapter 3.1 and 3.2). This pattern allows us to draw two inferences: first, that detectability is closely related to abundance, as previously suggested (McCarthy et al. 2013; Tempel and

Gutiérrez 2013); and second, that given the detectability of red foxes in a situation of midrank density, scented hair snare might be effective for studies of red fox population occupancy throughout the Iberian Peninsula (Bailey et al. 2007). Regardless, the low detection rates obtained for other carnivore species suggest that the response exhibited by the target species was not strong enough to cause hair to be plugged from the animal, the hair snare structure did not efficiently plugged the animals' hair, or the time between station revisits was too long and the collected hair was not efficiently seized in the hair snaring structure. Hair snaring rub-pads applied to carnivore surveys provide contrasting results (Burki et al. 2010; Castro-Arellano et al. 2008; Comer et al. 2011; Downey et al. 2007; Long et al. 2007; Steyer et al. 2012), however the potential information encapsulated in such biological samples motivates the continuous refinements in this sampling method.

Searching, identifying, mapping and analyzing the contents of carnivore scats are the main steps of one of the most commonly used noninvasive traditional methods (Heinemeyer et al. 2008; Kelly et al. 2012; Wilson and Delahay 2001). Extensive scat-based research studies have been published on European carnivore species describing their distributional and abundance patterns (Barea-Azcón et al. 2006; Cavallini 1994; Sadlier et al. 2004), habitat selection (Lozano et al. 2003; Virgós et al. 2002) and feeding ecology (Barrientos and Virgós 2006; Carvalho and Gomes 2004; Delibes-Mateos et al. 2008a; Malo et al. 2004). However, while species identification based on scat morphology and situation is sometimes accurate (Prugh and Ritland 2005), other studies have shown that the misidentifications often occur (Davison et al. 2002; Harrington et al. 2010). We observed high variability in the accuracy of species assignment to mesocarnivore scats. The low variability explained by our models (25%) suggests that accuracy rates are most likely context-specific. This was further supported by the covariates included in the top-ranked models of scat accuracy, which were the scats' morphological characteristics, season and study area (chapter 2.2). It has been argued that scats' misidentification rates increase when target species are rare or when scats are difficult to detect (Bulinski and McArthur 2000; Harrington et al. 2010; Prugh and Ritland 2005). In general, a meta-analysis of the accuracy patterns of mesocarnivore scats' species assignment over the entire study period with respect to target species abundance, as determined by camera-trap success rates (see chapter 2.2), supported this pattern. Overall, 1490 carnivore scats were analyzed by genetic methods, and 1086 produced adequate species identification (72.8%). A Spearman rank correlation between mesocarnivores' trap success and the proportion of correctly assigned species to collected scat revealed a highly significant relationship between abundance and species assignment accuracy ($r = 0.75; p < 0.001$; table 4.1). These results further support that target species abundance and conspicuity are major factors influencing observers' accuracy in the identification of their scats.

Table 4.1. Overall camera-trapping success (TS; detections/100 trapping-days) and accuracy (AC; percent of accurately identified scats) in mesocarnivore scats across study areas. CNP - Cabañeros National Park; GVNP - Guadiana Valley Natural Park; SANP - Serra de Andújar Natural Park; PGNP - Peneda-Gerês National Park; MNR - Muniellos Natural Reserve.

Study area	*Vulpes vulpes*		*Lynx pardinus*		*Felis sp.*		*Martes sp.*		*Meles meles*		*Genetta genetta*		*Herpestes ichneumon*	
	TS	AC	TS	AC	TS	AC	TS	AC	TS	AC	TS	AC	TS	AC
CNP	28.93	0.83	0.00	NA	0.50	0.00	2.98	0.74	1.04	0.0	1.67	NA	0.27	0.0
GVNP	3.20	0.89	0.00	NA	2.30	0.10	4.21	0.83	0.96	NA	2.13	0.0	2.25	0.0
SANP	4.49	0.94	2.72	0.64	0.19	0.00	0.19	0.0	1.59	0.80	0.37	NA	0.00	NA
PGNP	1.71	0.30	0.00	NA	0.40	0.40	3.77	0.95	0.05	0.0	1.01	0.0	0.00	NA
MNR	1.24	0.47	0.00	NA	0.71	0.85	3.47	0.93	0.13	NA	0.40	NA	0.00	NA

The severity of bias associated with misidentifications of carnivore scats may have serious consequences for the management of threatened species, especially if the data leads to unrealistic estimates of species' distribution and conservation status (Birks et al. 2005; Miller et al. 2011). A practical example applied to the Iberian Peninsula concerns the European wildcat. This species' populations in Iberia have declined over the last years, which justified scaling it to the "vulnerable" conservation status in Portugal (Cabral et al. 2005) and "near threatened" status in Spain (García-Perea 2007). Furthermore, a severe lack of information on this species prevents an adequate assessment of its distribution (Cabral et al. 2005; García-Perea 2007). Nevertheless, most research on this small felid's ecology in the Iberian Peninsula is mainly based in morphologically identified scats (e.g. Lozano 2010; Lozano et al. 2003; Malo et al. 2004). Our results indicate a high variability in the accuracy of wildcats' scats, which ranges from zero to 85% (table 4.1). Furthermore, the lowest identification rates were obtained in the Mediterranean study areas (CNP, GVNP and SANP). Disregarding these potential biases could lead to severe overestimations of wildcat populations, especially in the Mediterranean region of the Iberian Peninsula, with subsequent drastically unadjusted conservation plans.

Noninvasively collected biological samples such as hairs and scats could support studies on carnivore occupancy, abundance, movement, genetic variation, gene flow, social structure and mating system, or the impact of environmental stressors (Kelly et al. 2012; Schwartz and Monfort 2008). For instance, while the discrimination between sympatric pine and stone marten scats is impossible by morphological characteristics alone (Rosellini et al. 2008; Ruiz-González et al. 2007), using molecular methods Posluszny et al. (2007) were able to evaluate their diets in areas of co-occurrence and Balestrieri et al. (2010a) were able to document the expansion of pine martens in NW Italy, and document their diet (Balestrieri et al. 2010b). Noninvasive methods can also be used to evaluate patterns of species interactions and infer about interspecific competitive interactions. Using genetically identified scats, Dalen et al. (2004) were able to detect constraints in the spatial niche of arctic foxes (*Alopex lagopus*) imposed by competitive interactions with the dominant red fox. Although we did not explore hair samples to address any biological question, we were able to use genetically identified scats from sympatric pine and stone martens to evaluate their trophic and spatial niche relations (chapter 3.4). This evaluation, only possible with the advent of genetic species identification, provided original information that defies the assumption of pine martens competitive dominance over stone martens (Balestrieri et al. 2010a; López-Martin 2003; Ruiz-Olmo and López-Martín 2001) and that seasonally adjustments in the formers' trophic niche could be involved in maintaining species coexistence.

The observed relatively low genetic identification success of hair samples when compared to scats - 25.2% *vs*. 78.8% (chapter 2.2) or 72.8% (from all analyzed scats) - suggests that while scat-based studies could promptly be used for large-scale studies of Iberian carnivore species and to address specific biological hypothesis concerning co-occurring species (Broquet et al. 2006; Dalen et al. 2004; Janečka et al. 2011; Schwartz and Monfort 2008), hair-snares are a promising tool that requires further developments to increase efficiency. Specifically, better quality DNA must be collected and hair capture rates need to be improved in order to achieve adequate detection probability for less common species.

4.2 Ecological interactions among sympatric mesorcarnivores in SW European communities

The ecological traits exhibited by mammalian carnivores are strongly influenced by the abundance and accessibility to feeding resources, habitat structure, human disturbance and by the relations with other intraguild species (Carter and Shrestha 2012; Gittleman and Harvey 1982; Hebblewhite et al. 2005; Ritchie et al. 2012; Ritchie and Johnson 2009; Schoener 1974). Furthermore, availability (i.e. abundance and accessibility) of prey may be a determinant factor shaping carnivore interspecific relations (Estes et al. 2011; Prugh et al. 2009; Ritchie and Johnson 2009), as competitive stress among sympatric species when a shared resource becomes limiting (Donadio and Buskirk 2006; Palomares and Caro 1999). While spatial dimension of the ecological niche is the most frequently used by competing species to reduce competitive stress (Schoener 1974), recent research has demonstrated that the temporal segregation is often used among terrestrial carnivores to promote coexistence (Di Bitetti et al. 2009; Gerber et al. 2012; Lucherini et al. 2009; Rasmussen and Macdonald 2012).

The spatial dimension

We evaluated the spatial interactions between three sympatric mesocarnivores (the red fox, stone marten and common genet) with a trophic generalist behavior and found no evidence of competitive exclusion in neither of the analyzed species pairs (chapter 3.3). Furthermore, although high competitive relation has been reported between pine and stone martens, often leading to competitive exclusion of the latter (Balestrieri et al. 2010a; López-Martin 2003; Rosellini et al. 2008; Ruiz-Olmo and López-Martín 2001), our occupancy models suggest that these two congeneric mustelids often co-occur at the PGNP study area (chapter 3.4). Among the two-species occupancy models only in stone martens and common genets did we detect responses due to interspecific interactions. Stone martens displayed higher detectability in areas of co-occurrence with pine martens in PGNP, and lower detectability in the areas occupied by red foxes. While the higher detectability of stone martens in areas with pine martens may be related to a higher abundance achieved by the former in these areas (see chapter 3.4), it suggests that the behavior (translated by its conspicuity) of stone martens is not affected by the presence of the congeneric competitor. Notwithstanding, red foxes seem to impose a landscape of fear (Brown et al. 1999; Laundré et al. 2001) over stone martens, compelling to become more inconspicuous in the areas of co-occurrence. The behavioral pattern observed between stone martens and common genets across our study areas was comparable to what we observed between stone and pine martens at PGNP. While we did not find spatially segregated distributions between stone martens and common genets, our results suggest that the common genet is more conspicuous in the areas of co-occurrence.

Previous studies focusing on the spatial relations among European mesocarnivores have reported contrasting results (Pereira et al. 2012; Ruiz-González et al. 2007; Sarmento et al. 2010; Trewby et al. 2008; Zabala et al. 2009). Globally, our analyses of the spatial relations among coexisting generalist mesocarnivores in the Iberian Peninsula suggest that competitive exclusion among mesocarnivores is unlikely in their southwestern distribution in Europe. Moreover, species that share habitat preferences, such as the pine marten, stone marten and common genet, all preferentially forest dwelling species, become more conspicuous in areas of co-occurrence. Their similar body size, habitat and preference for small mammals as staple prey (López-martín 2006; Zhou et al. 2011) deemed these species as potential competitors (Barrientos and Virgós 2006; López-Martin 2003; Ruiz-Olmo and López-Martín 2001; Zabala et al. 2009). However, we found that spatial segregation was not a common strategy. Our case study on pine and stone martens' niche relations at PGNP revealed that seasonal trophic segregation most likely mediates the strength of interspecific competitive interactions between these two species. Adjustments in the trophic niche have already been reported as reducing the competitive interactions between sympatric carnivores, such as American minks and Eurasian otters (Harrington et al. 2009), pumas and bobcats (Hass 2009) or between jaguars and pumas (Moreno et al. 2006). However, when predators share prey species, then spatial adjustments may be unavoidable (Fedriani et al. 2000; Fedriani et al. 1999; Lovari et al. 2013; Mitchell and Banks 2005; Wilson et al. 2010).

The trophic dimension

The stone martens' feeding ecology, evaluated by analyzing genetically identified scats collected at CNP, GVNP and PGNP (table 4.2), shows the plasticity in this species feeding behavior and, most importantly, allows us to speculate on the strategies for coexistence with other species. Since the staple prey of common genets are rodents in it's European range (López-martín 2006; Virgós et al. 1999), rodents are expected to be the main drivers of competitive interactions. Our analyses of the spatial interactions revealed that stone martens and genets tended to be spatially associated at PGNP and CNP. At CNP, where rodents constitute less than 10% of ingested biomass of the stone marten, its diet is mostly based on fruits and seeds (table 4.2). However, at PGNP, stone martens have to cope with two potentially competing species: the pine marten and common genets. Interactions with pine martens are dealt with by trophic and temporal adjustments (chapter 3.4). Competitive stress with common genets might be mitigated by similar responses. However, we don't have data available that could provide us such information. At GVNP, the spatial occupancy pattern of stone martens and common genets appears to be independent (chapter 3.3). In this study area, where European rabbits are very abundant and widely distributed (chapter 3.1; Monterroso et al. 2009), they constitute over 80% of all ingested biomass by stone martens (table 4.2). However, given the extensive availability of this highly profitable feeding resource (Aldama et al. 1991; Malo et al. 2004) competitive stress can be reduced even if both species share the same prey (Heithaus 2001).

Table 4.2. Percent ingested biomass of each considered food item by stone martens (*Martes foina*) in Peneda Gerês National Park (PGNP), Cabañeros National Park (CNP) and Guadiana Valley Natural Park (GVNP), during the non-breeding (NB) and the breeding (B) seasons.

		PGNP			CNP			GVNP	
	NB	**B**	**Total**	**NB**	**B**	**Total**	**NB**	**B**	**Total**
Unidentified mammals	0.00	0.02	0.00	0.52	0.03	0.35	0.00	0.00	0.00
Rodentia	**16.44**	**59.09**	**30.32**	**9.92**	**7.99**	**9.24**	**0.93**	**0.53**	**0.70**
Unidentified rodents	0.00	0.00	0.00	0.17	0.00	0.11	0.25	0.00	0.10
Apodemus sylvaticus	10.92	44.74	21.92	0.00	0.73	0.26	0.00	0.00	0.00
Mus sp.	0.00	1.19	0.39	0.00	0.00	0.00	0.00	0.00	0.00
Microtus sp.	5.52	13.16	8.01	9.75	7.26	8.87	0.68	0.53	0.59
Insectivora	**0.00**	**1.90**	**0.62**	**0.00**	**0.00**	**0.00**	**4.24**	**0.00**	**1.75**
Talpidae.	0.00	1.90	0.62	0.00	0.00	0.00	4.24	0.00	1.75
Lagomorpha	**0.00**	**0.00**	**0.00**	**13.74**	**0.17**	**8.92**	**70.77**	**97.08**	**86.22**
Unidentified leporids	0.00	0.00	0.00	0.07	0.17	0.10	0.26	1.57	1.03
Lepus granatensis	0.00	0.00	0.00	8.49	0.00	5.48	0.00	3.96	2.33
Oryctolagus cuniculus	0.00	0.00	0.00	5.18	0.00	3.34	70.51	91.55	82.86
Artiodactyla (carrion)	**0.08**	**2.08**	**0.73**	**18.94**	**0.61**	**12.44**	**0.00**	**0.07**	**0.04**
Suidae	0.00	0.00	0.00	18.94	0.33	12.34	0.00	0.05	0.03
Cervidae	0.00	1.04	0.34	0.00	0.28	0.10	0.00	0.02	0.01
Bovidae	0.08	1.04	0.39	0.00	0.00	0.00	0.00	0.00	0.00
Aves	**0.01**	**3.22**	**1.06**	**0.03**	**16.77**	**5.97**	**0.73**	**0.69**	**0.71**
Unidentified birds	0.00	0.02	0.01	0.03	0.01	0.02	0.01	0.07	0.04
Columbiforme	0.00	0.14	0.05	0.00	0.00	0.00	0.39	0.00	0.16
Passeriforme	0.01	3.06	1.00	0.00	16.76	5.95	0.34	0.00	0.14
Galiforme	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.62	0.37
Ralliforme	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Reptilia	**0.00**	**1.84**	**0.60**	**0.10**	**0.03**	**0.08**	**0.04**	**0.00**	**0.02**
Unidentified reptiles	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00
Lacertidae	0.00	0.73	0.24	0.03	0.00	0.02	0.00	0.00	0.00
Colubridae	0.00	1.10	0.36	0.07	0.00	0.05	0.04	0.00	0.01
Amphibia	**0.00**	**0.06**	**0.02**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Gastropoda	**0.01**	**0.20**	**0.07**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Arthropoda	**0.19**	**4.99**	**1.75**	**2.42**	**3.48**	**2.80**	**0.35**	**0.01**	**0.15**
Fruits/Seeds	**83.01**	**13.91**	**60.53**	**52.13**	**55.60**	**53.36**	**19.19**	**0.00**	**7.92**
Vegetal matter	**0.25**	**12.69**	**4.30**	**2.20**	**14.52**	**6.57**	**2.26**	**1.57**	**1.86**
Eggs	**0.00**	**0.00**	**0.00**	**0.00**	**0.06**	**0.02**	**0.76**	**0.03**	**0.33**
Mushrooms	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	**0.01**	**0.00**	**0.03**	**0.02**
Unidentified material	**0.00**	**0.00**	**0.00**	**0.00**	**0.71**	**0.25**	**0.72**	**0.00**	**0.30**

The temporal dimension

Behavioral adjustments along the temporal niche have been reported to be an important strategy for sustaining coexistence among sympatric carnivores (Azlan and Sharma 2006; Di Bitetti et al. 2010; Di Bitetti et al. 2009; Gerber et al. 2012; Harrington et al. 2009; Rasmussen and Macdonald 2012; Wang and Fisher 2012).

According to the optimal foraging theory, animals should forage so that they can maximize their caloric intake per time unit (MacArthur and Pianka 1966; Pyke et al. 1977). We found that mammalian mesocarnivores, as a community, synchronize their activity patterns with that of rodents and partially with European rabbits (chapter 3.1), which are the preferred preys among most European mesocarnivores (Díaz-Ruiz et al. 2013; López-martín 2006; Lozano et al. 2006; Zhou et al. 2011). Alternative items significantly consumed by European mesocarnivores are fruits (Rosalino and Santos-Reis 2009), which are available throughout the entire diel cycle during their fructification period, and consequently not requiring any specific adjustment in predators daily behavior. However, as previously stated, varying availability of feeding resources and community structure, should lead to differences in the competitive stress among intervening species (Heithaus 2001; Linnell and Strand 2000; Roemer et al. 2009; Wilson et al. 2010). Accordingly, we found that the activity patterns of most mesocarnivores were not constant between study areas or seasons, suggesting behavioral adjustments to local conditions. The significant decrease of the mean interspecific activity overlap with increasing community diversity (chapter 3.2) further suggests that these shifts in activity patterns could consist of behavioral responses to the presence of competing species. Particularly, low overlap in activity patterns and high asynchrony in activity peaks were obtained at GVNP, where community evenness was the highest (chapter 3.1) and where most species exploit a common and widely abundant prey, the European rabbit (table, 4.2; Monterroso et al. 2006; Monterroso 2006).

While circadian separation among coexisting species should be rapidly exhausted with increasing diversity (Schoener 1974), phylogenetic constrains in the regulation of species endogenous clocks may additionally confine the exhibited activity patterns (Kronfeld-Schor et al. 2001; Roll et al. 2006). Nevertheless, we found that strictly nocturnal species (chapter 3.2) were able to have activity shifts contained within their preferred part of the diel cycle (Kronfeld-Schor and Dayan 2003), and that temporal segregation is effectively used at a community level, probably to minimize the probability of agonistic encounters (Gerber et al. 2012; Linnell and Strand 2000; Palomares and Caro 1999), while maintaining access to main prey (chapter 3.1).

The SANP was the only study area in the Mediterranean region that included an apex predator. Iberian lynxes are extant in this study area, which includes five female home ranges (Gil-Sánchez, personal communication). The mammalian carnivore community in this study area is simplified, and there is consistent presence of lynxes, red foxes and Eurasian badgers. This kind of community structure was expected as Iberian lynxes have already been reported to suppress the populations of smaller mesocarnivores, often killing them (Palomares et al. 1996; Palomares et al. 1995; Palomares and Caro 1999). Given that human disturbance is low in this study area due to its limited access, no human induced constrains are imposed in the diel activity of occurring animals. However, in spite of the high risks that encounters with Iberian lynxes pose to the integrity of red foxes, no significant differences were observed between the activity patterns of these two species. However, using data from cameras where at least one of the species was detected, we found a statistically significant negative correlation between the trapping-success rates of red foxes and Iberian lynxes, in the non-breeding season ($r = -0.86, p < 0.001, n = 13$). A similar tendency was detected in the breeding season, however it was not significant ($r = -0.38, p < 0.178, n = 14$). These findings are in accordance with previous research on these two species, which suggests that red foxes are able to avoid competition with Iberian lynxes through fine-scale adaptations (Fedriani et al. 1999; Palomares et al. 1996). Nonetheless, a detailed analysis of these species trophic niche could provide deeper insights into the strategies that mediate their coexistence. The contrasting results obtained from the Iberian lynx / red fox pair at SANP with those obtained from the pine marten / stone marten at PGNP make some hypotheses inevitable to postulate. First, the interactions among coexisting species are dynamic both in asymmetrical and mutual reciprocal competitive relations, and the strength of these interactions may vary according to season, probably mediated by feeding resources availability (Donadio and Buskirk 2006; Linnell and Strand 2000; Palomares and Caro 1999; Ritchie and Johnson 2009). Secondly, spatial segregation appears to be more effective in asymmetrical relationships, but trophic and activity pattern adjustments may be preferred among similar sized species. Finally, our results from the PGNP (chapter 3.4) suggest that the relative dominance between similar-sized species may not be constant across study areas, and it may change according to site-specific conditions. The interactions among predators and with their prey are dynamic and multidimensional (Linnell and Strand 2000; Schoener 1974), and the complexity of carnivore community functioning can only be grasped with holistic approaches that simultaneously evaluate the three main dimensions of the ecological niche (Fedriani et al. 2000; Fedriani et al. 1999; Scognamillo et al. 2003).

5 Conclusions

With this wok we provided relevant contributions for the understanding of the carnivore communities in southwestern Europe from a methodological and ecological level. The following main conclusions could be drawn from the work developed throughout this thesis:

1. Although several attractants may be used for species-specific studies in European carnivore communities, Lynx (*Lynx lynx* or *Lynx pardinus*) urine showed the most efficient results for community-wide surveys. Furthermore, lynx urine and Valerian extract provide complementary effectiveness in the attraction of European mammalian carnivores, and elicit investigative behavior and rubbing responses in Iberian wolves, European wildcats, Eurasian badgers, polecats and red foxes.
2. While eliciting rubbing behavior in enclosure trials, the low detectability of hair-snares when compared to camera traps suggest that this behavior must not be strong under natural conditions. Consequently, this method may not be efficient for short-term occupancy studies of target populations. Neverheless, hair collection structures may enable long-term monitoring of mammalian carnivores using a combination of adequate sampling designs and molecular analyses of DNA extracted from the collected biological samples. Particularly, the detectability rates of red foxes in midrank density situations suggest that hair snares could be useful for monitoring of red fox populations.
3. Our results highlight the potential errors of traditional scat-based sampling methods. The accuracy of species assignment of scats based on their morphology is highly variable (ranging from 0 to 95%) and depends on the abundance of target and other ecologically similar species, and on context-specific circumstances. Such variability prevents extrapolation of accuracy rates over areas, and stresses the importance of using genetic methods for assigning species identifications to scats in order to adequately draw inferences from the patterns observed in nature.

4. Mammalian mesocarnivores in the Iberian Peninsula are predominantly nocturnal, displaying a high overlap with the activity patterns of murid rodents and partially with European rabbits. The high overlap between the activity patterns of mammalian mesocarnivores and their prey is in accordance with optimal foraging theory, suggesting that predators forage when they can maximize accessibility to the most profitable prey.
5. Mammalian mesocarnivores, as a community, exhibit a high activity overlap with that of murid rodents, even when a more profitable prey (the European rabbit) is available. This fact appears to be linked either to temporal restrictions imposed by intraguild competitors, or to a balance between an adequate access to European rabbits during a suboptimal period and accessibility to rodent prey.
6. Three distinct groups of Iberian mesocarnivores could be identified regarding their activity patterns: strictly nocturnal, facultative nocturnal and strictly diurnal species. The first group includes the stone marten, Eurasian badger and common genet, and consists of species that reveal particularly strong selection indices towards nighttime, with little activity during the twilight periods, and strongly avoid being active during daytime. The second group includes the red fox, European wildcat, pine marten and Iberian lynx, and consists of species that positively select nighttime, but also use the twilight periods as expected by chance. Daytime is used less than expected by chance, but is not strictly avoided. The Egyptian mongoose was the only strictly diurnal species.
7. Activity patterns exhibited by mesocarnivores are not constant among study areas or seasons, suggesting behavioral adjustments to local conditions, probably facilitating coexistence. However, the activity shifts observed were contained within the preferred parts each species' daily cycle, supporting an endogenous regulation of their diel activities. This regulation appears to be particularly constraining in stone martens, common genets and Eurasian badgers.
8. Segregation along the temporal niche constitutes a recurrent strategy among co-occurring Iberian mesocarnivores. This behavior appears to facilitate carnivores' coexistence and is more pronounced in more complex communities.

9. Adjustments along the spatial dimension of the ecological niche are not a frequent strategy among co-occurring similar sized mesocarnivores in the Iberian Peninsula. Such adjustments only occur in asymmetrical competitive relations, where the dominant species is clearly defined, as is the case of the Iberian lynx and the red fox.

10. We found no evidence that similar sized mesocarnivores segregate spatially in mesocarnivore-dominated communities. However, behavioral responses take place in areas of co-occurrence, where subordinate species may adopt a more elusive behavior. In these situations, potentially stressful interactions are preferably handled by displacements along the temporal and trophic niche dimensions, allowing sympatric intraguild competitors to spatially co-occur.

11. In the study area where we were able to evaluate the niche relations between the two marten species (PGNP), the stone marten appears to be the dominant competitor over the pine marten, contrasting to what has been reported in other areas of sympatry. This observation suggests that, in similar sized competitors, the relative dominance position is not constant and may change due to context-specific factors.

12. The interactions between co-occurring Iberian terrestrial carnivores are dynamic, and their strength and direction may vary seasonally and geographically, fact that should be taken into account in community-wide studies.

13. Intraguild interspecific interactions significantly influence the spatial, temporal and trophic expression of a species ecological niche, and therefore must be accounted for in species-specific studies.

6 Future directions

In the last decades years several outbreaks of primary consumers have been reported in the Iberian Peninsula. For example, an outbreak of common voles (*Microtus arvalis*) in central Spain in 2007 has produced extensive damages in agricultural fields. More recently, in 2012, European rabbit outbreaks have affected extensive areas in central and south Spain, destroying large areas of cultivated fields and altering the hunting economy at a regional level. Although it has been argued that these disproportional irruptions were related to changes in land use, these human-altered ecosystems lack structured predator assemblages which could buffer its effects. Furthermore, the high economic value of European rabbits (Ferreira et al. 2013) motivates the generalized employment of predator control in the Iberian Peninsula, depressing predator populations and reducing diversity (Beja et al. 2008; Casanovas et al. 2012). However, the effectiveness such methods in releasing rabbits from top-down control enforced by predators is currently dependent on humans (Beja et al. 2008; Delibes-Mateos et al. 2008b), because the otherwise overgrowth of generalist predators often drives rabbits into a predator-pit effect (Pech et al. 1992; Pech and Hood 1998). Restoration of apex predators has been argued as an effective and less costly tool to release primary prey from mesocarnivore enforced top-down control, while stabilizing its populations (Estes et al. 2011; Ritchie et al. 2012). However, the complex web of interactions that link coexisting carnivores is still largely unknown. With this work, we have given one step further towards the understanding of interspecific interactions within mammalian carnivore communities in terrestrial ecosystems of the Iberian Peninsula. However, there is still a long road ahead. Revolutionary advances in noninvasive methods are rapidly widening the research possibilities, enabling us to pursue previously unthinkable hypothesis (Kelly et al. 2012; Long et al. 2008). However, the success of such research is only possible through a symbiotic relationship between effective field sampling methods and evolving disciplines such as conservation genetics (Avise and Hamrick 1996) and conservation physiology (Wikelski and Cooke 2006). Noninvasive endocrine tools are rapidly emerging, and provide information of the physiologic responses of animals to the environment (Kelly et al. 2012; Schwartz and Monfort 2008). Particularly, the concentration of glucorticoids (stress hormones) in noninvasive samples (such as scats, hair or urine) can be used to evaluate stress levels, and identify environmentally induced chronic or acute stressors that can ultimately affect fitness or survival (Wikelski and Cooke 2006). The assessment of the physiological status could provide valuable insights in identifying and quantifying competitive relations between coexisting competitors, especially when the behavioral expression of such effects is particularly subtle.

Our results suggest that interspecific interactions are dynamic, and may produce adjustments over several dimensions of the ecological niche. Furthermore, these responses appear to be subtle in mesocarnivore-dominated communities, where most species are similar sized. However, we found strong signals suggesting that the ultimate expression of mesocarnivores' ecological traits is influenced by competitive interspecific interactions. Therefore, we suggest that future research on carnivore conservation should be integrative and multidimensional, simultaneously evaluating the niche relations along the three main dimensions: spatial, trophic and temporal. However, because symmetrical interspecific interactions among carnivores are exceptionally challenging to identify and quantify (Pereira et al. 2012; Šálek et al. 2013; Sarmento et al. 2010), higher efforts should be employed to increase methods' sensitivity.

In light of our findings, we stress that methodological refinements focused in increasing detectability are still required for hair-snaring methods, as the combined use of efficient hair snares and camera traps in mixed stations could provide complementary information. Particularly we suggest that future research focusing in interspecific interactions between terrestrial carnivores should be based on:

- *Long term* studies - Interspecific relations dynamic. Therefore, long term monitoring programs may allow the identification of the factors that might cause shifts in the relative stability of such relations;
- *Landscape scale* - The spatial responses of interacting species could be expressed at the landscape scale, by evident exclusion from certain habitats, or at fine scale, such as avoidance of the competitors' core areas. Therefore, the sampling methods should provide suitable information across an adequate spatial scale, which is dependent on the target species home-range (Maffei and Noss 2008);

- *Multidimensional approaches* - Behavioral responses to the presence of intraguild competitors can be expressed over several dimensions of the ecological niche. Therefore, multidimensional approaches that simultaneously evaluate the spatial, trophic and temporal dimensions are required to provide “the full picture”, and thus preventing misinterpretations about the patterns of coexistence between potential competitors.
- *Multiple sites* - The strength and relative dominance position between competing species is context-dependent, especially in symmetrical relations. Multiple-sites approaches dilute site-specific effects and allow the predominant patterns to emerge.
- *Multidisciplinary* methodologies - No single method can provide the required information to evaluate interspecific relations. However, a better grasp of this subject in carnivore communities can be achieved using complementing disciplines. Camera trapping provides valuable data on occupancy and activity, however biological samples are required for deeper insights. Conservation genetics and physiology applied to noninvasively collected samples offer means to reduce bias (e.g. through species, gender or individual identification), increase sample sizes and evaluate animals’ responses (e.g. trophic or stress) to the environment.

In the current context of climate change and habitat degradation, it is crucial to efficiently determine the effect of carnivores in the ecosystems and how they shift with community structure, to adequately forecast the impact of species loss (extinction) or gain (recolonization) to maintain biodiversity and foster adjusted management plans. Therefore, continuous and deeper research on the functioning of terrestrial carnivore communities is still largely required, particularly focusing in mesocarnivore-dominated ecosystems and in developing cutting-edge noninvasive disciplines.

7 References

Aldama J, Beltrán JF, Delibes M (1991) Energy expenditure and prey requirements of free-ranging Iberian lynx in southwestern Spain. J Wildl Manage 55:635–641.

Avise JC, Hamrick JL (1996) Conservation Genetics. Springer, Boston..

Azlan JM, Sharma DSK (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40:36.

Bailey LL, Hines JE, Nichols JD, MacKenzie DI (2007) Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. Ecol Appl 17:281–290.

Balestrieri A, Remonti L, Ruiz-González A, Gómez-Moliner BJ, Vergara M, Prigioni C (2010a) Range expansion of the pine marten (*Martes martes*) in an agricultural landscape matrix (NW Italy). Mamm Biol - 75:412–419.

Balestrieri A, Remonti L, Ruiz-González A, Vergara M, Capelli E, Gómez-Moliner BJ, Prigioni C (2010b) Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). Acta Theriol 56:199–207.

Barea-Azcón JM, Virgós E, Ballesteros-Duperón E, Moleón M, Chirosa M (2006) Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodivers Conserv 16:1213–1230.

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

Beja P, Gordinho L, Reino L, Loureiro F, Santos-Reis M, Borralho R (2008) Predator abundance in relation to small game management in southern Portugal: conservation implications. Eur J Wildl Res 55:227–238.

Birks JDS, Messenger JE, Braithwaite T, Davison A, Brookes R, Strachan C (2005) Are scat surveys a reliable method for assessing distribution and population status of pine martens? In: Harrison DJ, Fuller AK, Proulx G (eds) Martens Fish. human-altered Environ. Springer, pp 235–252.

Di Bitetti MS, De Angelo CD, Di Blanco YE, Paviolo A (2010) Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica 36:403–412.

Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pérez IJ (2009) Time Partitioning Favors the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes (*Lycalopex gymnocercus*). J Mammal 90:479–490.

Broquet T, Ménard N, Petit E (2006) Noninvasive population genetics: a review of sample source, diet, fragment length and microsatellite motif effects on amplification success and genotyping error rates. Conserv Genet 8:249–260.

Brown JS, Laundré JW, Mahesh G (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399.

Bulinski J, McArthur C (2000) Observer error in counts of macropod scats. Wildl Res 27:277 – 282.

Burki S, Roth T, Robin K, Weber D (2010) Lure sticks as a method to detect pine martens *Martes martes*. Acta Theriol 55:223–230.

Cabral MJ, Almeida J, Almeida PR, Dellinger T, Ferrand N, Oliveira M, Palmeirim JM, Queiroz A, Rogado L, Santos-Reis M (2005) Livro Vermelho dos Vertebrados de Portugal, 2nd ed. Instituto da Conservação da Natureza/Assírio Alvim, Lisboa.

Carlsson NOL, Jeschke JM, Holmqvist N, Kindberg J (2009) Long-term data on invaders: when the fox is away, the mink will play. Biol Invasions 12:633–641.

Carter N, Shrestha B (2012) Coexistence between wildlife and humans at fine spatial scales. Proc Natl Acad Sci U S A 109:15360–15365.

Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). J Zool 263:275–283.

Casanovas JG, Barrull J, Mate I, Zorrilla JM, Ruiz-Olmo J, Gosàlbez J, Salicrú M (2012) Shaping carnivore communities by predator control: competitor release revisited. Ecol Res 27:603–614.

Castro-Arellano I, Madrid-Luna C, Lacher TE, León-Paniagua L (2008) Hair-Trap Efficacy for Detecting Mammalian Carnivores in the Tropics. J Wildl Manage 72:1405–1412.

Cavallini P (1994) Faeces count as an index of fox abundance. Acta Theriol 39:417–424.

Comer CE, Symmank ME, Kroll JC (2011) Bobcats Exhibit Low Detection Rates at Hair Collection Stations in East Texas. Wildl Biol Pract 7:116–122.

Cupples JB, Crowther MS, Story G, Letnic M (2011) Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? J Mammal 92:590–600.

Dalen L, Elmhagen B, Angerbjorn A (2004) DNA analysis on fox faeces and competition induced niche shifts. Mol Ecol 13:2389–2392.

Davison A, Birks JDS, Brookes RC, Braithwaite TC, Messenger JE (2002) On the origin of faeces: morphological versus molecular methods for surveying rare carnivores from their scats. J Zool 257:141–143.

Delibes-Mateos M, Fernandez de Simon J, Villafuerte R, Ferreras P (2008a) Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. Eur J Wildl Res 54:71–78.

Delibes-Mateos M, Ferreras P, Villafuerte R (2008b) Rabbit (*Oryctolagus cuniculus*) abundance and protected areas in central-southern Spain: why they do not match? Eur J Wildl Res 55:65–69.

Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martín JM, Ferreira C, Ferreras P (2013) Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian Peninsula. Mamm Rev 43:59–70.

Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat 167:524–36.

Downey PJ, Hellgren EC, Caso A, Carvajal S, Frangioso K (2007) Hair Snares for Noninvasive Sampling of Felids in North America: Do Gray Foxes Affect Success? J Wildl Manage 71:2090–2094.

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond Wj, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA (2011) Trophic downgrading of planet Earth. Science 333:301–306.

Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric Mediterranean carnivores. Oecologia 121:138–148.

Ferreira C, Touza J, Rouco C, Díaz-Ruiz F, Fernández-de-Simón J, Ríos-Saldaña CA, Ferreras P, Villafuerte R, Delibes-Mateos M (2013) Habitat management as a generalized tool to boost European rabbit *Oryctolagus cuniculus* populations in the Iberian Peninsula: a cost-effectiveness analysis. Mamm Rev (in press)

Ferreras P, Monterroso P, Alves PC (2011) Situación de las poblaciones de zorro en el Parque Nacional de Cabañeros. Technical report. IREC, Ciudad real.

García-Perea R (2007) *Felis silvestris*. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libr. Rojo los Mamíferos Terr. España. Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid, Spain, pp 333–338.

Garrote G, Gil-Sánchez JM, McCain EB, Santiago L, Tellería JL, Simón MA (2012) The effect of attractant lures in camera trapping: a case study of population estimates for the Iberian lynx (*Lynx pardinus*). Eur J Wildl Res 58:881–884.

Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. J Mammal 93:667–676.

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. Behav Ecol Sociobiol 10:57–63.

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297.

Harrington LA, Harrington AL, Hughes J, Stirling D, Macdonald DW (2010) The accuracy of scat identification in distribution surveys: American mink, *Neovison vison*, in the northern highlands of Scotland. Eur J Wildl Res 56:377–384.

Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald DW (2009) The impact of native competitors on an alien invasive: temporal niche shifts to avoid interspecific aggression? Ecology 90:1207–1216.

Harrington LA, Macdonald DW (2008) Spatial and temporal relationships between invasive American mink and native European polecats in the southern United Kingdom. J Mammal 89:991–1000.

Hass CC (2009) Competition and coexistence in sympatric bobcats and pumas. J Zool 278:174–180.

Hebblewhite M, White CA, Nietvelt CG, McKenzie JA, Hurd TE, Fryxell JM, Bayley SE, Paquet PC (2005) Human activity mediates atrophic cascade caused by wolves. Ecology 86:2135–2144.

Heinemeyer KS, Ulizio TJ, Harrison RL (2008) Natural sign: tracks and scats. In: Long RA, MacKay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, USA, pp 45–75.

Heithaus MR (2001) Habitat selection by predators and prey in communities with asymmetrical intraguild predation. Oikos 92:542–554.

Hunt RJ, Dall DJ, Lapidge SJ (2007) Effect of a synthetic lure on site visitation and bait uptake by foxes (*Vulpes vulpes*) and wild dogs (*Canis lupus dingo* , *Canis lupus familiaris*). Wildl Res 34:461.

Janečka JE, Munkhtsog B, Jackson RM, et al. (2011) Comparison of noninvasive genetic and camera-trapping techniques for surveying snow leopards. J Mammal 92:771–783.

Kays RW, Slauson KM (2008) Remote cameras. In: Long RA, Mackay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, pp 110–140.

Kelly MJ, Betsch J, Wultsch C, et al. (2012) Noninvasive sampling for carnivores. In: Boitani L, Powell RA (eds) Carniv. Ecol. Conserv. A Handb. Tech. Oxford University Press, Oxford, pp 47–69.

Kendall KC, Mckelvey KS (2008) Hair collection. In: Long RA, MacKay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, USA, pp 141–182.

Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu Rev Ecol Evol Syst 34:153–181.

Kronfeld-Schor N, Dayan T, Elvert R, Haim A, Zisapel N, Heldmaier G (2001) On the Use of the Time Axis for Ecological Separation: Diel Rhythms as an Evolutionary Constraint. Am Nat 158:451–457.

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Can J Zool 79:1401–1409.

Laundré JW, Hernández L, Ripple WJ (2010) The Landscape of Fear: Ecological Implications of Being Afraid. Open Ecol J 3:1–7.

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

Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS (2007) Comparing Scat Detection Dogs, Cameras, and Hair Snares for Surveying Carnivores. J Wildl Manage 71:2018–2025.

Long RA, Mackay, Zielinski WJ, Ray J (2008) Noninvasive survey methods for carnivores. Island Press, Washignton DC.

López-Martin JM (2003) Comparación de la ecología de la Marta (*Martes martes* L. 1758) y la Garduña (*M. foina* Erx.1777) en el N.E. Ibérico, e interacciones con la Gineta. PhD thesis. Universitat de Barcelona, Barcelona.

López-martín JM (2006) Comparison of feeding behaviour between stone marten and common genet: living in coexistence. In: Santos-Reis M, Birks JDS, O'Doherty EC, Proulx G (eds) Martes Carniv. Communities. Alpha Wildlife Publications, Alberta, Canada, pp 137–155.

Lovari S, Minder I, Ferretti F, Mucci N, Randi E, Pellizzi B (*in press*) Common and snow leopards share prey, but not habitats: competition avoidance by large predators? J Zool.

Lozano J (2010) Habitat use by European wildcats (*Felis silvestris*) in central Spain : what is the relative importance of forest variables ? Anim Biodivers Conserv 33:143–150.

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

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

Lucherini M, Reppucci J, Walker R, Villalba ML, Wurstten A, Gallardo G, Iriarte A, Villalobos R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal 90:1404–1409.

MacArthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat 101:377–385.

MacArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. Am Nat 100:603–609.

Maffei L, Noss AJ (2008) How Small is too Small? Camera Trap Survey Areas and Density Estimates for Ocelots in the Bolivian Chaco. Biotropica 40:71–75.

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

McCallum J (2013) Changing use of camera traps in mammalian field research: habitats, taxa and study types. Mamm Rev 43:196–206.

McCarthy MA, Moore JL, Morris WK, Parris KM, Garrard GE, Vesk PA, Rumpff L, Giljohann KM, Camac JS, Bau SS, Friend T, Harrison B, Yue B (2013) The influence of abundance on detectability. Oikos 122:717–726.

Mccoy JC, Ditchkoff SS, Steury TD (2011) Bias associated with baited camera sites for assessing population characteristics of deer. J Wildl Manage 75:472–477.

Miller D, Nichols J, McClintock B, Grant E, Bailey L, Weir L (2011) Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. Ecology 92:1422–1428.

Mitchell BD, Banks PB (2005) Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. Austral Ecol 30:581–591.

Monterroso P (2006) Distribuição, selecção de habitat e actividade do gato-bravo (*Felis silvestris*) no Parque Natural do Vale do Guadiana. MSc thesis. University of Porto, Porto.

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

Monterroso P, Moreira P, Castro D, Nery F, Alves PC (2006) Predação sobre o coelho-bravo (*Oryctolagus cuniculus*) em ecossistemas mediterrâneos. In: Ferreira C, Alves PC (eds) Gestão Popul. coelho-bravo (*Oryctolagus cuniculus algirus*). Federação alentejana de caçadores, pp 51–79.

Moreno RS, Kays RW, Samudio R (2006) Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. J Mammal 87:808–816.

O'Connell AF, Nichols JD, Karanth KU (2011) Camera Traps in Animal Ecology: Methods and Analyses. Springer.

Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:492–508.

Palomares F, Ferreras P, Fedriani JM, Delibes M (1996) Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. J Appl Ecol 33:5–13.

Palomares F, Gaona P, Ferreras P, Delibes M (1995) Positive Effects on Game Species of Top Predators by Controlling Smaller Predator Populations: An Example with Lynx, Mongooses, and Rabbits. Conserv Biol 9:295–305

Pasanen-Mortensen M, Pyykönen M, Elmhagen B (2013) Where lynx prevail, foxes will fail - limitation of a mesopredator in Eurasia. Glob Ecol Biogeogr 22:868–877.

Pech RP, Hood GM (1998) Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. J Appl Ecol 35:434–453.

Pech RP, Sinclair ARE, Newsome AE, Catling PC (1992) Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. Oecologia 89:102–112.

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

Posluszny M, Pilot M, Goszczyński J, Gralak B (2007) Diet of sympatric pine marten (*Martes martes*) and stone marten (*Martes foina*) identified by genotyping of DNA from faeces. Ann Zool Fennici 44:269–284.

Prugh LR, Ritland CE (2005) Molecular testing of observer identification of carnivore feces in the field. Wildl Soc Bull 33:189–194.

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

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal Foraging: A Selective Review of Theory and Tests. Q Rev Biol 52:137–154.

Rasmussen GSA, Macdonald DW (2012) Masking of the zeitgeber: African wild dogs mitigate persecution by balancing time. J Zool 286:232–242.

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

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998.

Roemer GW, Gompper ME, Van Valkenburgh B (2009) The Ecological Role of the Mammalian Mesocarnivore. Bioscience 59:165–173.

Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining activity patterns of rodents. Evol Ecol 20:479–490.

Rosalino LM, Santos-Reis M (2009) Fruit consumption by carnivores in Mediterranean Europe. Mamm Rev 39:67–78.

Rosellini S, Osorio E, Ruiz-González A, Piñeiro A, Barja I (2008) Monitoring the small-scale distribution of sympatric European pine martens (*Martes martes*) and stone martens (*Martes foina*): a multievidence approach using faecal DNA analysis and camera-traps. Wildl Res 35:434–440.

Ruiz-González A, Rubines J, Berdión O, Gómez-Moliner BJ (2007) A non-invasive genetic method to identify the sympatric mustelids pine marten (*Martes martes*) and stone marten (*Martes foina*): preliminary distribution survey on the northern Iberian Peninsula. Eur J Wildl Res 54:253–261.

Ruiz-Olmo J, López-Martín J (2001) Relaciones y estrategias ecológicas de los pequeños y medianos carnívoros forestales. In: Camprodon J, Plana E (eds) Conserv. la Biodivers. y gestión For. Edicions de la Universitat de Barcelona, pp 397–414.

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

Šálek M, Červinka J, Padyšáková E, Kreisinger J (2013) Does spatial co-occurrence of carnivores in a Central European agricultural landscape follow the null model? Eur J Wildl Res.

Salo P, Nordström M, Thomson RL, Korpimäki E (2008) Risk induced by a native top predator reduces alien mink movements. J Anim Ecol 77:1092–8.

Sarmento PB, Cruz J, Eira C, Fonseca C (2010) Modeling the occupancy of sympatric carnivorans in a Mediterranean ecosystem. Eur J Wildl Res 57:119–131.

Schlexer F V (2008) Atracting animals to detection devices. In: Long RA, Mackay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, pp 263–292.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185:27–39.

Schwartz MK, Monfort SL (2008) Genetic and Endocrine Tools for Carnivore Surveys. In: Long RA, Mackay P, Zielinski WJ, Ray JC (eds) Noninvasive Surv. methods Carniv. Island Press, Washignton DC, USA, pp 238–262.

Scognamillo D, Maxit IE, Sunquist M, Polisar J (2003) Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. J Zool 259:269–279.

Steyer K, Simon O, Kraus RHS, Haase P, Nowak C (2012) Hair trapping with valerian-treated lure sticks as a tool for genetic wildcat monitoring in low-density habitats. Eur J Wildl Res 59:39–46.

Tempel DJ, Gutiérrez RJ (2013) Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl. Conserv Biol 00:1–9.

Thorn M, Scott DM, Green M, Bateman PW, Cameron EZ (2009) Estimating brown hyaena occupancy using baited camera traps. South African J Wildl Res 39:1–10.

Trewby ID, Wilson GJ, Delahay RJ, Walker N, Young R, Davison J, Cheeseman C, Robertson PA, Gorman ML, McDonald RA (2008) Experimental evidence of competitive release in sympatric carnivores. Biol Lett 4:170–172.

Virgós E, Llorente M, Cortés Y (1999) Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. Mamm Rev 29:119–128.

Virgós E, Tellería J, Santos T (2002) A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. Biodivers Conserv 11:1063–1079.

Wang Y, Fisher D (2012) Dingoes affect activity of feral cats, but do not exclude them from the habitat of an endangered macropod. Wildl Res 39:611–620.

Wikelski M, Cooke SJ (2006) Conservation physiology. Trends Ecol Evol 21:38–46.

Wilson GJ, Delahay RJ (2001) A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildl Res 28:151–164.

Wilson RR, Blankenship TL, Hooten MB, Shivik JA (2010) Prey-mediated avoidance of an intraguild predator by its intraguild prey. Oecologia 164:921–929.

Zabala J, Zuberogoitia I, Martínez-climent JA (2009) Testing for niche segregation between two abundant carnivores using presence-only data. Folia Zool 58:385–395.

Zhou Y, Newman C, Xu W, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie ZQ (2011) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr 38:137–147.