Journal of Zoology

ZSL

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Spatio-temporal patterns of carnivore guild related to their prey in a Mediterranean landscape

A. Peris[1], T. Mampel[1], M. Vilella[2], D. Pons[1], J. Real[3] & R. Puig-Gironès[3,4]

[1]Servei de Gestió de Parcs Naturals, Diputació de Barcelona, Barcelona, Catalonia, Spain
[2]BiBio Research Group, Natural Sciences Museum of Granollers, Francesc Macià 51, Granollers, Spain
[3]Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals & Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Barcelona, Catalonia, Spain
[4]Departament de Ciències Ambientals, Universitat de Girona. C. Maria Aurèlia Capmany 69, Girona, Catalonia, Spain

Keywords
activity patterns; detectability; mesocarnivores; population dynamics; predator–prey relationships; dynamic occupancy models; small mammals.

Correspondence
Roger Puig-Gironès, Equip de Biologia de la Conservació, Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals & Institut de la Recerca de la Biodiversitat (IRBIO), Universitat de Barcelona, Av. Diagonal 643, Barcelona 08028, Catalonia, Spain.
Email: roger.puig.girones@gmail.com

Editor: Hazel Nichols
Associate Editor: Stéphanie Périquet

Received 31 July 2023; revised 15 November 2024; accepted 21 November 2024

doi:10.1111/jzo.13246

Abstract

Small mammal populations fluctuate significantly in abundance over time, affecting the entire food web. However, changes in their occupancy across a landscape receive less attention. While habitat features are relevant for some predators, diet specialization and prey distribution and abundance might play an important role in shaping predator populations. Using a multi-season occupancy analysis, we examined the spatio-temporal patterns of Mediterranean mesocarnivores—common genet, stone marten and red fox—focusing on the factors that influence their occupancy dynamics, particularly small mammal occupancy as a prey resource. Data was collected from December 2020 to May 2021 in the Sant Llorenç del Munt i l'Obac Natural Park using a camera-trap grid. We analysed small mammal occupancy dynamics and used these as covariates in predator occupancy models to explore predator–prey relationships. Additionally, we included the occurrence of each carnivore as a predictor for interspecific analysis, and kernel density functions were used to assess daily activity overlaps. Results showed that interspecific competition significantly affected mesocarnivore occupancy, as genet occupancy was negatively correlated with the red fox occupancy. Although prey occurrence did not influence mesocarnivore occupancy, it did affect detectability, with genet and stone marten detectability being positively related to small mammal presence and high daily activity overlap between predators and prey. This suggests that mesopredators respond rapidly to prey abundance, highlighting the intricate temporal dependence between predator activity and prey occupancy. Dynamic occupancy and activity models provide a deeper understanding of predator–prey relationships at the local scale.

Introduction

Understanding ecosystem functioning and, therefore, effectively devising conservation strategies, requires studying population dynamics and interspecific relationships within communities (Kandziora et al., 2013; Tilman et al., 1997). While large predators have received more attention in ecological studies, mesocarnivores also play a pivotal role in ecosystem dynamics and often serve as crucial drivers of ecosystem function, structure and dynamics as seed dispersers, small mammal population regulators and scavengers (Roemer et al., 2009). On the other hand, small mammals, like rodents and insectivores, play key roles as seed dispersers, burrowers or prey (Hayward & Phillipson, 1979; Lacher Jr et al., 2019), despite often being considered pests in anthropogenic ecosystems (Stenseth et al., 2003). The complex top-down and bottom-up regulatory mechanisms of small mammal populations provide valuable insights for studying the spatial and temporal dynamics of mesocarnivores, which may be influenced by these prey populations (Krebs, 2009; Meserve et al., 2003; Sinclair & Krebs, 2002).

Current landscape and climate changes are causing shifts in small mammal assemblages (Muhly et al., 2011; Rowe & Terry, 2014; Sokolova et al., 2024; Torre et al., 2020, 2023), highlighting the need for new management strategies to conserve ecosystems. Identifying factors influencing prey and predator presence is key for conservation assessment. Both biotic and abiotic elements may play a significant role in

spatio-temporal predator–prey interactions and interspecific relationships (Doherty et al., 2022; Puig-Gironès & Pons, 2023; Sunyer et al., 2013; Torre et al., 2007). For instance, predator habitat selection can be conditioned by prey abundance in a certain environment (Carvalho & Gomes, 2004; Puig-Gironès & Pons, 2020; Vilella et al., 2020), while prey species may exhibit seasonal spatial patterns based on the maturation of fruits that are part of their diet (Díaz et al., 2010; Puig-Gironès et al., 2023).

In the Mediterranean basin, which is defined by highly variable weather patterns, this variability can potentially determine predator–prey dynamics (Fargallo et al., 2009; Previtali et al., 2009; Torre et al., 2020, 2023; Wilmers et al., 2007). Drought and habitat interactions may reduce food availability, decreasing small mammal populations (Espelta et al., 2008; Puig-Gironès et al., 2023), which could affect the mesocarnivore guild, especially the species that rely the most on small mammals for food (Burgos et al., 2023; Hernandez-Puentes et al., 2022; Vilella et al., 2020). However, despite their relevance to the ecosystem and the need for their management, predator–prey and carnivore intra-guild interactions remain understudied in Mediterranean landscapes (Carvalho & Gomes, 2004; Díaz et al., 2005; Puig-Gironès, 2023; Vilella et al., 2020).

Predators and prey usually operate at different temporal and spatial scales, with prey having more rapid reproductive cycles and predators often having larger home ranges (Palomo et al., 2007). Dynamic occupancy models (MacKenzie & Nichols, 2004) are a valuable tool for assessing seasonal variations in rodent occupancy (i.e. species presence probability per sampling unit at each defined period), acting as a surrogate for abundance and studying how this variable influences both predator occupancy and detectability (i.e. the likelihood of detection of a species during each sampling period) (Bailey et al., 2007; MacKenzie et al., 2017; MacKenzie & Nichols, 2004). Additionally, occupancy models may be useful to assess how the presence of each predator species influences the occurrence of others.

In this study, we focused on a mesocarnivore guild comprised of three generalist predator species: the red fox (*Vulpes vulpes* L.), stone marten (*Martes foina* Erxleben) and common genet (*Genetta genetta* L.). Our aim was to describe how forested habitat, prey availability and intra-specific competition influence the occupancy and detectability of these common mesocarnivores in a Mediterranean area, using camera traps in Sant Llorenç del Munt i l'Obac Natural Park (NE of the Iberian Peninsula) during five months between 2020 and 2021. We tested the following hypotheses: (1) predator occurrence is driven by seasonal dependence on food availability and the short-term prey density fluctuations on a carnivore home-range scale. If it is supported, we expect that mesocarnivore detectability and occupancy will be affected by intra-annual variations in small mammal occurrence, as well as predator–prey activity patterns showing overlaps, particularly impacting mesocarnivores that specialize in small mammal prey (Barrientos & Virgós, 2006; Carbone & Gittleman, 2002; Virgós et al., 1999). (2) Predator occurrence is driven by intra-specific competition with niche partitioning structuring carnivore coexistence and activity patterns. Consequently, we would expect to see spatial and temporal niche partitioning among mesocarnivores (Vilella et al., 2020). (3) Habitat factors, specifically the amount of forest cover, positively influence predator occurrence. If supported, we should see mesocarnivore occupancy increase with greater forest cover, based on the habitat preferences of each focal species (Díaz et al., 2005; Mangas et al., 2008; Muñoz et al., 2009; Puig-Gironès & Pons, 2020).

Materials and methods

Study area and target species

The study area was Sant Llorenç del Munt i l'Obac Natural Park (henceforth PNSLL; Fig. 1), a 13 694-ha protected area in the Catalan Prelitoral Mountain Range (NE of Iberian Peninsula). With an altitudinal range of 280–1103 m a.s.l. it has a mid-altitude Mediterranean montane climate, precipitation around 500 mm per year and average temperatures remain around 15°C (Puig-Gironès et al., 2023). Forest covers 60% of its surface area, a consequence of multi-decadal rural abandonment since the 1950s (Carnicer et al., 2021). It is characterized by rocky outcrops and cliffs, whose crags and ridges are clothed chiefly by holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.) woodland with an evergreen oak understory (Pintó & Panareda, 1995).

Since 2018, the Biodiversity Monitoring Centre of Mediterranean Mountains (CMBMM), have extensively monitored biodiversity indicators in the Natural Park (Puig-Gironès & Real, 2022). The terrestrial mammal community is one of the biodiversity elements that is monitored, particularly the mesocarnivore guild consisting of three potential predators of small mammals weighing from 1 to 15 kg (Prugh et al., 2009): genet, stone marten and red fox. These carnivores are widespread in the sampling area (Peris et al., 2011; Torre & Díaz, 2004), however, the common genet stands out as the most specialized rodent predator among them (Dupuy et al., 2009; Hanski et al., 1991). The European badger (*Meles meles* L.) and the least weasel (*Mustela nivalis* L.) are also present in the system but were not included in this study due to their low representation and/or a generalist and rodent-poor diet (Fig. 2). Small mammals, such as rodents and insectivores under 120 g, present in the system include mice, voles and shrews (Delany, 1974).

Camera trap survey

A 22-square grid (1.5 km sides) defined camera placement, based on the common Mediterranean carnivore species' average home ranges (Santos-Reis et al., 2005). A camera trap (Browning BTC-5HDPX) was strategically placed near (±150 m) of the centre of each 2.25-km^2 square, forming a 4950-ha continuous sampling area (Fig. 1). Camera trapping has been effectively used for surveying medium and large mammals (Rovero & Zimmermann, 2016; Tobler et al., 2008), and is increasingly recognized as an efficient technique for identification and studying small mammals, such as rodents (Hopkins et al., 2024; Lamelas-López & Salgado, 2021; Swann & Perkins, 2014; Villette et al., 2016). Using camera traps in

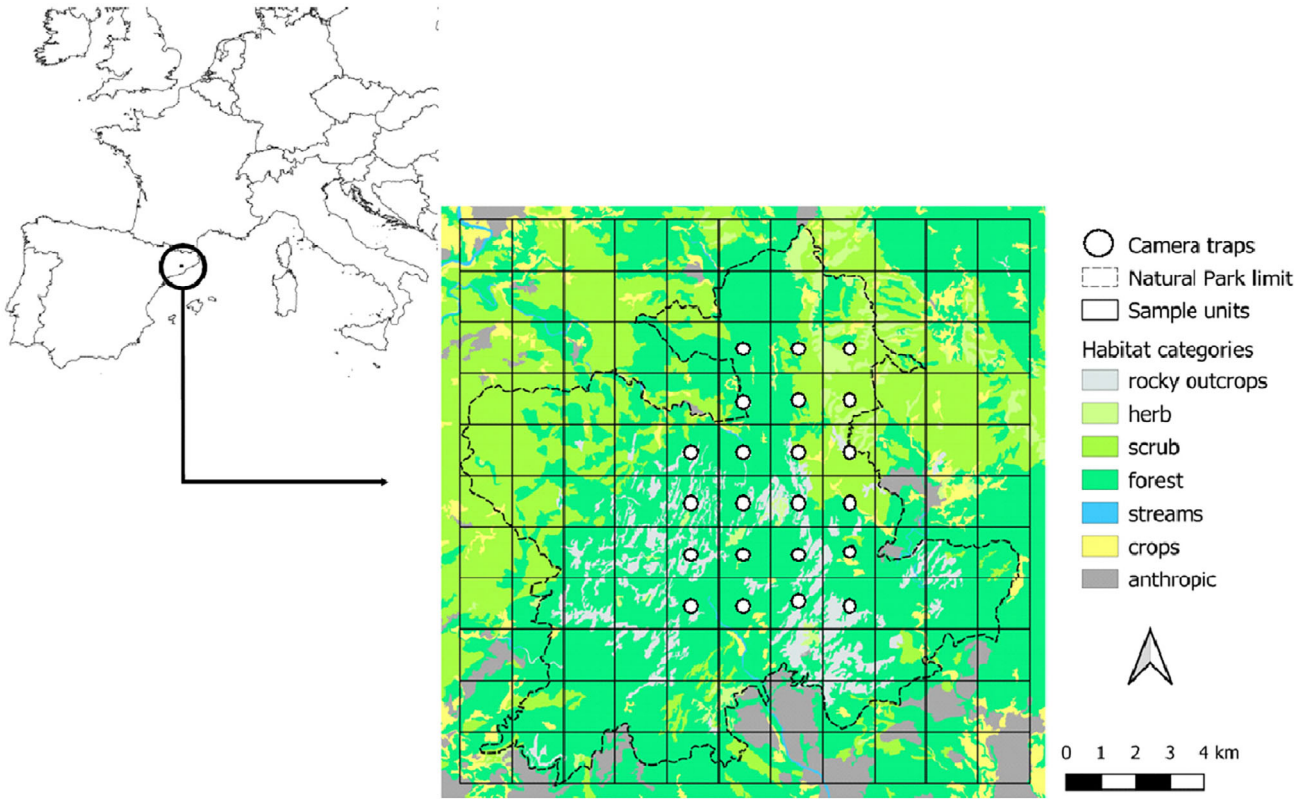

Figure 1 Study area at Sant Llorenç del Munt i l'Obac Natural Park, Catalonia, northeast Spain and the sampling unit grids, camera trap locations and habitat categories considered.

this study, the detection probability of small mammals was adequate for occupancy modelling (average of 0.46; 95% CI 0.32–0.59). Moreover, during dry and hot conditions, camera traps detected more small mammals than live Sherman traps in PNSLL, whereas both methods captured similar numbers during wet periods when their abundance was greater (unpublished data). Cameras were selectively placed along wildlife paths and trails within the squares to maximize the likelihood of detecting the target species. This placement strategy aimed to optimize the natural movement corridors of animals, enhancing the chances of capturing them without the use of lures or baits. By applying this strategy, cameras were positioned 20–50 cm above ground, oriented downward and focusing the camera at rocks or roots, which allowed for effective capture both medium-sized and small mammals (Taylor et al., 2014; Viviano et al., 2022). We obtained authorization from the Servei de Gestió de Parcs Naturals of the Diputació de Barcelona, local administration responsible for managing the Natural Park, to conduct this study.

Cameras operated 24-h a day, capturing three-photo bursts with a 10-s time interval between consecutive bursts. They recorded data for approximately five consecutive months (from December 2020 to May 2021). Considering that the target mesocarnivores do not have a preference for a specific small mammal species (Padial et al., 2002), and the wood mouse (*Apodemus sylvaticus* L.) represents over 89% of the live captures in the area (Puig-Gironès et al., 2023), small mammals were not classified to the species level assuming that the vast majority of the photographs corresponded to this species. Therefore, we assumed wood mouse occupancy data as a proxy of small mammal abundance at locations and periods.

Data analyses

Spatial analysis

For dynamic spatial relationships between species, we used multi-season occupancy models in an unmarked R package (Fiske & Chandler, 2011) within R software (R Development Core Team, 2017). These dynamic models allowed simultaneous assessment of multiple sampling periods, showing variations in occupancy and detectability over time. Capture histories, required for occupancy models, were generated using the *camtrapR* package (Niedballa et al., 2016). Capture histories were represented as binary values indicating species detection (1) or absence (0) at each sampling station (i.e., camera trap) on every capture occasion. To improve detection probability and reduce capture occasions, surveys were structured hierarchically in time. Primary occasions (season), each lasting 15 days, were considered as the highest temporal level. Within each season, three-day data were collapsed into a visit or capture occasions. This approach maintains consistency with

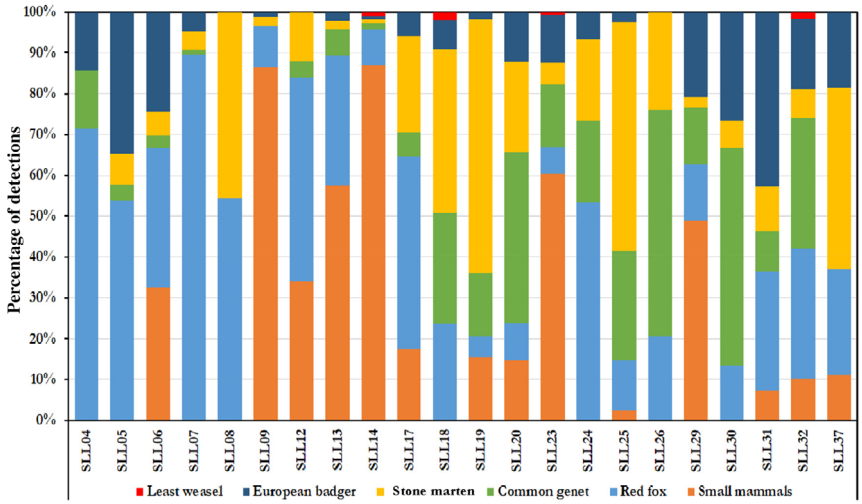

Figure 2 Percentage of independent camera trapping detections for each carnivore and small mammal species at each camera trap site.

carnivore models and applying the same method to small mammals allows for model comparison, enhances model homogeneity, increases detection probability and reduces temporal autocorrelation (Burton et al., 2015; Kleiven et al., 2023; Windell et al., 2024).

Dynamic models for prey were calibrated with primary occasions (seasons) used as a categorical season-site-covariate influencing detection probability (p), colonization probability (gamma) and extinction probability (epsilon). Habitat categories were not considered for small mammals due to insufficient resolution in available cartography (i.e. one hectare) to influence their occupancy. Prey occupancy estimates for each season and site were used as covariates in predator species occupancy models.

In mesocarnivore occupancy models (red fox, stone marten and common genet), small mammal occupancy estimates served as both occupancy and detection covariates. Therefore, it was considered that predator detectability could vary across sites within each season (15-day period). Colonization and extinction parameters also were contemplated that could vary between seasons for small mammal models, consistent with their rapid adaptability and population dynamics (Puig-Gironès & Pons, 2023; Rosário & Mathias, 2004). Conversely, for mesocarnivores, both parameters were assumed constant in the occupancy models due to the relatively short study period. Forest percentage was used as the site habitat variable, discarding all other habitats considered open (scrub, herbaceous, rocky and crops) in the carnivores analysed. To include forest habitat features, habitat percentages were extracted within each 1.5-km square of the camera grid (Fig. 1) from the PNSLL 1:10 000 habitat cover map (Mercadé & Ferré, 2019). Lastly, to assess possible interspecific relationships between carnivores, the estimates of the occupancy of each predator species were introduced as site covariates into the occupancy models of the other species.

Our model selection was ranked using the Akaike information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002) employing the AICcCmodavg (Mazerolle, 2023) R package. A model was considered most plausible in explaining the data if the next best models ΔAICc score was >2.0 (Burnham & Anderson, 2002).

Temporal analysis

Camera-trapping data was also used to calculate mesocarnivore and small mammal daily activity patterns using the kernel density function, a nonparametric method. Nycthemeral prey–predator and predator–predator temporal segregation were calculated using overlap coefficients in pairwise comparisons. Thereby, independent detections were only considered when two same-species pictures from the same camera were separated by a minimum one-hour interval. This interval is commonly used in camera-trapping studies and allows for maximizing independent contacts and obtaining an accurate estimate of daily activity patterns (Azevedo et al., 2018; Bu et al., 2016). Coefficients of overlap (Δ) ranged from 0 (no overlap) to 1 (total overlap). We categorized activity overlap based on the percentiles of overall pairwise comparisons (Monterroso et al., 2014), with 'low' overlap as $\Delta \leq$ 50th percentile, 'moderate' overlap as 50th percentile $< \Delta \leq$ 75th percentile and 'high' overlap as $\Delta >$ 75th percentile. The overlap coefficient is defined as the area under both curves, taking the minimum of the two density functions at each time point. The analyses were performed using the *camtrapR* package (Niedballa et al., 2016) applying the *Dhat* 4 (Δ_4) estimate since we had more than 75 observations for all species (Meredith & Ridout, 2018).

Results

Between December 2020 and May 2021, 3291 trap-nights provided 1251 independent records of target species: small mammals (451), genet (239), stone marten (214) and red fox (347). During this period, the small mammals were registered on

63.6% (n = 14) of sampling sites, red fox was photographed at all sampling points (100%; n = 22), while both stone marten (95.4%; n = 21) and genet (86.4%; n = 19) were detected at most sites (Fig. 2).

Although, our results showed that the best dynamic model for explaining small mammal occupancy incorporates within-season variation in detectability (Table 1), our first hypothesis—that small mammal availability influences mesocarnivore occupancy—was not supported, as mesocarnivore occupancy remained unaffected by small mammal occupancy. However, we observed clear evidence that mesocarnivore detectability was influenced by the multi-season modelled occupancy of small mammals, with both genet (β = 0.923: 95% CIs = 0.412 to 1.433) and stone marten (β = 0.785: 95% CIs = 0.315 to 1.255) showing a positive significant effects (Fig. 3). In contrast, red fox detectability and occupancy was not influenced by any of the tested variables.

Regarding daily activity patterns, focal species were predominantly nocturnal, with small mammal activity peaking at midnight, while mesocarnivores showed activity peaks at twilight

Table 1 The models with variables that affect occupancy and detectability, the degrees of freedom (d.f.), the difference in the Akaike Information Criterion corrected for small sample (ΔAIC), the AIC weight (AICω) and the cumulative AICω (∑AICω)

	Candidate models	d.f.	AICc	ΔAICc	AICω	∑AICω
Small mammal model	ρ(season); γ(.) and ε(.)	14	732.17	0	0.89	0.89
	γ and ρ(season); ε(.)	23	736.45	4.28	0.11	1.0
	γ, ε and ρ(season)	32	747.25	15.08	0.0	1.0
	Null	4	752.73	20.56	0.0	1.0
	γ(season); ε (.) and ρ(.)	13	755.52	23.35	0.0	1.0
	ε(season); γ(.) and ρ(.)	13	761.87	29.7	0.0	1.0
	γ and ε(season); ρ(.)	22	763.89	31.72	0.0	1.0
Genet model	ρ(SMamml); ψ(.)	5	735.85	0	0.77	0.77
	ρ(SMamml); ψ(SMamml)	6	738.38	2.53	0.22	0.99
	Null	4	745.23	9.38	0.01	1.0
	ρ(.); ψ(forest)	5	747.45	11.6	0.0	1.0
	ρ(season); ψ(.)	14	820.02	84.17	0.0	1.0
	ρ(season+SMamml); ψ(.)	15	823.89	88.04	0.0	1.0
	ρ(SMamml+season); ψ(forest+SMamml)	17	899.04	163.18	0.0	1.0
Stone marten model	ρ(SMamml); ψ(.)	5	820.55	0	0.82	0.82
	ρ(SMamml); ψ(SMamml)	6	823.82	3.27	0.16	0.97
	Null	4	827.83	7.27	0.02	1.0
	ρ(.); ψ ~ (forest)	5	831.05	10.49	0.0	1.0
	ρ(season); ψ(.)	14	891.55	70.99	0.0	1.0
	ρ(season+SMamml); ψ(.)	15	904.78	84.22	0.0	1.0
	ρ(SMamml+season); ψ(forest+SMamml)	16	934.65	114.1	0.0	1.0
Red fox model	Null	4	1054.85	0	0.7	0.7
	ρ(.); ψ(forest)	5	1058.01	3.16	0.15	0.85
	ρ(SMamml); ψ(.)	5	1058.22	3.37	0.13	0.98
	ρ(SMamml); ψ(SMamml)	6	1061.85	6.99	0.02	1.0
	ρ(season); ψ(.)	14	1118	63.15	0.0	1.0
	ρ(season+SMamml); ψ(.)	15	1139.75	84.89	0.0	1.0
	ρ(SMamml+season); ψ(forest+SMamml)	16	1170.11	115.25	0.0	1.0
Genet carnivore interactions model	ρ(SMamml); ψ(vulvul)	6	732.33	0	0.55	0.55
	ρ(SMamml); ψ(marfoi+vulvul)	7	733.39	1.06	0.32	0.87
	ρ(SMamml); ψ(.)	5	735.85	3.52	0.09	0.97
	ρ(SMamml); ψ(mar_foi)	6	737.9	5.57	0.03	1.0
Stone marten carnivore interactions model	ρ(SMamml); ψ(.)	5	820.55	0	0.69	0.69
	ρ(SMamml); ψ(vulvul)	6	823.46	2.9	0.16	0.85
	ρ(SMamml); ψ(gengen)	6	823.96	3.41	0.13	0.97
	ρ(SMamml); ψ(gengen+vulvul)	7	827.16	6.61	0.03	1.0
Red fox carnivore interactions model	ρ(.); ψ(.)	4	1054.85	0	0.66	0.66
	ρ(.); ψ(gengen)	5	1057.43	2.57	0.18	0.85
	ρ(.); ψ(marfoi)	5	1058.24	3.39	0.12	0.97
	ρ(.); ψ(gengen+marfoi)	6	1061	6.15	0.03	1.0

Where ρ represents the probability of detection, ψ is the probability of occupancy, γ represents the colonization and ε is the extinction probability. Dot (.) denotes no covariate effect on the parameter. SMamml corresponds to the small mammal modelled occupancy results, whereas gengen (genet), marfoi (stone marten) and vulvul (red fox) correspond to the carnivore best occupancy model.

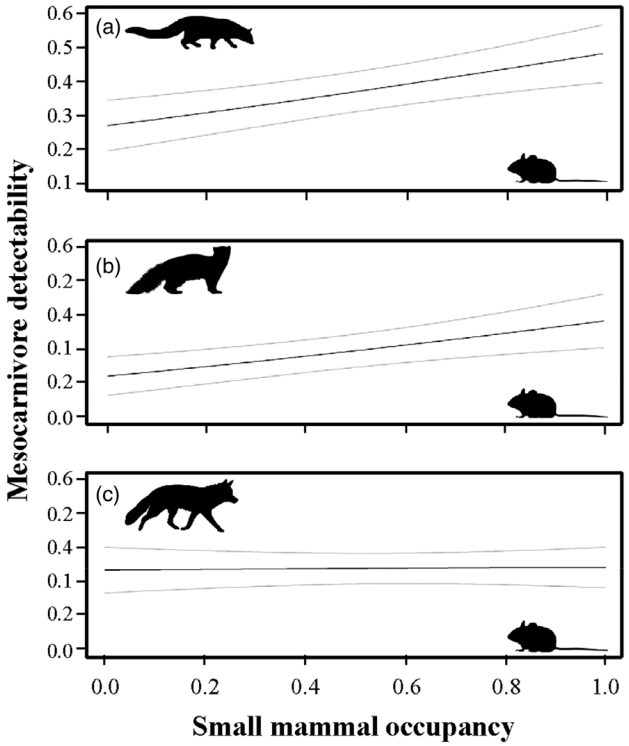

Figure 3 The variation in mesocarnivore detectability (line) and its corresponding confidence intervals (shadow) depending on wood mouse multi-season occupancy is shown in figure (a) for genet, (b) for stone marten and (c) for red fox.

and dawn (Fig. 4). Overlap values differed between the three prey–predator dyads: there was high overlap between small mammals and common genet ($\Delta_4 = 0.91$), moderate overlap with stone marten ($\Delta_4 = 0.85$) and low overlap with red fox ($\Delta_4 = 0.69$).

Considering our second hypothesis regarding mesocarnivore competition, the spatial influence of co-occurring carnivores on individual mesocarnivore occupancy revealed that genet occupancy was impacted by both red fox and stone marten presence, with the former negatively affecting genet occupancy ($\beta = -6.625$: 95% CIs = −12.912 to −0.338) and the latter having a non-significant positive effect ($\beta = 5.445$: 95% CIs = −3.443to 14.335; Fig. 5). Stone marten and red fox occupancy was unaffected by other carnivores in our study area.

Referent to temporal overlaps between predators (Fig. 4), common genet and stone marten presented high overlap as potential small mammal predators and competitors ($\Delta_4 = 0.88$), whereas the red fox showed low overlap with genet ($\Delta_4 = 0.75$) and stone marten ($\Delta_4 = 0.79$).

Finally, no models supported our third hypothesis. Thus, forest cover does not appear to be a variable that significantly influences the occupancy or detectability of mesocarnivores, although, for the red fox, it was the second-best model.

Discussion

Prey distribution has been shown to influence predator occupancy (Dias et al., 2019; Kleiven et al., 2023; Moreno-Sosa et al., 2022; Sharief et al., 2022). However, our study did not find that relationship, but instead found it influenced predator detectability. A possible explanation includes small mammal occupancy variations in spring and summer, influenced by their rapid reproductive cycles (Palomo et al., 2007). Detecting changes in occurrence influenced by specific food availability on slower-life-cycle predators, especially common species that appear in more than 85% of the study area, is challenging. Nevertheless, our dynamic occupancy models showed a positive relationship between prey occupancy and predator detectability, specifically for small mammals-common genet and small mammals-stone marten dyads. The predator–prey relationship, wherein the occurrence of small mammals increases predator detectability, suggests a more predictable response to a food resource expressed by a more active behaviour of genets and stone martens in areas with greater small mammal availability. This could be explained by the seasonal dependence of both mesocarnivores on small mammals in their diet (Barrientos & Virgós, 2006; Virgós et al., 1999). However, this relationship was not observed in the red fox, a more generalist species (Padial et al., 2002), which further supports the link between diet specialization and response to prey.

Predation and anthropogenic disturbances lead to segregation in species' daily activity patterns (Barrientos & Virgós, 2006; Frey et al., 2017; Monterroso et al., 2013; Smith et al., 2019). Consistent with dynamic occupancy models, our results showed high overlaps in carnivore-small mammal activity patterns, particularly for the stricter nocturnal carnivores like the common genet and stone marten. Supporting our hypothesis, the genet, the most trophic specialist among the mesocarnivores studied (Rosalino & Santos-Reis, 2002) showed greater synchrony with small mammal activity, while stone marten, a medium specialist predator, showed moderate overlap. As expected, the red fox, known for its generalist behaviour (Carvalho & Gomes, 2004), exhibited the least activity overlap with small mammals. Small mammals were more active than predators at midnight, consistent with other studies in the same season and geographical region (Monterroso et al., 2013; Vilella et al., 2020). Shifts in the activity peaks of prey have been described as an avoidance strategy to evade predation (Brown et al., 2001; Díaz et al., 2005; Ferreiro-Arias et al., 2021).

Despite differences in reproductive rates, lifespan and home-range size, we provide evidence of the predator–prey relationship in the Mediterranean mountains, an ecosystem characterized by seasonal food availability and irregular population dynamics (Díaz et al., 2010). Small mammals were identified as the main factor to determine both genet and stone marten detectability, indicating the presence of clear predator–prey interactions (Puig-Gironès & Pons, 2020; Torre & Díaz, 2004; Vilella et al., 2020).

Interspecific competition for common resources among carnivores can significantly influence species' spatio-temporal

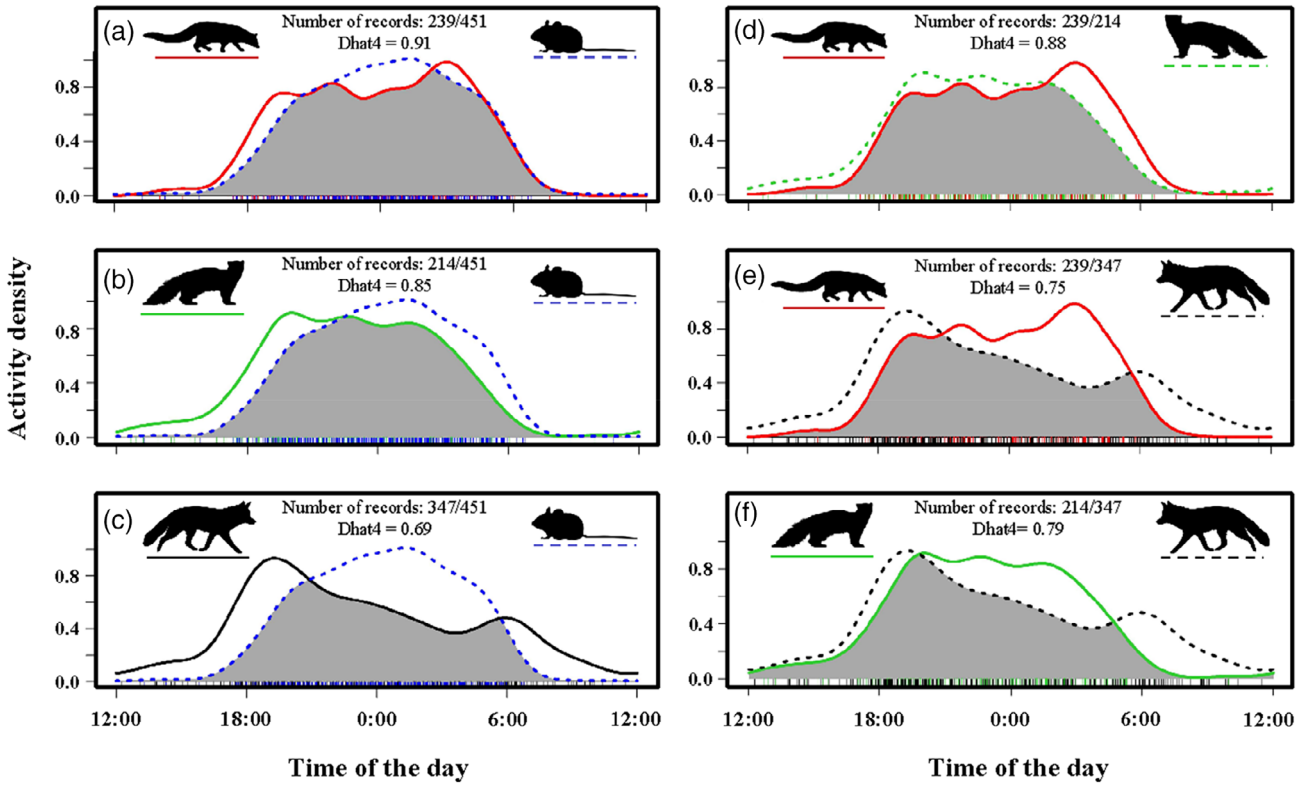

Figure 4 Activity overlap between carnivore species and wood mice (panels on the left): for (a) genet, (b) stone marten and (c) red fox. On the other side (panels on the right), the activity overlap among carnivores for (d) genet and stone marten, (e) genet and red fox and (f) stone marten and red fox.

dynamics (Ferreiro-Arias et al., 2021; Karanth et al., 2017), causing perceptible changes in occupancy patterns and abundance. Variation in the degree to which predators rely on specific prey species can result in separation in habitat use by different predator species. We found that common genet occupancy was inversely related to red fox. This spatio-temporal pattern may be explained by the habitat preferences, as the genet is a more specialized forest species compared to the generalist red fox. Although the red fox can predate on smaller carnivores (Casteneda et al., 2022), and genets do spend time on the ground hunting prey and taking shelter in rocky outcrops (Virgós & Casanovas, 1997), they are primarily arboreal. Genets often spend considerable time climbing trees to hunt birds (Carvalho et al., 2014) and resting in thickets and trees within areas of very dense vegetation, which are practically inaccessible to potential predators (Camps, 2011; Carvalho et al., 2014). This arboreal behaviour makes them less accessible to red foxes. Additionally, trophic segregation reinforces this relationship. The common genet, a specialist in small mammals, exhibits activity patterns that differ from the generalist red fox. These factors contribute to the observed low diel activity overlap, as other authors found (Ferreiro-Arias et al., 2021; Vilella et al., 2020). The second-best model for common genet occurrence included stone marten occupancy as predictor. The positive influence of stone marten occupancy on genet occupancy could be a response to joint predation on small mammals during certain seasons of the year and a similar habitat selection (Vilella et al., 2020).

Genet and stone marten exhibit different degrees of preference for forest environments, while red fox and wood mice, the most abundant small mammal species in the study area, are habitat generalist species (Díaz et al., 2005; Mangas et al., 2008; Muñoz et al., 2009; Puig-Gironès & Pons, 2020; Sunyer et al., 2016; Torre et al., 2022). However, in our carnivore occupancy models, the forest habitat variable did not appear as relevant in the best models for these species. The relative ubiquity of forest habitat—covering approximately 60% of the study area—may complicate the detection of selectivity or occupancy patterns. When a preferred habitat type is widely available, it becomes less likely to be identified as selected or influential (Åberg et al., 2000). Additionally, the wide ranges of predator species within the predominantly forested sampling area may contribute to the lack of clear patterns in habitat selection for mesocarnivores. In addition, several factors beyond simple habitat types, like latitude, historical biogeography, macroclimatic variables and human impact may potentially influence mammal species richness (Ceballos & Brown, 1995; Fløjgaard et al., 2011).

Mesocarnivores have a significant impact on ecosystem function, structure and dynamics (Ritchie & Johnson, 2009). Therefore, the diversity observed in resource and habitat use within this carnivore guild (Roemer et al., 2009), may be

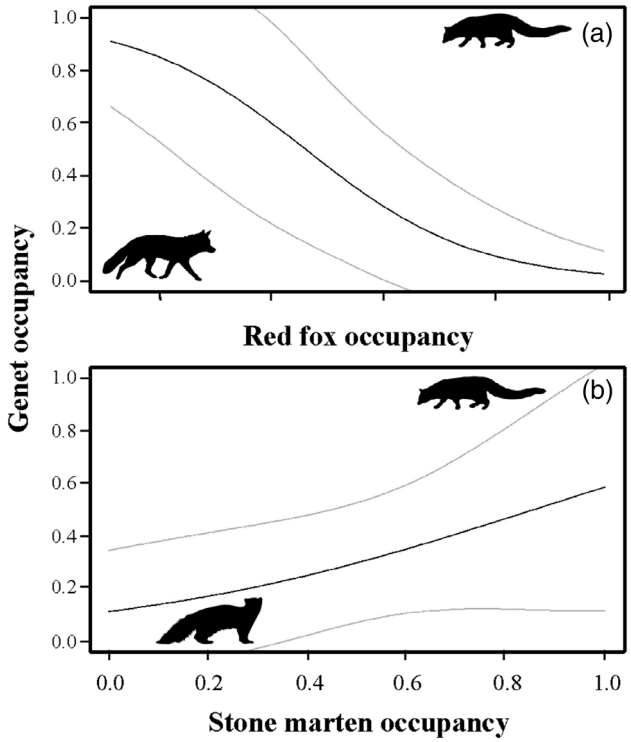

Figure 5 The variation in genet occupancy (line) and its corresponding confidence intervals (shadow) depending on (a) red fox and (b) stone marten occupancy.

crucial in maintaining intra-guild relationships and shaping species' ecological niches (Chesson, 2000). Our study reveals the spatial and temporal dynamics of predator guild and examines how interspecific relationships and predator–prey interactions facilitate and structure the coexistence of mesocarnivore assemblage. Understanding these species interactions is fundamental for biodiversity conservation in apex predator-free communities (Ripple et al., 2014) and for effective decision-making.

Our results highlight the usefulness of camera trapping, a well-established method for monitoring medium- and large-sized unmarked animals (Gilbert et al., 2021), in simultaneously obtaining data on smaller mammals (Ferreiro-Arias et al., 2021; Lamelas-López & Salgado, 2021; Vilella et al., 2020). Traditionally, the inclusion of small mammals in photographic analyses was limited by device sensitivity. Currently, aligning the methodology with predator detection not only improves modelling but also expands the focus, leading to a more comprehensive and realistic understanding of the ecosystem. Nevertheless, further studies should explore other variables such as additional food resource availability, and extend the results across full-year and inter-annual scales.

Acknowledgements

This work has been carried out through the Biodiversity Monitoring Centre of Mediterranean Mountains (CMBMM) thanks to a convention of Diputació de Barcelona and Universitat de Barcelona (Exp. 2021/0016157). So, we are grateful to Joana Barber and Angel Miño for their support. We thank the two anonymous reviewers whose comments and suggestions have allowed us to substantially improve the manuscript. We would also like to thank Jesús Scrofa for their help and support during the project, as well as to Michael Lockwood for the remarkable improvements in document readability.

Author contributions

AP, TM, MV and RP-G designed the methodology, the manuscript visualization and conceptualized the study. AP data curation and analysed the data. AP, MV and RP-G wrote the manuscript draft with inputs from TM, DP and JR. AP and RP-G wrote the review manuscripts and editing. JR and DP found the economic resources and project administration. All authors contributed critically to the draft manuscript and gave final approval for publication.

Conflict of interests

The authors declare no conflict of interest.

Data availability statement

Data are available on request.

References

Åberg, J., Jansson, G., Swenson, J. E., & Mikusinski, G. (2000). Difficulties in detecting habitat selection by animals in generally suitable areas. *Wildlife Biology*, **6**(2), 89–99. https://doi.org/10.2981/2lb.2000.004

Azevedo, F., Lemos, F., Freitas-Junior, M., Rocha, D., & Azevedo, F. (2018). Puma activity patterns and temporal overlap with prey in a human-modified landscape at southeastern Brazil. *Journal of Zoology*, **305**(4), 246–255. https://doi.org/10.1111/jzo.12558

Bailey, L. L., Hines, J. E., Nichols, J. D., & MacKenzie, D. I. (2007). Sampling design trade-offs in occupancy studies with imperfect detection: Examples and software. *Ecological Applications*, **17**(1), 281–290. https://doi.org/10.1890/1051-0761(2007)017[0281:SDTIOS]2.0.CO;2

Barrientos, R., & Virgós, E. (2006). Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. *Acta Oecologica*, **30**(1), 107–116. https://doi.org/10.1016/j.actao.2006.02.006

Brown, J. S., Kotler, B. P., & Bouskila, A. (2001). Ecology of fear: Foraging games between predators and prey with pulsed resources. *Annales Zoologici Fennici*, **38**(1), 71–87.

Bu, H., Wang, F., McShea, W. J., Lu, Z., Wang, D., & Li, S. (2016). Spatial co-occurrence and activity patterns of mesocarnivores in the temperate forests of Southwest China. *PLoS One*, **11**(10), e0164271. https://doi.org/10.1371/journal.pone.0164271

Burgos, T., Salesa, J., Fedriani, J. M., Escribano-Ávila, G., Jiménez, J., Krofel, M., Cancio, I., Hernández-Hernández, J., Rodríguez-Siles, J., & Virgós, E. (2023). Top-down and bottom-up effects modulate species co-existence in a context of top predator restoration. *Scientific Reports*, **13**(1), 4170. https://doi.org/10.1038/s41598-023-31105-w

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, **52**(3), 675–685. https://doi.org/10.1111/1365-2664.12432

Camps, D. (2011). Resting site selection, characteristics and use by the common genet *Genetta genetta* (Linnaeus 1758). *Mammalia*, **75**(1), 23–29. https://doi.org/10.1515/mamm.2010.061

Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, **295**(5563), 2273–2276. https://doi.org/10.1126/science.1067994

Carnicer, J., Vives-Ingla, M., Blanquer, L., Méndez-Camps, X., Rosell, C., Sabaté, S., Gutiérrez, E., Sauras-Yera, T., Peñuelas, J., & Barbeta, A. (2021). Forest resilience to global warming is strongly modulated by local-scale topographic, microclimatic and biotic conditions. *Journal of Ecology*, **109**(9), 3322–3339. https://doi.org/10.1111/1365-2745.13752

Carvalho, F., Carvalho, R., Mira, A., & Beja, P. (2014). Use of tree hollows by a Mediterranean forest carnivore. *Forest Ecology and Management*, **315**, 54–62. https://doi.org/10.1016/j.foreco.2013.12.013

Carvalho, J., & Gomes, P. (2004). Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). *Journal of Zoology*, **263**(3), 275–283. https://doi.org/10.1017/S0952836904005266

Casteneda, I., Doherty, T. S., Fleming, P. A., Stobo-Wilson, A. M., Woinarski, J. C. Z., & Newsome, T. M. (2022). Variation in red fox *Vulpes vulpes* diet in five continents. *Mammal Review*, **52**(3), 328–342. https://doi.org/10.1111/mam.12292

Ceballos, G., & Brown, J. H. (1995). Global patterns of mammalian diversity, endemism, and endangerment. *Conservation Biology*, **9**(3), 559–568. https://doi.org/10.1046/j.1523-1739.1995.09030559.x

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**(1), 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Delany, M. J. (1974). *The ecology of small mammals* (Vol. 51). Edward Arnold.

Dias, D., Massara, R., De Campos, C., & Rodrigues, F. (2019). Feline predator–prey relationships in a semi-arid biome in Brazil. *Journal of Zoology*, **307**(4), 282–291. https://doi.org/10.1111/jzo.12647

Díaz, M., Torre, I., & Arrizabalaga, A. (2010). Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse *Apodemus sylvaticus* populations. *Acta Theriologica*, **55**(3), 251–260. https://doi.org/10.4098/j.at.0001-7051.046.2009

Díaz, M., Torre, I., Peris, A., & Tena, L. (2005). Foraging behavior of wood mice as related to presence and activity of genets [article]. *Journal of Mammalogy*, **86**(6), 1178–1185. https://doi.org/10.1644/04-mamm-a-127r1.1

Doherty, T. S., Geary, W. L., Jolly, C. J., Macdonald, K. J., Miritis, V., Watchorn, D. J., Cherry, M. J., Conner, L. M., González, T. M., & Legge, S. M. (2022). Fire as a driver and mediator of predator–prey interactions. *Biological Reviews*, **97**, 1539–1558. https://doi.org/10.1111/brv.12853

Dupuy, G., Giraudoux, P., & Delattre, P. (2009). Numerical and dietary responses of a predator community in a temperate zone of Europe. *Ecography*, **32**(2), 277–290. https://doi.org/10.1111/j.1600-0587.2008.04930.x

Espelta, J. M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B., & Retana, J. (2008). Masting mediated by summer drought reduces acorn predation in mediterranean oak forests. *Ecology*, **89**, 805–817. https://doi.org/10.1890/07-0217.1

Fargallo, J. A., Martínez-Padilla, J., Viñuela, J., Blanco, G., Torre, I., Vergara, P., & De Neve, L. (2009). Kestrel-prey dynamic in a Mediterranean region: The effect of generalist predation and climatic factors. *PLoS One*, **4**(2), e4311. https://doi.org/10.1371/journal.pone.0004311

Ferreiro-Arias, I., Isla, J., Jordano, P., & Benítez-López, A. (2021). Fine-scale coexistence between Mediterranean mesocarnivores is mediated by spatial, temporal, and trophic resource partitioning. *Ecology and Evolution*, **11**(22), 15520–15533. https://doi.org/10.1002/ece3.8077

Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1–23. https://doi.org/10.18637/jss.v043.i10

Fløjgaard, C., Normand, S., Skov, F., & Svenning, J. C. (2011). Deconstructing the mammal species richness pattern in Europe–towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans. *Global Ecology and Biogeography*, **20**(2), 218–230. https://doi.org/10.1111/j.1466-8238.2010.00604.x

Frey, S., Fisher, J. T., Burton, A. C., & Volpe, J. P. (2017). Investigating animal activity patterns and temporal niche partitioning using camera-trap data: Challenges and opportunities. *Remote Sensing in Ecology and Conservation*, **3**(3), 123–132. https://doi.org/10.1002/rse2.60

Gilbert, N. A., Clare, J. D., Stenglein, J. L., & Zuckerberg, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation Biology*, **35**(1), 88–100. https://doi.org/10.1111/cobi.13517

Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *The Journal of Animal Ecology*, **60**, 353–367. https://doi.org/10.2307/5465

Hayward, G., & Phillipson, J. (1979). Community structure and functional role of small mammals in ecosystems. In M.

Stoddart (Ed.), *Ecology of small mammals* (pp. 135–211). Springer. https://doi.org/10.1007/978-94-009-5772-5_4

Hernandez-Puentes, C., Torre, I., & Vilella, M. (2022). Spatio-temporal interactions within a Mediterranean community of Mesocarnivores. *Mammalian Biology*, **102**(2), 357–373. https://doi.org/10.1007/s42991-022-00230-w

Hopkins, J., Santos-Elizondo, G. M., & Villablanca, F. (2024). Detecting and monitoring rodents using camera traps and machine learning versus live trapping for occupancy modeling. *Frontiers in Ecology and Evolution*, **12**, 1359201. https://doi.org/10.3389/fevo.2024.1359201

Kandziora, M., Burkhard, B., & Müller, F. (2013). Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators—A theoretical matrix exercise. *Ecological Indicators*, **28**, 54–78. https://doi.org/10.1016/j.ecolind.2012.09.006

Karanth, K. U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., & Kumar, N. S. (2017). Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. *Proceedings of the Royal Society B: Biological Sciences*, **284**(1848), 20161860. https://doi.org/10.1098/rspb.2016.1860

Kleiven, E. F., Barraquand, F., Gimenez, O., Henden, J.-A., Ims, R. A., Soininen, E. M., & Yoccoz, N. G. (2023). A dynamic occupancy model for interacting species with two spatial scales. *Journal of Agricultural, Biological and Environmental Statistics*, **1-17**, 466–482. https://doi.org/10.1007/s13253-023-00533-6

Krebs, C. J. (2009). Population dynamics of large and small mammals: Graeme Caughley's grand vision. *Wildlife Research*, **36**(1), 1–7. https://doi.org/10.1071/WR08004

Lacher, T. E., Jr., Davidson, A. D., Fleming, T. H., Gómez-Ruiz, E. P., McCracken, G. F., Owen-Smith, N., Peres, C. A., & Vander Wall, S. B. (2019). The functional roles of mammals in ecosystems. *Journal of Mammalogy*, **100**(3), 942–964. https://doi.org/10.1093/jmammal/gyy183

Lamelas-López, L., & Salgado, I. (2021). Applying camera traps to detect and monitor introduced mammals on oceanic islands. *Oryx*, **55**(2), 181–188. https://doi.org/10.1017/S0030605319001364

MacKenzie, D. I., & Nichols, J. D. (2004). Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation*, **27**(1), 461–467.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence* (2nd ed.). Elsevier Inc.

Mangas, J. G., Lozano, J., Cabezas-Díaz, S., & Virgós, E. (2008). The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. *Biodiversity and Conservation*, **17**(1), 43–51. https://doi.org/10.1007/s10531-007-9229-8

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. In R package version 2.3.3. https://cran.r-project.org/package=AICcmodavg.

Mercadé, A., & Ferré, A. (2019). *Cartografia digital dels hàbitats CORINE i dels Hàbitats d'Interès Comunitari del Parc Natural de Sant Llorenç del Munt i l'Obac a escala*. 1:10.000.

Meredith, M., & Ridout, M. (2018). *Overview of the overlap package. R project*. In (pp. 1-9).

Meserve, P. L., Kelt, D. A., Milstead, W. B., & Gutiérrez, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *Bioscience*, **53**(7), 633–646. https://doi.org/10.1641/0006-3568(2003)053[0633:TYOSTA]2.0.CO;2

Monterroso, P., Alves, P. C., & Ferreras, P. (2013). Catch me if you can: Diel activity patterns of mammalian prey and predators. *Ethology*, **119**(12), 1044–1056. https://doi.org/10.1111/eth.12156

Monterroso, P., Alves, P. C., & Ferreras, P. (2014). Plasticity in circadian activity patterns of mesocarnivores in southwestern Europe: Implications for species coexistence. *Behavioral Ecology and Sociobiology*, **68**, 1403–1417. https://doi.org/10.1007/s00265-014-1748-1

Moreno-Sosa, A. M., Yacelga, M., Craighead, K. A., Kramer-Schadt, S., & Abrams, J. F. (2022). Can prey occupancy act as a surrogate for mesopredator occupancy? A case study of ocelot (*Leopardus pardalis*). *Mammalian Biology*, **102**(1), 163–175. https://doi.org/10.1007/s42991-022-00232-8

Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator-prey space race. *PLoS One*, **6**(3), e17050. https://doi.org/10.1371/journal.pone.0017050

Muñoz, A., Bonal, R., & Díaz, M. (2009). Ungulates, rodents, shrubs: Interactions in a diverse Mediterranean ecosystem. *Basic and Applied Ecology*, **10**(2), 151–160. https://doi.org/10.1016/j.baae.2008.01.003

Niedballa, J., Sollmann, R., Courtiol, A., & Wilting, A. (2016). camtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution*, **7**(12), 1457–1462. https://doi.org/10.1111/2041-210X.12600

Padial, J., Avila, E., & Sanchez, J. (2002). Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. *Mammalian Biology*, **67**(3), 137–146. https://doi.org/10.1078/1616-5047-00021

Palomo, L. J., Gisbert, J., & Blanco, J. C. (2007). *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU.

Peris, A., Tena, L., & Villena, A. (2011). Abundancia de ginetas (*Genetta genetta*) en un encinar mediterráneo. Estimación mediante trampeo fotográfico. *Galemys*, **23**(1), 73–79.

Pintó, J., & Panareda, J. M. (1995). *Memòria del mapa de la vegetació de Sant Llorenç del Munt*. Aster.

Previtali, M. A., Lima, M., Meserve, P. L., Kelt, D. A., & Gutiérrez, J. R. (2009). Population dynamics of two sympatric rodents in a variable environment: Rainfall, resource availability, and predation. *Ecology*, **90**(7), 1996–2006. https://doi.org/10.1890/08-0405.1

Prugh, L., Stoner, C., Epps, C., Bean, W., Ripple, W., Laliberte, A., & Brashares, J. (2009). The rise of the mesopredator. *Bioscience*, **59**(9), 779–791. https://doi.org/10.1525/bio.2009.59.9.9

Puig-Gironès, R. (2023). Can predators influence small rodent foraging activity rates immediately after wildfires? *International Journal of Wildland Fire*, **32**, 1391–1403. https://doi.org/10.1071/WF23023

Puig-Gironès, R., Muriana, M., Real, J., & Sabaté, S. (2023). Unravelling the influence of annual weather conditions and Mediterranean habitat types on acorn production, availability and predation. *Forest Ecology and Management*, **543**, 121149. https://doi.org/10.1016/j.foreco.2023.121149

Puig-Gironès, R., & Pons, P. (2020). Mice and habitat complexity attract carnivorans to recently burnt forests. *Forests*, **11**(8), 855. https://doi.org/10.3390/f11080855

Puig-Gironès, R., & Pons, P. (2023). Mice population dynamics and structure over time and space after wildfires. *Journal of Zoology*, **321**(2), 128–141. https://doi.org/10.1111/jzo.13101

Puig-Gironès, R., & Real, J. (2022). A comprehensive but practical methodology for selecting biological indicators for longterm monitoring. *PLoS One*, **17**(3), e0265246. https://doi.org/10.1371/journal.pone.0265246

R Development Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., & Nelson, M. P. (2014). Status and ecological effects of the world's largest carnivores. *Science*, **343**(6167), 1241484. https://doi.org/10.1126/science

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Roemer, G. W., Gompper, M. E., & Van Valkenburgh, B. (2009). The ecological role of the mammalian mesocarnivore. *Bioscience*, **59**(2), 165–173. https://doi.org/10.1525/bio.2009.59.2.9

Rosalino, L., & Santos-Reis, M. (2002). Feeding habits of the common genet Genetta genetta (Carnivora: Viverridae) in a semi-natural landscape of central Portugal. *Mammalia*, **66**(2), 195–205. https://doi.org/10.1515/mamm.2002.66.2.195

Rosário, I. T., & Mathias, M. L. (2004). Annual weight variation and reproductive cycle of the wood mouse (*Apodemus sylvaticus*) in a Mediterranean environment. *Mammalia*, **68** (2–3), 133–140. https://doi.org/10.1515/mamm.2004.014

Rovero, F., & Zimmermann, F. (2016). *Camera trapping for wildlife research*. Pelagic Publishing.

Rowe, R. J., & Terry, R. C. (2014). Small mammal responses to environmental change: Integrating past and present dynamics. *Journal of Mammalogy*, **95**(6), 1157–1174. https://doi.org/10.1644/13-MAMM-S-079

Santos-Reis, M., Santos, M. J., Lourenço, S., Marques, J. T., Pereira, I., & Pinto, B. (2005). Relationships between stone martens, genets and cork oak woodlands in Portugal. In D. J. Harrison, A. K. Fuller, & G. Proulx (Eds.), *Martens and fishers (Martes) in human-altered environments: An international perspective* (pp. 147–172). Springer. https://doi.org/10.1007/b99487

Sharief, A., Kumar, V., Singh, H., Mukherjee, T., Dutta, R., Joshi, B. D., Bhattacharjee, S., Ramesh, C., Chandra, K., & Thakur, M. (2022). Landscape use and co-occurrence pattern of snow leopard (Panthera uncia) and its prey species in the fragile ecosystem of Spiti Valley, Himachal Pradesh. *PLoS One*, **17**(7), e0271556. https://doi.org/10.1371/journal.pone.0271556

Sinclair, A., & Krebs, C. J. (2002). Complex numerical responses to top–down and bottom–up processes in vertebrate populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **357**(1425), 1221–1231. https://doi.org/10.1098/rstb.2002.1123

Smith, Y. C. E., Smith, D. A. E., Ramesh, T., & Downs, C. T. (2019). Novel predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species. *Behavioural Processes*, **159**, 9–22. https://doi.org/10.1016/j.beproc.2018.12.005

Sokolova, N. A., Fufachev, I. A., Ehrich, D., Shtro, V. G., Sokolov, V. A., & Sokolov, A. A. (2024). Expansion of voles and retraction of lemmings over 60 years along a latitudinal gradient on Yamal peninsula. *Global Change Biology*, **30**(2), e17161. doi:10.1111/gcb.17161

Stenseth, N. C., Leirs, H., Skonhoft, A., Davis, S. A., Pech, R. P., Andreassen, H. P., Singleton, G. R., Lima, M., Machang'u, R. S., & Makundi, R. H. (2003). Mice, rats, and people: The bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment*, **1**(7), 367–375. https://doi.org/10.1890/1540-9295(2003)001[0367:MRAPTB]2.0.CO;2

Sunyer, P., Muñoz, A., Bonal, R., & Espelta, J. M. (2013). The ecology of seed dispersal by small rodents: A role for predator and conspecific scents. *Functional Ecology*, **27**(6), 1313–1321. https://doi.org/10.1111/1365-2435.12143

Sunyer, P., Muñoz, A., Mazerolle, M. J., Bonal, R., & Espelta, J. M. (2016). Wood mouse population dynamics: Interplay among seed abundance seasonality, shrub cover and wild boar interference. *Mammalian Biology*, **81**(4), 372–379. https://doi.org/10.1016/j.mambio.2016.03.001

Swann, D. E., & Perkins, N. (2014). Camera trapping for animal monitoring and management: A review of applications. In P. D. Meek & P. J. Fleming (Eds.), *Camera trapping: Wildlife management and research* (pp. 3–11). CSIRO Publishing.

Taylor, B. D., Goldingay, R. L., & Lindsay, J. M. (2014). Horizontal or vertical? Camera trap orientations and recording modes for detecting potoroos, bandicoots and pademelons. *Australian Mammalogy*, **36**, 60–66. https://doi.org/10.1071/AM13012

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, **277**(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tobler, M. W., Carrillo-Percastegui, S. E., Leite-Pitman, R., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, **11**(3), 169–178. https://doi.org/10.1111/j.1469-1795.2008.00169.x

Torre, I., Bastardas-Llabot, J., Arrizabalaga, A., & Díaz, M. (2020). Population dynamics of small endotherms under global change: Greater white-toothed shrews *Crocidura russula* in Mediterranean habitats. *Science of the Total Environment*, **705**, 135799. https://doi.org/10.1016/j.scitotenv.2019.135799

Torre, I., & Díaz, M. (2004). Small mammal abundance in Mediterranean post-fire habitats: A role for predators? *Acta Oecologica*, **25**(3), 137–142. https://doi.org/10.1016/j.actao.2003.10.007

Torre, I., Díaz, M., Martínez-Padilla, J., Bonal, R., Vinuela, J., & Fargallo, J. A. (2007). Cattle grazing, raptor abundance and small mammal communities in Mediterranean grasslands. *Basic and Applied Ecology*, **8**(6), 565–575. https://doi.org/10.1016/j.baae.2006.09.016

Torre, I., Puig-Montserrat, X., & Díaz, M. (2023). Global change effects on Mediterranean small mammal population dynamics: Demography of Algerian mice (Mus spretus) along land use and climate gradients. *Science of the Total Environment*, **863**, 160875. https://doi.org/10.1016/j.scitotenv.2022.160875

Torre, I., Pulido, T., Vilella, M., & Díaz, M. (2022). Mesocarnivore distribution along gradients of anthropogenic disturbance in Mediterranean landscapes. *Diversity*, **14**(2), 133.

Vilella, M., Ferrandiz-Rovira, M., & Sayol, F. (2020). Coexistence of predators in time: Effects of season and prey availability on species activity within a Mediterranean carnivore guild. *Ecology and Evolution*, **10**(20), 11408–11422. doi:10.1002/ece3.6778

Villette, P., Krebs, C. J., Jung, T. S., & Boonstra, R. (2016). Can camera trapping provide accurate estimates of small mammal (*Myodes rutilus* and *Peromyscus maniculatus*) density in the boreal forest? *Journal of Mammalogy*, **97**(1), 32–40. https://doi.org/10.1093/jmammal/gyv150

Virgós, E., & Casanovas, J. G. (1997). Habitat selection of genet Genetta genetta in the mountains of central Spain. *Acta Theriologica*, **42**(2), 169–177.

Virgós, E., Llorente, M., & Cortés, Y. (1999). Geographical variation in genet (*Genetta genetta* L.) diet: A literature review. *Mammal Review*, **29**(2), 117–126. https://doi.org/10.1046/j.1365-2907.1999.00041.x

Viviano, A., Scarfò, M., & Mori, E. (2022). Temporal partitioning between Forest-dwelling small rodents in a Mediterranean deciduous woodland. *Animals*, **12**, 279. https://doi.org/10.3390/ani12030279

Wilmers, C. C., Post, E., & Hastings, A. (2007). The anatomy of predator-prey dynamics in a changing climate. *Journal of Animal Ecology*, **76**, 1037–1044. https://doi.org/10.1111/j.1365-2656.2007.01289.x

Windell, R. M., Bailey, L. L., Livieri, T. M., Eads, D. A., Biggins, D. E., & Breck, S. W. (2024). Coyote use of prairie dog colonies is most frequent in areas used by American badgers. *Journal of Mammalogy*, **105**, 1309–1321. https://doi.org/10.1093/jmammal/gyae066