

Article

Intraguild Predation by the Eagle Owl Determines the Space Use of a Mesopredator Carnivore

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Abstract: Top predators shape the communities of sympatric predators by killing and displacing smaller predators. Predation risk pushes smaller predators to select enemy-free spaces irrespective of food availability, which results in changes in their behaviour, space use, distribution, and abundance. Although the landscape of fear dynamics are known for top predators such as the eagle owl and its impact on smaller raptors, the effect of the presence and abundance of the eagle owl on the space use of mesopredator carnivores remains poorly understood. Here, we studied this effect on the space use of the stone marten in a Mediterranean ecosystem where it shares rabbits as main prey with the eagle owl. We also accounted for the presence of another sympatric carnivore, the red fox. Using a multi-model inference, we found stone martens avoided areas with a higher abundance of eagle owls and rabbits, which suggested a hyperpredation process and a cognitive association by stone martens between rabbit hotspots and owl presence. We found a positive relationship between the space use of the red fox and the stone marten, which suggested foxes behaved as competitors and not predators of martens. Understanding intraguild predation can assist the conservation and management of predators and their prey.

Keywords: eagle owl; enemy-free space; hyperpredation; landscape of fear; rabbit; red fox; stone marten

1. Introduction

Intraguild predation is a type of asymmetrical interaction with important consequences on the structuring of predator communities [1,2]. Top predators kill and displace smaller predators; consequently, individuals of these smaller species (hereafter mesopredators) can perceive the risk of being predated in a specific area (i.e., the landscape of fear [3,4]), which ultimately contributes in shaping their space use, diversity, and abundance. Considerable research has identified intraguild predation in a wide variety of taxa, regions, and habitats [5–7]. Still, less is known about how the presence and abundance of top predators shape the space use of smaller predators (e.g., [8–10]). Mesopredators search for spaces free of enemies [4,11–13]. Therefore, in a complex landscape with several levels of perceived predation risk, lower species in the rank of intraguild interactions may tend to prioritise the selection of low-risk habitat or conditions over other niche components such as food resources [4,13–15]. For instance, the grey fox (*Urocyon cinereoargenteus*) behaves as a highly selective habitat specialist in areas with a high density of coyotes (*Canis latrans*) [16], and the tawny owl (*Strix aluco*) shows more clumped nesting in enemy-free spaces [14]. Overall, understanding these dynamics is essential to further our knowledge of the ecological roles of predators and thus, to assist in their conservation and that of their prey [9,17,18].

The eagle owl (*Bubo bubo*) is one of the most important and abundant top generalist predators in the Palearctic [19,20], especially in the Mediterranean region [21], where its abundance varies throughout heterogeneous landscapes [22,23]. This variation in the eagle owl's presence and abundance as a top predator may lead to changes in the landscape of fear perceived by mesopredator species. In this vein, the role of the eagle as a predator of other smaller raptors has been largely documented [7,11]. For instance, the presence and abundance of the eagle owl in a given area is a significant determinant of the habitat use, reproductive success, abundance, and behavioural traits of smaller diurnal raptors [7,14,24] such as kites (*Milvus* spp.), grey falcons (*Falco peregrinus*), or buzzards (*Buteo buteo*) [11,25–27]. The eagle owl can also kill small-to-medium size carnivores (mesocarnivores) [7,28] such as martens (*Martes* spp.), genets (*Genetta genetta*), red foxes (*Vulpes vulpes*), or cats (*Felix silvestris*) [19,28–30]. However, much less is known about the impact of the eagle owl on carnivores, although similar effects to those caused on small raptors could be expected. In this relationship between the eagle owl and carnivore species, interspecific interactions among carnivore species may also play a role. For instance, species such as the red fox (*Vulpes vulpes*) are also top predators of smaller species such as martens, which added to the impact caused by the eagle owl creates a complex scenario of multiple interactions between species of diverse taxa [31–33].

The eagle owl is a generalist predator, although the wild rabbit (*Oryctolagus cuniculus*) is its staple prey in Mediterranean environments [21,34–36]. In this region, eagle owl abundance is low in areas where rabbits are scarce or absent [35]. The red fox is also a generalist predator that behaves like a rabbit specialist if this prey is abundant [37]. On the other hand, the stone marten preys on low proportions of rabbits, although this is also a relevant resource (in terms of biomass) in some regions and seasons [38,39]. Since the eagle owl and red fox may use rabbit patches intensively, spatial changes in rabbit abundance could have consequences for the landscape of fear of mesopredators. To avoid top predators, mesopredators could show a numeric and behavioural response to food resources.

In this research, we analysed the changes in the space use of a mesocarnivore, the stone marten, in a region with a varied abundance of eagle owl and wild rabbit. The stone marten could perceive a predation risk in areas with a higher density of eagle owls, and thus, it would tend to avoid these areas regardless of containing a greater abundance of rabbits. We predicted that the stone marten selected areas free of enemies (i.e., with less presence of eagle owls) irrespective of the availability of rabbits. We also tested how the abundance of another sympatric predator, the red fox, influences the relationship between the stone marten and the eagle owl.

2. Materials and Methods

2.1. Study Area

We conducted research in the southeast of the province of Madrid in central Spain (Figure 1). In this area, mosaics of remnant wild vegetation and crops characterise a highly deforested and transformed landscape. The dominant vegetation was a Mediterranean shrubland of kermes oak (*Quercus coccifera*), and an arboreal stratum of holm oak (*Quercus ilex*), riparian species such as silver poplar (*Populus alba*), and reforested pinewoodlands (*Pinus halepensis*). The natural vegetation areas were surrounded or mixed with a combination of olive groves and cereals. Crops and anthropogenic landscapes were associated with high rabbit densities [40,41], which was an abundant species in this study area. The average annual temperature and accumulated rainfall in the study area was 15 °C and 400 mm, respectively. The elevation varied between 400 and 700 m, with the presence of steep lands and cliffs where the eagle owl and other cliff-nesting birds were abundant.

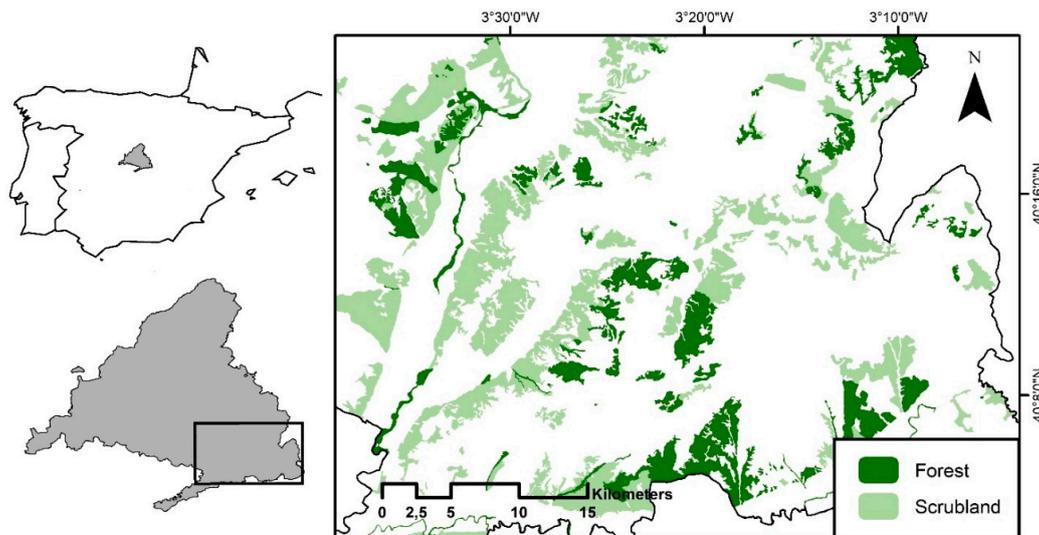


Figure 1. Location of the study area in the Autonomous Region of Madrid (grey colour, maps to the left) in Spain, Iberian Peninsula (top-left map). Characterisation of the land cover categories (map to the right) considered in this study as providers of refuge from predation for the stone marten in the study area.

2.2. Sampling Procedure and Explanatory Variables

During 2007 and 2008, we sampled once 30 transects of 1.5 km lengths during the period of high vocalisation activity of the eagle owl between mid-November and the first week of January [35]. All transects were located in areas that included cliffs and separated by a minimum distance of 2 km to ensure the spatial independence of home ranges of stone martens, as this distance is the reported typical size of a home range for this species in Mediterranean environments [42,43].

We conducted an acoustic census of the eagle owl to quantify its abundance [44]. Two operators listened for spontaneous calls and considered that calls belonged to an owl couple (see also [45]). We started sampling 5 min before sunset and continued for 40–50 min to complete the transect. We stopped and listened for 2 min every 100 m and whenever we heard any new call. Although spontaneous calls may underestimate the density of non-breeding males [44], we considered that during this season, most of the population was composed of reproductive pairs with a lower proportion of bachelors. The sampling of breeding pairs of eagle owls was carried out only once in each transect except for three transects sampled in the first year where windy days of suboptimal hearing conditions impaired census conditions. Consequently, we repeated this sampling. Transects were walked at a constant speed with both operators sampling separately at each side of the path to avoid repeated counts.

In each transect, we counted the number of stone marten and red fox scats and used it as a habitat use index, which is considered a useful method for red foxes and stone martens [46,47]. In addition, we counted the number of rabbit latrines in each transect as a proxy for rabbit abundance [48]. We sampled one-metre wide transects with similar visibility conditions to search for and count scats and latrines.

Several studies identified tree cover and other vegetation as resources providing refuge, and thus, this is the most critical landscape feature for the stone marten [49,50]. Therefore, we quantified the percentage of forest and scrubland cover in ArcGIS 10.2 (ESRI, Redlands, CA, USA) by overlaying a detailed 1:50,000 land use map from the Madrid community [51] with each transect and perform a buffer of 570 ha, which covered several standard stone marten home ranges [42,51]. This area may include between 1 and 4 owl pairs [52]. However, in areas of higher rabbit density, the number of pairs can increase at a decrease of home range size [53]. Therefore, in areas of high rabbit density, the owl territories tend to be highly packed and it is possible to find even 4 pairs in 1.5 km. Although

it cannot be discarded some pairs may have an influence on two separated transects, we assumed this was an uncommon situation in our study area of potential minor effects in the results. Similarly, if owl territories did not stretch over the whole transect, we still expected to identify a direct effect on the space use because in each of the small segments (e.g., 400 m) martens are under the presence of owls and the effect on marten scats would be cumulative. Consequently, we considered this potential circumstance was not relevant to our objective on identifying how a higher owl presence shapes the space use strategy of a small mammalian predator. Thus, we assumed in our analyses and conclusions that the observed distribution of marten and fox scats indicated the use of the different transects. Specifically, the detectability of scats was not lower in transects with a high abundance of rabbits and eagle owls. Also, the differences between transects in the space use of martens and foxes were not caused by different abundance of rodents. We also assumed the abundance of rodents was not inversely related to rabbits and the predation pressure by eagle owls in each transect was measurable by the number of roosting owls detected. Lastly, we assumed all eagle owls detected along each transect hunted over the entire transect and rarely in neighbour transects (where they were not detected).

2.3. Statistical Analyses

We carried out a multi-model selection procedure to quantify the effect of variations in the abundance of eagle owls and other accessory variables on the stone marten habitat use. The models included the scaled explanatory variables of “number of eagle-owl pairs”, “number of red fox scats”, “rabbit abundance”, “percentages of tree cover”, and “percentage of shrub cover”. We proposed a total of eight models representing alternative hypotheses about predators and competitors, food resources, and habitat coverage, as well as the null and global model (containing all the variables used). We ranked the models using an Akaike’s Information Criterion for small sample sizes (AICc) and selected only those top-ranked models with $\Delta\text{AICc} < 2$ [54]. Then, we averaged the selected top-ranked models [55]. All models were generalised linear models (GLM) with a negative binomial distribution to correct for the over-dispersion identified in preliminary analyses using a Poisson distribution for counts.

We also tested causality in the intensity of the red fox’s space use due to the interaction between eagle owl and the abundance of rabbits. Here, we also applied a negative binomial GLM. Finally, we tested the relationship between the number of eagle owl pairs and rabbit abundance using a GLM with a Poisson distribution. Statistical analyses were conducted in R [56].

3. Results

We identified 39 pairs of eagle owl in the acoustic census conducted across 30 transects ($\bar{x} \pm \text{SE} = 0.97 \pm 0.18$ owl/transect). The sampling of these transects also reported a total of 179 scats of stone marten ($\bar{x} \pm \text{SE} = 5.35 \pm 0.97$ scat/transect) and 216 of fox ($\bar{x} \pm \text{SE} = 6.71 \pm 1.22$ scat/transect). The total number of rabbit latrines counted was 1611 ($\bar{x} \pm \text{SE} = 55.40 \pm 10.11$ latrine/transect). No pairs of eagle owls were reported in five transects, and only one transect reported a maximum of four pairs (Table 1). One eagle owl pair was the most common value identified (in 16 transects out of 30) (Table 1). The scats of stone marten and red fox were less abundant in transects with three and four pairs of eagle owl (Table 1).

Table 1. Summary of the number of transects where a different number of pairs of eagle owl were heard using acoustic census, as well as of the average number of stone marten scats, fox scats, and rabbit latrines per transects grouped by pairs of owls.

Eagle Owl Pairs CATEGORY	No. of Eagle Owl Pairs	No. of TRANSECTS	Stone MARTEN ($\bar{x} \pm \text{SE}$)	Fox ($\bar{x} \pm \text{SE}$)	Rabbit ($\bar{x} \pm \text{SE}$)
0	0	5	9.8 ± 3.4	8.2 ± 2.4	46.6 ± 23.1
1	16	16	4.8 ± 1.1	6.9 ± 1.9	51 ± 13.7
2	10	5	8.8 ± 2.6	9.4 ± 3.0	40.4 ± 18.2
3	9	3	1.4 ± 0.4	5.7 ± 4.7	104.3 ± 58.8
4	4	1	0	1	47

Multi-model selection to test the impact of the eagle owl and other variables on the distribution and habitat use of stone martens revealed two top-ranked models with $\Delta\text{AICc} < 2$ (Table 2). The first-ranked model contained the variables “number of eagle owl pairs”, “the number of red fox scats”, and “rabbit abundance” ($\text{AICc} = 167.8$). This model explained a deviance of 0.36. The second-ranked model included the “number of eagle owl pairs” and the “number of red fox scats” ($\text{AICc} = 169.0$) and explained a deviance of 0.27. The averaging of these two models revealed that the stone marten was negatively and significantly related (i.e., confidence intervals, CI, did not contain zero) to the number of eagle owl pairs ($\beta_{\text{eagle owl}} = -0.389 \pm 0.174$; 95% CI $[-0.747, -0.031]$) and with the rabbit abundance ($\beta_{\text{rabbit}} = -0.326 \pm 0.162$; 95% CI $[-0.660, -0.007]$), and it was positively and significantly related with the number of red fox scats ($\beta_{\text{red fox}} = 0.479 \pm 0.143$; 95% CI $[0.184, 0.773]$).

Table 2. Model selection rank on the distribution and habitat use of the stone marten considering the number of eagle owl pairs as the marten’s predator, red fox as predator or competitor, the abundance of the rabbit as the staple prey of owls and a marten prey, and natural habitat (referred cover of forest and shrublands).

Models	AICc	ΔAICc	d.f	wAIC
owl + rabbit + fox	167.8	0.0	5	0.4
owl + fox	169.0	1.2	4	0.2
global	170.2	2.4	5	0.1
rabbit + natural habitat	170.3	2.5	7	0.1
owl + fox + natural habitat	172.5	4.7	6	0
natural habitat	173.3	5.5	4	0
rabbit	174.5	6.7	3	0
null model	174.8	7.0	2	0

The model to test causality on the intensity of space use by the red fox due to the interaction between eagle owl and rabbit abundance revealed a negative relationship between the red fox and the abundance of eagle owl pairs ($\beta_{\text{eagle owl}} = -0.142 \pm 0.183$ SE; 95% CI $[-0.522, 0.249]$). This relationship was also negative with the abundance of rabbits ($\beta_{\text{rabbit}} = -0.077 \pm 0.169$ SE; 95% CI $[-0.432, 0.288]$) and with the interaction between both variables ($\beta_{\text{eagle owl:rabbit}} = -0.253 \pm 0.180$ SE; CI $[-0.625, 0.110]$). However, neither of these relationships was significant (i.e., confidence intervals (CI) contained zero). The results of the GLM for testing the relationship between the number of eagle-owl pairs and rabbit abundance showed a positive but not significant relationship between these two variables ($\beta_{\text{rabbit}} = 0.102 \pm 0.141$ SE; $p = 0.466$; CI $[-0.191, 0.364]$).

4. Discussion

Our results provide further support on how mesopredators can change space use to avoid predation and agonistic interactions with top predators, and how the search of enemy-free spaces has implications for their distribution and abundance. It is known that the presence and abundance of the eagle owl induce individual and population changes in other raptors [27]. Our research furthers knowledge on how these affect changes that occur in a carnivore and a scenario of shared prey with the eagle owl. We identified that the stone marten, a sympatric mesopredator, avoids areas with a greater presence of eagle owls where there are also greater availabilities of rabbits, which are the main prey of the eagle owl and an important resource for the stone marten in Mediterranean environments. Although effects are mainly observed with more than two pairs, the net effect is large enough to be confident on the negative association between owl abundance and stone marten habitat use. Indeed, we did not expect a monotonic response, and probably negative effects are only evident with a moderate-high owl density.

Our results suggest that patches with high densities of rabbits where the stone marten can hunt may also expose it to a greater risk of predation by eagle owls or other predators. Consequently, the stone marten would tend to avoid these patches irrespective of the high-density of rabbits. Concerning other

carnivore predators, we identified no effect on the stone marten caused by the presence of the red fox. This result suggests the red fox might play a role as a sympatric predator with the stone marten in this environment instead of being a top predator. The adaptive feeding behaviour of stone martens and red foxes might also explain the infrequent interactions between the two predators in this area.

Small carnivores represent an average of 1% of the diet of diurnal and nocturnal raptors [57]. Although this figure is not significant from an energy point of view, it could be enough for their prey to perceive raptors as a high risk of death. Golden eagles and eagle owls are the most prominent raptors that prey on carnivores [30,57]. A relevant example of the strong effect of a raptor's predation on carnivores was that of the golden eagle (*Aquila chrysaetos*) on littoral grey foxes (*Urocyon cinereoargenteus littoralis*) and spilogale (*Conepatus*) in the Channel Islands, California [58]. The predation by the golden eagle threatened the viability of the littoral grey fox, and management measures were taken to control golden eagles in favour of foxes [59,60]. This severe impact was mediated by the abundance of introduced pigs (*Sus scrofa*), which enhanced the reproductive success and survival of golden eagles and increased its population as well as predation on a secondary prey, the grey fox [58,61]. An increased predation on a secondary prey when there is a surplus of primary prey is called hyperpredation [62,63], which has been documented in predator-prey systems of raptors, red-legged partridges (*Alectoris rufa*), and rabbits in Mediterranean environments [64]. According to these hyperpredation processes, changes in prey abundance can produce an indirect effect on how predators interact with each other, leading to the different impacts caused by large predators on small ones.

Our study can be considered as an example of this hyperpredation process involving an apex predator, a mesopredator, and a shared prey, the rabbit. The stone martens avoided areas of higher abundance of eagle owls and also rabbits. Since the rabbit is a main food item of the eagle owl in Mediterranean Spain [22,36], its abundance affects the density and reproductive success of this raptor [23,65]. A high density of eagle owls in the area would be associated with a higher average abundance of rabbits (6 rabbit/ha on average) than the mean density of rabbits density in typical Mediterranean habitats [66]. Although we found a non-significant association between eagle owl abundance and rabbit abundance, the high regional abundance of eagle owls is a consequence of high rabbit density, which is its preferred prey [36]. Stone martens are not rabbit specialists; however, there is no apparent reason for these to avoid areas of substantial rabbit abundance. We found no differences in habitat composition between sites of high and low abundance of rabbits and owls. Consequently, based on these habitat composition results (which may correlate with food resource availability), we expected to observe a uniform distribution of the stone marten. However, this was not the case, which suggests that an ultimate driver of space use for the stone marten might be the real or perceived presence of eagle owls. The avoidance of these hotspots of rabbits by the stone marten could respond to a cognitive association between a high abundance of rabbits and a higher presence of owls or other top predators; that is, a warning of substantial predation risk. Nevertheless, to discard a potential effect on the habitat use of martens in a landscape of fear due to changes in the abundance of other food resources (e.g., rodents), further research is required to quantify these resources and to address their impact on the space use of smaller predators. Thus, our conclusions should be viewed as the most probable (but not definitive) explanation of the observed patterns. Unlike eagle owls, we found no effect caused by the red fox on the stone marten's habitat use. Previous studies conducted in Fennoscandia on a larger scale and using hunting bags identified opposite effects of the red fox on pine martens (*Martes martes*) [67,68]. It could be suggested that this effect can be very context-dependent (e.g., differences in food supply or relative abundances).

We acknowledge our results cannot discriminate between reductions in stone marten presence and abundance and changes in habitat selection due to predation risk; however, we found strong evidence of the effect of the eagle owl on the space use of stone martens. Eagle owl predation on the stone marten could lead to a reduction in the abundance of martens and the low use of the habitat that we found in areas with a high density of owls and rabbits.

The possibility of small predators perceiving different levels of fear across the landscape has been documented in different systems and classic predator–prey relationships [3,69–72]. Individuals of smaller predators and prey species are forced to select enemy-free spaces [73] to escape from predators, which could be a selective force in habitat selection processes equal to or greater than the selection of food or other resources [69,70]. Overall, although it cannot be discarded other non-quantified factors in our research may influence the habitat use of the stone martens, our results support that the space use of this species in this Mediterranean region is mostly shaped by the perceived differences in predation risk mediated by the abundance of eagle owls and their main prey, the wild rabbit.

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