

Shift in microhabitat use as a mechanism allowing the coexistence of victim and killer carnivore predators

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ABSTRACT

It has been suggested that spatial heterogeneity is key to the coexistence at local spatial scales of subordinate and dominant predator species by allowing the former to shift to more protective habitats when the risk of intraguild predation exists. Here, we show how the smaller carnivore Egyptian mongoose (*Herpestes ichneumon*) may coexist on a local scale with its intraguild predator, the Iberian lynx (*Lynx pardinus*), by using places with different microhabitat characteristics. We expect that mongooses living within lynx home ranges will use denser and more protective habitats when active in order to diminish their risk of being killed by lynx compared to those living in areas similar in vegetation and prey availability but where lynx are absent. The scrubland cover of points used by mongooses outside lynx areas, and that of points located within lynx areas but not used by mongooses, were significantly lower than, or similar to, cover of points used by mongooses within lynx areas. The probability of finding mongoose tracks was constant across levels of scrubland cover when lynx were absent, but more mongoose tracks were likely to be found in thicker scrubland within lynx areas, especially if these areas were intensively used by lynx. This result agrees with the hypothesis on shifts in microhabitat use of subordinate carnivores to prevent fatal or risky encounters with dominant ones.

Keywords: Carnivore Coexistence; Egyptian Mongoose; Iberian Lynx; Interspecific Competition; Intraguild Predation; Microhabitat Shift; Spatial Heterogeneity

1. INTRODUCTION

Interspecific interactions among predators can greatly shape community structure [1,2]. In particular, competition and predation have been recognized as major factors affecting population dynamics [3]. Intraguild predation [4-6] represents a convergence of both features and it has been hypothesized that this ecological process involves more complex effects than competition or predation per se [1,7]. In victim species, the risk of direct or offspring killing drives behavioural responses in order to minimize the probability of being preyed upon (reviewed in [8-9]).

It has been suggested that spatial heterogeneity at small scales is key in allowing the coexistence of both subordinate (victims) and dominant (killers) species by allowing the former to shift to safe habitats [10-14]. This topic has gained attention in recent decades and it has been reported that victim species may use habitats that are little or not used by killers [15-19], favouring the coexistence of both species at local scales. However, the underlying mechanisms allowing the coexistence when victim and killer species that overlap home ranges, and therefore apparently use the same habitat types, are still unclear [20]. In fact, despite empirical evidence suggesting that long-term local coexistence among vertebrate predators involved in intraguild predation relationships may be favoured by spatial heterogeneity and/or shifts in habitat use by victims [21-25], no study offers clear support for this hypothesis.

Here, we show how the Egyptian mongoose (*Herpestes ichneumon*) may on a local scale coexist with its intraguild predator, the Iberian lynx (*Lynx pardinus*), by using places that differ in microhabitat characteristics. The Iberian lynx often kills mongooses and other mesocarnivores such as red foxes (*Vulpes vulpes*), genets (*Genetta genetta*), domestic cats (*Felis catus*) or Eurasian otters (*Lutra lutra*) [4,15]. In areas where lynx reach high densities, mongooses are almost absent even in optimal

habitat [15,26]. However, when lynx occur at lower densities, both species may be found [26]. Lynx and mongooses are habitat specialists that use Mediterranean scrubland [27-29] and feed on wild rabbits (*Oryctolagus cuniculus*), either as a specialist predator (the Iberian lynx) or as an opportunistic one (the Egyptian mongoose), when rabbits are abundant [30,31].

Under a scenario of low density of lynx, we propose that mongooses can coexist locally with lynx by shifting microhabitat selection during activity, which would diminish the probability of encounters with lynx. Thus, compared with mongooses living in areas without lynx, we predicted that mongooses living within lynx areas would use denser and more protective habitats during activity to decrease the risk of being killed. Furthermore, because mongooses are practically absent in areas with high density of lynx [26] and subordinate carnivores may use more intensively the gaps and the borders of the dominant's home ranges [21,22], we also predicted that this pattern (shift in microhabitat) would be modulated by the spatial use of lynx, being in the areas highly used by lynx stronger than in the periphery of lynx home ranges (*i.e.* in the areas where the probability of encounters with lynx decreases).

2. METHODS

2.1. Study Area

The study was carried out in the Doñana Biological Reserve (approximately 6700 ha), a flat area with sandy soils located in SW Spain (37°N, 6°30'W). Although three main biotopes are found in this area: dunes, marshes and scrubland [32]; lynx and mongooses mainly use the scrubland [27,29]. Scrubland is dominated by *Halimium halimifolium* and *Ulex* spp. (shorter scrubs) or *Erica* spp. heaths (taller scrubs) depending on the underground water level. As a consequence, at small scale, scrubland vegetation is composed of alternating short and tall scrub patches (Figure 1).

2.2. Data Collection

2.2.1. Microhabitat Use by Active Mongooses

Between January and February 2007 we searched for mongoose tracks by slowly walking (ca. 1.5 km/h) along sandy paths within 5100 ha of scrubland. Sampling was based on a 1 × 1 km grid cell (a total of 51 squares). We selected the winter season for surveys due to optimal conditions of sand (damp) for detecting tracks. All mongoose tracks were georeferenced using a GPS (Garmin, Inc.). Tracks clearly produced by the same individual were counted only once. When some rain fell, surveys were resumed a minimum of three days later in order to allow mongooses to leave tracks. On average, we sampled 85 minutes per cell (sd = 15.13, n = 51).

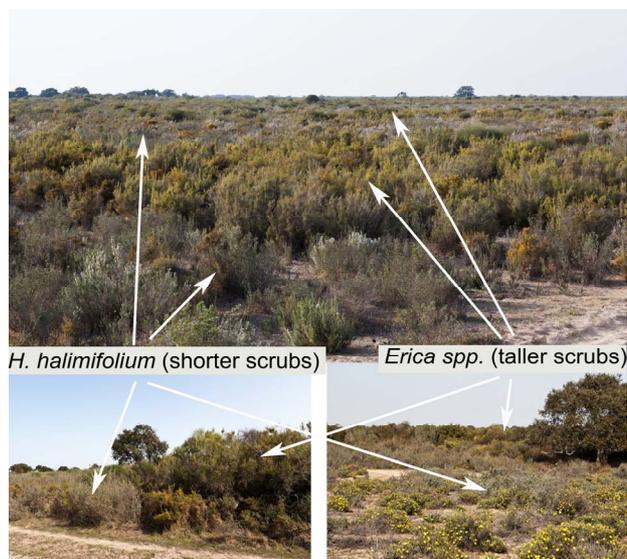


Figure 1. Photos of the most common scrubland types and a view from a higher place to show how they are interspersed in the study area.

During spring 2007 we estimated vegetation cover at points where mongoose tracks were and were not detected. Points without mongoose tracks were randomly generated leaving at least 15 m from a known mongoose track.

Vegetation cover was visually estimated in two areas of 15 m × 4 m centred on the position of the track (one on each side of the path). To avoid re-sampling the same points, only mongoose tracks separated by at least 15 m were considered (we estimated that our GPS error was <4 m in the area). Each of these two areas was subdivided into six squares of 5 m × 2 m, totalling 12 sampling squares in which ground cover by scrubland species was estimated. For visual estimation of the ground cover we used shadow drawn patterns of known percentages for comparison. An index of scrubland cover was assigned to each of the 12 sampling squares according with the following scale: 1, bare ground; 2, <10% cover; 3, 11% - 25% cover; 4, 26% - 50% cover; 5, 51% - 75%; and 6, >75%. Areas with the scores 1, 2 and 3 were attributed to open or relatively open areas; those with scores of 4 and 5 as intermediate, and finally, the score 6 was considered as dense scrubland vegetation.

2.2.2. Areas Used by Lynx

Information on areas used by lynx was obtained by radio tracking all the lynx living in the study area as a part of a parallel study aimed at examining the effect of a supplementary feeding program on lynx conservation (see [32-36] for details of these program, trapping, tagging, handling and radio-tracking procedure of the lynx). At the time of the present study only 3 lynx were present in the area [33]: one sub-adult male, one sub-adult fe-

male and one adult female. Trapping and radio tagging of lynx used in this research complied with the norms of the Spanish Animal Protection Regulation, RD1201/2005, regarding protection of animals used in scientific research, which conforms to European Union Regulation 2003/65. Methods of capture and handling of wild lynx were specifically approved by the competent administration (Regional Government of Andalusia and the Doñana National Park) under permit N° RS-2093/04.

2.3. Data Analyses

For each lynx, we used the extension Animal Movement for ArcView GIS 3.2 [37] to calculate the size of fixed kernel estimates of home ranges (area with 90% of positions) and core areas (area of highest use defined by 60% of positions). For range estimations we only used the positions obtained between two months before and after the sampling of mongoose tracks, that is, between November 2006 and April 2007. Then, each site where vegetation cover was sampled was assigned to a level of lynx use (absent, boundary of home ranges or core areas) pooling the spatial use of all lynx as they were relatives sharing the same territory. All sites outside the 90% kernel estimates were assigned as lynx absence, whereas those within the belt obtained between the 90% and 60% kernel estimates were assigned to lynx home range boundaries.

We generated a single index of scrubland cover for each site as the mean value of the 12 quadrants sampled. We then built a Generalized Linear Model (GLM) with normal error distribution and identity link to test for differences in scrubland cover between sites where we included as predictors lynx presence (three levels: absent, boundaries and core areas), mongoose presence (two levels: presence/absence), and their interaction. Post hoc multiple pairwise comparisons (Tukey-Kramer test) were used to identify significant differences in the mean scrubland cover indices between different combinations of lynx and mongoose presence. The indices of scrubland cover were log-transformed to meet the assumption of normality. On the other hand, we generated a set of competing models (Table 1) to test whether the probability of mongoose occurrence (tracks) was determined by

lynx presence, scrubland cover, or their interaction. We built a set of logistic regressions and compared their explanatory power. We also included a null model, as the intercept-only model, representing that mongoose occurrence was irrespective of lynx presence and scrubland cover. The Akaike's information criterion was used to detect the most parsimonious model according with their ability to explain our data. Models with $\Delta AICc < 2.0$ were considered to have substantial support. We also used Akaike weights (ω_i) to estimate the probability of a given model to be the best. This analysis provided additional information on different responses in the use of microhabitat by mongooses in relation with lynx spatial use. All statistical analyses were performed with the R software 2.6.0 [38].

3. RESULTS

A total of 965 mongoose tracks were found in the overall 137.6 km sampled. We found that scrubland cover was significantly different depending on the category of use of mongooses ($F_{1, 420} = 21.79$, $P < 0.0001$) and its interaction with lynx use of the area ($F_{4, 420} = 3.48$, $P < 0.01$; Figure 2). Pair-wise comparisons showed that, as expected, scrubland cover indices were either lower or

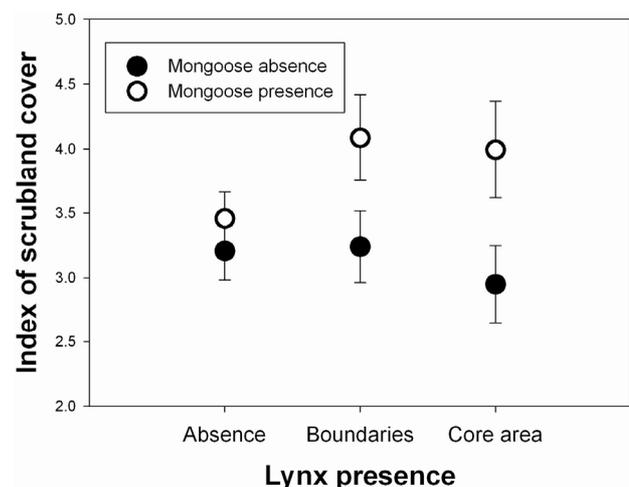


Figure 2. Mean values and 95% confidence intervals for scrubland cover in areas differing in lynx spatial use in relation to presence of Egyptian mongoose.

Table 1. Model selection. Results of a set of competing models on the probability of Egyptian mongoose occurrence (tracks) according to lynx presence and scrubland cover. The intercept-only model was considered as the null model. Models are sorted in increasing order according to $\Delta AICc$. The best approximating model is marked in bold.

Model	AIC	$\Delta AICc$	ω_i
Lynx presence + Scrubland cover + Interaction term	561.5	0	0.986
Lynx presence + Scrubland cover	570.1	8.6	0.013
Null model	588.8	27.3	0.001
Lynx presence	590.2	28.7	0.001

similar at points located within areas classified as any of the three levels of lynx use when not selected for mongooses and in those selected by mongooses but where lynx were absent. Scrubland cover was either higher or similar in points situated within lynx areas where mongooses were detected.

When we modelled the probability of occurrence of mongoose tracks, the only model that fitted well our data was the model incorporating lynx presence, scrubland cover and their interaction (Wald statistics: $\chi^2_3 \times 25 = 28.09$, $P < 0.001$; **Tables 1** and **2**). The rest of the models were poorly supported (**Table 1**). The probability of occurrence of mongoose tracks was constant across levels of scrubland cover when lynx were absent, but this probability increased in thicker scrubland areas within lynx areas; being highest within lynx highly used areas (**Figure 3**).

4. DISCUSSION

When mongooses coexisted with lynx, and were active, they selected scrubland areas thicker than those used by mongooses where lynx were absent, despite cover availability was similar in areas used and not used by lynx. This result is in agreement with the hypothesis of shifts

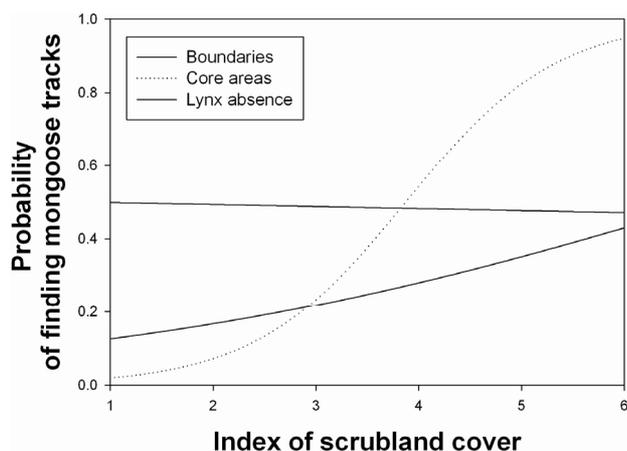


Figure 3. Predicted probability of Egyptian mongoose occurrence (tracks) for different scenarios of lynx spatial use (absent, home range boundaries, core areas) against scrubland cover.

Table 2. Estimates of coefficients ($\beta \pm SE$) for the variables included in the model selected to explain the probability of Egyptian mongoose occurrence (tracks) according to lynx presence and scrubland cover. Estimates of levels included in the intercept are not showed. Significant factors are marked in bold.

Model-effect		$b \pm SE$	df	Z	P
Intercept		-0.74 \pm 0.41			
Lynx presence	Home range boundaries	-0.54 \pm 0.69	2	-2.23	0.28
	Core area	-4.56 \pm 1.71		-2.66	
Scrubland cover		0.18 \pm 0.11	1	1.6	<0.001
Interaction term	Home range boundaries \times Scrubland cover	0.33 \pm 0.18	2	1.82	<0.001
	Core area \times Scrubland cover	1.37 \pm 0.49		2.8	

in microhabitat use of subordinate carnivores to prevent fatal or risky encounters with dominant ones. Selection of thicker vegetation by the potential victim species minimizes the chance of encounter with the killer species [4,15]. Furthermore, the behavioural response observed in mongooses, selecting denser scrubland sites, was stronger in areas where the probability of lynx encounters was higher. This result suggests that mongooses could perceive the risk associated with using the same areas of its potential killer. A few studies have shown the importance of landscape attributes or vegetation structure and complexity in allowing the coexistence of victim and killer predators at small spatial scales [18,19]. However, to our knowledge this is the first empirical evidence showing such a pattern of microhabitat shift in subordinate carnivore predators.

Although in recent times it has been reported that intraguild predation is widespread and can have important effects on subordinates (see reviews in [4-6,39]), almost no studies show the behavioural responses and mechanisms adopted by victims to diminish or avoid the probability of intraguild predation. Among the most outstanding findings, some studies have reported that victims can decrease the probability of encounters with intraguild predators by reducing their daily movements [40] and hunting activity [13,41] as well as by foraging in suboptimal habitats [17-19,42].

Our study was based on tracks left by active mongooses, so it could be argued that the behavioural response observed cannot be extrapolated to every mongoose. However, in the study area mongooses live in family groups of 4 - 5 members, moving within home ranges of 300 - 400 ha [43,44]. Therefore, the probable number of individuals sampled was 12 - 20 mongooses within lynx areas sampled whereas it could be 20 - 34 mongooses in the areas not used by lynx.

In terms of prey availability, the shift in microhabitat imposed by lynx spatial use may not be beneficial for mongooses. For example, in dense scrubland mongooses have a lower access to wild rabbits. Rabbits are one of the most profitable prey for mongooses in the study

area [31], but both the abundance of wild rabbits and their activity are lower in thicker scrublands compared to other habitat types present in the study area [45]. This result agrees with empirical and theoretical findings of game theory, which suggests that subordinates use the less profitable microhabitats for foraging due to the presence of dominants [46,47].

In this study, we show an interesting behavioural mechanism that allows the local coexistence of Egyptian mongooses and Iberian lynx. Our results are in agreement with the density-dependent relationship between both species [15,26]: mongooses are absent when lynx reach high densities whereas coexistence is possible at lower lynx densities provided that habitat (scrubland) heterogeneity is present. Landscape heterogeneity would allow for microhabitat shifts by subordinates favouring the coexistence between victims and killers [48]. We hypothesise that this mechanism could be generalized to other pairs of competitive predators living in heterogeneous landscapes.

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