Spatial segregation between Iberian lynx and other carnivores

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Abstract

Spatial segregation between Iberian lynx and other carnivores. The Iberian lynx (*Lynx pardinus*) is a specialist predator. Rabbits represent the bulk of its diet as for many other Iberian predators. This study addresses how the presence of the Iberian lynx affects the spatial distribution of the mesocarnivore community at landscape scale in the Sierra de Andújar. We studied mesocarnivore presence by sampling at 230 camera trapping stations, located in areas with and without lynx. We used a χ^2–test to compare the proportion of stations in which each species of carnivore were recorded in the zones with and without lynx. The proportion of camera trapping stations in which red fox (*Vulpes vulpes*), Egyptian mongoose (*Herpestes ichneumon*), beech marten (*Martes foina*), wildcat (*Felis sylvestris*) and common genet (*Genetta genetta*) were detected was significantly lower in the area where lynx were present than in the area where it was absent. No significant differences between the two types of areas were found for badgers (*Meles meles*). Our results highlight the role of the lynx as apex predators and the benefits that the recovery of Iberian lynx populations would entail in terms of trophic interactions and restored disrupted ecosystems processes.

Key words: Intraguild competition, Carnivores, Phototrapping, Apex predator

Resumen

Segregación espacial entre el lince ibérico y otros carnívoros. El lince ibérico (*Lynx pardinus*) es un depredador especialista. El conejo constituye el grueso de su dieta, al igual que la de otros depredadores ibéricos. Este estudio analiza cómo la presencia del lince ibérico afecta a la distribución espacial de la comunidad de mesocarnívoros a escala de paisaje en la sierra de Andújar. Se estudió la presencia de mesocarnívoros mediante 230 cámaras de fototrampeo, instaladas en zonas con y sin presencia de lince. Se utilizó la prueba de la χ^2 para comparar la proporción de cámaras en las que se detectó cada una de las especies de carnívoros en las zonas con y sin lince. La proporción de cámaras que detectaron zorros (*Vulpes vulpes*), meloncillos (*Herpestes ichneumon*), garduñas (*Martes foina*), gatos monteses (*Felis sylvestris*) y ginetas (*Genetta genetta*) fue significativamente menor en las zonas con presencia de lince que en las zonas donde este estaba ausente. No se encontraron diferencias significativas en cuanto a la presencia de tejones (*Meles meles*) entre ambos tipos de zona. Nuestros resultados ponen de relieve la importancia del lince como depredador apical y los beneficios que podría reportar la recuperación de las poblaciones de lince ibérico en lo que concierne a las interacciones tróficas y el restablecimiento de los procesos ecosistémicos interrumpidos.

Palabras clave: Competencia intragremial, Carnívoros, Fototrampeo, Depredador apical

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Introduction

Direct interactions between predators and other species can have indirect consequences further down the food web via trophic cascades (Ripple et al., 2016). Large carnivores play a key role in terrestrial ecosystems when they exert an influence on herbivores and so indirectly prevent overgrazing (McShea, 2005). They can also influence carnivore communities via intraguild interactions (Ritchie and Johnson, 2009) and indirectly prevent excessive predation on prey species by meso-carnivores (Elmhagen et al., 2010). This top–down cascade can influence ecosystem structures and biodiversity at both local and larger scales (Terborgh, 2001; Elmhagen et al., 2010). If healthy populations of top predators are to be maintained within ecosystems, these ecosystems should also contain healthy communities and populations of the many species that perform ecosystem services at lower trophic levels (Dobson et al., 2006; Haswell et al., 2017). However, the functional roles of top predators cannot be fully appreciated in isolation from bottom–up processes because the effects of nutrients, productivity (Pace et al., 1999) and anthropogenic habitat may bring about change (Litvaitis and Villafuerte, 1996; Estes, 1998; Elmhagen and Rushton, 2007).

Competitive intraguild interactions have been proposed as highly important organizing mechanisms since, due to similarities in ecological niches, they limit the number of species that can be packed into an assemblage (Jaksic and Marone, 2007). Similar ecological preferences increase the risk of competition, whereas mechanisms such as resource partitioning, temporal or spatial avoidance strategies (Voigt and Earle, 1983; Johnson and Franklin, 1994; Kozlowski et al., 2008), or alternative foraging strategies (Husseman et al., 2003) facilitate coexistence. Interference interactions, harassment and injury caused by larger carnivores pose a risk to smaller mesopredators (Linnell and Strand, 2000; Haswell et al., 2018). Furthermore, as a result of interference competition, subordinate species are frequently restricted to suboptimal habitats (Tannerfeldt et al., 2002; Macdonald et al., 2004; Mitchell and Banks, 2005), which can have important implications for the demography and distribution of the species involved (Thompson, 1988; Holt and Polis, 1997; Atwood and Gese, 2008).

The Iberian lynx (*Lynx pardinus*) is the top predator of the terrestrial vertebrate community in the Mediterranean ecosystem (Valverde, 1963). Listed as Endangered by the IUCN (Rodríguez and Calzada, 2015), the species reached its all–time minimum in the first years of the twenty–first century, when only 100 individuals in just two isolated populations –Andújar–Cardeña and Doñana– were known to exist (Guzmán et al., 2004; Simón et al., 2012). Since then, however, the Iberian lynx has undergone a significant increase in population size and range due to the measures implemented as part of conservation projects for the species (Simón et al., 2012), which include the creation of new populations through reintroduction.

The Iberian lynx is a specialist predator. Rabbits represent the bulk of its diet in a similar manner to that of many other Iberian predators (Cabezas–Díaz et al., 2011), possibly leading to interference or food competition. Previous studies of the relationships between Iberian lynx and other carnivores performed in Doñana have found that the Egyptian mongoose (*Herpestes ichneumon*) and genet (*Genetta genetta*) avoid lynx, while the Eurasian badger (*Meles meles*) is apparently indifferent to its presence. Although foxes (*Vulpes vulpes*) and lynx exhibit temporal segregation in their use of habitat (Fedriani et al., 1999), their spatial relationship remains unclear (Palomares et al., 1996). The relationship between wildcat (*Felix sylvestris*) and lynx has not been studied.

This study addresses how the presence of the Iberian lynx affects the spatial distribution of the mesocarnivore community at a landscape scale in the Sierra de Andújar. We studied the spatial distribution of several species of mesocarnivores in areas where the lynx is absent and where it is present, taking into account the abundance of rabbits.

Material and methods

Study area

The study area lies in the eastern Sierra Morena (SE Spain; fig. 1) and consists of a mountainous area with an altitudinal range of 200–1,500 m covered by well–preserved Mediterranean forests (*Quercus ilex, Q. faginea* and *Q. suber*) and scrublands (*Quercus coccifera, Pistacia lentiscus, Arbutus unedo, Phillyrea angustifolia* and *Myrtus communis*). The area is managed for big–game hunting and has high densities of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*). It is partially protected by the Parque Natural Sierra de Andújar. During the study period, the Andújar–Cardeña Iberian lynx population consisted of 60–110 individuals, distributed over an area of 15,000 ha (Guzmán et al., 2004).

Camera trapping survey

The spatial distribution of the carnivore community was estimated by sequential camera trapping surveys performed in December 1999–February 2000, November 2000–February 2001 and November 2001–February 2002. We used camera trapping data from the annual national Iberian lynx survey (Guzmán et al., 2004), which covers 85 % of the area potentially used by the Iberian lynx.

We divided the study area into 12 survey blocks, each of which were surveyed by camera trapping for periods of two months. Once one block was finished, cameras were moved to the next survey block. We surveyed an almost continuous surface area of 7,800 ha using a total of 230 camera trapping stations (1999/2000: n = 28; 2000/2001: n = 168; 2001/2002: n = 39). In all, 115 out of 230 stations were located in areas in which the lynx are present, as defined by Guzman et al. (2004), and the other 115 stations were placed in areas without lynx (fig. 1).
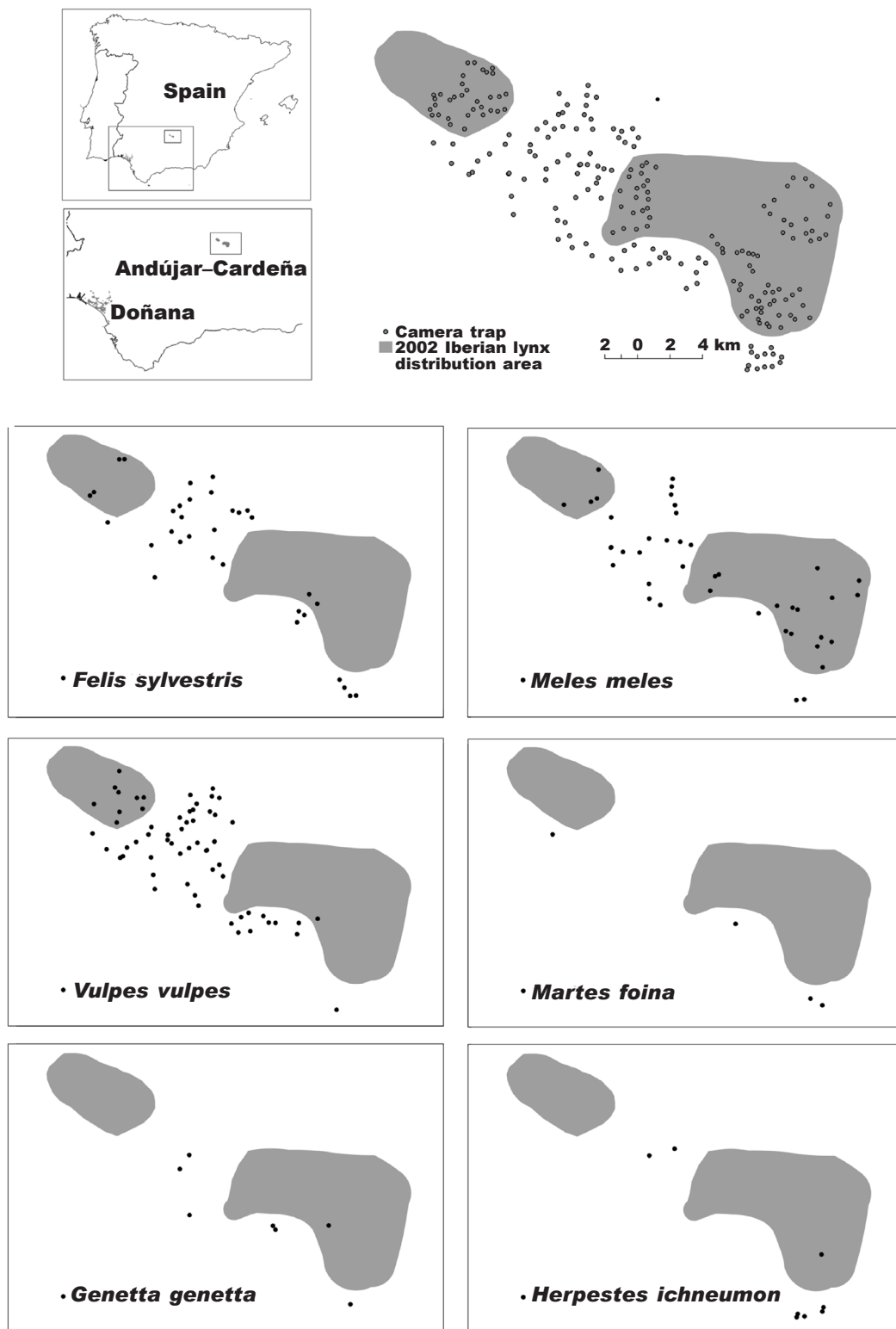
Fig. 1. Study area map. Camera trap stations located in areas with and without lynx, and stations in which each species of carnivore was recorded.

Fig. 1. Mapa de la zona de estudio donde se representa la ubicación de las estaciones de fototrampeo en zonas con y sin lince, así como las estaciones donde se detectó cada una de las especies de carnívoros.

We used 212 35–mm Canon Prima© classic photo film cameras with data registers and automatic flashes. The cameras were modified to allow activation via an external 25×25 cm pressure plate, positioned at a distance of 170 cm that was triggered when stepped on by an animal (Garrote et al., 2011). The cameras were placed in a small wooden box on pillars 30 cm above ground level. Urine from captive Iberian lynx, placed on an inert adjacent support, 50 cm above ground level and the pressure plate, was used as a lure. Lynx urine has been reported to be an excellent attractant for all carnivore species (Garrote et al., 2011; Monterroso et al., 2016). This attractant was replaced every 3–6 days. The distance between camera traps was 400–800 m. Camera–trap locations were located along suspected lynx travel routes (Garrote et al., 2012) such as roads or paths, chosen to maximize capture probabilities (Karanth and Nichols, 1998). Each camera was continuously active throughout the entire survey period for each block (two months).

To describe the species distribution in the area, we calculated occupancy as the proportion of stations at which a species was detected in relation to the total number of stations (Sogbohossou et al., 2018).

Rabbit abundance and habitat variables

Rabbit abundances were estimated for each survey block by on–foot constant–speed itineraries lasting three hours. Rabbit latrines were counted every 15', and these counts were taken as the survey unit for the statistical analysis. Indirect surveys were carried out at the same time of the year (end of spring, when rabbit populations peak) under similar weather conditions. Every 15' we estimated, in a 25 m radius plot, the percentage of land surface covered by the following habitat categories: trees, scrubland lower than 50 cm in height, scrubland higher than 50 cm in height, pastureland and rocks. The percentage of covered land was divided into four categories scored as follows: 1 (0–25 %), 2 (> 25–50 %), 3 (> 50–75 %) and 4 (> 75).

Statistical analysis

We compared the mean values for rabbit abundance and for each habitat category obtained in the areas with and without lynx using a Mann–Whitney U–test. We used a χ^2–test to compare the proportion of stations in the zones with and without lynx in which each species of mesocarnivore was present. The carnivores with lower capture rates were grouped together to perform statistical analysis (minimum five expected records).

Results

The following carnivores were detected in this study: (*Lynx pardinus*, 9–15.9 kg), Eurasian badger (*Meles meles*), red fox (*Vulpes vulpes*), Egyptian mongoose (*Herpestes ichneumon*), beech marten (*Martes foina*), wildcat (*Felis sylvestris*), and common genet

(*Genetta genetta)*. The proportion of camera trapping stations in which the fox and wildcat were detected was significantly lower in the area with lynx than in the area without lynx (table 1; fig. 1); no significant differences were found for the presence of the badger between both areas. Genet, beech marten and Egyptian mongoose were grouped together to perform the statistical analysis. The presence of this group of mesocarnivores was found to be significantly lower in the areas where lynx were present.

No significant difference was found between zones with and without lynx for the habitat variables (table 2). As expected, rabbit abundance in areas with lynx was significantly higher than that in lynx–free areas since lynx distribution is dependent on rabbit abundance (table 2).

Discussion

With the exception of the badger, the presence of the Iberian lynx determines the distribution at the landscape scale of the mesocarnivores community in the study areas. No significant habitat differences were found between areas with and without lynx, while the highest rabbit abundances were detected in areas with lynx. As mentioned above, Iberian mesocarnivores preferably select rabbits as prey (Cabezas–Díaz et al., 2011). The most probable explanation for the observed distribution of mesocarnivores at a landscape scale is the interference competition between species in which the lynx is the dominant species.

This is the first study to address a relationship between the Iberian lynx and wildcat, the only two sympatric wild felids present in the Iberian peninsula. Competition becomes greater as eco–morphological similarities or phylogenetic proximity between competing species increase (Cruz et al., 2018), and generally the larger dominant species exclude smaller or subordinate species from their territories by interference competition. Therefore, as expected, the larger Iberian lynx exerts strong interference competition on the smaller wildcat. This leads to fewer wildcats in those areas where lynx are present. Similar relationships of dominance have been described for other species of felines, such as the ocelot (*Leopardus pardalis*), which acts as a dominant carnivore over other smaller sympatric cats such as margay (*Leopardus wiedii*) and jaguarundi (*Puma yagouaroundi*) and so influences their ecological parameters (de Oliveira et al., 2010; Cruz et al., 2018).

Previous studies have shown a high overlap in the diets, activity levels, habitat use and home range in radio–tracked foxes and lynx (Fedriani et al., 1999). Although it has been suggested that foxes mitigate lynx predation by modifying their spatial behaviour at home range level, no spatial segregation in these species has ever been found. Using a landscape approach, the present study demonstrates significant spatial segregation between foxes and lynx. These differences with previous work might be attributable to scale since certain studies have concluded that approaches at different scales can generate different

Table 1. Total number of camera stations, positive stations for each species in zones with/without lynx, and positive stations per species. Genet, beech marten and Egyptian mongoose are grouped in 'others'. χ^2 results are shown.

Tabla 1. Número total de estaciones de fototrampeo, número de estaciones positivas para cada especie en las zonas con y sin lince y estaciones totales positivas para cada especie. Las ginetas, las garduñas y los meloncillos están agrupados en la categoría "Others" (otras). Se muestran los resultados de las pruebas de la χ^2.

	Total	Badger	Fox	Wildcat	Others
With lynx	115	20	10	6	2
Without lynx	115	26	53	29	17
Total	230	43	63	35	19
p		0.5	< 0.0001	0.0038	0.016

conclusions regarding interspecific interactions between species (e.g. (Tannerfeldt et al., 2002) for the Arctic red fox (Cruz et al., 2018). Previous studies (Palomares et al., 1996; Fedriani et al., 1999) have covered smaller areas than our study, which was performed at a much greater landscape scale. On the other hand, the relative densities of the mesocarnivores and their prey may also influence interactions (Creel, 2001; Berger and Gese, 2007). However, although no information is available for fox densities to compare these two study areas, the density of Matasgordas rabbit population (8 rabbits/ha; Villafuerte et al., 1997) is greater than that of Andújar (Simón et al., 2012). In areas or during periods of lower prey abundance, competition may play a more important role and interspecific interactions may change, resulting in increased interference competition (Creel, 2001). Lower prey densities can result in lower lynx tolerance toward foxes and, consequently, greater interference competition. Similar conclusions were reached by (Gese et al., 1996) in Yellowstone National Park, where coyotes tolerate red foxes during high prey years but not at other times.

Although data regarding the presence of the smaller mesocarnivores (Mongoose, martens and genets) are scarce, our results concur with previously reports from Doñana, where mongoose and genets avoid areas where lynx are present.

Iberian lynx and badgers seem to be particularly well predisposed to coexist (Palomares et al., 1996; Fedriani et al., 1999), and our results suggest that there is a complete spatial overlap between the species. Kleiman and Eisenberg (1973) suggest that this coexistence occurs as a result of a separation in their ecological niches, which is likely a consequence of evolution of different social systems. Similar interactions have been described between Eurasian lynx and wolves in Białowieza Forest (Schmidt, 2008) and between lynx and wolverine in northern Sweden (Schmidt, 2008). The Iberian lynx is a crepuscular species that preys mainly on rabbits (Fedriani et al., 1999), whereas badgers are much more nocturnal and are generalists with the capacity to survive on a

greater diversity of resources (Roper, 1994; Neal and Cheeseman, 1996; Revilla and Palomares, 2002). The food available for badgers in Mediterranean habitats varies greatly and badgers respond by shifting their diets accordingly between prey items (Virgós et al., 2004). However, niche differences alone cannot completely explain this coexistence. Foxes are even more adaptable than badgers and could potentially develop resource partitioning, temporal avoidance strategies (Voigt and Earle, 1983; Johnson and Franklin, 1994; Kozlowski et al., 2008), or different foraging strategies (Husseman et al., 2003) to facilitate coexistence. However, fox distribution is clearly influenced by the presence of lynx while badger distribution is not. The outcome of direct encounters between lynx and badgers is unknown but probably involves a risk of injury for both species. Therefore, the observed sympatry between Iberian lynx and badger is probably facilitated by a combination of both factors –the avoidance of injury and different foraging strategies.

Table 2. Mann–Whitney U–test results for the variables of habitat and rabbit abundance.

Tabla 2. Resultados de las pruebas U de Mann–Whitney para las variables del hábitat y la abundancia de conejos.

	Z	*p*–level
Pasture	−0.64	0.52
Scrub < 50cm	0	1
Scrub > 50 cm	0.96	0.33
Tree	−0.48	0.63
Rocks	1.28	0.2
Rabbit	2.08	0.03

As a result of being a trophic specialist on rabbits, the abundance of its staple prey determines the lynx's basic demographic parameters (Monterroso et al., 2016) and distribution (Guzmán et al., 2004), which thus implies that there is bottom–up control over Iberian lynx dynamics. Likewise, the presence or absence of the Iberian lynx, which is determined by rabbit abundance, affects the dynamics of subordinate carnivore species via a top–down control effect. The foraging theory suggests that animals adjust their behaviour accordingly to optimize foraging efficiency and overall fitness, and trade–off harvesting rates with fitness costs (Haswell et al., 2018). In the absence of Iberian lynx, sympatric mesocarnivores should ideally be distributed on the basis of habitat quality and preferred food availability (Van Der Meer and Ens, 1997; Roemer et al., 2009). The presence of the lynx forces smaller species to invest in antipredator behavioural strategies (Lima, 1998; Haswell et al., 2017) that can have negative consequences. For example, their access to high–quality foraging areas can be restricted (Ritchie and Johnson, 2009), which forces them to seek an alternative diet, adopt their life cycles to those of their new prey items, and adjust their feeding behaviour (Durant, 2000; Hayward and Slotow, 2009; Wikenros et al., 2014). This in turn can affect the size of the home range, increase travel costs or lead to shifts in habitat use (Caro and Stoner, 2003). The fitness costs of these antipredator responses could affect survival and reproduction, thereby ultimately having an impact on population dynamics (Creel and Christianson, 2008). On the other hand, a fall in lynx numbers is expected following rabbit declines, which will lead to a lessening of the top–down control on mesocarnivores numbers (Estes et al., 2011; Monterroso et al., 2016).

Conservation implications

Numerous studies have drawn attention to the importance of apex predators in suppressing populations of smaller predators (mesopredators) and thus their roles in moderating the impact of predation on smaller prey species (Crooks and Soulé, 1999; Johnson et al., 2007; Berger et al., 2008). The recovery and re–establishment of apex predator populations contribute not only to their conservation but also benefit biodiversity conservation via a relaxing of the impact of mesopredators on their prey (Ritchie and Johnson, 2009). This is positive for the restoration of disrupted ecosystem processes (Estes et al., 2011; Ritchie et al., 2012), particularly in terms of trophic interactions (Monterroso et al., 2016) but also for economic and social reasons (ecosystem services). Some areas in rural Spain have high rabbit densities and suitable habitat for the lynx. Most such areas are occupied by private, intensively managed, small–game hunting areas (rabbit and partridge; Delibes–Mateos et al., 2009). In these hunting estates strong predator control is traditional and still persists nowadays, both legally (leg–hold traps and snares when authorised under certain exceptional circumstances) and illegally (Villafuerte et al., 2000; Virgós and Travaini, 2005). Despite the possible negative effect on non–target species, this practice requires important time and monetary expenditure, although the desired results are not always achieved (Harding et al., 2001). Lynx are viewed negatively by many hunters in the Iberian Peninsula since, as a trophic specialist that preys on rabbits, it competes for this highly important small–game species. Nevertheless, the Iberian lynx presence could be an effective, natural and inexpensive tool for predator control since it suppresses populations of smaller predators and thereby mitigates the impact that these mesopredators will have on game species (Palomares et al., 1995). This is a key argument for changing game managers' opinions and for ensuring a favourable response to any lynx reintroduction project in its past range from where, ironically, it was eradicated by indiscriminate predator control (Gil–Sánchez and McCain, 2011).

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