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<http://www.italian-journal-of-mammalogy.it>

doi:10.4404/hystrix-00372-2020

Research Article

Adapt or perish: how the Iberian lynx reintroduction affects fox abundance and behaviourPedro SARMENTO^{1,*}, Victor BANDEIRA², Pedro GOMES², Carlos CARRAPATO¹, Catarina EIRA², Carlos FONSECA²¹Instituto da Conservação da Natureza e das Florestas. Centro Polivalente de Divulgação da Casa do Lanternim. Rua D. Sancho II, nº 15 | 7750-350 Mertola, Portugal.²Departamento de Biologia and CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

Keywords:
reintroduction
camera trapping
occupancy models
intraguild competition

Article history:

Received: 24 August 2020

Accepted: 13 February 2021

Acknowledgements

This work was supported by the Life+ project “Recovery of the Historical Distribution for Iberian Lynx” (*Lynx pardinus*) in Spain and Portugal (LIFE09NAT/ES/570) co-funded by the European Commission. Thanks are due to Foundation of Science and Technology/Ministério da Ciência, Tecnologia e Ensino Superior (FCT/MCTES) for the financial support to CESAM (UIDP/50017/2020+UIDB/50017/2020), through national funds and to the project Selectpredators financed by national and European funds. Thanks to Jinpa Smith for the English revision.

Abstract

The Iberian lynx (*Lynx pardinus*) reintroduction in the Guadiana valley (Portugal) began in 2015. By 2019 more than 100 lynxes were in the wild, dispersed over 300 km². The arrival of a new top predator (the lynx had been extinct from this region for decades) may have affected red fox populations (*Vulpes vulpes*) as a result of intraguild competition. The aim of this study was to evaluate the effects of the lynx reintroduction on the spatial, temporal and spatial-temporal dimensions of local fox abundance and behaviour. Camera trapping results revealed a clear decrease in fox abundance. Also, co-occurrence occupancy models indicated a higher probability of fox occupancy in areas where lynxes were absent, as well as a greater fox detectability in places where lynxes were absent, rather than in places where lynxes were present. In the temporal dimension, there were no significant effects on fox behaviour. However, the spatial-temporal dimension revealed a competitive exclusion since foxes avoided areas that had recently been used by lynxes.

Introduction

Dissimilarities among sympatric species in the exploitation of trophic, temporal and spatial resources are basic mechanisms that allow species co-occurrence (Davies et al., 2007). In the case of sympatric carnivores with analogous morphology, behaviour and ecological requirements, differences in body size can reduce competition for trophic resources (Carbone and Gittleman, 2002). Habitat (Sollmann et al., 2012) and space (Palomares et al., 1996) segregation, or differences in activity patterns (Romero-Munoz et al., 2010), allowing species with equivalent feeding ecology to coexist.

In this context, interspecific competition may affect populations and shape the evolution of interacting species (Palomares et al., 1996). Potential competitors can either kill each other (intraguild predation) or persist together (Karanth and Sunquist, 2000). The competition between species with analogous ecological requirements tends to decrease through changes in the use of trophic, temporal and spatial resources (Schoener, 1983). The coexistence of sympatric carnivores showing analogous morphology and hunting strategies relies on space segregation (Palomares et al., 1996; Creel and Creel, 1996) and on adjusting activity patterns (Karanth and Sunquist, 2000; Arjo and Pletscher, 1999).

In a top predator reintroduction context, quantitative and behavioural changes in the populations of potential competitors are to be expected, especially if the reintroduced species has a larger body mass than native predators (Yiu et al., 2018). Therefore, post-release monitoring is critical and should also cover potential effects on species interactions, which is particularly important for large carnivores, due to their influence on predator-prey dynamics (Hayward et al., 2007).

Over the last 10 years, an Iberian lynx (*Lynx pardinus*) reintroduction project, using captive born animals (aimed at preventing the species extinction) led to the establishment of six new populations in Spain and in Portugal. Previously, the species was confined to the south of Spain (Doñana and Andújar) and occupied only 100 km² (Guzmán et al., 2005). Since then, the total population has increased from 90 to more than 600 individuals, which is spread over an area of more than 500 km² (Life+IBERLINCE, 2020). From 2015 till 2019, 40 lynxes were released in the southeast of Portugal (Guadiana valley) and at least 99 lynxes were born in the wild during 4 breeding seasons. Most lynxes established stable home ranges (Sarmento et al., 2019) and by 2019, over 100 lynxes had dispersed through more than 300 km² (Sarmento et al., 2019).

The establishment of a new top predator population may have caused ecological adjustments in the community of native predators and prey (Hayward et al., 2007; Yiu et al., 2018). These potential effects may be more conspicuous in red fox populations (*Vulpes vulpes*), particularly because the fox is the most abundant carnivore species in lynx territories and because foxes and lynxes may display similar feeding habits (Palomares et al., 1996). Direct competition, via aggression, was documented between lynxes and foxes (Palomares et al., 1996). Considering the larger body mass of lynxes, they are expected to be dominant, while foxes could reduce their abundance and covered area, or adjust their habitat use and daily activity patterns. These changes in habits can be achieved through active avoidance upon recognition of olfactory signals (Arjo and Pletscher, 1999), after antagonistic encounters. Since lynxes were previously absent from the study area, a certain period of time should be expected to occur before foxes begin to effectively recognise the lynx scent as a threat.

As a predator, the fox is a keystone species with a high importance in the ecosystem (Soe et al., 2017). Nevertheless, the fox is usually accused of creating conflict with human activities that rely on small game

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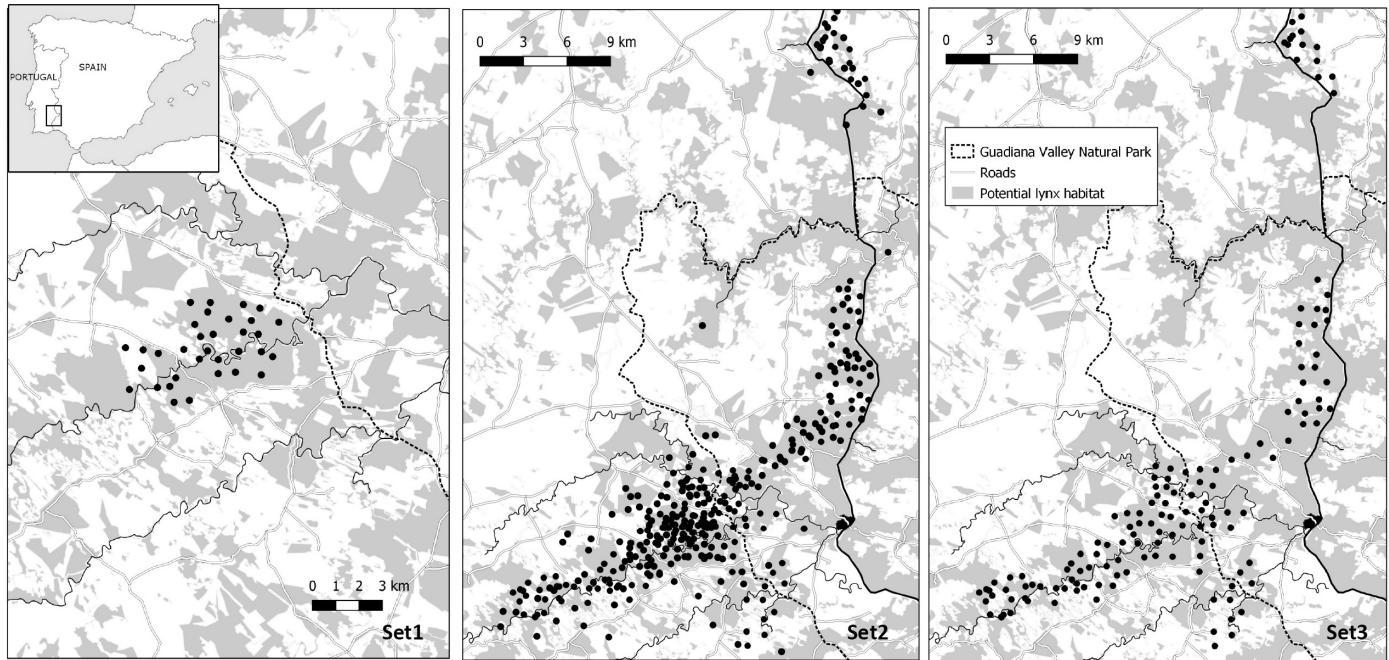


Figure 1 – Study area and locations of camera traps used for studying temporal variation of fox abundance (set 1), temporal partition between lynxes and foxes (set 2) and co-occurrence mechanisms between lynxes and foxes (set 3), in the Guadiana Valley (Portugal).

and poultry rearing. On the other hand, lynxes are generally accepted by the local human population, even though the lynx reintroduction has added one more predator species to the ecosystem (Lopes-Fernandes et al., 2018).

Using camera trapping, we studied the effects of the new lynx population on fox abundance and behaviour in the Guadiana valley up to 4 years after the reintroduction onset. The main objectives of our study were to evaluate if the effect of competition would result in: 1) a decrease of fox abundance, 2) a change of behaviour, particularly in daily activity patterns and space use, or 3) a combination of fox abundance and behavioural changes.

Study area

The study area was situated in southeast Portugal and it comprised around 850 km² corresponding to the Guadiana Valley Natural Park and its surroundings (Fig. 1). The area is covered by scrublands, characteristic of the dry thermo-Mediterranean environment. The *Myrto communis*-*Querceto rotundifoliae* S. series is dominant. Scrublands are fragmented by cereal, pasturelands and forestations of *Pinus pinea* L. and *Quercus rotundifolia* L. subsp. *ballota*. These vegetation patches occur mostly on the Guadiana riverbanks, in its bordering valleys and in the main elevations. Wild rabbits (*Oryctolagus cuniculus*) are abundant in most of the area, presenting spring densities >4 individuals/ha. Ungulates are also present (fallow deer *Dama dama* and red deer *Cervus elaphus*) in most of the area and red partridges (*Alectoris rufa*) are abundant.

Materials and methods

Time variation in lynx and fox abundance

Fox relative abundance was estimated between October 2014 and October 2018 using camera-trapping on a 25-camera grid installed over a 20.9 km² area (set 1; Fig. 1). A 750 m–1000 m distance was kept between cameras in order to guarantee their spatial independence (Garrote et al., 2010). It was therefore possible to estimate fox abundance in the study area before the lynx reintroduction, which started later on in February 2015 (Sarmento et al., 2019). It was also possible to evaluate how the fox abundance varied over time in relation to an increasing number of lynxes. Considering that set 1 cameras were the only cameras that were never moved during the 4-year period, this was the

only set of cameras that could be used for that purpose (see information about camera sets 2 and 3 below).

Cameras (SpyPoint Force 11-D®, Stealth Cam®, Bushnell Trophy Cam® and Browning trail Cameras®) were installed about 40 cm above the ground in places with greater probability of detecting the target species, such as at watering points, and on wild animal trails.

The Relative Abundance Index (RAI) was used to estimate lynx and fox relative abundances. For each species, RAI is the total number of monthly independent detections multiplied by 100 and divided by the total number of camera-days (O'Brien et al., 2003). Detections were considered independent if the time between two consecutive encounters was greater than 0.5 h (O'Brien et al., 2003).

Lynx and fox temporal overlap

We used kernel density estimation to generate the activity patterns and the overlap between lynxes and foxes, using camera trapping data from all active stations from February 2015 till October 2018, including set 1 cameras (n=972; set 2; Fig. 1). The overlap coefficient (Δ), which varies from 0 (no overlap) to 1 (complete overlap) was estimated and confidence intervals were calculated at 95%, using 10000 bootstraps (Ridout and Linkie, 2009). The statistical analysis was performed with the software R 3.3.2, using the Overlap package, applying an adaptation of the script used by Ridout and Linkie (2009) (<http://www.kent.ac.uk/ims/personal/msr/overlap.html>). We considered 3 overlap categories: 1) low ($\Delta \leq 0.5$); 2) medium ($0.5 < \Delta \leq 0.75$); and 3) high ($\Delta > 0.75$). We used the Δ_4 method since our sample size was larger than 75 records (Ridout and Linkie, 2009). Significant differences between coefficients of overlap were measured using the Watson's two-sample test of homogeneity (U^2) used for circular data (Jammalamadaka and Sengupta, 2001), following conversion of solar time data to radians (varying from 0 to 2π). The analyses were divided in three periods: 1) March to September (the period of lynx juvenile dependence), 2) October to February, and 3) the entire year. This approach aimed to assess if lynx behaviour during the juvenile dependence period (while protecting cubs) could affect fox activity.

Lynx and fox spatial overlap

Co-occurrence was also studied using the two species conditional occupancy model (MacKenzie et al., 2004) using an adaptation by Richmond et al. (2010). We used 178 camera traps (sampling sites) on a

1×1 km grid operating in the field for 45 consecutive days between July and September 2019 (set 3; Fig. 1).

No detection of a species in a sampling unit (camera) may indicate a true absence or it may indicate non-detection. Therefore, repeated visits to these same units were used to determine the probability of detection conditioned to the occupation (MacKenzie et al., 2004). In this study, one visit corresponded to each day of photo-trapping, resulting in a total of 45 replicates.

The conditional two-species occupancy model assumes that species A is dominant (the lynx), and species B is subordinate (the fox). The parameters included in this model are:

- ψ^A – probability of occupancy for lynx
- ψ^{BA} – probability of occupancy for fox, given lynx is present
- ψ^{Ba} – probability of occupancy for fox, given lynx is absent
- p^A – probability of detection for lynx, given fox is absent
- p^B – probability of detection for fox, given lynx is absent
- r^A – probability of detection for lynx, given both species are present
- r^{BA} – probability of detection for fox, given both species are present and lynx is detected
- r^{Ba} – probability of detection for fox, given both species are present, and lynx is not detected

Some of these parameters can be derived (see MacKenzie et al., 2004). The fox unconditional probability of occupancy can be calculated as: $\psi^B = \psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba}$, which corresponds to fox occupancy independent of lynx presence. The unconditional probability of both species being present can be calculated as: $\psi^{AB} = \psi^A \psi^{BA}$. These parameters also allow calculating the species interaction factor or SIF (φ) (Richmond et al., 2010):

$$\varphi = \frac{\psi^{AB}}{(\psi^A \psi^B)} \quad (1)$$

If SIF is equal to 1 the two species occur independently. If SIF<1, species B (fox) is less likely to occur when species A (lynx) is present in comparison to an independent occurrence hypothesis. If SIF>1, species B has a higher probability of occupancy if species A is present in comparison to an independent occurrence hypothesis (Royle et al., 2013).

Contender models were ranked using the Akaike Information Criterion adjusted for small sample sizes (AICc) by estimating their Akaike weights (Burnham and Anderson, 2002). We tested a total of 12 models that allowed all the combinations between occupancy and detection probabilities within each species.

Lynx and fox spatial-temporal overlap

We applied two methods to evaluate spatial-temporal exclusion among lynxes and foxes (Karanth et al., 2017). Using set 3 (Fig. 1), we started by designing a matrix of both species' detections per hour for each camera station (rows=sampling sites; columns=hourly intervals of the diel cycle). Individual cells included the total number of detections of each species at a particular site during a particular hour. Then, we calculated the proportion of sites, at each hourly interval, where each species was detected in the absence of the other, and where both species were detected. Confidence intervals for the observed proportions were calculated using empirical bootstrapping (Efron and Tibshirani, 1999) using available R codes (Karanth et al., 2017).

We then estimated the parameter "time-to-encounter" (Karanth et al., 2017) using multi-response permutation processes (Mielke et al., 1976). For each detection of one of the two species at a given station we calculated the minimum time to encounter the other species, obtaining a series of observed times-to-encounter. Then, we produced expected statistical distributions of that parameter by randomly assigning encounter times to each station, using 1000 simulations. Next, the median observed time-to-encounter was compared with the simulated distribution of expected times-to-encounter. A higher observed time-to-encounter in comparison to the respective expected value indicated avoidance, while the opposite indicated aggregation. As above, we used the R codes provided by Karanth et al. (2017).

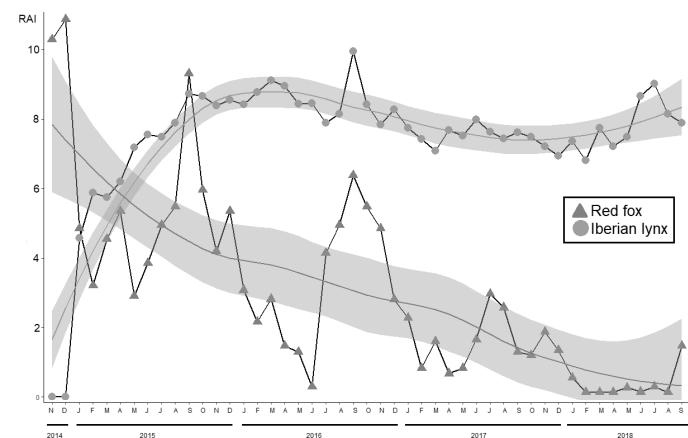


Figure 2 – Temporal variation of red fox and Iberian lynx relative abundance index (RAI) obtained from camera trapping (set) in the Guadiana Valley (Portugal), 2015–2018. The grey areas represent the tendency with an exponential smoothing factor of 0.05 using a LOESS regression.

Intraguild predation

We analysed 7 fox carcasses suspected to have been predated by lynxes and that we found in lynx territories. We compared the injuries, particularly the distance between canines, with the dimensions observed in lynxes, and we looked for lynx signs such as footprints and excrement.

Behavioural observations

We used four observations of interactions between lynxes and foxes that were obtained either by camera trapping (using de video mode) or directly in the field, in order to describe behaviour. Even though these observations were circumstantial in nature, they are important to support the data.

Results

Time variation in lynx and fox abundance

In set 1, a total of 27967 camera-days resulted in 1029 fox and 2542 lynx independent detections, corresponding to a trapping success of 3.68 and 9.09 independent detections/100 camera-days for each species, respectively.

Despite the large fluctuations, the fox's RAI decreased over time, reaching minimum values in 2018 (Fig. 2). This parameter exhibited annual peaks in late summer, corresponding to the fox's juvenile dispersal period, whereas the lowest values were coincident with the lynx juvenile dependence period, between March and September (Fig. 2). The growth rate observed between the highest RAIs of 2018 and 2014 was -2.00. The growth rate observed between the lowest values of 2018 and 2015 (for 2014 registrations started in November) was -3.08. In both cases, the obtained values correspond to a considerable decrease in fox relative abundance. On the other hand, the observed lynx RAI initially increased until September 2015 and stabilized from that date onwards, when the number of adult lynxes in the area began to stabilize (Fig. 2), reaching a maximum of 8 adults. A significant negative correlation was observed between the lynx RAI and the fox RAI ($r^2=0.82$; $F=16.33$; $p<0.001$).

Lynx and fox temporal overlap

In set 2, a total effort of 42683 camera-days resulted in 2600 and 842 independent lynx and fox captures, respectively. These values correspond to a trapping success of 6.09 and 1.97 independent captures for 100 trap-days for lynx and fox, respectively. During the three analysed periods (March to September corresponding to the juvenile dependence period, October to February, and the entire year), lynx activity was mostly crepuscular with activity peaks around sunrise and sunset (Fig. 3). There were no significant differences in lynx activity between the juvenile dependence period and the rest of the year, with a high activity overlap between both periods ($\Delta_4=0.86$; $CI=0.84–0.88$;

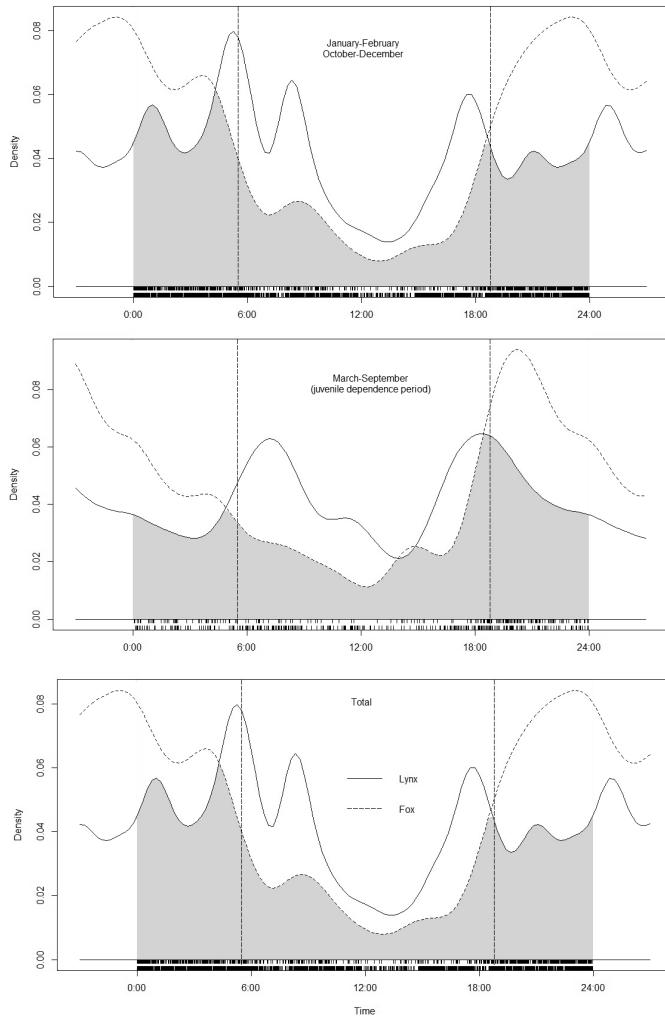


Figure 3 – Temporal activity overlap (grey area) between Iberian lynx and red fox in the Guadiana Valley (Portugal), 2015–2018.

Watson's test, $U^2=0.99$, $p>0.1$). Fox activity was mainly nocturnal and there were no significant differences in the species activity between the above-mentioned periods ($\Delta_4=0.75$; CI=0.72–0.76; $U^2=0.99$, $p<0.1$) (Fig. 3) and between areas with and without lynx detection. For the total set of observations, there was a medium level of overlap between fox and lynx activity with significant differences ($\Delta_4=0.70$; CI=0.68–0.72; $U^2=0.99$, $p<0.1$).

Lynx and fox spatial overlap

In set 3, a total effort of 7210 trap-days produced 218 and 129 independent lynx and fox captures, respectively. Trapping success was 3.0 and 1.8 independent captures for 100 trap-days for lynx and fox, respectively. Lynxes were detected in 110 stations (naïve occupancy of 0.62) and foxes in 71 (naïve occupancy of 0.40). We detected both species simultaneously at 10 (6%) camera sites.

The most supported model for co-occupancy had an AICc weight of 1 (Tab. 1), showing significant differences in all occupancy and detection parameters (Tab. 2).

The level of spatial interaction between lynxes and foxes (SIF) was significantly lower than 1 (Tab. 2), showing that foxes are less likely to inhabit places where lynxes are present. In fact, while the total probability of fox occupancy (ψ^B) was 0.49, the probability of fox occupancy was 2.0 times higher in sites where lynxes are absent (ψ^{Ba}) and 2.1 times lower in sites where lynxes are present (ψ^{BA}).

Foxes' detection probabilities were significantly lower in sites where it co-occurred with lynxes (r^{BA} ; r^{Ba}) than where only foxes were present (ρ^B), which was more evident in sites where both species were detected (r^{BA}) (Tab. 2). Lynx detection probability was 3.3 times higher

Table 1 – Model selection results for the best 4 fitted models ranked by AICc to evaluate co-occupancy of Iberian lynx and fox in Guadiana Valley (Portugal), in 2018. K: number of parameters; LL: log-likelihood; wi: AICc weight.

Model	AICc	ΔAICc	wi	LL	K	Deviance
$\psi^A \psi^{BA} \psi^{Ba} \rho^A \rho^B r^A r^{BA} r^{Ba}$ *	1283.09	0	1	1	8	1265.27
$\psi^A \psi^{BA} \psi^{Ba} \rho^A \rho^B$	1323.75	40.65	0	0	5	1313.01
$\psi^A \psi^{BA} \psi^{Ba} \rho^A \rho^B r^A$	1324.91	41.82	0	0	6	1311.87
$\psi^A \psi^{BA} \psi^{Ba} \rho^A \rho^B r^{BA} r^{Ba}$	1325.24	42.14	0	0	7	1309.83

* The best ranking model indicates that fox occupancy in areas where lynx is present (ψ^{BA}) is significantly different of fox occupancy in areas where lynx is absent (ψ^{Ba}), the probability of detection for lynx, given fox is absent (ρ^A) is significantly different than the probability of detection for lynx, given both species are present (r^A), the probability of detection for fox, given lynx is absent (ρ^B) is significantly distinct from the probability of detection for fox, given both species are present and lynx is detected (r^{BA}) and from the probability of detection for fox, given both species are present and lynx is not detected (r^{Ba}).

in sites where only this species was present (ρ^A) than in sites where both species co-occurred (r^{BA} ; r^{Ba}) (Tab. 2).

Lynx and fox spatial-temporal overlap

When considering the temporal and spatial dimensions simultaneously, the proportion of overlap between lynx and fox was much lower than those observed when analysing the temporal and spatial dimensions separately. Both species were detected simultaneously in fewer than 5% of the sites at each time interval whereas isolated detections occurred in more than 85% of the sites at each time interval (Tab. 3). Furthermore, avoidance behaviour was particularly apparent when spatial-temporal overlap was observed, with a medium time-to-encounter between lynxes and foxes of 6.1 days (SE=2.66) (Fig. 4). Foxes can therefore co-occur with lynxes but they avoid areas recently used by lynxes. The proportion of randomly generated times-to-encounter values that were greater than the observed time-to-encounter was estimated at 0.11 (Fig. 4).

Intraguild predation

From 2015 to 2019 we found seven dead foxes that seemed to have been killed by lynxes, revealing intraguild predation. In all the cases, injuries were mostly concentrated in the neck and the distance between canines varied between 22 mm–25 mm, which is compatible with lynx intercanine distance. Also, lynx scat was found near the fox carcasses in 4 of these events. One of these events occurred in May 2017, during the lynx breeding season, and it consisted of a female fox and its three cubs, which had been killed near a lynx burrow by a male lynx, as confirmed by molecular analysis (J. Godoy *pers. comm.*) (Fig. 5).

Table 2 – Real and derived parameter estimates for the most supported model to describe lynx and fox co-occurrence in the Guadiana Valley (Portugal).

Parameters	Estimate	SE	Lower	Upper
Real				
ψ^A	0.66	0.05	0.55	0.75
ψ^{BA}	0.23	0.06	0.13	0.35
ψ^{Ba}	1.00	0.00	1.00	1.00
ρ^A	0.19	0.02	0.15	0.23
ρ^B	0.37	0.02	0.31	0.42
r^A	0.62	0.04	0.53	0.70
r^{BA}	0.05	0.02	0.02	0.12
r^{Ba}	0.3	0.07	0.18	0.45
Derived				
φ	0.46	0.09	0.29	0.63
ψ^B	0.49	0.05	0.37	0.6
ψ^{AB}	0.15	0.04	0.09	0.24

Table 3 – Proportions of time when each species was exclusively active, and when the activity of both species overlapped. Bootstrapped 95% confident intervals in parentheses.

Species activity	Proportions of sites at each hourly interval	
Lynx alone	0.96	(0.92–0.99)
Fox alone	0.88	(0.84–0.93)
Lynx and Fox	0.03	(0.01–0.04)

Behavioural observations

Two encounters between foxes and lynxes were directly observed during the first year of lynx releases. One of these encounters occurred on day 1 after the first lynx pair had been released. A fox crossed paths with the female lynx, facing it in an antagonistic posture, and eventually was attacked and escaped. In the second encounter, the fox came within a few meters of the lynx and then moved away in response to an aggressive posture by the lynx. Two years after the first lynx release, two more interactions between lynxes and foxes were observed. In both cases, foxes immediately escaped once they detected the lynx, indicating an emergence and evolution of fox defensive behaviour in response to lynx.

Discussion

Our study clearly reveals that the reintroduction of the lynx has had an effect on fox abundance and behaviour. Fox abundance steadily decreased as the number of lynxes increased and behavioural changes were observed in the spatial-temporal dimensions.

The large dataset included in the present study strongly validates the competitive exclusion between the lynx and the fox already described in Garrote and Ayala (2019) and Jiménez et al. (2019). However, a reintroduction effect on another predator's abundance and spatial and time use was not reported in Garrote and Ayala (2019), since the lynx was never completely absent from the study area. Nonetheless, spatial segregation between lynxes and foxes was also observed in Garrote and Ayala (2019). As for Jiménez et al. (2019), the authors did analyse the effect of lynx reintroduction on foxes and also small game abundances. However, the authors did not include behavioural aspects, such as daily activity patterns adaptations or behavioural avoidance, which constitute the main focus of the present study. Furthermore, we used a wider timeframe and a larger lynx population. In fact, Jiménez et al. (2019) used a 2-year dataset and a lynx population of 23 lynxes with 3 breed-

ing females, whereas we used a 4-year dataset and a population of 54 lynxes with 9 breeding females. The larger lynx population allowed us to obtain more robust data for studying behavioural adaptations.

Our study further emphasises the multidimensional character (space, time and space-time) of competitive exclusion. The overlap in temporal, spatial and spatiotemporal patterns are not necessarily equivalent. In fact, conclusions generated from separate analyses of each dimension may fail to explain species co-occurrence patterns (Karanth et al., 2017). Lynx presence alone is not sufficient to inhibit fox occurrence (Garrote and Ayala, 2019). However, fox occupancy and detection probability are much lower (indicating lower fox density) in lynx occurrence areas.

In the present study, lynx presence influenced fox abundance, as revealed by a continuously decreasing fox detection rate. The fox detec-

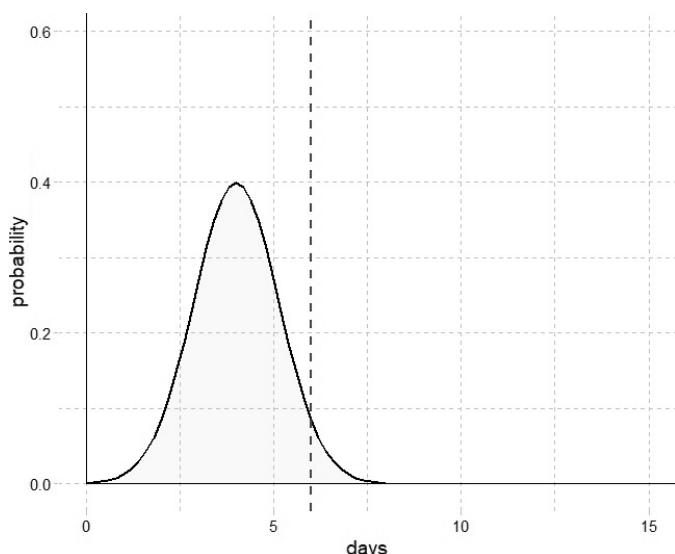


Figure 4 – Spatial-temporal interaction between Iberian lynx and red fox represented as times-to-encounter produced from multi-response permutation procedures in the Guadiana Valley (Portugal), 2015–2018. The grey area represents randomly simulated times-to-encounter, and the vertical line is the median minimum time-to-encounter between the two species.

Figure 5 – A female fox and three cubs killed by a lynx (A) and details of fatal neck wounds in one of the cubs (B).

tion rate was even lower during the lynx juvenile dependence period, when females probably displayed more intense aggressive behaviour to protect their offspring. The detection of a female fox and 3 of her cubs killed by a lynx, during that period, can support this conclusion. The spatial-temporal dimension of their competitive exclusion relationship clearly shows how foxes avoid areas that have recently been used by lynxes. This behaviour could be the result of antagonistic encounters, which are corroborated by the detection of foxes certainly killed by lynxes.

The spatial analysis resulting from the co-occurrence models revealed two circumstances:

1. a higher probability of fox occupancy in areas where the lynx is absent (about 5 times higher), which validates the negative effect of lynx presence on fox occupancy
2. a greater fox detectability in places where lynx is absent than in places with lynx occurrence (whether lynx had been detected or not)

With respect to the fox abundance peaks detected during late summer and early autumn, these are possibly due to the dispersal period of juvenile foxes (Cavallini, 1994), and to the fact that fox hunting season does not start until winter.

Considering the direct effect of lynx abundance on fox detection probability, results revealed that where lynxes occurred in low abundance (leading to lynx non-detection) the probability of fox detection was higher than in areas where lynxes were detected. Therefore, higher lynx abundance means lower fox abundance, which corroborates the results obtained through set 1. In summary, lynx reintroduction seems to have influenced fox population in the numerical and spatial-temporal dimensions, with no latent impacts on the temporal dimension. Foxes may avert danger by increasing their vigilance behaviour and by reacting to menace signals, which may constrain habitat use and reduce food consumption (Haswell et al., 2018; Lesmeister et al., 2015).

The effect of large predators on limiting the impacts, distribution and space use of mesopredators has been previously described for several species (Prugh et al., 2009; Levi and Wilmers, 2012; Pasanen-Mortensen and Elmhagen, 2015) and even for the relationship between the lynx and other predators (Jiménez et al., 2019). The latter authors observed that the reintroduction of the lynx in Toledo (Spain) led to a marked abundance decrease of some mesopredators, such as foxes and Egyptian mongooses (*Herpestes ichneumon*) which, in turn, led to an increase in wild rabbit abundance/availability (Jiménez et al., 2019).

As observed for other top predators (Terborgh et al., 2001), the lynx disappearance from its historical range could have led to damaging outcomes at the ecosystem level. The effects of large carnivore declines can lead to ecosystem degradation through the release of top-down control upon mesopredators Prugh et al. (2009). The mesopredator release hypothesis states that a reduction in the abundance of top-order predators allows for an increase in mesopredators' abundance, due to a decrease in intraguild predation (a phenomenon observed in our study) and competitive suppression (Ritchie et al., 2012). Therefore, lynx reintroduction in areas where it once existed may be a key step in restoring ecological balance (Smith and Bangs, 2009).

If stable lynx populations are to be maintained, ecosystems must also contain healthy populations of other predators that fulfill important ecosystem services at lower trophic levels (Dobson et al., 2006). The return of the lynx should not cause local fox population extinction, although a decrease in fox abundance is expected along with the adoption of defensive strategies that allow for their co-occurrence. Maintaining adequate fox density remains important for ecosystem balance, as this species is an important rodent predator and regulates its abundance (Egle et al., 2017).

Finally, the present study emphasises that predator control should not be required in areas where lynx is abundant, as predator abundance can be regulated through intraguild competition. Considering that legal methods for the control of foxes and Egyptian mongoose populations are widely applied in the region, the presence of lynx alone should motivate a change in the management strategies of game estates located in lynx occurrence areas. 

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Associate Editor: S. Grignolio