

## Restoring apex predators can reduce mesopredator abundances

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### ABSTRACT

The role that apex predators play in ecosystem functioning, disease regulation and biodiversity maintenance is increasingly debated. However, the positive impacts of their presence in terrestrial ecosystems, particularly in human-dominated landscapes, remain controversial. Limited experimental insights regarding the consequences of apex predator recoveries may be behind such controversy and may also impact on the social acceptability towards the recovery of these species. Using a quasi-experimental design and state-of-the-art density estimates, we show that mesopredator abundances were reduced after the restoration of an apex predator, with evidence of resonating positive impacts on lower trophic levels. Iberian lynx *Lynx pardinus* reintroduction was followed by the reduction of the abundance of mesocarnivores (red foxes *Vulpes vulpes* and Egyptian mongooses *Herpestes ichneumon* by ca. 80%) and the recovery of small game of high socio-economic value (European rabbits *Oryctolagus cuniculus* and red-legged partridges *Alectoris rufa*). The observed mesopredator reduction resulted in an estimated 55.6% less rabbit consumption for the entire carnivore guild. Our findings have important implications for the social acceptability of Iberian lynx reintroductions, which crucially depend on the perception of private land owners and managers. Under certain circumstances, restoring apex predators may provide a sustainable and ethically acceptable way to reduce mesopredator abundances.

### 1. Introduction

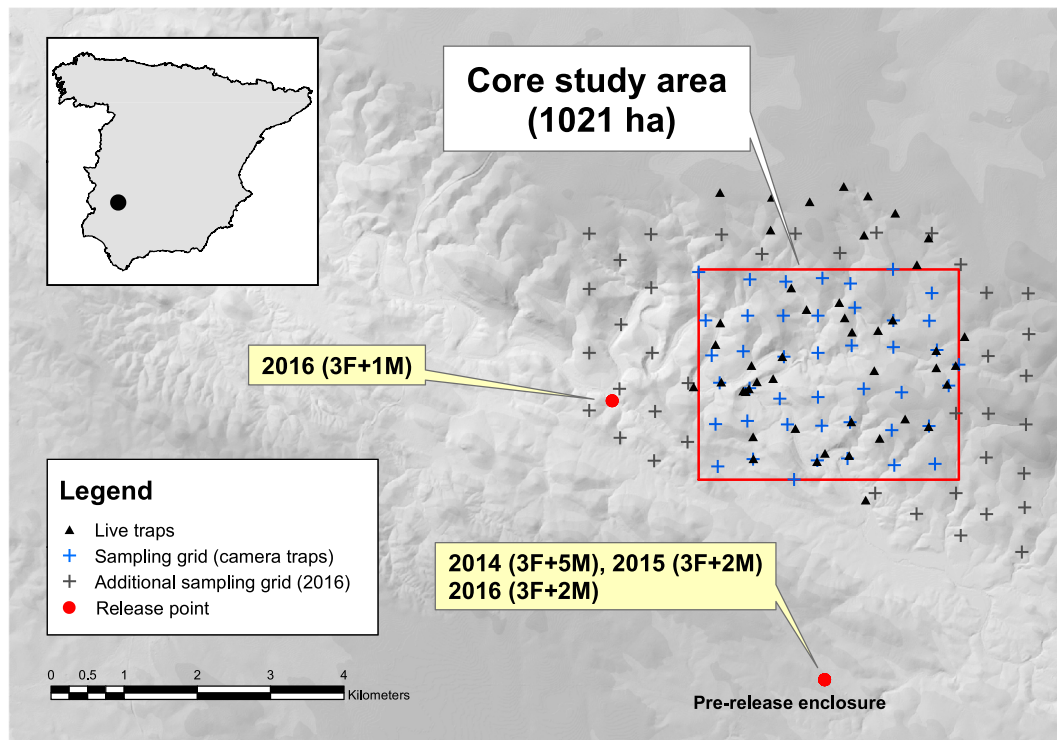
Apex carnivores generate considerable interests both within the scientific community and the general public, with an ongoing debate about the robustness of the available evidence regarding their ecological roles (Allen et al., 2017; Bruskotter et al., 2017), such as ecosystem functioning and structuring, disease regulation or biodiversity maintenance (Ripple et al., 2014; Stier et al., 2016; O'Bryan et al.,

2018). The socio-ecological consequences of such roles are difficult to quantify (Allen et al., 2017; Brackzkowski et al., 2018), impacting on the acceptability of these species (Bruskotter and Wilson, 2014), particularly when their recovery occurs in human-dominated landscapes (Chapron et al., 2014). Current debate may be in part motivated by limited sound evidence (i.e., experimental insights) regarding the consequences of apex predator presence and recoveries (Morris and Letnic, 2017; Suraci et al., 2016), social conflicts over sharing the

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**Fig. 1.** Map showing the location of the core study area (red rectangle) and lynx reintroductions. Yellow panels indicate the location (red dots), year and number of female (F) and male (M) lynx that were released. The grid of detector devices used to study the carnivore community is also shown (live traps = black triangles; camera-traps = blue crosses; additional camera traps deployed in 2016 = black crosses). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

landscape with these species (Woodroffe and Redpath, 2015; López-Bao et al., 2017) and the controversy around the effectiveness and acceptability of large-scale conservation actions, such as reintroductions (Hayward and Somers, 2009).

Numerous studies have addressed the regulatory role of apex carnivores in ecosystems and have identified that they act on lower levels through trophic cascades (Ripple et al., 2016a), and on the same guild through the regulation of mesopredators (Ritchie et al., 2012; Ripple et al., 2014). For example, the return of the wolf *Canis lupus* in Yellowstone (USA) has had cascading effects on herbivory pressure and plant formations through regulatory effects on ungulate populations (Ripple and Beschta, 2012), whereas the presence of lions *Panthera leo* reduces pack size in wild dogs *Lycaon pictus* through intraguild interactions (Groom et al., 2016). The debate about the reliability of evidence regarding the ecological roles of apex carnivores is well illustrated by the case of the Yellowstone wolves, for which there is disagreement about the mechanisms involved in the trophic cascades mediated by this species (e.g. Creel et al., 2005; Hebblewhite and Merrill, 2007; Kauffman et al., 2013).

We report here on a quasi-experiment investigating the short-term ecological changes associated with the restoration of an apex predator, the Iberian lynx *Lynx pardinus* in a Mediterranean ecosystem, focusing on population trends of mesopredators and species of lower trophic levels. The Iberian lynx (6.1–15.9 kg; Table A1) is one of the most threatened carnivore species worldwide (Rodríguez and Calzada, 2015). By the end of the twentieth century, eight out of 10 lynx populations had gone extinct (Palomares et al., 2011). In 2002, two lynx-breeding areas remained (Doñana and Sierra Morena) with ca. 52 breeding individuals left (Rodríguez and Calzada, 2015). After intense conservation efforts, including reintroductions, breeding populations recovered to ca. 400 individuals in 2016 (Life + IBERLINC, 2017). The best areas for lynx reintroduction are private estates primarily managed for hunting big (mainly red deer *Cervus elaphus* and wild boar *Sus*

*scrofa*) and small game (red-legged partridges *Alectoris rufa* and European rabbits *Oryctolagus cuniculus* - a key multifunctional species of the Iberian Peninsula; Delibes-Mateos et al., 2008). The extent to which the presence of lynx is acceptable to landowners is therefore key for the long-term recovery of this endangered felid.

We took advantage of a lynx reintroduction program in Extremadura, Spain, where the species has been absent since the late twentieth century (Guzmán et al., 2004; Rodríguez and Delibes, 1992) to carry out a quasi-experimental assessment of the response of terrestrial mesocarnivores and main prey species to the lynx restoration. The targeted study area had no other apex predator for decades, as the Iberian wolf *Canis lupus signatus* became extinct in mid-late twentieth century (López-Bao et al., 2018).

The Iberian lynx is a rabbit specialist (Delibes-Mateos et al., 2008; López-Bao et al., 2010). Territorial lynx maintain exclusive and well-defined territories to buffer possible fluctuations in rabbit abundance (López-Bao et al., 2014). In Mediterranean ecosystems, the most abundant mesopredators are medium-sized (1–6 kg, Table A1) and generalists (e.g. red fox *Vulpes vulpes*; Egyptian mongoose *Herpestes ichneumon*). Although intraguild interactions between lynx and several mesocarnivores have been empirically described previously (a negative association between mesocarnivore and lynx abundances; Palomares et al., 1996; Palomares and Caro, 1999) the impact of the restoration of the species on mesocarnivores' densities and lower trophic levels remains unexplored. With our quasi-experimental design, our aim was to confirm that the reintroduction of the Iberian lynx should be associated with a reduction of mesopredator abundances that could further affect lower trophic levels (prey species), helping the recovery of small game species of high socio-economic and ecological importance.

## 2. Methods

### 2.1. The lynx reintroduction program in the Matachel river valley and surroundings

The study area is located in the Matachel river valley (altitude: 498 m above sea level, range: 346–667; Sierra Morena, Badajoz, Spain). The landscape is a mixture of cultivated lands, open oak woodlands ('dehesa') and scrubs. Vegetation is dominated by holm oak *Quercus ilex* and olive *Olea europea* trees, with a shrub layer of *Cistus ladaniferus*. Human population density in this area is low, 12.9 inhabitants/km<sup>2</sup> (INE, 2017). The main land uses include extensive farming (cereal crops and vineyards), livestock farming, and estates managed for large and small game hunting.

The lynx reintroduction was conducted by Life + IBERLINC (2017), with released animals coming from the Ex-situ Conservation Program (LYNXESITU, 2019). The first reintroduction in this valley (3 females and 5 males) was on July 13th 2014. All the released animals were fitted with telemetry collars and were monitored.

Soft-releases were performed in a pre-release enclosure located at 5.3 km from our core study area (Fig. 1). On July 30, 2014, one female lynx appeared for the first time in this core area, followed by a male detected on August 26, 2014. Both settled their territories in the area and had 3 kittens in 2015 (and 4 kittens in 2016). In 2015 another lynx pair established their territories west of the core study area, with a distance of 7.5 km between the activity centres of both territorial males (spatial overlap in the Iberian lynx between individuals of the same sex is very low; López-Bao et al., 2014). This pair gave birth to 3 kittens in 2015 and 2 kittens in 2016.

In 2015, 5 lynx (2 males and 3 females) were released from the pre-release enclosure point (Fig. 1). One of the females released in 2015 gave birth in 2016 (3 kittens). In 2016, 9 lynx (3 males and 6 females) were released again (5 from the pre-release enclosure and 4 during a hard-release action). In 2017 and 2018, another 8 (4 males and 4 females) and 6 (3 males and 3 females) lynx were released, respectively. One long disperser from Vale do Duoro (Portugal) also established in Matachel Valley.

Overall, from the 36 lynx released in the Matachel Valley until 2018, 10 individuals died (4 were road-killed, 1 poisoned, and 5 died from diseases). Another 2 individuals disappeared (their transmitters failed and they were never recorded by camera trapping again, so their fate was unknown). One lynx was translocated, and three individuals were long-distance dispersers, establishing their territory outside the study area (one of them in Toledo Mountains, Central Spain, at 197 km). In December 2018, the remaining 19 released lynx were still occupying the reintroduction area in the Matachel Valley. A total of 41 kittens were produced during 2015–2018, of which 7 died, 4 had an unknown-fate, and 30 survived.

### 2.2. Carnivore abundance estimates

We used a quasi-experimental approach because replication and contemporary controls were logistically difficult to achieve. Within the area where the lynx reintroduction program took place, we used knowledge on the habitat conditions favourable for lynx (i.e., high rabbit density and dense vegetation cover; Palomares et al., 2001) to select *a priori* a 1021 ha core study area to run our experiment (Fig. 1). We worked at the scale of the lynx's home range (850–1800 ha for adult female and male, respectively; Palomares et al., 2001), which is relevant from a landowner's point of view: hunting estates are on average of 1075 ha (MAPA, 2018), and cover 70% of the land surface in Spain (Arroyo et al., 2012).

We estimated the density of Iberian lynx and mesocarnivores in the core study (Fig. 1) area just before lynx settled there in 2014, one year (2015) and two years (2016) later. Every year, estimates were carried out from May 22nd to August 15th. During this period, which was after

the time of birth and before the dispersal of mesocarnivores, we could consider the populations to be demographically closed. We worked at a spatial scale that is sufficient to describe a typical mesocarnivore community in Mediterranean habitats (Jiménez et al., 2017).

We used a combination of camera-trapping, telemetry, and spatially explicit capture-recapture models to estimate carnivore densities (Efford, 2004; Royle et al., 2014).

We set up 43 camera traps of similar characteristics (ScoutGuard and Ltl-Acorn 5210) regularly spaced over the core study area (average distance of 436 m between cameras). Cameras were attached to trees or fence poles. Lynx urine (collected from captive breeding facilities) was used as an olfactory attractant and was sprayed onto a cork piece and placed on a 0.3–0.4 m metal pole support. The attractant was renewed every 20 days. Lynx urine, either alone or in combination with valerian extracts, has proved to be an effective attractant for most Iberian mesocarnivores (Monterroso et al., 2011; Jiménez et al., 2017; Ferreras et al., 2018). Camera-traps remained at the same exact location throughout the study. In addition, we set 45 live-traps (4 Belisle, 11 Collarum, 8 handmade cages and 22 Tomahawk Live Traps® 80 × 26 × 32 cm) spread over the whole core study area (Fig. 1) to capture and tag individuals of the different mesocarnivore species. The live-traps were used only in 2014, prior to the first lynx release.

The size of the selected core study area (1021 ha) was adequate for all the mesocarnivore species considered in this study, given their home range sizes (Sollmann et al., 2012). We could *a priori* detect in our working state space an estimated 24 mesocarnivores (11 foxes, 7 mongooses and 6 stone martens) based on density estimates carried out in a nearby location with a similar Mediterranean landscape (36 km away from our core study area; Jiménez et al., 2017). For Iberian lynx the home range of a territorial male released in 2014 was of 1053 ha in 2015 (95% kernel density estimator using GPS and telemetry locations); and subsequently increased to 1714 ha in 2016. Thus, the size of the core study area was under the minimum limit for reliably estimating lynx density in 2015. Following this observation, we increased in 2016 the size of the core study area up to 2892 ha (larger than the home range of the settled lynx) but exclusively in order to get optimal estimates of lynx density. This was done by adding 40 camera traps around the core study area using the same above-mentioned criteria (Fig. 1). For mesocarnivore species, we used only camera trappings within the core study area in order to report abundances trends within the same area.

Camera-trap pictures were classified in order to create a database of detection events (Jiménez et al., 2017). We considered these as independent when they were separated by at least 30 min. Pictures with more than one individual were considered as different detection events (one per observed individual). We used the events of each species as a reference of their spatial use of the territory.

We used spatial capture-recapture (SCR) methods (Efford, 2004; Royle and Young, 2008) on recognizable species to model capture probability as a function of the distance between activity centres and detectors (camera traps), and calculating abundance estimates that are linked to a predefined area using thinned spatial point process models (Royle et al., 2014). SCR models postulate that the encounter probability of individuals ( $\lambda_{ijk}$ ) is a decreasing function of the distance between the activity centre ( $s_i$ ) of individual  $i$  and the location of survey devices  $j$  at the occasion  $k$ . Our observation models were assumed to be Bernoulli outcomes when we had one detection of each individual at a particular detector on any occasion, or Poisson outcomes when we had repeated detections:

$$y \sim \text{Bernoulli}(\lambda_{ijk}) \text{ or } y \sim \text{Poisson}(\lambda_{ijk})$$

The link function between the location of survey devices and the activity centres for individuals follows a half-normal distribution:

$$\lambda_{ijk} = \lambda_0 \exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

where  $d_{ij}$  is the Euclidean distance between the activity centre for each individual and camera-trap,  $\sigma$  is the parameter of movement, and  $\lambda_0$  is the baseline encounter rate. Integrating the underlying point process, we estimated the number of activity centres in the prescribed state-space. If only a fraction of the animals can be uniquely identified, we used the extension of SCR developed by Sollmann et al. (2013): the spatial mark–resight (SMR) model. In this model, the recognizable fraction is modelled as in SCR, and the unmarked events ( $n_{jk}$ ) were used as reduced information of latent encounter histories of individuals as accumulated counts:  $n_{jk} \sim \sum_i^n y_{ijk}$ . If we had information about capture and marking process, we used generalized SMR (Whittington et al., 2017), with different basal detection rate for marking and resight. When individual recognition was not possible, we used another SCR extension: Spatial Count (SC) developed by Chandler and Royle (2013), using only the latent encounter histories of individuals. For the latter two types of models, we used telemetry data, adding a description of the bivariate normal model. If we have a coordinate dataset *locs* from some *ind* individuals:

$$\text{locs}[r] \sim \text{Normal}(\text{sm}[\text{ind}[r]], 1/\sigma^2)$$

where *sm* are coordinates within the state space (Royle et al., 2014). All these spatially explicit methods have been used to assess density for multiple species simultaneously (Jiménez et al., 2017; Rich et al., 2019)

We implemented spatially-explicit models in a Bayesian framework (Royle et al., 2014) using R (R Core Team, 2018) and the package *nimble* (De Valpine et al., 2017; NIMBLE Development Team, 2017). For the Iberian lynx and feral cat *Felis silvestris catus*, all the individuals were identifiable, so we used spatial capture-recapture (SCR) models. For the red fox and the European badger *Meles meles*, only some individuals were identifiable, so we used spatial mark-resight (SMR) models (Royle et al., 2014). For the stone marten *Martes foina*, we had one marked individual, captured near the limit of the study area, so we used a generalized-SMR model (Whittington et al., 2017). For the Egyptian mongoose, individual recognition was not possible, so we used spatial count (SC) models (Chandler and Royle, 2013; Royle et al., 2014). In order to enhance estimation of the detection parameters, we also used telemetry data from tagged red foxes and stone martens (Sollmann et al., 2013).

For red fox, we selected the best spatially explicit model comparing those that included or not covariates affecting the basal probability of detection ( $\lambda_0$ ) using the Kuo & Mallick criteria (Kuo and Mallick, 1998). We also used the Watanabe-Akaike criterion (Watanabe, 2010) from the package *nimble* that closely approximates Bayesian cross-validation. In order to improve parameter estimates when sample sizes (spatial recaptures) were small (Da Rocha et al., 2016; Gelin et al., 2017; Morin et al., 2018), we used models for each species with shared movement parameter  $\sigma$  among years (for lynx, feral cat, stone marten and badger). When the capture history of a species included only zeros in a given year (e.g. feral cat and stone marten in 2016), we used a baseline detection rate ( $\lambda_0$ ) that was shared among years. Posterior probabilities were calculated using 3 independent MCMC chains, with at least 50,000 iterations each, and a burn-in of 1000 iterations. We assessed MCMC convergence and mixing by visually inspecting trace plots and calculated the Gelman-Rubin statistic R-hat (Gelman et al., 2003) using the R package *coda* (Plummer et al., 2006).

For red foxes and Egyptian mongooses, we additionally collected information on changes over time in group sizes, using camera-trapping from the breeding season. This information was used as an indicator of family size and reproductive output. Foxes form family groups consisting of the male and/or female with young (Cavallini, 1996; Macdonald, 1979). Egyptian mongooses also typically form family groups (Palomares and Delibes, 1993). We also report all the cases of intraguild killing (Palomares and Caro, 1999) after lynx reintroduction.

### 2.3. Prey trends

We used abundance indices to study the population trends of European rabbits and red-legged partridges in areas occupied by lynx (treatment areas) or not occupied by lynx (control areas) before and after the initial lynx reintroduction (Appendix B). Between 2014 and 2016, a set of transects were repeated each year to count rabbit latrines and partridges (Appendix B).

For rabbit trends, we used 49 transects repeated across 12,773 ha (average transect length:  $843 \pm 224$  m, range: 504–2042 m). Twenty transects (treatment) overlapped with the home range (kernel 95%) of two male territorial lynx and their associated females and kittens, one of them in the core study area (Appendix B). Twenty-nine transects were adjacent to these (control), but located in areas known to be unoccupied by lynx (Appendix B). A latrine was defined as a group of at least 20 rabbit pellets within an area of  $20 \times 30$  cm<sup>2</sup> (Ferreira et al., 2010). Latrine counts were conducted between June and October. This survey method is reliable to determine rabbit trends or to map abundance at the landscape scale (Delibes-Mateos et al., 2008; Ferreira et al., 2010).

Similarly, red-legged partridges were counted annually in September over 9297 ha along 9 transects of  $14,347 \pm 3729$  m (range 9460–22,143 m). Transects were carried out by driving vehicles at low speed (< 20 km/h) without a priori knowledge of where lynx would settle. We categorized each transect a posteriori according to a “lynx area” factor using two groups: those entirely within areas occupied by lynx after reintroduction and overlapping with the 95% kernel area (representing the area of higher lynx activity; López-Bao et al., 2010, 2014), and those with no or an overlap < 50% with the kernel 95%. Partridge counts along transects have also been shown to provide reliable abundance estimates of red-legged partridge in habitats similar to those of our study area (Caro et al., 2015).

Variation in rabbit and partridge abundances in relation to lynx presence over time was analysed using generalized linear mixed models with a negative binomial error distribution. Models were fitted using the *glmer.nb* function from the *lme4* R package (Bates et al., 2015). We tested for spatial correlation in rabbit and partridge abundances using Moran tests and Monte-Carlo simulations (R package *spdep*; Bivand and Wong, 2018). We found evidence for spatial autocorrelation for rabbit (Moran's  $I = 0.172$ ,  $p = 0.001$ ) but not for partridge ( $I = -0.381$ ,  $p = 0.921$ ) abundances. To take this into account, we used an additional level of random effect in our analyses of rabbit trends, by re-grouping spatially transect into 4 clusters (2 treatments and 2 controls; see Appendix B). We included the predictors year (three levels: 2014–2015–2016), lynx area (binary factor: lynx presence-lynx absence) and their interaction to test whether prey population trends differed between areas with or without lynx presence. Models were fitted for each prey species separately and included transect length (log-transformed) as an offset. The proportion of generalized variance explained by the fixed predictors was calculated using the R package *r2glmm* (Jaeger, 2017). For the rabbit model, we performed a Moran test on the model's residuals and confirmed that adding the cluster level random effect correctly dealt with the spatial autocorrelation issue (Moran's  $I = 0.0042$ ,  $p = 0.189$ ).

### 2.4. Rabbit consumption by mesocarnivores and the Iberian lynx

We estimated the number of rabbits eaten by lynx in the core study area, and those that would have been consumed by the mesocarnivores displaced by the lynx during the study period, using the methodology described by Palomares et al. (1995).

To do this, we used our estimates of carnivore abundance and reviewed published information on: 1) the daily food requirements (Table C2), 2) the proportion of rabbits in the diet during the same season (Tables C2 & C3), and 3) the proportion of three rabbit sizes (small: < 200 g, medium: 200–800 g and large: > 800 g) in the diet of

each carnivore species (Table C4). These figures are fundamental in order to approximate the number of rabbits preyed by each carnivore species, because more rabbits will be required if the diet has to be satisfied with smaller rabbits and because of the different hunting strategies used by carnivores. For example, the Egyptian mongoose preys mostly on juvenile rabbits through burrowing and digging (Palomares et al., 1995). By contrast, the Iberian lynx feeds on subadult and adult rabbits (Palomares et al., 1995), hunted by stalking and ambushing (Delibes and Hiraldo, 1981). A full-size rabbit is close to the lynx daily food requirement (Aldama et al., 1991).

Rabbit consumption by carnivores was estimated for the same period (3 months; mid-May to mid-August) when the camera-trap sampling was carried out to estimate carnivore densities (Appendix C).

### 3. Results

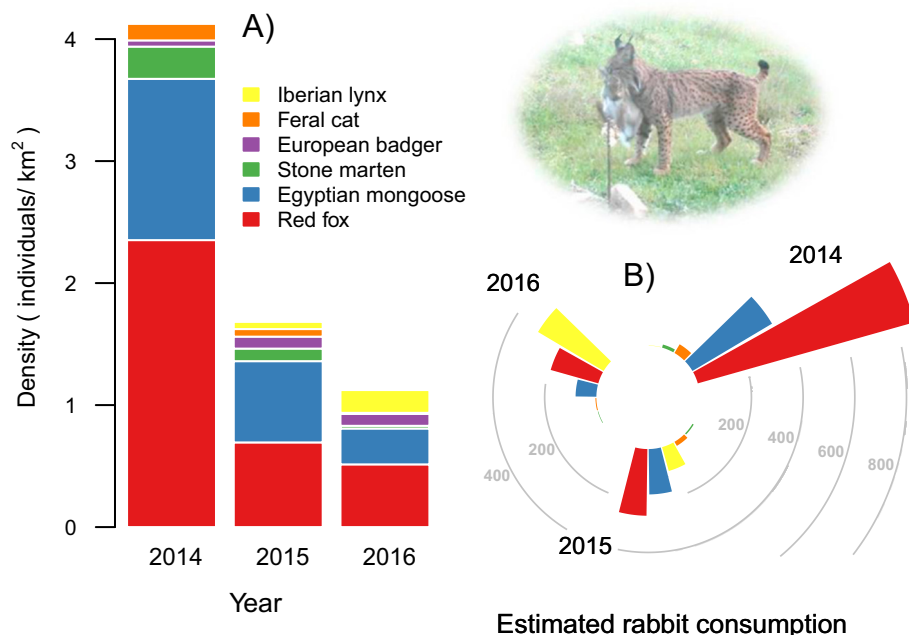
After lynx reintroduction in 2014, lynx densities in the core study area increased from 0.06 (Bayesian credible interval BCI: 0.04–0.1) to 0.19 (BCI: 0.13–0.27) individuals/km<sup>2</sup> in 2015 and 2016, respectively (Fig. 2). These figures were consistent with the known lynx population size in the area (Appendix D). Before lynx reintroduction and settlement in the core study area, the community included 9 mesocarnivores. We estimated the density of 5 species (Table 1). The red fox and the Egyptian mongoose dominated, with 2.35 (BCI: 1.50–3.42) and 1.34 (BCI: 0.69–2.39) individuals/km<sup>2</sup>, respectively. However, after lynx establishment fox and mongoose densities decreased by 78%: 0.51 (BCI: 0.28–0.83) and 0.27 (BCI: 0.12–0.56) individuals/km<sup>2</sup>, respectively; (Fig. 2, Appendix D). Moreover, two species, feral cats and stone martens, almost disappeared from the area, while the European badger slightly increased (from 0.06 BCI: 0.04–0.14 individuals/km<sup>2</sup> in 2014 to 0.1 BCI: 0.10–0.27 individuals/km<sup>2</sup> in 2016) (Figs. 2 & 4; Table C1). The lynx settlement was associated with a spatial displacement of foxes and mongooses, visible through changes in the occurrence of camera-trapping events. Capture rate was of 23.46 foxes/100\*camera-day in 2014, before lynx reintroduction. In 2015, fox capture rates averaged 18.60 vs 10.61 in areas inside vs. outside the lynx home ranges, respectively. By 2016, fox capture rates were of 1.88 vs 14.54 in areas inside vs. outside lynx home ranges, respectively. The same occurred for mongooses, with 7.86 mongooses/100\*camera-day in 2014, 3.51 vs. 1.38 in 2015, and 1.23 vs. 4.09 in areas inside vs. outside lynx ranges,

respectively (Fig. 3). Overall, the establishment of lynx in the core study area translated into an estimated disappearance of 33 mesocarnivores: 18.8 foxes, 10.5 mongooses, 2.5 stone martens and 1.3 feral cats (Appendix C).

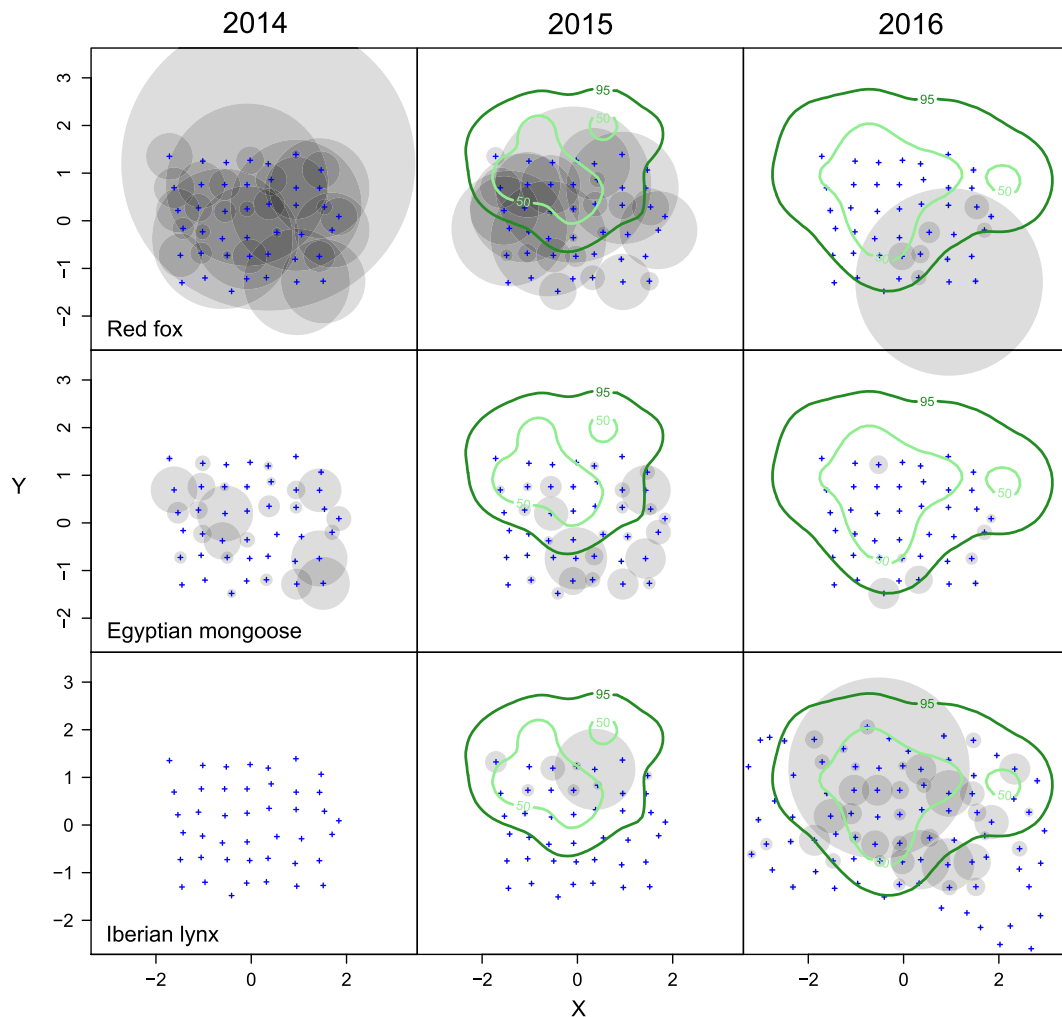
For foxes, a population reduction occurred one year after the initial lynx reintroduction (2015), with the maintenance of a low abundance compared with 2014. In 2016, some foxes established outside the lynx home ranges (Fig. 3) where rabbits were also abundant. For mongooses, the population reduction was sustained until at least two years post-reintroduction (Figs. 2, 3 & 4). Seventeen events of intraguild predation were detected (Fig. F1, Table F1), of which three were direct observations of lynx killing mongooses or feral cats, and 14 were putative killings by the lynx (lynx present near the event and the corpse showing neck bites with an intercanine distance ~32 mm consistent with a lynx killing; LIFE project unpublished data). We also observed a decrease in the productivity of foxes and mongooses following the lynx return based on information from camera-traps. From 2014 to 2016, the number red fox family groups camera-trap detections dropped from 9 to 1. Similarly, the number of detections of Egyptian mongoose family groups dropped from 37 to 8 (Fig. D1).

Apparently, the lynx selected for settlement in 2014 those areas with highest rabbit density (Fig. 4). The presence of lynx was also associated with differences in rabbit and partridge population trends, particularly during 2015–2016 (Fig. 4, Table 2). In 2014–2016, rabbit abundance varied with year ( $X_2 = 22.20$ ;  $df = 2$ ,  $p < 0.001$ ) and lynx presence (lynx area:  $X_2 = 5.58$ ,  $df = 1$ ,  $p = 0.018$ ), with no significant interaction between the presence of lynx and the year ( $X_2 = 5.20$ ,  $df = 2$ ;  $p = 0.074$ ; variance explained by fixed effects: 41%). In 2015, rabbit abundance decreased irrespective of lynx presence but in 2016, rabbits recovered (increased) only in areas occupied by lynx (see Table 2; significant Year2016 \* Lynx Area effect). Partridge abundance varied with the interaction between year and lynx area ( $X_2 = 16.03$ ,  $df = 2$ ;  $p < 0.001$ ; variance explained by fixed effects: 60%). This interaction was significant in 2015–2016 when partridge abundance decreased in areas without lynx, but not in areas where lynx had established (Fig. 4, Table 2).

The reduction of mesopredator abundance after the initial lynx reintroduction resulted in an estimated 55.6% net reduction (averaged value) in rabbit consumption by all carnivores (Fig. 2). Considering rabbit size, small rabbit consumption was reduced by 67%, whereas this



**Fig. 2.** A) Carnivore community densities (estimated using spatial-capture-recapture models in the 1021 ha study area) before lynx reintroduction (2014), one year (2015) and two years (2016) later (left). B) Estimated number of rabbit consumed by the lynx and mesocarnivores each year (right) along the study period. Colours used for carnivore species are the same in A (density) and B (rabbit consumption).



**Fig. 3.** Spatio-temporal variation in the number of photo-capture events for red fox (top row), Egyptian mongoose (central row) and Iberian lynx (lower row). Events are shown before the reintroduction of the Iberian lynx (2014); 1-year later (2015), and 2-years later (2016). Circle size is proportional to the number of captures per 100 camera-days (same scale for all species) and centred at the location of the camera trap (shown with crosses: +). The home range area (50% and 95% kernels; green and dark green contour lines, respectively) of the male territorial lynx is also shown as a reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

figure was 45 and 46% for medium and larger-size rabbit consumptions, respectively (Appendix C).

#### 4. Discussion

We have reported multiple changes associated with the reintroduction of Iberian lynx: changes in mesopredator densities, relations between lynx presence and prey trends, changes in fox and Egyptian mongoose family group size before and after lynx settlement, several evidences of intraguild killing, and also changes in mesocarnivore space use. Below we discuss these findings and their implications for the acceptability of Iberian lynx restoration.

During the early stages of lynx reintroduction, mesopredator abundances were drastically reduced at the scale of our study area, with a concomitant recovery of prey species of socio-economic (as small game) and ecological value (rabbits and partridges) in areas where lynx established. The core study area selected for our quasi-experimental design was representative of places with high rabbit density: dense Mediterranean scrub cover and interspersed crop fields. Its size was similar to that of many privately-owned hunting estates. The magnitude of carnivore density changes at the scale of this study area was quantified using an estimation of the density of both the apex predator (Iberian lynx) and 5 common mesocarnivore species, before the

reintroduction, and one and two years later, in the same core study area. For prey trends, we could only use abundance indices, not measured abundances, but these informed on trends at a larger spatial scale.

The lynx reintroduction was associated with a recovery of the main prey for lynx (rabbits), and of an alternative prey, the red-legged partridge. After a general decline in 2014–2015 (Fig. 4), prey population trajectories differed in 2015–2016 between areas without lynx, where they continued to decline, and areas with lynx, where prey abundance stabilized or increased (Fig. 4). In 2015, rabbit abundance decreased regardless of lynx presence when the new variant of rabbit haemorrhagic disease virus (RHDV) affected the study population (Delibes-Mateos et al., 2014). In 2016, however, rabbit populations recovered in areas occupied by lynx, but not in other areas. This recovery could be partially due to a net reduction in predation pressure on rabbits, which we estimated to average 55.6%, following the reduction of mesopredators associated with the lynx return (Palomares et al., 1995; Appendix C). The presence of lynx was the most likely explanation for the marked observed reduction of mesopredators, as predicted by previous empirical evidence described by Palomares et al. (1996). The rabbit population declines that occurred in 2015 (caused by the RHDV) were unlikely to explain the marked mesocarnivore decline that we reported, because rabbit declines were minimal in areas with lynx (Fig. 4). In 2016, the rabbit practically returned to 2014 levels in lynx areas, but

**Table 1**

Camera trapping effort and species-specific detection rates during the 3-year study period. The species are organized in two groups: those for which the camera trapping data allowed to calculate density estimates (Estimable) and those for which data were insufficient (Not estimable).

	Year	Camera trapping days	Captures/100 cam-days
<b>Estimable</b>			
Red fox	2014	2634	23.46
	2015	3048	14.80
	2016	3211	3.61
Stone marten	2014	1511	1.46
	2015	3048	0.30
	2016	3211	0.00
European badger	2014	2634	1.03
	2015	3048	1.90
	2016	3211	1.68
Egyptian mongoose	2014	2634	7.90
	2015	3048	5.64
	2016	3211	1.62
Feral cat	2014	2634	1.64
	2015	3048	0.26
	2016	3211	0.00
Iberian lynx	2014	2634	0.00
	2015	3048	2.32
	2016	5801	6.24
<b>Not estimable</b>			
Common weasel	2014	2634	0.00
	2015	3048	0.03
	2016	3211	0.06
European polecat	2014	2634	0.26
	2015	3048	0.00
	2016	3211	0.00
Eurasian otter	2014	2634	0.08
	2015	3048	0.16
	2016	3211	0.03
Common genet	2014	2634	0.04
	2015	3048	0.07
	2016	3211	0.06
Wildcat	2014	2634	0.04
	2015	3048	0.07
	2016	3211	0.00

mesopredators continued to decline. The reduction of partridge abundance in 2015 was possibly due to a spring drought (Casas et al., 2009; Borralho et al., 1998) and was also unlikely to explain the generalist mesocarnivore reductions we observed, given their feeding habits in areas with high rabbit availability (Appendix C) where partridge consumption should be low. The most likely explanation was an eviction or removal of mesocarnivores by the lynx, probably mediated via behavioural and demographic effects. We indeed had evidence that by 2016 fox and mongoose capture event reductions were much more pronounced inside than outside the lynx home ranges within our core study area (Fig. 3), that family groups were reduced, and that mesopredator killings by lynx occurred (Appendix E & F).

Around 60% of the world's largest carnivores are threatened with extinction (Ripple et al., 2016b), and most species have undergone dramatic range contractions, resulting in intact carnivore guilds only occupying an estimated 34% of the world's land area (Wolf and Ripple, 2017). Consequently, mesopredators have dramatically increased and the impacts of the mesopredator release are widely acknowledged (Prugh et al., 2009).

Although apex carnivores are experiencing declines in many developing countries, some populations are recovering in the Western world (e.g., Europe, USA; Chapron et al., 2014; Bruskotter et al., 2017). Both situations are associated with controversy and, in each scenario, one of the most contentious issues of debate relates to the ecological roles of these species (Kuijper et al., 2016; Allen et al., 2017). In the first case, the debate is mainly linked to the negative consequences for biodiversity and ecosystem functioning of declining apex predator populations, whereas in the second case, it is more related to the benefits

and social acceptability of recovering predator populations. Preliminary information suggests that, in the case of the Iberian lynx, there is an a priori favourable social context for reintroductions (Lafuente, 2008; Delibes-Mateos et al., 2018; see also Lopes-Fernandes et al., 2018). For example, a high level of support towards lynx reintroduction (> 90% and > 80%, respectively) has been reported from a sample of hunters and the general public in two areas of S Spain (Delibes-Mateos et al., 2018). Further investigations are however needed, focusing on different stakeholders and potential conflicts after reintroductions (e.g., Garrote et al., 2013).

The prey species trends we describe are relevant for the social acceptability of the lynx reintroduction. Many wildlife managing authorities and land owners have traditionally promoted the killing of terrestrial mesopredators as a fundamental game management strategy. In Spain, ca. 200,000 red foxes are being hunted annually (between 207,317 and 248,537 foxes/year during in 2014 and 2016, respectively; MAPA, 2018). In most Spanish hunting estates, red fox killing is widely implemented to favour small-game populations, with up to  $2.69 \pm 2.30$  foxes/km<sup>2</sup> killed yearly in intensive commercial hunting estates (Arroyo et al., 2012). However, the cost-effectiveness of this intervention is recurrently debated because its implementation is very expensive, time-consuming, increasingly ethically unacceptable and sometimes not effective or even counterproductive in achieving the expected goals (e.g. Côté and Sutherland, 1997; Lennox et al., 2018).

Although our findings should be replicated in other contexts, and over a longer period of time and at greater spatial scales to generalize the evidence, the reported early outcomes highlight key benefits of restoring apex predators from multiple perspectives, from species conservation to broad ecological and socio-economic benefits. Reintroductions of apex predators are complex processes, and different conservation conflicts can emerge at different stages of a reintroduction program. We acknowledge that although evidence for ecological impacts may have potential to influence attitudes towards Iberian lynx reintroductions, and may improve the acceptability of lynx reintroductions by landowners -which is key to guarantee a long-term sustainable future for this endangered felid- further research is needed to shed light on other potential factors influencing lynx acceptability (Young et al., 2010; Redpath et al., 2013; Lopes-Fernandes et al., 2018).

In this regard, our findings of mesopredator reductions and prey trends after lynx populations' recovery support the perception already stated by some managers of Spanish hunting estates who increasingly acknowledge in the media that the presence of lynx is indeed beneficial for small game (Redacción JyS, 2019). Accordingly, in the Mediterranean Iberian Peninsula, a more sustainable management of predation should consider the short term as well as longer term impacts of the recovery of apex predators, such as Iberian lynx, on mesopredators. The benefits of restoring apex predators may not be exclusive to the Iberian context, since human dimensions are paramount within the apex predator recovery puzzle (Treves and Bruskotter, 2014). For example, in the USA a tiny portion (< 5%) of the land of the Midwest is publicly held (Natural Resources Council of Maine, 2018). Therefore, the acceptability of apex predators by landowners there is fundamental for their future, such as in the case of the Florida Panther *Puma concolor*, persisting mainly on private lands (Maehr et al., 2002).

Since the first reintroduction program of a large carnivore (brown bear *Ursus arctos*) motivated by conservation goals in 1937 (Samojlik et al., 2018), different reintroductions have been implemented across the world involving an important number of carnivore species, driven by different motivations, from ethical and moral responsibilities to utilitarian uses (Hayward et al., 2007; Levine et al., 2017). Conservation actions such as reintroductions or translocations are not exempt from controversy (e.g., Baker et al., 2019; Pérez et al., 2012), particularly in the case of apex carnivores (Hayward and Somers, 2009). However, our study illustrates potential multiple benefits of these actions under certain circumstances, with positive impacts not only on the conservation status of a threatened species, but also on the successful

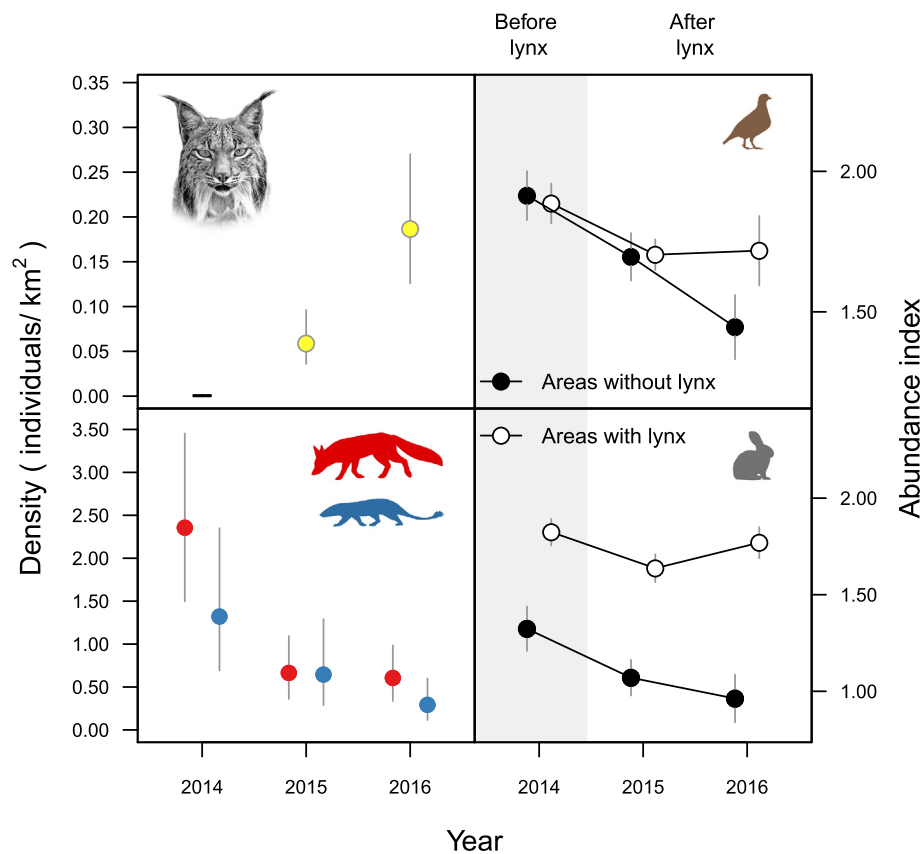


Fig. 4. Density of Iberian lynx (apex predator), red fox (red) and Egyptian mongoose (blue) (meso-carnivores), and prey abundance estimates before lynx reintroduction (2014, grey shadow), one year (2015) and two years (2016) later. For carnivores, error bars represent Bayesian Credible Intervals. For prey species, mean (Standard Error) abundance indices are shown for areas with and without lynx (log-transformed counts of individuals/km for partridges and latrines/km for rabbits). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

restoration of their ecological functions.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108234>.

**Declaration of competing interest**

The authors whose names are listed immediately below certify that they have NO affiliations with or involvement in any organization or entity with any financial interest, or non-financial interest in the subject matter or materials discussed in this manuscript.

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**Table 2**

Summary statistics of the negative binomial GLMMs carried out to test for the effect of lynx presence/absence on temporal variations in rabbit and red-legged partridge abundance.

Parameters	European rabbit			Red-legged partridge		
	Estimate ± SE	z-	p	Estimate ± SE	z-	p
Intercept	3.13 ± 0.32	9.65	***	4.41 ± 0.19	22.58	***
Year = 2015	-0.74 ± 0.18	-4.18	***	-0.50 ± 0.14	-3.47	***
Year = 2016	-0.72 ± 0.19	-3.90	***	-1.07 ± 0.15	-7.31	***
Lynx = Present	1.11 ± 0.47	2.36	*	-0.06 ± 0.26	-0.22	n.s.
Year = 2015 × Lynx = Present	0.30 ± 0.26	1.14	n.s.	0.09 ± 0.19	0.44	n.s.
Year = 2016 × Lynx = Present	0.61 ± 0.27	2.28	*	0.72 ± 0.20	3.68	***

\*\*\*p < 0.001; \*\*: p < 0.01; \*: p < 0.05; n.s.: p > 0.05.



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