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ORIGINAL ARTICLE

Wildcat population density in NE Portugal: A regional stronghold for a nationally threatened felid

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Abstract

Population density data on depleted and endangered wildlife species is an essential tool to assure their effective management and, ultimately, conservation. The European wildcat is an elusive and threatened species inhabiting the Iberian Peninsula, with fragmented populations and living in low densities. We fitted spatial capture-recapture (SCR) models on camera-trap data, to provide the first estimate of wildcat density for Portugal and assess the most influential drivers determining it. The study was implemented in Montesinho Natural Park (NE Portugal), where we identified 9 individuals, over a total effort of 3477 trap-nights. The mean density estimate was 0.032 ± 0.012 wildcat/Km², and density tended to increase with distance to humanized areas, often linked to lower human disturbance and domestic cat presence, with forest and herbaceous vegetation cover, and with European rabbit abundance. Although, this density estimate is within the range of values estimated for protected areas elsewhere in the Iberian Peninsula, our estimates are low at the European level. When put in context, our results highlight that European wildcats may be living in low population densities across the Iberian Mediterranean biogeographic region. No phenotypic domestic or hybrid cats were detected, suggesting potentially low admixture rates between the

two species, although genetic techniques should be performed to corroborate this assertion. We provide evidence that Montesinho Natural Park may be a suitable area to host a healthy wildcat population, and thus be an important protected area in this species' conservation context.

KEYWORDS

conservation, european wildcat, population density, portugal, spatial capture-recapture model

1 | INTRODUCTION

A keystone requirement to efficiently manage and conserve wildlife species is to have robust abundance and/or density estimates available (Stephens, Pettoirelli, Barlow, Whittingham & Cadotte, 2015), which are keystone metrics to assess demographic variations (Wright & Hubbell, 1983) and extinction risk (Purvis, Gittleman, Cowlishaw & Mace, 2000). The International Union for Conservation of Nature (IUCN) criteria for defining a species' threat status are intrinsically linked to its population size (IUCN, 2012), highlighting the importance of these metrics to guide conservation. While these parameters are particularly difficult to obtain for threatened or rare species (Foster & Harmsen, 2012; Royle, Chandler, Sollmann & Gardner, 2014), they remain essential to conservation policies. Incorrect estimates may lead to inaccurate assessment of population status and, consequently, to inefficient conservation actions (López-Bao et al., 2018; Popescu, Artelle, Pop, Manolache & Rozyłowicz, 2016) with potentially severe impacts for rare species due to the low number of individuals in the wild.

The European wildcat (*Felis silvestris silvestris*, Schreber, 1777) is a good example of a species for which density estimates are often unavailable. It natively occurs from the Iberian Peninsula to Eastern Europe, and British Isles (Yamaguchi, Kitchener, Driscoll & Nussberger, 2015), but the current distribution is fragmented across much of its range as a result of significant declines (Yamaguchi et al., 2015) due to habitat loss, roadkills, disease transmission, and hybridization with its domestic counterpart (Beaumont et al., 2001, Macdonald et al., 2010; Yamaguchi et al., 2015). It is listed as 'Least Concern' by the IUCN, but its status varies across many of its range countries, being considered threatened in Portugal, Spain, Germany or Switzerland (Cabral et al., 2005; Nussberger, Currat, Quilodran, Ponta & Keller, 2018; Palomo, Gisbert & Blanco, 2007;). This legal protection has contributed to reducing and locally inverting some of the above-mentioned threats (Streif, Kraft, Veith, Kohnen & Suchant, 2012), leading to the recent recovery of a few wildcat populations across Europe (Nussberger et al., 2018; Steyer et al., 2016). This apparent turnover in European wildcats' population trends has led to the identification of locally-dense populations in some European regions, where densities have been estimated to be as high as 0.29 and 0.26

ind/Km² in Switzerland (Kéry, Gardner, Stoeckle, Weber & Royle, 2011; Maronde, McClintock, Breitenmoser & Zimmermann, 2020) or 0.28 – 1.36 ind/Km² in Sicily (Anile, Amico & Ragni, 2012; Anile, Ragni, Randi, Mattucci & Rovero, 2014). However, this trend appears not to be occurring across much of the Iberian Peninsula where wildcat populations are suspected to continue declining (Cabral et al., 2005; Gil-Sánchez et al., 2020; Sobrino, Acevedo, Escudero, Marco & Gortázar, 2009). The loss of its main prey in the Mediterranean region-the European rabbit, *Oryctolagus cuniculus* (Gil-Sánchez, Valenzuela & Sanchez, 1999)-adds to the common threats affecting European wildcats across its range as a major player in the decline of the Iberian metapopulation of this small felid (Gil-Sánchez et al., 2020; Lozano, Virgós, Malo, Huertas & Casanovas, 2003). The low densities observed across the Mediterranean region of Iberia (0.038 – 0.069 wildcat/Km²; Ferreras et al., submitted; Gil-Sánchez et al., 2020) further support that European wildcats might be under serious threat. In Portugal, the European wildcat is listed as ‘Vulnerable’ due to a suspected population decline $\geq 30\%$ over 24 years (Cabral et al., 2005). The identified threats continue acting in Iberia and highlight the instrumental role protected areas (PAs) in safeguarding this peripheral European wildcat metapopulation (Matias, 2020). However, the profound information gap that persists regarding the status, density and trends of the remnant Iberian wildcat populations, namely within PAs, preclude the implementation of efficient conservation actions, and potentially invert the ongoing silent extinction.

Remotely triggered cameras (henceforth camera-traps) have emerged as successful tool to overcome the limitations in the study of mammalian carnivore density, and are currently of widespread use (Rich et al., 2017; Sollmann et al., 2011). Camera-traps are a noninvasive method (Long, MacKay, Ray & Zielinski, 2012), allowing survey designs encompassing large areas, hence make the study of carnivore species feasible (Noss et al., 2012). Alongside the widespread use of camera trap-based surveys, new analytical tools have emerged to cope with the large amounts of data produced by these methods, particularly under the framework of hierarchical models (Kéry & Royle, 2015; Royle et al., 2014), such as Spatial Capture-Recapture models (SCR) that estimate densities while accounting for detectability variations (Royle, Chandler, Gazenski & Graves, 2013). European wildcat habitat preferences are known to differ between the two Iberian bioclimatic regions (Temperate and Mediterranean): it is more likely found close to forests (Klar et al., 2008) in the Temperate bioclimatic region, while preferring scrublands and scrub-pasturelands mosaics in the Mediterranean region (Lozano et al., 2003; Oliveira et al, 2018). However, human disturbance is negatively related to wildcat presence in both bioclimatic regions (Klar et al., 2008; Oliveira et al., 2018). Our study area is a transitional area between both bioclimatic regions exhibiting mixed characteristics. Therefore, it emerges as a privileged setting to comprehend what occurs in these gradients.

Although several studies have recently shed light into some important aspects of European wildcat's ecology in the Iberian metapopulation (Monterroso, Brito, Ferreras & Alves, 2009; Oliveira et al., 2018; Oliveira et al., 2018; Sarmiento, 1996; Sarmiento, Cruz, Tarroso & Fonseca, 2006), robust assessments of its abundance, density range and trends are still missing. This study aims to contribute to bridge this information gap by estimating European wildcat population density, as well characterizing the drivers of spatial variation density in a transitional Iberian protected area. We formulated two hypotheses based on our previous knowledge about European wildcat ecology and about our study area: i) European wildcat density at Montesinho Natural Park (MNP) is within the range estimated for other Iberian protected areas, and ii) European wildcat density will be negatively associated with anthropic activities but positively associated with native forests (Klar et al., 2008; Monterroso et al., 2009; Oliveira et al., 2018) and prey availability (Lozano et al., 2003).

2 | MATERIAL AND METHODS

2.1 | Study area

We carried out the study in MNP (NE Portugal), which extends over an area of *ca.*748 Km² (Figure 1). It is also classified as European Union Natura 2000 Site (Montesinho-Nogueira; PTCON0002) and is mostly dominated by Northwest Iberian montane forests (Dinerstein et al., 2017) in a natural wooded landscape within a mountainous landscape, ranging from 438 to 1481 m a.s.l. The annual average temperature ranges between 3°C and 21°C, and the precipitation between 600 and 1500mm (Castro et al., 2010). MNP is covered by highly diverse forests that include several arboreal species such as holm oaks (*Quercus rotundifolia*), Pyrenean oaks (*Q. pyrenaica*), sweet chestnuts (*Castanea sativa*) and different Pine species (*Pinus silvestris*, *P. nigra* and *P. pinaster*). The understory layer is dominated by gorse (*Ulex europaeus* and *U. minor*), gum rockrose (*Cistus ladanifer*) and heather (*Erica* spp.). The park is crossed by two main rivers, Sabor and Onor and several streams accompanied by riparian vegetation, mainly composed by ash (*Fraxinus angustifolia*), white willow (*Salix salviifolia*), common alder (*Alnus glutinosa*) and black poplar (*Populus nigra*; Castro et al., 2010). There are multiple small villages (i.e., < 8000 people) scattered through the landscape (Valente et al., 2014). This region contains a highly diverse carnivore community, including nationally threatened species, such as the Iberian wolf (*Canis lupus signatus*) and European wildcat (*Felis silvestris silvestris*) (Cabral et al., 2005).

2.2 | Data collection

We conduct the fieldwork between October 2019 and March 2020. We deployed 34 camera-traps equipped with heat and motion PIR sensor. Three camera models were used: Cuddeback Model H-1453 (n = 14, Cuddeback Digital, De Pere, WI, USA), Moultrie M-990i (n = 14, Moultrie Products, Alabaster, AL, USA; used to substitute the Cuddeback model due to logistic constraints) and Browning Strike Force HD Pro model BTC-5HDP (n = 20, Prometheus Group, Birmingham, AL, USA), which were placed at an inter-camera distance of 1590 ± 650 m (range: 1001 – 4344 m). Cameras were attached to wooden sticks or tree trunks, at 40–80 cm above ground level to achieve the best angle for capturing wildcat's pelage characteristics. We set cameras to take three consecutive photos per trigger, with a delay of 10 seconds between triggering events, recording the date and time of each photograph. All stations were lured with valerian extract and domestic cat urine, deployed on a wood stick 2m from the camera. These lures are known to be effective attractants for wildcats (Monterroso, Alves & Ferreras, 2011; Steyer, Simon, Kraus, Haase & Nowak, 2013). We checked the cameras every 15-20 days, to replace SD cards, lures, exchange batteries and for troubleshooting. Putative European wildcat records were classified based on pelage characteristics as defined by Kitchener, Yamaguchi, Ward, and Macdonald (2005) and Ragni and Possenti (1996), which have revealed highly diagnostic in other Iberian wildcat populations (Ballesteros-Duperón, Virgós, Moleón, Barea-Azcón & Gil-Sánchez, 2015; Supporting Information Figure S1). European wildcat records deprived of identification (i.e., not possible to identify the individual) were excluded from the statistical analysis. Because we used unpaired cameras, two datasets were generated-left and right flank – with their respective individual detection histories. A detection record was considered as independent event if a record of the same species in the same camera had a minimum time interval greater than 30 minutes (unless animals were undoubtedly individually distinguishable; Rich et al., 2017).

2.3 | State covariates

We selected four candidate covariates for explaining the density variations in the study area, linked to three drivers: land cover, disturbance and prey availability (Table 1). Land cover and disturbance data were obtained from the Copernicus Global Land Cover raster with 100 m resolution (GLC; Buchhorn et al., 2020). We hypothesized that forest and herbaceous vegetation, e.g., meadows and pastures, were the most relevant habitat features for wildcats in Mediterranean (Lozano et al., 2003, Monterroso et al., 2009, Oliveira et al., 2018) and Temperate regions of Iberia (Klar et al., 2008; Wittmer, 2001). Forest patches provide sheltering, resting and breeding conditions (Jerosch, Götz, Klar & Roth, 2010), whereas herbaceous vegetation tend to host higher rodent abundance (Osbourne, Anderson & Spurgeon, 2005) and are privileged hunting grounds for wildcat (Klar et al., 2008). Forest landcover units were identified as the sum of all forest types defined in the GLC. All landcover covariates were calculated as the total area

encompassed by circular 1 km buffer around each camera station (see data analysis). Site-level prey availability was estimated as local European rabbit abundance derived from camera trapping records and calculated for each station using the Royle-Nichols parametrization for occupancy models (Royle & Nichols, 2003, see description below). Small mammal availability was not estimated because such data was not available. We selected one covariate (distance to the nearest human-buildup area) as a surrogate of human-induced disturbance (Ferreira, Leitão, Santos-Reis & Revilla, 2011; Germain, Benhamou & Poulle, 2008). This covariate was calculated as the Euclidean distance between each camera location and the nearest feature edge. We included camera placement on or off animal/human trail as a binary covariate to account for this effect on baseline detection probability, one of the SCR model components (see Statistical analysis).

All spatial analysis were implemented using the R Studio©, version 1.1.463, on R, version 3.5.3 (R Development Core Team, 2017), software.

2.4 | Data analysis

In a first step, we calculated nonparametric Spearman's correlation (ρ) to test for multicollinearity among continuous covariates, using the psych R package (Revelle, 2015). When a high correlation between two covariates was detected ($|\rho| \geq 0.7$; Zuur, Ieno, Walker, Saveliev & Smith, 2009), the pair was not included simultaneously in the same model on the subsequent modeling procedure. All retained continuous predictors were scaled to 'z-scores' to avoid dispersion bias, to facilitate numeric convergence, and to allow direct coefficient comparisons among models (MacKenzie et al., 2017; Shiffler, 1988). European rabbit abundance in each station, was determined by fitting the abundance-induced detection heterogeneity occupancy under the Royle-Nichols parameterization (Royle & Nichols, 2003) using a maximum likelihood framework, assuming constant detection probability and abundance. These models were fitted with the "unmarked" package for R software (Fiske & Chandler, 2015).

We then fitted SCR models to estimate wildcat density and detection probability using the "oSCR" package for R software (Sutherland, Royle & Linden, 2019). Conceptually, SCR assumes that each individual from a population has an activity center i during the survey distributed in the landscape as a realization of a spatial point process (Royle et al., 2013) and following a homogenous distribution $i \sim \text{Uniform}(S)$, where S is the 'state-space' (Royle & Young, 2008). Hence, the SCR model assumes that a total of N individuals has their activity center within the state-space S , encompassing all camera-traps and neighboring area such that all individuals have a reasonable probability of being detected during the survey (Royle et al., 2013). Within the SCR framework, the baseline detection probability (p_0) is assumed to decay as a function of the Euclidean distance between individual's activity center i and the camera trap

location j at a rate related to wildcats' movement (σ) within S , such that the probability of detecting an individual decreases with increasing distance between its activity center and camera-trap position (Efford, Borchers & Byrom, 2009; Royle et al., 2014). Consequently, the density estimate \hat{D} can be calculated as $\hat{D} = \hat{N}/S$. These models account for the spatial components related to trap location and animal movement, representing an upgrade from traditional capture-recapture models (Royle, Sutherland, Fuller & Sun, 2015).

The extent of the state-space was defined by creating a buffer of 1.5 times the mean maximum distance moved by detected individuals around camera-trap locations (Royle et al., 2013). The state-space resolution was calculated following Sutherland et al., (2019), where grid cells are suggested to be half of target species' movement parameter ($\sigma = 2860$ m), resulting in a resolution of ca. 1.4 km. We defined the 1km grid since is approximately the minimum known wildcat home-range in Iberia (1.22 km²; Oliveira et al., 2018). Both parameters (density and detection probability) were estimated over 157 occasions, representing the total number of days that camera-traps were deployed and operational at MNP. Both capture histories (left and right side) were combined into one dataset, and models were fitted as independent sessions in oSCR but constrained to provide the same state and detection parameters.

We created a set of candidate models including all covariate combinations and a null model. We included the camera placement as a detection covariate in the null model because its effect has already been sufficiently demonstrated in the literature (Bruggeman, Garrot, White, Watson & Wallen, 2007; Rafiq et al., 2020; Sunquist & Sunquist 2017). To avoid model overparameterization, we use the criterium of a maximum 1:10 ratio between the number of estimated parameters (covariates coefficients) and sample size ($n = 34$), and thus, we used a maximum of two state and one detection covariates (Burnham & Anderson, 2002).

Model parameters were estimated using a maximum likelihood estimation (MLE) approach. Model selection was based on Akaike's Information Criterion for small samples size (AICc) and on Akaike model weights (ω_i) (Burnham & Anderson, 2002). Models with a $\Delta AICc < 7$ were considered as having substantial support for being the best models (Burnham & Anderson 2002). Whenever more than one model comprised a $\Delta AICc < 7$, the model-averaged coefficients were calculated to obtain the best estimates of covariate effects from the candidate model set. The covariates estimate from the model-averaged were determined using the conditional averaged procedure (Burnham & Anderson, 2002). As an additional measure of each covariate's effect on wildcat's density and detection probability, the relative variable importance (RVI) was calculated as the sum of Akaike weights (ω_i) among all models that included that covariate over the total ω_i of the considered model set (Arnold, 2010). RVI is scaled

between 0 and 1, with values near 1 indicating a high support for a covariate to be highly influential to response variable variability, while RVI near 0 indicates little support (Burnham & Anderson, 2002). All statistical analysis were implemented using R Studio© version 1.1.463 on R version 3.5.3 (R Development Core Team, 2017).

3 | RESULTS

We registered 24 independent European wildcat records, obtained in nine stations over a total sampling effort of 3477 trap-nights. These detection records allowed us to identify a minimum of nine individuals, five from the left side and 9 from the right. The individuals identified by the left flank had an average number of encounters of 2.2 and an average number of spatial locations of 1.6, with a mean maximum distance moved of 3012.55 m. The wildcat's identified by the right side presented an average number of encounters of 1.78, an average spatial number of 1.22, and a mean maximum distance moved of 2633.17 m.

A total of 2457 independent detections from other wildlife were also obtained. The red fox (*Vulpes vulpes*, $n = 767$), European roe deer (*Capreolus capreolus*, $n = 614$), and red deer (*Cervus elaphus*, $n = 593$) were the species with a highest number of independent records (Supporting Information Table S1). The mean maximum distance moved (mmdm) by the European wildcat in our study area was 1430.4 m. Thus, we used a 4.3 km buffer to create the state-space (Sutherland et al., 2019), resulting in an effectively sampled area of *ca.* 423 Km² (Supporting Information Figure S2). The analysis of collinearity did not reveal any significant correlation among potential covariates.

We generated 10 models (Table 2), containing all combinations of the four considered state covariates and camera-trap placement for detection probability (p_0). All candidate models were comprised within a $\Delta AICc < 7$, and therefore were all considered in the subsequent model-averaging procedure (for further detail see Supporting Information Table S2). The best model comprised the covariates prey availability (rabbit abundance) and camera placement, for density and detection probability, respectively, with $\omega = 0.20$ (Table 2). Although with relatively low precision, all state covariates from the model-averaged, appear to have a positive effect (Figure 2), with a relative variable importance (RVI) of 0.43 for prey availability, 0.30 for distance to human patches, and 0.34 for forest and herbaceous vegetation cover (Table 3). Camera placement on trails also had a positive effect on wildcat detection probability. The mean European wildcat's density estimate (D) obtained from the model-averaged was 0.032 ± 0.012 ind/Km² [IC95: 0.016 – 0.067], resulting in an estimate of 14 ± 5 [IC95: 7 – 29] wildcats for our effectively sampled area. The baseline daily detection probability from the model averaged was $p_0 =$

0.002 \pm 0.001 and $p_{trail} = 0.003 \pm 0.001$, for camera-traps placed off and on trail, respectively (Figure 2). The spatial scale parameter was estimated to be $\hat{\sigma} = 2878.9 \pm 474.9$ [IC95: 2083.6 – 3978.0].

A comparison of our density estimate with other wildcat populations elsewhere in Iberia (n=3) and across Europe (n=22) revealed that MNP exhibits wildcat density within the range of values of Mediterranean Iberia (< 0.1 ind/Km²). However, it is at the lower end of the density estimates found across Europe, namely in the Temperate bioclimatic region (Figure 3).

4 | DISCUSSION

Density and abundance are key parameters needed for effective species conservation, especially when aiming to identify high priority conservation areas (Veloz et al., 2015). The lack of such information for elusive and threatened species, such as European wildcat, can be critical since the assessment of conservation status strongly relies on population trend, which is only assessable through continued monitoring of abundance or, ideally, density. We provide the first density estimates of a European wildcat population in Portugal. The relevance of this study is further exacerbated by focusing in one of the most threatened wildcat metapopulations-the Iberian metapopulation (Matias, 2020)-and in a region (NW Iberia), where research on this small felid is severely lacking. This study also illustrates the feasibility of using camera-trap data to estimate the density of an elusive and low-abundance species, and therefore, be a pivotal tool to generate baseline information to delineate management and conservation strategies.

European rabbit has been suggested as a key driver of wildcat's population density in other Portuguese populations (Monterroso et al., 2009). Although European rabbit abundance was lower in our study area than observed in typical Mediterranean Iberian ecosystems (Delibes-Mateos, Ferreras & Villafuerte, 2008), it still had a positive effect on wildcat density and suggests that rabbits may still act as a cornerstone feeding resource for wildcats even in Mediterranean-temperate transitional regions. The positive effect of herbaceous vegetation supports that European wildcats use agricultural patches, pastures and meadows as preferred hunting grounds for small mammals, in Temperate regions (Klar et al., 2008; Rodríguez et al., 2020), and for European rabbits, in Mediterranean regions (Lozano et al., 2003). We found forest cover to have a positive effect on wildcat's density. Native forests are important landscape components for wildcats by providing prey, refuge and shelter (Germain et al., 2008; Jerosch et al., 2010; Jerosch, Kramer-Schadt, Götz & Roth, 2018; Klar et al., 2008; Lozano, 2010; Sarmiento et al., 2006) and emerge as near-compulsory landscape features for wildcats to establish home-ranges (Klar et al., 2008; Oliveira et al., 2018). However, these results need to be interpreted with caution, due to high variability in the covariate effect, caused by the low wildcat recapture rate during the survey. We found distance to

human-buildup areas to have a positive effect on wildcat's density, also corroborating our initial hypothesis. Anthropogenic areas act as a source of disturbance and of domestic animals (Germain et al., 2008, Klar et al., 2008) and have been shown to be avoided by European wildcats throughout Europe (Germain et al., 2008; Klar et al., 2008, Klar, Hermann & Kramer-Schadt, 2009; Oliveira et al., 2018). Also, we detected several domestic dogs and cats surrounding villages during our survey, which can add a significant disturbance effect constraining wildcat presence (Klar et al., 2008).

Finally, our results evidenced higher detection probability when cameras were deployed on animal/human trails. Camera-trap deployment on trails have been shown to increase detectability of several felids (e.g., Fonteyn et al., 2020; Harmsen, Foster, Silver, Ostro & Doncaster, 2010; Kolowski & Forrester, 2017), likely because these are preferred sites for social communication (Rafiq et al., 2020; Sunquist & Sunquist 2017) and for energy-efficient travelling (Bruggeman et al., 2007). Our study demonstrates this pattern also applies for European wildcats. Although a purely trail-based targeted design may not be appropriate for estimating occupancy or richness, it is suited for designs targeting SCR density estimation through optimizing effort and leading unbiased results (Burton et al., 2015),

Paired camera deployment is recommended in photographic SCR designs to allow recording both flanks, because individual's marks are usually bilaterally asymmetric (McClintock, Conn, Alonso & Crooks, 2013). This was not possible in our study due to logistics constraints. Nevertheless, our unpaired camera design still allowed to reliably estimate European wildcat's density through combining the left and right flank datasets to provide a single density estimate (Maronde et al., 2020).

One potential caveat regards to the ability to unambiguously distinguish individuals as wildcat, domestic or hybrid from external characteristics alone (Daniels et al., 2001). During our survey, no phenotypic domestic cats were detected, and all cat photos exhibited the main phenotypic characteristics of European wildcats (Kitchener et al., 2005). Although we are confident on our results, we acknowledge that the use of genetic profiling techniques can provide a complementary means to overcome this obstacle (Anile et al., 2014).

Our estimate of 0.032 ± 0.012 ind/Km² is low, although within the range of values estimated elsewhere in the Mediterranean Iberia (Ferrerias et al., submitted; Gil-Sánchez et al., 2020). However, is well below the estimates for the temperate region of the Iberian Peninsula (Sayol, Vilella, Bagaria & Puig, 2018) and for other metapopulations of Europe. Nevertheless, inter-study comparisons need to be done cautiously, because analytical methods and data used can lead estimates to vary. These discrepancies may be further exacerbated by the misidentification of 'pure' wildcat and hybrids (e.g., Kilshaw et al., 2015). For example, in Spain, Ferrerias et al. (submitted) captured five individuals with 'pure' characteristics, one of

which was genetically identified as an F1 hybrid. Such bias could pose a serious threat since density might be overestimated.

Taken together, these results suggest that the Mediterranean Iberian metapopulation is characterized by low density populations with a fragmented distribution (Gil-Sánchez et al., 2020). Together with a relatively high admixture rate found throughout contemporary European wildcat populations in Iberia (Matias, 2020; Oliveira et al., 2008) these data are suggesting that this metapopulation may be undergoing a silent extinction and should be target of a detailed status assessment.

Human-related mortality is a major cause of wildcat mortality throughout its entire distribution range, with roadkills and poaching representing 62% and 15% of the total annual mortality, respectively (Bastianelli et al., submitted). However, the region has relatively strict wildlife protection and low human population density (Valente et al., 2014). Therefore, direct human persecution and road mortality should not be an important driver of this felid's low density.

Reduced prey availability may be concurring to the low wildcat density in MNP. The reduced abundance of its staple prey in the Mediterranean Iberian – the European rabbit – and the relatively lower rodent density and diversity found in this bioclimatic region relative to the temperate regions of Europe (Kryštufek & Griffiths, 2002) may be key players in suppressing wildcat's density locally.

Therefore, despite being a protected area, the low European wildcat density and population size in MNP suggests that this peripheral/edge population (Iberia) may be fragile and potentially threatened.

The main limitations of our study regard to the use of unpaired cameras, the reduced number of wildcat records and the fact that European wildcat's identification is not supported by genetic analyses. The former two limitations lead to low detection probabilities, potentially compromising model convergence. However, this was mitigated by integrating the two datasets (left and right flank) in a shared modeling approach which provided sound abundance estimates. Although genetic techniques could allow confirming the genetic integrity of wildcats, it would still be challenging to assign specific samples to each camera trapping record. Therefore, although useful, genetic monitoring techniques would need to be implemented independently of the camera trapping sampling.

The current data available about European wildcat's density at its southwestern range (Ferrerias et al., submitted; Gil-Sánchez et al., 2020), depicts a concerning scenario. Therefore, it is urgent to assess and quantify the causes of this threatened felid's possible decline. The development of improved sampling protocols and establishment of long-term monitoring surveys targeting wildcat's density throughout the Iberian metapopulation range could be a valuable tool to quantify the species trend, allow early detection of population fluctuations and the implementation of adaptative management approaches to adjust conservation guidelines and protected areas' management plans to actions outputs.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

P.M. and G.M. conceived the ideas; G.M., J.L.R. and P.M. collected the data; P.M. and G.M. analyzed the data; P.M., G.M., J.L.R. and L.M.R. discussed the results and contributed to the writing of the manuscript.

AVAILABILITY OF DATA

The datasets generated during the current study are available from the corresponding author on reasonable request.

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643 SUPPORTING INFORMATION

644 **FIGURE S1** - Example of individual identification using the coat pattern of the right leg, and body (e.g.,
 645 shape, position and number of spots), at Montesinho Natural Park.

646 **FIGURE S2** - Visualization of the prescribed state space. Blue circle are the locations of the detectors
 647 (camera-trap) and grey points are the pixel centroids (hypothetically individual's activity center). The
 648 state space resolution is 1 km, and the buffer is 4.3 km.

649 **TABLE S1** - Number of independent events for all species detected and proportion of occupied stations,
 650 at Montesinho Natural Park (ranked by the number of events).

651 **TABLE 1** Candidate covariates used in the modelling procedure to assess wildcat's density (D) and detection probability (p0), with the
652 corresponding acronym, units and observed range, hypothesis reasoning, description, source, and references supporting the presented reasoning.

Spatial capture-recapture model components	Covariate	Range and Units	Hypothesis	Description	Source	References
Density (D)	Proportion of Forest Patches (For)	[0.05-0.97] %	European wildcat density increases in areas with high forest patches cover. This habitat is expected to be suitable for wildcat's population, since it as a higher prey and refuge availability, contributing to a higher wildcat density.	Proportion of forest patches in 1 km buffer around each station	Global Land Cover https://lcviewer.vito.be/	Klar et al., 2008 Monterroso et al., 2009 Oliveira et al., 2018
	Proportion of Herbaceous Patches (Herb)	[0.01-0.75] %	European wildcat density increases in areas with high herbaceous patches cover. This habitat is a <i>proxy</i> of small mammal availability, thus is expected to contribute for wildcat density due to higher food resource.	Proportion of herbaceous patches in 1 km buffer around each station	Global Land Cover https://lcviewer.vito.be/	Klar et al., 2008 Osbourne et al., 2005
	Local Rabbit abundance (Rabbit)	[0.0-2.0]	European wildcat density increases in areas with high rabbit availability. Higher prey availability is expected to contribute for wildcat density due to higher food resource.	Local rabbit abundance determined for each station	Field-collected	Lozano et al., 2003
	Distance to Human Influenced Patches (D_urb)	[0.17-8.53] Km	European wildcat density decreases near humanized regions. These regions are avoided by wildcats due to human disturbance and possible competition with domestic cat.	Euclidean distance from nearest urban area	Global Land Cover https://lcviewer.vito.be/	Klar et al., 2008
Detection (p0)	Trail (trail)	0/1	Detection probability increases when detectors are located in or at edge of trails. Trails can be used as energy efficient travel routes and may increase scent mark encounter rate, facilitating individual communication.	On/off trail	Detector position	Kolowski & Forrester 2017 Rafiq et al., 2020 Bruggeman et al., 2007

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TABLE 2 Models explaining wildcats' density (D) and detection probability (p_0) variation, which included the covariates distance to forests (For), distance to herbaceous patches (Herb), local rabbit abundance (Rabbit), distance to human buildup (D_urban), and detector position (trail).

Model	LogL	K	AICc	Δ AICc	ω_i	Cum ω_i
D(~Rabbit) p(~trail) sig(~1)	204.74	5	419.47	0	0.20	0.20
D(~For + Herb) p(~trail) sig(~1)	203.89	6	419.78	0.3	0.17	0.36
D(~D_urban + Rabbit) p(~trail) sig(~1)	203.96	6	419.92	0.45	0.16	0.52
D(~Herb) p(~trail) sig(~1)	205.18	5	420.37	0.90	0.13	0.65
D(~For + Rabbit) p(~trail) sig(~1)	204.68	6	421.35	1.88	0.08	0.72
D(~1) p(~trail) sig(~1)	206.73	4	421.47	1.99	0.07	0.79
D(~D_urban) p(~trail) sig(~1)	205.81	5	421.61	2.14	0.07	0.86
D(~For) p(~trail) sig(~1)	205.90	5	421.81	2.33	0.06	0.92
D(~D_urban + Herb) p(~trail) sig(~1)	205.14	6	422.28	2.80	0.05	0.97
D(~D_urban + For) p(~trail) sig(~1)	205.62	6	423.23	3.76	0.03	1

Abbreviations: LogL, log-likelihood; K, degrees of freedom; AICc, Akaike's information criterion; Δ AICc, variation between the AICc from each model and the lower AICc value; ω_i , Akaike weight; Cum ω_i , cumulative Akaike weight.

TABLE 3 Coefficient estimates, on the logarithmic scale, included in the model-averaged process to explain the wildcat's density and detection probability, in the natural scale, standard error (SE) and relative importance (RVI) (variables acronyms are described in Table 1).

Sub-model	Parameter	$\hat{\beta} \pm SE$	RVI
Detection	\hat{p}_0	0.002 ± 0.001	1.000
	trail	0.920 ± 0.460	1.000
	$\hat{\sigma}$	2.879 ± 0.475	1.000
Density	\hat{D}_0	0.012 ± 0.018	1.000
	Rabbit	3.050 ± 1.000	0.430
	D_urban	0.360 ± 0.360	0.300
	For	1.880 ± 3.600	0.340
	Herb	2.300 ± 3.080	0.340

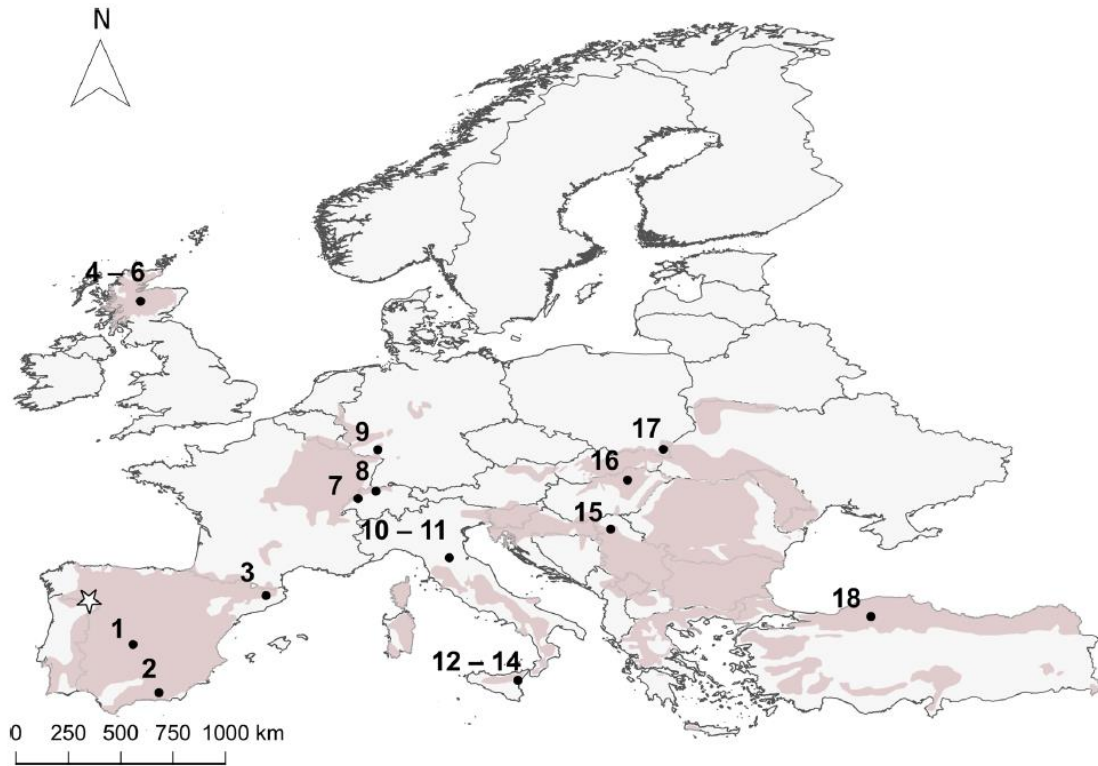


FIGURE 1 Location of the study area at Montesinho Natural Park (white star). European wildcat distribution is highlighted in gray, adapted from IUCN Red List of Threatened Species, version 2013.2 (<http://www.iucnredlist.org>). Representation of the European wildcat's density studies (black dots) across its range. Studies number: 1-Ferreras et al., submitted; 2-Gil-Sánchez et al., 2020; 3-Sayol et al., 2018; 4-6-Corbett, 1979; Scott et al., 1993; Kilshaw et al., 2015; 7-8-Weber et al., 2008; Kéry et al., 2011; 9-Heller, 1992; 10-11-Ragni, 2006; Velli et al., 2015; 12-14-Anile et al., 2010, 2012, 2014; 15-Dimitrijevic, 1980; 16-Heltai et al., 2006; 17-Okarma et al., 2002; 18-Can et al., 2011.

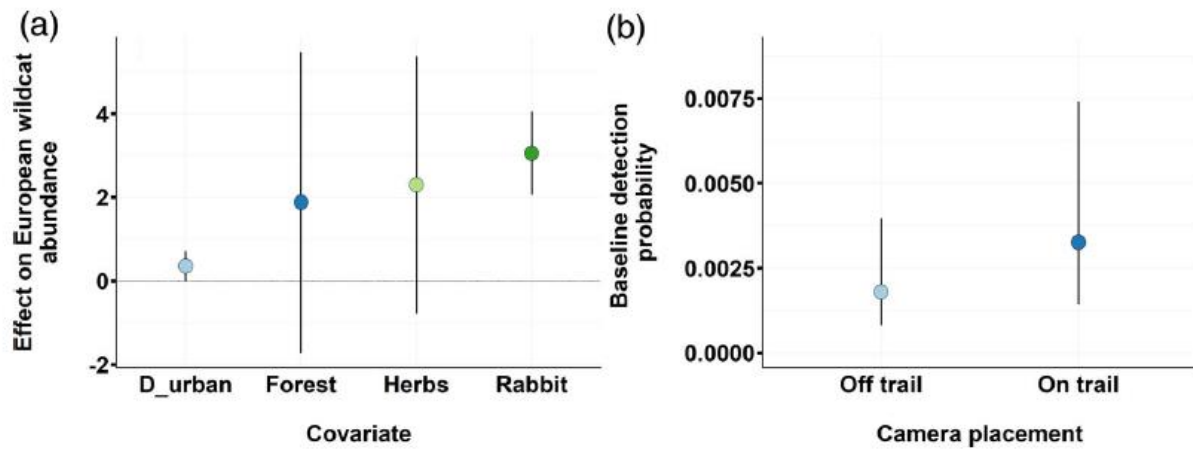


FIGURE 2 (a) Coefficient estimates, on logarithmic scale, from model-averaged procedure of state covariates on European wildcat density: distance to urban (D_urb), forest cover (For), herbaceous cover (Herb) and prey availability (Rabbit). (b) European wildcat baseline detection probability on and off trail.

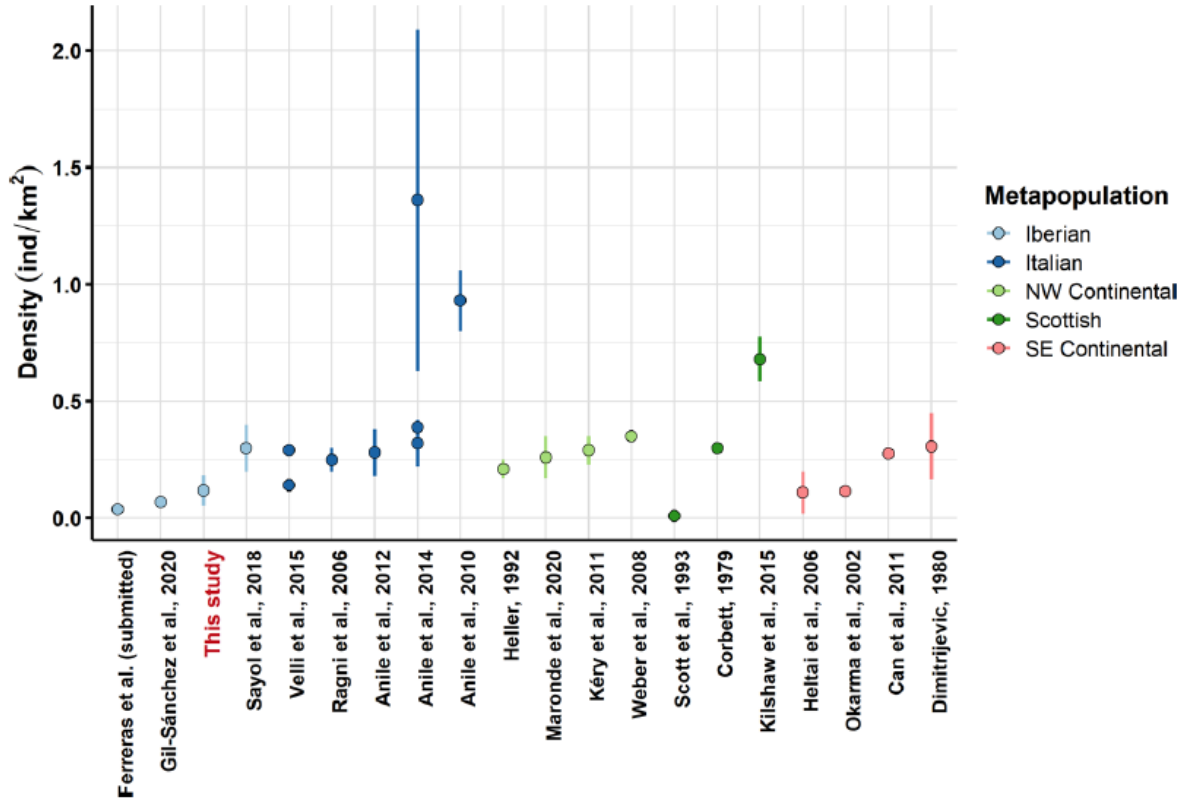


FIGURE 3 European wildcat's density (Ind/Km²) as obtained in different wildcat's populations of Europe, expressed as estimate \pm SE (whenever available). Metapopulations countries: Iberian-Portugal (this study) and Spain; Italian-Italy; NW Continental-Germany and Switzerland; Scottish-Scotland; SE Continental-Hungary, Poland, Serbia and Turkey. Source data: CT-Camera trapping; LT-Live capture; TEL-Telemetry; GH-Genetically identified hairs; RSS-Radioactive scat survey; NR-Not reported.