

Modelling the European wildcat (*Felis silvestris*) density across Europe

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Todas as correções determinadas pelo júri, e só essas, foram efetuadas.

O Presidente do Júri,





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Resumo

O gato-bravo é um mesocarnívoro elusivo que tem sofrido um declínio na sua distribuição nos últimos três séculos, dando origem a populações fragmentadas e ao desfavorável estado de conservação em alguns países do continente Europeu. No entanto, ainda não estão em prática medidas eficazes de conservação para espécie, particularmente no que diz respeito à informação disponível sobre o estado atual das populações e respetivos tamanhos e tendências populacionais.

A densidade populacional é uma quantidade fundamental na ecologia da vida selvagem, embora seja difícil de obter estimativas robustas para espécies elusivas. Métodos de amostragem não intrusivos, como as armadilhas fotográficas, permitem a recolha de dados ao longo de grandes áreas territoriais e permitem a identificação de indivíduos de espécies com padrões de pelagem notáveis, sendo possível estimar densidade através da captura-recaptura espacial. Alternativamente, registar dados de presença-ausência ou o número total de deteções requer menos esforço e recursos. Desta forma, os índices de abundância relativa e as abordagens de modelação que fazem uso de dados de presença-ausência são mais fáceis de usar, partindo do princípio de que abundância e distribuição das espécies tendem a estar relacionadas, e assim que se possam usar dados mais facilmente acessíveis para estimar a abundância.

O objetivo deste estudo é obter estimativas de densidade do gato-bravo Europeu através da modelação de dados provenientes de diferentes populações em toda a Europa, particularmente para populações onde os dados são escassos. Neste contexto, foram compilados e sistematizados dados de armadilhas fotográficas previamente recolhidos em 22 regiões. Desta forma, foram realizadas, pelo mesmo observador, identificações individuais dos gatos-bravos a partir de imagens provenientes de armadilhagem fotográfica. As estimativas de densidade para o gato-bravo europeu foram obtidas através de modelos de captura-recaptura espacial no pacote oSCR do R, quando possível obter recapturas espaciais. Adicionalmente, foi usada a formulação de Royle-Nichols para ajustar modelos de abundância aos nossos dados de ocupação e gerar estimativas de abundância local média, assim como os respetivos índices de abundância relativa foram obtidos para todas as áreas de estudo disponíveis. Estes resultados foram então integrados em modelos lineares generalizados para investigar a relação entre esses parâmetros e as estimativas de densidade obtidas através da modelação de capturas-recapturas espaciais. Desta forma, foi possível gerar previsões de densidade para populações que à partida não teriam informação suficiente disponível.

Foram obtidas estimativas de densidade através da captura-recaptura espacial para 10 (45.45%) áreas de estudo, inclusivamente para populações que nunca tinham sido estudadas antes. As densidades mais altas foram encontradas na Alemanha Central (33.30 \pm 6.14 indivíduos/100km²) e as mais baixas no Parque Natural de Montesinho (1.13 \pm 0.44 indivíduos /100km²). A relação logarítmica encontrada entre as estimativas de densidade e abundância local média foi usada para obter pela primeira vez previsões de densidade para populações pobres em deteções de gato-bravo.

Nova informação sobre as diferentes populações de gato-bravo Europeu foi obtida devido à colaboração e integração de dados de vários projetos. Nomeadamente, foi possível avaliar comparativamente a densidade - um parâmetro populacional pouco conhecido para esta espécie elusiva – fundamental para determinar o seu estado de conservação. Para adicionar, a relação entre a abundância local média e a densidade permitiu-nos gerar mais informação, ao fazer uso tanto dos dados de ocupação como dos dados de captura-recaptura espacial, o que é de grande importância, visto que é muito difícil obter dados para esta espécie. No entanto, os nossos resultados mostram que a maioria das populações de gato-bravo ocorre a baixas densidades populacionais, inferior ao esperado para populações europeias. Este resultado é preocupante para a conectividade entre as populações e a viabilidade da espécie. Esta abordagem demonstra também a necessidade de desenvolver métodos de recolha de dados adeguados, incluindo uma larga área territorial e duração da recolha de dados, para conseguir resultados robustos de densidade para espécies elusivas, como é o caso do gato-bravo Europeu. No caso de tais metodologias estarem limitadas por condições logísticas, métricas alternativas que não requerem a identificação individual devem ser exploradas, sempre na condição de ser testada a sua validade. Deve ser posto em prática um protocolo unificado, padronizado e em grande escala para avaliar com detalhe a distribuição e o estado das populações de gato-bravo Europeu.

Palavras-chave

Abundância local média, armadilhagem fotográfica, captura-recaptura espacial, conservação, dados de ocupação, densidade populacional, Gato-bravo Europeu, identificação individual, índice de abundância relativa, trabalho colaborativo

Abstract

The wildcat is a medium-sized elusive carnivore that has been suffering a range decline for the last three centuries, resulting in fragmented populations and unfavourable conservation status at the national level in many European states. However, the conservation of this species is still an issue, particularly regarding the lack of information available about the current status, population sizes and trends.

Animal population density is a fundamental quantity in wildlife ecology, but reliable estimates are hard to obtain for elusive species. Non-invasive sampling methods such as camera trapping allow the collection of data over large geographic areas and enable the identification of individuals for species with distinguishable coat patterns, allowing the estimation of density through spatial capture-recapture. Alternatively, recording the occurrence of species requires fewer resources and effort than does the estimation of local population densities. Therefore, indices of relative abundance and models that make use of presence-absence data are often easier to use, and as the abundance and distribution of species tend to be related, results that abundance may be estimated from more easily accessible data.

The goal of this study is to obtain density estimates of the European wildcat (*Felis silvestris silvestris*) through the modelling of data from several populations across Europe, particularly for populations where data is scarce. For this purpose, camera trapping data previously collected from 22 different study areas were compiled and systematized to estimate European wildcat density across its distribution range. Individual identifications of putative wildcats from camera-trapping images were performed by the same observer, and spatial capture-recapture density estimates were obtained using the oSCR package in R. We used the Royle-Nichols formulation to fit abundance models to our occupancy data and generate mean local abundance estimates, as well as obtained relative abundance indexes for all study areas available. These results were then used in a GLM to formulate a relationship between these parameters and the density estimates obtained through SCR modelling, which enabled us to generate density predictions for populations that did not have enough available information.

Density estimates were obtained for 10 (45.45%) study areas across Europe, including for populations that have never been studied before. The highest densities were found in central Germany (33.30 ± 6.138 individuals/100km²) and the lowest at Montesinho Natural Park (1.130 ± 0.437 individuals/100km²). A logarithmic relationship was found between density estimates and mean local abundance, which was used to

obtain for the first time density predictions for populations poor in wildcat detections. By modelling these relationships through a GLM, we were able to make use of all information available: occupancy data, number of total wildcat detections, and spatial captures-recaptures, thereby contributing with new information on wildcat populations across Europe.

New information regarding different European wildcat populations was obtained due to the collaboration and integration of data from several projects. Namely, we were able to comparatively assess an understudied population parameter - density - for an elusive felid, key to the assessment of its conservation status. Further, the relationship between mean local abundance and density allowed us to generate more information by making use of both the occupancy data and spatial capture-recapture data, which is significant since data is very hard to obtain for this species. However, our results show that most wildcat populations occur in low density, even lower than expected for European populations, which is concerning for the connectivity between populations and viability of the species. Our approach also exposes that adequate survey designs, including a large spatial extent and survey duration, are required to allow reliable density estimates for elusive species such as the European wildcat. When such designs are not possible due to logistic constraints, alternative metrics accounting for records without individual identification or that do not require recaptures should be explored as proxies, upon proper testing of their validity. A unified, standardized, large-scale protocol should be put in practice to assess with detail the European wildcat distribution and status.

Keywords

Camera trapping, collaborative work, conservation, density, European wildcat, generalized linear model, individual identification, mean local abundance, occupancy data, relative abundance index, spatial capture-recapture

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List of Abbreviations

- AIC Akaike information criterion
- BF Bavarian Forest
- CNP Cabañeros National Park
- Crb Carabaña
- EDF Encounter data file
- EIA Eastern Italian Alps
- Etn Etna
- GLM Generalized linear model
- GVNP Guadiana Valley Natural Park
 - HR Home range
 - MB Melsunger Bergland
- MLA Mean local abundance
- MMDM Mean maximum distance moved
- MMNP Massis del Montseny Natural Park
- MNR Muniellos Natural Reserve
- MtNP Montesinho Natural Park
 - NC Northern Catalunha
- NCAG Northern Catalunha, Alta Garrotxa
- NSJM Northern Swiss Jura Mountains
 - Pgl Penyagolosa
- PGNP Peneda-Gerês National Park
 - PNP Prespa National Park
 - RAI Relative abundance index
 - RN Royle-Nichols
- SANP Sierra de Andújar Natural Park
 - SCR Spatial capture-recapture
 - SF Spatial capture-recapture frame
 - SP Sierra de Picón
 - SS State space
 - SS Southern Slovenia
 - SV Serra de la Virgen
 - TDF Trap deployment file
 - WJ Wachau Jauerling



1.General introduction

1.1. The European wildcat

The European wildcat (*Felis silvestris* Schreber, 1777) is a medium-sized carnivore from the family Felidae. Among the three subspecies of wildcats, the European wildcat (*Felis silvestris silvestris* Schreber, 1777) occurs throughout mainland Europe from Portugal to eastern Europe, including Bulgaria, Rumania, southern Poland, western Russia (Kitchener *et al.*, 2017)(Figure 1). However, wildcat populations are fragmented throughout most of the central and western European countries (Lozano & Malo, 2012; Mitchell-Jones *et al.*, 1999).

Among the many morphological features of this felid, the ones that stand out are its long body with short limbs, a tail length greater than half of the body, and a brownishgrey coat with pelage patterns that, to a certain extent, allow us to distinguish between wild, hybrid and domestic individuals (Krüger *et al.*, 2009; López-Martín *et al.*, 2007). The main diagnostic pelage characteristics have been described by several authors who have developed marking systems that enable a more efficient morphological description of wildcats (Table 1).



Figure 1 – Known wildcat (Felis silvestris) distribution in the European continent (Source: (European Comission, Eurostat, & GISCO, 2018; IUCN, 2015)).

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Table 1 – Main wildcat pure phenotypic characters common to the three marking systems (Kitchener et al., 2005; Ragni & Possenti, 1996; Spassov, Simeonovski, & Spiridonov, 1997). Other features have been identified by each of the authors. Namely, (Ragni & Possenti, 1996) additionally described the nose with upper black margin, ears uniformly coloured and without the formation of dark hair in the apex, and a white aureole with or without collars in the gular region. While (Spassov, Simeonovski, & Spiridonov, 1997) describes the colour of the muzzle differing from the frontal part, none or 1 or 2 stripes on the lateral side of the foreleg, a dark spot on the armpit, and the plantar surface of the metatarsus varying from brown to ochre, among other characters as well.

Somatic region	(Ragni & Possenti, 1996)	(Kitchener <i>et al.</i> , 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
Nape	4 longitudinal stripes and 1 median thin stripe	4 thick stripes	1 to 4 stripes
Shoulder	2 parallel longitudinal stripes and 1 intermediate thin stripe	2 thick stripes	1 to 3 stripes
Dorsal line	Longitudinal median stripe flanked or not by bars and/or maculae	Stops at the base of the tail	Does not cross the tail rings
Flanks and hindquarters	The cephalic half with vertical stripes and the caudal half with macular and/or bars	Stripes on flanks and hindquarters are less than 25% broken and without spots	No stripes or scarcely notable and rarely broken
Tail	Without longitudinal markings or a dorsal longitudinal median evanescent bar on the proximal ½ to ¼	The tip is blunt, the bands are distinct	Short terminal ring, 2 to 3 dark rings), 0 to 6 pale rings, blunt tip

In addition to the description of wild phenotypes, these authors also allude to morphological indications of hybrid individuals. These include the extent of the dorsal stripe (which continues onto the tail, sometimes even crossing the rings), a long and sharp tail tip, the distinctiveness of tail bands (indistinct or fused), the shape of the stripes on the nape and shoulders (thin, indistinctive, or disordered), and highly broken stripes on flanks and hindquarters (or presence of spots) (Kitchener *et al.*, 2005; Spassov, Simeonovski, & Spiridonov, 1997).

However, continued interbreeding between domestic and wild individuals have produced a continuum in phenotypic variation and caused some characters to be typical in both forms, making it particularly difficult to distinguish hybrids from pure genotypes using morphological features (Krüger *et al.*, 2009). This is evident when the use of the different marking systems might lead to different conclusions of the same individual (Ballesteros-Duperón *et al.*, 2014). Hence, without the genetic analysis of individuals, one can only refer to phenotypic-like or putative wildcats.

Ecology of the European wildcat

The wide geographic distribution of the European wildcat extends through different bioclimatic regions, comprising a variety of different habitats (Bolnick *et al.*, 2007; Stahl & Léger, 1992) and the species has been recorded to occur in altitudes that

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range from the sea level up to 2250 meters (López-Martín et al., 2007). European wildcats are known to occur mostly in mosaic environments (Easterbee, Hepburn, & Jefferies, 1991; Lozano et al., 2003), usually comprised by open areas and closed vegetation patches, which allow wildcats to find high prey availability and shelter, respectively (Easterbee, Hepburn, & Jefferies, 1991; Klar et al., 2008; Lozano, 2010). Open areas generally include forest clearings, grasslands and croplands (Easterbee, Hepburn, & Jefferies, 1991; Klar et al., 2008; Lozano, 2010; Mattucci et al., 2013; Silva et al., 2013), whereas areas of enclosed vegetation structure are usually comprised of formations of scrubland, broad-leaved or mixed forests, and rocky areas of difficult access (Easterbee, Hepburn, & Jefferies, 1991; Klar et al., 2008; Lozano, 2010; Lozano et al., 2003; Mattucci et al., 2013; Monterroso et al., 2009; Yamaguchi et al., 2015). Such heterogeneous environments seem to play a significant role in wildcat abundance (Easterbee, Hepburn, & Jefferies, 1991; Lozano et al., 2007; Lozano et al., 2003). Particularly, in cases where shelter is available, this subspecies has been reported to occur in riparian and agricultural landscapes which are connected with forest habitats, since in these settings there might be a higher diversity and density of prey (Alain, Gilles, & Yannick, 2006; Chapman & Ribic, 2002; Jerosch, Götz, & Roth, 2017; Jerosch et al., 2018; Lozano, 2010; Šálek et al., 2014). European wildcats are also known to prefer areas with low human population density and at intermediate altitudes (300 to 800 meters), which are determined by avoiding humanized areas and snow cover, respectively (López-Martín et al., 2007; Yamaguchi et al., 2015).

Populations living in the Temperate and Mediterranean bioclimatic regions experience different climate, habitat and food resources. This promotes divergent local adaptations (Mattucci *et al.*, 2013) and is reflected in their feeding behaviour and spatial behaviour (Anile *et al.*, 2017; Biró, Szehethy, & Heltai, 2004; Corbett, 1979; Jerosch *et al.*, 2018; Lozano, Moleón, & Virgós, 2006; Malo *et al.*, 2004; Monterroso *et al.*, 2009; Oliveira *et al.*, 2018).

As active predators, European wildcats are strongly associated to their prey communities, which vary in diversity across their geographic range and latitude (Lozano, Moleón, & Virgós, 2006; Mattucci *et al.*, 2013; Sunquist & Sunquist, 2002; Széles *et al.*, 2018). Small mammals (such as rodents) are the staple prey in the Temperate region, whereas lagomorphs (when available) are preferred in the Mediterranean region (Apostolico *et al.*, 2016; López-Martín *et al.*, 2007; Lozano, Moleón, & Virgós, 2006; Monterroso *et al.*, 2020; Oliveira *et al.*, 2018; Sunquist & Sunquist, 2002; Széles *et al.*,



2018). Still, other prey such as birds, reptiles, and invertebrates can be significantly consumed, especially towards the southern regions of Europe (Lozano, Moleón, & Virgós, 2006; Sunquist & Sunquist, 2002; Széles *et al.*, 2018). Hence, in Mediterranean climates, the feeding ecology of the European wildcat tends to be more diversified, contrasting with the one exhibited in Temperate climates where the rodents are the bulk of its diet (Lozano, Moleón, & Virgós, 2006). Therefore, this species is considered a facultative specialist displaying an optional feeding strategy, with a specialization on rodents only when European rabbits (*Oryctolagus cuniculus*) are not available (Lozano, Moleón, & Virgós, 2006; Lozano, Virgós, & Cabezas-Díaz, 2013; Malo *et al.*, 2004).

Local prey densities, habitat, population structure and individual features, have a strong impact on the species home range, making it highly variable across its distribution range (Anile *et al.*, 2017; Biró, Szehethy, & Heltai, 2004; Corbett, 1979; Jerosch *et al.*, 2018). Reported home range sizes vary from 1.22 to 59.78 km² (Monterroso *et al.*, 2009; Oliveira *et al.*, 2018), with the female home-range size being generally smaller than the male home-range size (Monterroso *et al.*, 2009). Throughout their whole distribution, wildcats tend to live in low population densities and are elusive in behaviour (Anile *et al.*, 2017; Anile *et al.*, 2019; Piñeiro *et al.*, 2012), being most active during the night and crepuscular hours (Corbett, 1979; Daniels *et al.*, 2001; Germain, Benhamou, & Poulle, 2008; Monterroso, Alves, & Ferreras, 2014). European wildcats are solitary and territorial carnivores and both genders only come together during the reproductive season, between December and March (Biró, Szehethy, & Heltai, 2004; Germain, Benhamou, & Poulle, 2008; López-Martín *et al.*, 2007; Smit & van Wijngaarden, 1981).

European wildcat populations trends and estimates

Sound knowledge about European wildcat populations remains scarce (Lozano, Virgós, & Cabezas-Díaz, 2013): they are largely fragmented, and the species' presence is uncertain in many places (Lozano & Malo, 2012). In some regions of central Europe, including France, Germany, and adjacent areas, wildcats seem to be expanding their range (Driscoll *et al.*, 2011; Hartmann *et al.*, 2013; Nussberger *et al.*, 2014; Say *et al.*, 2012; Steyer *et al.*, 2016). Additionally, the European wildcat was considered extinct in Austria since 1989, although recent data has confirmed the species has returned (Gerngross, Slotta-Bachmayr, & Hagenstein, 2021; Slotta-Bachmayr, Meikl, & Hagenstein, 2016). In the Iberian Peninsula, the populations' decline and fragmented distribution (Lozano *et al.*, 2007; Sarmento *et al.*, 2009) urged the Vulnerable

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conservation status in Portugal (Cabral *et al.*, 2005) and Near Threatened in Spain (López-Martín *et al.*, 2007).

The highest densities recorded for the European wildcat are approximately 38 individuals/100km², and occur in areas considered optimal for the species. However, densities of around 20 individuals/100km² are more common in the Temperate bioclimatic region, whereas in the Iberian Peninsula densities are generally lower than 10 individuals/100km² (Gil-Sánchez *et al.*, 2020; López-Martín *et al.*, 2007; Matias *et al.*, 2021). The few studies in which local population densities have been estimated include a wide range of protocols (Figure 2), varying in the data collection (e.g., camera trapping, live capture, radio tracking, and scat collection) and analysis methods (e.g., spatial capture-recapture and random encounter model), resulting in some difficulty comparing results, as is suggested by (Anile *et al.*, 2014). Other studies have documented low local wildcat abundances (Beutel *et al.*, 2017; Soto & Palomares, 2014). Regardless, none of these studies provided large-scale assessments or integrated estimates of wildcat density.

Main threats and conservation actions

The European wildcat is facing major threats. Particularly, hybridization with the domestic cat (*Felis silvestris catus*) (Monterroso *et al.*, 2016; Yamaguchi *et al.*, 2015). Indeed, domestic cats omnipresent across almost the whole range of the European wildcat (Driscoll *et al.*, 2007; Driscoll *et al.*, 2011; Jiménez *et al.*, 2017; Nowell & Jackson, 1996; Yamaguchi *et al.*, 2015) and both subspecies hybridize, compete for resources (such as territory and food), and are affected by the same diseases (Nowell & Jackson, 1996; Széles *et al.*, 2018). This compromises the genetic integrity of the wild populations and, thus, leads to decreased fitness (Tiesmeyer *et al.*, 2020).

Anthropogenic threats, besides indirectly increasing hybridisation risk, include the loss of habitat to deforestation and the increase of infrastructures which are impactful for elusive species (Yamaguchi *et al.*, 2015). Furthermore, human-induced mortality, such as road and railway killings, and persecution by hunters as a predator control measure to foster game species, have contributed to the decrease of many European wildcat populations (Jerosch *et al.*, 2018; Nowell & Jackson, 1996; Yamaguchi *et al.*, 2015). In fact, a recent survival and cause-specific mortality assessment of this species has concluded that road kills and poaching represent 57% and 22% of the total annual mortality across Europe, respectively (Bastianelli *et al.*, 2021).





Figure 2 - Density estimates of the European wildcat populations per European region. Many estimates are outdated and vary in methodological approaches

Finally, ecological pressures in the Mediterranean region, such as a decrease in prey availability (mainly due to the rabbit haemorrhagic disease virus) and interspecific competition, have impacted wildcat abundance (Alonso & de Ayala, 2019; Monterroso *et al.*, 2020; Monterroso *et al.*, 2016). In fact, the European wildcat has overlapping habitats and similar diets as the Iberian lynx (*Lynx pardinus*) (Lozano, Moleón, & Virgós, 2006; Monterroso *et al.*, 2020; Oliveira *et al.*, 2018; Palomares, 2001; Schauenberg, 1981). This may lead to wildcat mortality due to lynx attacks (Ritchie & Johnson, 2009) and the possible displacement of the wildcat populations (Jiménez *et al.*, 2019; Lozano & Malo, 2012; Nájera *et al.*, 2019; Palomares *et al.*, 1995). Moreover, climate change is increasing desertification in the Mediterranean habitats where the European wildcat

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occurs, which can impact the small mammal communities they are associated with (Mattucci *et al.*, 2016).

Globally, the wildcat is classified as Least Concern by the International Union for the Conservation of Nature (IUCN) due to its wide distribution range and large global population size (Gerngross *et al.*, Submitted; Yamaguchi *et al.*, 2015). However, the above-identified threats have made its range contract over the last three centuries, resulting in a fragmented distribution with the presence of multiple isolated populations (Mitchell-Jones *et al.*, 1999; Nowell & Jackson, 1996). Hence, it is strictly protected across almost all its range (Nowell & Jackson, 1996) and through the Bern Convention and Habitats Directive (Gerngross *et al.*, Submitted; Yamaguchi *et al.*, 2015).

Despite its global favourable status, the conservation of the European wildcat is still a challenge. Of particular concern is the lack of information available about the current status, population sizes and trends (Yamaguchi *et al.*, 2015). Reliable information concerning the populations is crucial for the implementation of efficient conservation actions (Macdonald *et al.*, 2004; Maronde *et al.*, 2020). Therefore, more efforts are needed for regular monitoring of wildcat populations through robust sampling approaches (López-Martín *et al.*, 2007; Macdonald *et al.*, 2004; Tiesmeyer *et al.*, 2020; Yamaguchi *et al.*, 2015).

1.2. Camera trapping and the challenges of estimating population density

Monitoring data are essential to identify key issues for management goals, such as assessing conservation and land use priorities and informing wildlife managers, policymakers, and the general public about the state of nature (Heywood & Watson, 1995; Pellet & Schmidt, 2005; Stephens *et al.*, 2015). In this context, conservation efforts should be guided by metrics that reliably represent the population sizes and status of populations, such as population density (Hayward *et al.*, 2015; IUCN, 2012; Popescu *et al.*, 2016). This is a fundamental quantity in wildlife ecology (Efford, 2004; Stephens *et al.*, 2015), as this metric allows us to assess demographic variations and the extinction risk of populations (Purvis *et al.*, 2000; Wright & Hubbell, 1983). Unfortunately, reliable estimates are challenging to obtain for elusive species (Karanth & Chellam, 2009).

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Sampling methods such as remotely triggered cameras (camera traps) enable the study of biodiversity at a global scale to help answer urgent questions, particularly since they allow the monitoring of rare species, the general decline of biodiversity, and the decrease in geographic ranges of species, therefore having the potential to guide conservation policy (Steenweg et al., 2017). This is an increasingly popular technology in the field of ecology for several reasons: they are non-invasive (i.e., cause relatively low disturbance for animals), allow the collection of data over large geographic areas (Silveira, Jacomo, & Diniz-Filho, 2003), and they can stay on the field for long periods of time with little human effort, enabling more data to be collected while being cost-efficient (Choo et al., 2020; O'Connell, Nichols, & Karanth, 2011; Sollmann et al., 2013; Steenweg et al., 2017; Wearn & Glover-Kapfer, 2019). This makes camera traps the most effective sampling methods for detecting medium and large mammal species (Silveira, Jacomo, & Diniz-Filho, 2003; Steenweg et al., 2017; Wearn & Glover-Kapfer, 2019). Particularly, they are extremely useful for the study of elusive species occurring at low population densities (Augustine et al., 2018; Brassine & Parker, 2015; Gil-Sánchez, Jaramillo, & Barea-Azcón, 2015). This is the case of the European wildcat, which is very challenging to study because of its solitary and secretive behaviour (Brassine & Parker, 2015; Kilshaw et al., 2015; Maronde et al., 2020; Velli et al., 2015).

Estimating population density from camera trapping data

With the proper sampling design and statistical models, camera trapping data allow the conversion of detection rates into population parameters, such as abundance and distribution (Choo *et al.*, 2020; O'Connell, Nichols, & Karanth, 2011; Sollmann *et al.*, 2013; Soto & Palomares, 2014; Steenweg *et al.*, 2017). The most widely used index for camera-trapping data is the number of photographs of the focal species per trap day (i.e., relative abundance index, RAI) (O'Brien, Kinnaird, & Wibisono, 2003; O'Brien, 2011), as indices of relative abundance often are cheaper to estimate than absolute abundances and often are the goal of monitoring programs with broad spatial or temporal scales (Link & Sauer, 1998; Pollock *et al.*, 2002). However, this approach is controversial, as the uniform detection probability assumption (i.e., the assumption that our ability to detect animals is constant across space) is rarely tested (Williams, Nichols, & Conroy, 2002b).

Hierarchical models emerge as a solution to avoid violating this assumption. This modelling approach is characterized by building a set of sub-models that are conditionally related to each other, allowing for the representation of a more complex

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system than a single model would be able to represent (Kéry & Royle, 2015). Therefore, hierarchical models enable us to simultaneously account for the ecological process (i.e., the true state of nature that is not observable, or only partly so) and the observation process (i.e., the measurement error, given that detection is conditional on the occurrence of the species) (Kéry & Chandler, 2012; Kéry & Royle, 2015). This latter component takes into account our inability to detect all individuals in a sampling area (Royle & Dorazio, 2008).

The Royle-Nichols (RN) model formulation (Royle & Nichols, 2003) stands on this hierarchical modelling approach to infer abundance from detection/non-detection data. The RN model is based on the principle that detecting a species in a location is often a direct function of the number of individuals of the species inhabiting the location (i.e., animal abundance is an important source of heterogeneity in detection probability) (Kéry & Royle, 2015; Royle & Nichols, 2003). While this model accounts for the fact that most species are not observed perfectly in each habitat in which they occur (Duckworth & Altwegg, 2021; MacKenzie & Kendall, 2002; Pellet & Schmidt, 2005), thereby contrasting the relative abundance indexes (Sollmann *et al.*, 2013), it is still relatively easy to obtain, as it uses occupancy data.

As a further analytical development in hierarchical modelling, capture-recapture models account for imperfect detection of individuals (Augustine *et al.*, 2018), (i.e., the fact that we may not observe all individuals in the study area) and are additionally characterized by the use of individual encounter history data, which are obtained by identifying individuals and observing them over time (Otis *et al.*, 1978; Royle, Fuller, & Sutherland, 2018; White *et al.*, 1982). However, these models are not spatially explicit, i.e., do not allow information such as the locations of individuals, landscape features, and any spatially explicit biological processes to be modelled (Royle *et al.*, 2013b; Royle, Fuller, & Fuller, & Sutherland, 2018).

In this context, spatial capture-recapture (SCR) models arise as an extension of classical capture-recapture models (Royle, Fuller, & Sutherland, 2018) a provided framework for dealing with the main shortcomings in capture-recapture models, namely, accounting for spatially explicit data and heterogeneous detection probability (Augustine *et al.*, 2018; Royle, Fuller, & Sutherland, 2018; Sutherland, Royle, & Linden, 2019). Indeed, the SCR framework accounts for the interaction between the spatial organization of individuals (i.e., the individual encounter history) and the spatial organization of traps (Augustine *et al.*, 2018; Royle, Fuller, & Sutherland, 2018). Additionally, spatial

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recaptures of individuals are also fundamental in SCR models since they directly inform the state-space component of the models. This component is a probabilistic characterization of potential activity centres of individuals, which is determined by their spatial locations (expressed in the data by x and y coordinates). Therefore, the statespace (which defines where individuals can live and should represent activity centres of all detectable individuals) allows to explicitly model a heterogeneous detection probability, i.e., the probability that an individual is captured in each trap is conditional on its activity centre. Hence, detection probability varies according to the distance between the individual activity centre and traps, which improves the accuracy of density estimates (Royle, Fuller, & Sutherland, 2018).

This analytical approach is especially useful for camera traps, which enable the identification of individuals for species with distinguishable coat patterns. Hence, data from camera trapping surveys have the potential to be analysed through capturerecapture models to estimate the population density of elusive animals (Augustine et al., 2018; Sollmann et al., 2011). However, individual identifications often reduce the amount of data collected, which may be problematic when studying elusive species. The inability to obtain density estimates for datasets poor in number of individuals identified urge the use of simpler approaches (O'Brien, Kinnaird, & Wibisono, 2003; O'Brien, 2011), such as the above mentioned RAI and RN. This happens because recording the presence and absence of species requires fewer resources and effort than does the estimation of local densities (Burton et al., 2015; Gaston et al., 2000; Linden et al., 2017). However, analytical alternatives for obtaining reliable density estimates from camera-trapping data of unmarked populations are still limited and an ongoing focus of research (Sollmann et al., 2013). To address this issue, it is important to test the hypothesis in which the relationship between densities and occupancies indicates the former can be derived from the latter, i.e., it would be possible to estimate density from presence-absence data (Gaston et al., 2000; Linden et al., 2017).

The opportunity of scale

The larger the geographic range of an analytical approach, the greater the opportunity for understanding the underlying causes of population-level responses across multiple sites (Fraser *et al.*, 2013). Hence, linking local remote-camera projects into nationally or internationally coordinated efforts has the potential for allowing continent-level questions to be addressed from locally point-sampled data (Steenweg *et al.*, 2017).

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However, different survey protocols across projects limit the robustness and comparison of results (Fraser *et al.*, 2013; Liebhold & Gurevitch, 2002), as each approach has its strengths and weaknesses and biases may be introduced in several steps of data analysis (Choo *et al.*, 2020; Liebhold & Gurevitch, 2002). Particularly, in the individual identification step by inter-observer discrepancies (observer bias) (Choo *et al.*, 2020) and in the modelling step by the different analytical choices of researchers (Liebhold & Gurevitch, 2002). Hence, it is of great importance to use standardized data and to obtain comparable results in order to advance our understanding of general ecological principles and test large-scale hypothesis (Fraser *et al.*, 2013; Liebhold & Gurevitch, 2002).

1.3. Objectives

The main goal of this study is to quantify European wildcat density throughout its distribution range in Europe, through a set of secondary intermediate objectives:

- i) Obtain estimates with a single comparable approximation, reducing the effects of observer identification (observer bias),
- ii) To test the relationship between density and other metrics obtained from camera trapping data, as is the case of mean local abundance and relative abundance index, thereby providing support (or rejection) of the use of these metrics as density proxies in studies that resort to the use camera trapping
- iii) Obtain estimates for the first time for populations where data is scarce

To achieve these objectives, we hypothesized that i) both the mean local abundance and the relative abundance index are proportional to the estimated density and ii) these metrics can serve as density proxies, under calibrated conditions, to study populations where data is scarce.

For this purpose, camera trapping data previously collected under the scope of independent studies carried out across different regions and projects were compiled and harmonized, allowing the construction of hierarchical models for the European range (Figure 3). First, population-specific density estimates for the European wildcat will be obtained through spatial capture-recapture models, when possible. Second, a relationship will be tested between mean local abundance and density, as well as between the relative abundance index (RAI) and density. In case there is support for the



relationships, density estimates may be predicted for study areas where the spatial capture-recapture approach was not possible to be applied.



Figure 3 - Workflow adopted to obtain European wildcat population density estimates.



2.Methods

2.1. Study areas

Europe is characterized by its highly indented shape and complex coastline with many islands and peninsulas, which makes it susceptible to a large oceanic influence from the surrounding seas in the north, west and south. Although Europe has still some large wilderness areas, such as high mountains in the upper ranges of river systems, the landscape has never been so fragmented. Deeply influenced by a long history of cultivation and land use, this continent encompasses the largest urbanised area and densest infrastructure. Consequently, the effects of human activity are seen, directly or indirectly, throughout the whole continent, such as in the species compositions and disturbances in the most remote places (Condé & Richard, 2002).

The data included in this study were collected in several European countries, which comprise a variety of different biomes (Figure 4, Table 2), such as the Mediterranean forests, woodland, and scrub, the Temperate broadleaf and mixed forests, and the Temperate conifer forests (Dinerstein *et al.*, 2017). Although wildcat density has been studied in Scotland (Kilshaw *et al.*, 2015), this region was not included in this study as the population is known to be exposed to a high hybridization risk (Kilshaw *et al.*, 2016), resulting in lower genetic integrity of individuals (Tiesmeyer *et al.*, 2020).









Biome	Ecoregion	Study area	
	Iberian sclerophyllous and semi-	GVNP; MNP; CNP; SP;	
	deciduous forests	SANP; Pgl; SV	
Mediterranean forests, woodland, and scrub	Iberian conifer forests	Crb	
	Northwest Iberian montane forests	MtNP	
	Northeast Spain and southern France Mediterranean forests	NC; MMNP	
	Tyrrhenian-Adriatic sclerophyllous and		
	mixed forests	_ Etn	
	South Apennine mixed montane forests		
	Pindus Mountains mixed forests	PNP	
Temperate broadleaf and mixed forests	Cantabrian mixed forests	PGNP; MNR	
	Western European broadleaf forests	MB; BF; NSJM	
	Central European mixed forests	WJ	
	Pannonian mixed forests	<u>ee</u>	
	Dinaric Mountains mixed forests	- 33	
Tomporate and applifur forests	Alps conifer and mixed forests		
remperate and conner lorests	Dinaric Mountains mixed forests		

Table 2 – Study areas and correspondent ecoregions included in each biome (Dinerstein et al., 2017).

2.1.1. Mediterranean forests, woodland, and scrub

The Mediterranean forests, woodland, and scrub support a high level of endemism and diversity (Dinerstein *et al.*, 2017). They are typically located in the Mediterranean biogeographical region, which is characterized by a warm climate with hot summers and mild winters. However, water is becoming scarce here and, thus arid conditions are increasing (Condé & Richard, 2002; Rodriguez, Rivero, & Ballesta, 2005), endangering this biome and promoting biodiversity loss (Dinerstein *et al.*, 2017; Rodriguez, Rivero, & Ballesta, 2005). Among the great variety of ecoregions present in this biome, those that comprise the study areas in this work are the Iberian sclerophyllous and semi-deciduous forests, the Iberian conifer forests, the northwest Iberian montane forests, the northeast Spain and southern France Mediterranean forests, the Tyrrhenian-Adriatic sclerophyllous and mixed forests (Dinerstein *et al.*, 2017)(Table 2).

The Iberian Mediterranean forests are mainly dominated by *Quercus* species, although there are also beech dominated forests, which are generally restricted to the mountains. Sclerophyllous oak forests (e.g., *Quercus rotundifolia* and *Quercus suber*) covers the biggest part of the area (mainly in valleys or plateaus), while deciduous forests (e.g., the endemic *Quercus canariensis* and *Quercus pyrenaica*) mainly occur in mountain ranges. Furthermore, olive woodlands (*Olea europaea var. sylvestris*) also make an important part of the Sclerophyllous vegetation in this ecoregion (Gavilán *et al.*,



2018). Mountain conifers can be found in the mountains of the north and centre of the Iberian Peninsula. They are characterized by formations of species such as *Pinus sylvestris*, *Pinus uncinata*, and *Abies alba* (Benito Garzón, Sánchez de Dios, & Sainz Ollero, 2008).

In the Pre-Pyrenees and in the Iberian range conifer forests or mixed coniferhardwood forests are the main dominants of the landscape. These forested areas comprise stands of *Pinus sylvestris, Pinus pinea, Pinus nigra, Quercus faginea,* and *Quercus ilex* (Lasanta & Vicente-Serrano, 2012).

Eastern of the Iberian range, the forests of the Apennines are characterised by high canopy cover and high tree species diversity (Vacchiano *et al.*, 2017). Sclerophyllous and mixed forests of southwestern Italy are dominated by *Quercus ilex* together with mixed *Quercus suber* forests and coastal Mediterranean maquis with *Pistacia lentiscus*, *Juniperus oxycedrus*, *Juniperus phoenicea*, *Chamaerops humilis*, and *Olea europaea* var. *sylvestris*. Whereas deciduous forests are dominated by several species of oaks or *Fagus sylvatica* and *Ilex aquifolium* in moist volcanic substrata (Blasi *et al.*, 2014).

Finally, further east, the mixed forests of the Pindus Mountains are characterized by forests with black pine (*Pinus nigra*), fir (*Abies borisii regis*), beech (*Fagus sylvatica*), and white pine (*Pinus heldreichiii*) (Mertzanis, 1994).

In this biome, data has been gathered from 13 study areas: Guadiana Valley Natural Park; Cabañeros National Park; Monfrague National Park; Sierra de Picón; Sierra de Andújar Natural Park; Penyagolosa; Sierra de la Virgen; Carabaña; Montesinho Natural Park; Northern Catalonia; Massis del Montseny Natural Park; Mount Etna; and Prespa National Park.

Guadiana Valley Natural Park (GVNP), Portugal

The Guadiana Valley Natural Park (GVNP) is a protected area located in the southeast part of Portugal, where elevation varies between 9 and 370m (Vieira, 2008). This region presents the lowest precipitation levels in Portugal and very high levels of insolation (ICNF, 2020). The landscape is highly fragmented with cereal croplands and agroforestry systems (Montado) mainly associated with steeper slopes and elevation ridges (Costa *et al.*, 1998). There is a high level of hunting activity, where one of the most relevant game species is the European rabbit. Predator control measures are legally directed towards the red fox and the Egyptian mongoose (Monterroso, 2014). This is one



of the Iberian lynx (*Lynx pardinus*) reintroduction sites in the Iberian Peninsula (Sarmento *et al.*, 2019).

Cabañeros National Park (CNP), Spain

The Cabañeros National Park is a protected area located in Central Spain (between the provinces of Ciudad Real and Toledo), occupying a low mountain system, with altitudes ranging from 620 to 1500m above sea level (Barriga *et al.*, 2006; Ferreras *et al.*, 2017). The climate is typically Mediterranean, with the rainy season usually encompassing autumn, winter and spring, relatively mild winters, and hot and dry summers (Morales-Molino *et al.*, 2018). The central area of CNP is occupied by pastureland with a savanna-like open tree layer of cork and holm oaks (dehesas) (Ferreras *et al.*, submitted). Neither hunting activity nor predator control is allowed (Monterroso, 2014). Wild ungulates occur at high density, however, the main potential prey for wildcats are scarce in the Park (Ferreras *et al.*, submitted).

Monfrague National Park (MNP), Spain

Monfrague National Park is a large protected area located in western Spain, in Cáceres province, occupying a low mountain system, with altitudes from 250 to 750m above sea level (Ferreras *et al.*, 2017). The climate and vegetation are similar to Cabañeros National Park (Ferreras *et al.*, 2017; Ortín, Montes, & Martínez-Solano, 2019). This region has a low human density, but a half of the park is private property. The main anthropogenic activities include livestock and hunting, which is a very valuable activity in this area, mainly focused on big game species, such as red deer (Lozano *et al.*, 2007).

Sierra de Picón (SP), Spain

Ciudad Real province, in the centre of Spain, is a flat region with uniform vegetation. This area has a dry, continental climate and has extreme temperatures (Feo Brito *et al.*, 2007). This region is characterized by fragmented habitats of open grasslands for extensive cattle pasture in lowlands (LaHue *et al.*, 2016). These are savannah-like areas, called dehesas, marginal to mountainous lands, which are also used for hunting (LaHue *et al.*, 2016).

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Sierra de Andújar Natural Park (SANP), Spain

Andújar Natural Park is located within Sierra Morena (southeast Spain). This mountainous area comprises altitudes from 200 to 1500m above sea level, and the climate is Mediterranean with rainy mild winters and hot dry summers (Gil-Sánchez, Ballesteros-Duperón, & Bueno-Segura, 2006). The vegetation is dominated by Mediterranean shrubland and an arboreal stratum of holm oak (*Quercus ilex*) and olive tree (*Olea europaea* var. *sylvestris*) (Burgos *et al.*, 2019). Human activities in this area include game hunting, although only big game is allowed. In areas used for cattle raising, shrub vegetation has been almost eliminated and grasslands with scattered trees are dominant (Millán *et al.*, 2007). Here occurs the Iberian Lynx (*Lynx pardinus*), in what represents the main world Iberian lynx population (Gil-Sánchez, Ballesteros-Duperón, & Bueno-Segura, 2006). Therefore, intense European rabbit recovery efforts have been put in place to maintain prey availability for this population (Monterroso, 2014).

Penyagolosa (Pgl), Spain

Penyagolosa Natural Park is located in eastern Spain, in Castellón province, near the Mediterranean Sea. This Natural Park is characterized by its abrupt topography with numerous ravines throughout a territory that ranges between 1250 and 1814m above sea level. The combination of its geographical location and altitude lead to a humid Mediterranean climate (Albesa & Ros, 2019). The Park comprises a variety of flora and fauna species, such as the existence of large mammals and birds of prey. Penyagolosa and its surroundings support a population of 2623 inhabitants and the environment of hills, trails and ravines attract hikers and promote sport activities (Reddam, Olivares, & Bonfill, 2017).

Sierra de la Virgen (SV), Spain

Sierra de la Virgen, in the province of Zaragoza (north-eastern Spain), belongs to the Iberian System mountain range. The elevation varies between 900 and 1300m and the climate is typical continental Mediterranean with cold winters (Villar Pérez, 1990). This Mountainous area is located on the Iberian sclerophyllous and semi-deciduous forests ecoregion, being dominated by several species of oaks (*Quercus ilex, Quercus pyrenaica,* and *Quercus petraea*) and also pine (mostly *Pinus sylvestris, Pinus nigra* and *Pinus uncinata*) and beech (*Fagus sylvatica*) (Gavilán *et al.*, 2018; Martinez del Castillo *et al.*, 2015). Traditional human activities in this region include cattle raising and forest logging (Martinez del Castillo *et al.*, 2015).

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Carabaña (Crb), Spain

Carabaña is a municipality in central Spain in the province of Madrid. This region reaches an altitude of 625m above sea level with a population density of 29.63 inhabitants per km². This is a semi-arid region comprised mainly of open steppes dominated by alpha grass (*Stipa tenacissima*), holm oak (*Quercus ilex*), and scrub species such as *Quercus coccifera*, *Cistus ladanifer*, and *Lavandula stoechas*. Olive tree (*Olea europaea* var. *sylvestris*) plantations are very abundant (CM, 2019; Maestre, Ramírez, & Cortina, 2007).

Montesinho Natural Park (MtNP), Portugal

Montesinho Natural Park is located in a mountainous region of northeast Portugal, on the border with Spain. Elevation ranges from 436 to 1487m (Castro *et al.*, 2010) and the climate is influenced by the relief of the mountains and the continental effects from the inner Iberian Peninsula (Gonçalves, 1985). The landscape consists of natural woodlands, and traditional agriculture at lower altitudes (Castro *et al.*, 2010). However, in the mountains, above 1000 m elevation, human activity is almost non-existent and cultivated land almost disappears, with the appearance of upland pastures instead (Agroconsultores, 1991). This Natural Park includes 92 small villages inhabited by less than 8,000 people (Castro *et al.*, 2010). This region contains a very diverse carnivore community, including threatened species, such as the Iberian wolf (*Canis lupus signatus*) (Matias, 2020).

Northern Catalonia and Alta Garrotxa (NC and NCAG, respectively), Spain

Catalonia (Spain) is located northeast of the Iberian Peninsula (Sans-Fuentes & Ventura, 2000). The altitude ranges from sea level to 3143m (Hawkins & Pausas, 2004). In north Catalonia, the Pre-Pyrenees, relief strongly influences the climate, representing a barrier to humid and warm winds coming from the Mediterranean, which are forced to rise, causing high precipitation (Revelles *et al.*, 2018).

In Alta Garrotxa and its surroundings, the landscape is made up of mosaics of forests, crops, and pasture meadows (Sayol *et al.*, 2018), characterized by the predominance of evergreen humid sclerophyllous forests (deciduous oak and beech), in the middle mountains in the pre-Pyrenees, and the presence of conifer forests, in high mountain areas (Revelles *et al.*, 2018). The socio-economic dynamics of the territory are characterised by human abandonment and the decline of agricultural activity. This region



is well-preserved from urbanization due to the absence of road networks and its protection status. However, the isolation of the area plays a role in both biodiversity conservation and loss (Cohen *et al.*, 2011).

A little south of Alta Garrotxa, the Castell de Montesquiu Park is distributed among the municipalities of Montesquiu, Santa Maria de Besora, Sant Quirze de Besora and Sora. It is crossed by the river Ter and covers a narrow range of altitudes, between 565 and 800m. The vegetation consists mainly of pine and oak trees, riverside forests and cultivated areas (Espadaler *et al.*, 2013).

Massis del Montseny Natural Park (MMNP), Spain

The Montseny Natural Park is a UNESCO Biosphere Reserve (Otero *et al.*, 2018). This mountain range runs parallel to the Mediterranean Sea at about 30km off the Catalonian coast and 20 km northeast of Barcelona (Caritat *et al.*, 2006; Jump, Hunt, & Peñuelas, 2007). The topography is rough and the altitude ranges from 100m to 1700m (Caritat *et al.*, 2006; Otero *et al.*, 2018). In the lower areas, the climate is characterised by a dry season of approximately two months in the summer, while on the summits rainfall is more abundant and there is no dry summer season (Caritat *et al.*, 2006). This region has gone through a dramatic socio-economic transformation during the 20th century: crops and pastures decreased, while forests, urban and industrial areas have expanded. This has led to substantive changes in landscape ecology and biodiversity (Otero *et al.*, 2018).

Etna (Etn), Italy

The data was collected on an area of 10.1km² on the south-westside of Mount Etna, on the island of Sicily (Anile *et al.*, 2014), corresponding to the southernmost location of the wildcat occurrence in Italy (Nowell & Jackson, 1996). Elevation ranged from 900 to 2000m. The climate is typically Mediterranean, but snow cover is common in winter and rainfall is concentrated during autumn and winter. The volcanic activity has produced a landscape characterized by open fields formed recently due to large lava flows and inactive secondary cones of different ages, intermixed with large woodland patches. Human activity is low, with very restricted vehicle access mainly for the management of woodland, sheep farming, and tourist trekking. Its wide variety of flora and fauna species makes Sicily a relevant global biodiversity hotspot (Médail & Quézel, 1999). Potential wildcat refuges are widely available in cavities, which are characteristic



of the volcanic soil, and also represent the only available water in summer (Anile *et al.*, 2014).

Prespa National Park (PNP), Albania

The Prespa National Park is situated in the southeast of Albania on the national border with Macedonia (FYROM) and Greece. This Park covers large parts of the Mali i Thate and Mali i Ivanit mountains, as well as the Albanian parts of both Prespa Lakes. Altitude ranges from 850 m to 2288 m above sea level (Naumova, Hristovski, & Hristov, 2016) and the climate is influenced by the large water bodies, which create a less extreme microclimate, within the mountainous area with very harsh winter conditions. The main forests of the area include oak, beech, and mixed hardwoods (such as *Quercus* spp, *Juniperus* spp, *Ostrya* spp, *Fraxinus* spp, *Acer* spp, *Buxus* spp, and *Corylus* spp) (Catsadorakis & Malakou, 1997). This is a globally unique natural area due to its geomorphology, rich ecology, and biodiversity (Abeliotis, Detsis, & Pappia, 2013).

The National Park infrastructure for visitors is almost non-existent and the low number of inhabitants (1200 people from twelve villages) and the fact that human activities consist mainly of extensive land-use practices have allowed conditions that favoured high biodiversity. However, the recent intensification of agriculture in favour of bean croplands and the ousting of cereals threatens many bird species. Hunting is practised throughout almost all the forestlands and poaching of rare and protected species such as brown bears (*Ursus arctos*) and wolves (*Canis lupus*) is extensive. Furthermore, illegal methods, such as night-hunting with car lights, have been partly responsible for the decimation of hares (*Lepus europaeus*) (Catsadorakis & Malakou, 1997).

2.1.2. Temperate broadleaf and mixed forests

This biome typically occurs in the Atlantic and Continental biogeographical regions of Europe. The Atlantic region has a very long coastline and is under the influence of the Atlantic Ocean and the North Sea. Hence, the climate is mild and humid. As for the Continental region, it connects to most other biogeographical regions of Europe and is characterized by the warm summers and cold winters (Condé & Richard, 2002). In this biome, we can find ecoregions such as the Cantabrian mixed forests, the western European broadleaf forests, the central European mixed forests, the Pannonian



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mixed forests, and the Dinaric Mountains mixed forests (Dinerstein *et al.*, 2017) (Table 2).

Under the Atlantic influence, the north-western Iberia is dominated by deciduous oak woodlands (*Quercus robur*, *Quercus pyrenaica*, and *Quercus petraea*), heaths (Ericaceae), brooms (*Genista*) and gorses (*Ulex*) (Benito Garzón, Sánchez de Dios, & Sainz Ollero, 2008; Desprat *et al.*, 2006). *Fagus sylvatica* can be found in pure and mixed stands or coexisting in forests dominated by other species (such as *Quercus spp, Fraxinus excelsior, Castanea sativa*, or *Acer* spp) (Benito Garzón, Sánchez de Dios, & Sainz Ollero, 2008; Sánchez de Dios *et al.*, 2016).

The natural forest cover of Continental Europe is mostly deciduous, where the characteristic species include the beech (*Fagus sylvatica*), the hornbeam (*Carpinus betulus*), several oak species, the elm (*Ulmus glabra*), the lime (*Tilia cordata*), and the ash (*Fraxinus excelsior*)(Condé & Richard, 2002).

The Dinaric region is dominated by mixed montane forests of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*), although the Norway spruce (*Picea abies*) is also abundant (Boncina, 2011).

In this biome, data has been gathered from 7 study areas: Peneda-Gerês National Park; Muniellos Natural Reserve; Melsunger Bergland; Bavarian Forest; Wachau; Southern Slovenia; and Northern Swiss Jura Mountains.

Peneda-Gerês National Park (PGNP), Portugal

The only National Park in Portugal is Peneda-Gerês National Park. It is located in North-western Portugal, on the border with Spain, near the transition with the Mediterranean region, and comprises altitudes between 800 and 1400m (Carvalho & Gomes, 2004). The predominant Atlantic climate is characterized by high levels of precipitation and drainage, but the diversified orientation of the relief and altitude variations provide a wide variety of microclimates (Soares *et al.*, 2005). PGNP is a protected area with a diverse array of flora, fauna, ecosystem types, and landscapes (Honrado *et al.*, 2003). These have a strong human influence, with pastures, agricultural fields, and small villages found mainly along valleys and lower altitude locations (Carvalho & Gomes, 2004). However, traditional agricultural practices are declining due to the abandonment and increasing intensification of more fertile agricultural lands at lower altitudes. These factors are inducing losses of both traditional knowledge and biodiversity in these mountain landscapes (Cerqueira *et al.*, 2010). In this region there



are high levels of tourism in warmer months and hunting is allowed, but geographically restricted. This area harbours rich populations of carnivores in relation to others in Portugal (Soares *et al.*, 2005). Here, the food habits and trophic niche of the carnivores red fox (*Vulpes vulpes*) and common genet (*Genetta genetta*) are known to overlap with the European wildcat. (Carvalho & Gomes, 2004).

Muniellos Natural Reserve (MNR), Spain

This reserve is located in southwestern Asturias (north-western Spain), in the western range of the Cantabrian Mountains and is a designated Biosphere Reserve (Merino-Sáinz & Anadón, 2015). The altitudes range between 650 and 1680m and the relief is abrupt and irregular (Prieto & Sánchez, 1992). The climate of the reserve is temperate oceanic (Merino-Sáinz & Anadón, 2015). The landscape consists mainly of mountainous agricultural–forest mosaics, where mountain tops are dominated by scrublands and mountain slopes and valleys by oak forests (Villafuerte *et al.*, 1996). This region is a remote, undisturbed area, with few human infrastructures and has one of the lowest human population densities in Asturias, although there are some pastures, agricultural fields and small villages mainly along valleys and lower altitude locations (Suárez-Seoane & García-Rovés, 2004). Hunting and predator control measures are forbidden inside the integral reserve and human access is restricted (Monterroso, 2014). This region supports two apex predators, the wolf and the brown bear (Clevenger, Purroy, & Pelton, 1990; Rodríguez *et al.*, 2007).

Melsunger Bergland (MB), Germany

Here the data was collected in a low mountain range known as Melsunger Bergland, approximately located 20km southeast of the city of Kassel, in central Germany. The elevation ranges between 300m and 500m. The Melsunger Bergland is in the transition zone between Atlantic and continental climates with mild and humid winters. This region is almost all covered by forest, being fragmented only by the village of Kehrenbach (with a population of 320 inhabitants) and its surroundings, as well as by a small road. Even though the forest is used for timber production and recreation activities, it supports a diverse community of animal species, including large mammals (Wening *et al.*, 2019). One of which, a small population of Eurasian Lynx started to recolonize the area in 2009 (Wening *et al.*, 2019).



Bavarian Forest (BF), Germany

The Bavarian Forest National Park is the oldest national park in Germany, boasting a relatively natural state since 1972 (Lausch, Fahse, & Heurich, 2011). It is situated in south-eastern Germany along the border to the Czech Republic in a mountainous area, with a variation in elevation between 600 and 1453m above sea level. The climate is cold in winter (with a considerable amount of snowfall) and hot in summer (with a strong dry period). The forest is dominated by Norway spruce (*Picea abies*), which co-occurs with European beech (Fagus sylvatica) on the slopes, and silver fir (Abies alba) at low and intermediate elevations. This forest has been affected by a massive proliferation of the spruce bark beetle (Ips typographus), which resulted in the death of mature *Picea abies* stands over an extensive area (Cailleret, Heurich, & Bugmann, 2014). The basic principle underlying the National Park's is the concept of leaving nature to itself (Lausch, Fahse, & Heurich, 2011), and the locals value the conservation of the forest (Müller, 2011), allowing it to develop without human interference. The density of human habitation is very low: in the core areas, it is less than 30 inhabitants per km²; and, at the margins, approximately 70. Therefore, the Bavarian Forest National Park is fundamental for the protection of large wildlife species, such as the lynx (Lynx lynx) and the capercaillie (Tetrao urogallus). There have been efforts for wildlife management and preservation of this area through measures such as wildlife population control, restriction of public access and disturbance to certain areas, and reduction of winter feeding (Heurich et al., 2011).

Wachau (WJ), Austria

Wachau-Jauerling Nature Park is located in the Danube valley between Melk and Krems in Lower Austria, about 80km west of Vienna. It encompasses the river landscape along approximately 35km of the valley of the Danube and the adjacent highlands. The geological, climatic, and scenic diversity is reflected in the flora and fauna species richness. The near-natural forests that slope down towards the Danube offer important habitats for many rare animal species, including the European wildcat (Gerngross, Slotta-Bachmayr, & Hagenstein, 2021). The main income source in the Wachau region is tourism and agriculture (Kieninger, Gugerell, & Penker, 2016).

Southern Slovenia (SS), Slovenia

In Slovenia, the Dinaric mountains and the Pannonian Basin are the regions outside the Eastern Alps. In the northern Dinaric Mountains (southern Slovenia), altitudes

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range from sea level to 1796m and the climate is influenced by the Alps, the Mediterranean sea, and the Pannonian basin (Krofel, Huber, & Kos, 2011). The region is densely forested and dominated by mixed and broad-leaved forests followed by coniferous forests (Güthlin *et al.*, 2011). The average human density in the Dinaric area of Slovenia is 54 people per km² (Perko, Adamic, & Oroz, 1998). Most human settlements are located in the valley bottoms leaving uplands scarcely populated. The region supports large carnivore species such as the Eurasian lynx, brown bear, and grey wolf (Krofel, Huber, & Kos, 2011).

Northern Swiss Jura Mountains (NSJM), Switzerland

Data collection took place in the northern Swiss Jura Mountains, in the Cantons of Jura and Bern, where a 100km² study area was located south-west of the city of Delémont and west of the city of Moutier. Elevation ranges from 460 to 1,337m above sea level (Maronde *et al.*, 2020). The climate here is wet and cold (Do Linh San, Ferrari, & Weber, 2007) and snow generally covers the ground from December to March (Rion *et al.*, 2018). Half of the entire surface of this mountain chain is covered by forest (Maronde *et al.*, 2020), but the landscape is also dominated by open and semi-open areas where cattle breeding is the main agricultural activity (Do Linh San, Ferrari, & Weber, 2007). Potential interference between people and wildlife may occur due to economic (such as woodcutting and cattle) and recreational activities (such as tourism and hunting) (Do Linh San, Ferrari, & Weber, 2007). The population density in the study area ranges from about 54 inhabitants to 97 inhabitants per km² (Maronde *et al.*, 2020). According to a previous study (Weber, 2018), about 75% of the study area was considered suitable habitat for the wildcat (Maronde *et al.*, 2020).

2.1.3. Temperate conifer forests

Finally, the Temperate conifer forests are located in the European Alpine biogeographical region, comprised of mountains from the Mediterranean to western Siberia. These mountains are characterised by low productivity, isolation, and a high level of endemism. Specifically in the Alps, the annual and spatial distribution of rainfall is highly variable, being higher in the summer in the north, while the south is very dry in summers (except for thunderstorms that may cause severe erosion). Despite this variability, rainfall increases with altitude, being is more or less equal across the Alps at higher altitudes (Condé & Richard, 2002). In this biome, data has been gathered in the



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eastern Italian Alps. Ecoregions here include the Alps conifer and mixed forests and the Dinaric Mountains mixed forests (Dinerstein *et al.*, 2017) (Table 2).

Eastern Italian Alps (EIA), Italy

The Alps are the largest mountain range in Europe, their elevation goes up to more than 4000m above sea level (Güthlin *et al.*, 2011). The Alps exhibit complex geomorphology and an array of microclimates which contribute to a wide variety of habitats and high levels of biodiversity(Condé & Richard, 2002). The Eastern Alps are dominated by coniferous forests, followed by mixed and broad-leaved forests (Güthlin *et al.*, 2011). The forests of the alps are composed of a relatively low number of tree species, the main being the conifers silver fir (*Abies alba*), Norway spruce (*Picea abies*), larch (*Larix decidua*), and several pine species (*Pinus sylvestris, Pinus cembra, Pinus uncinata, Pinus mugo*, and *Pinus nigra*) (Condé & Richard, 2002). Agricultural production is almost limited to livestock husbandry since arable fields are rare and restricted to low elevations (Güthlin *et al.*, 2011). The Alps are possibly the mountain range most used for tourism in the world (Bätzing, 2003), but many fauna species have found the high altitudes as a retreat from the human presence (Condé & Richard, 2002).

2.2. Field methods

Camera trapping data was provided by researchers who conducted projects with different aims, either explicitly targeting the European wildcat or where its detection was merely considered as by-catch. Ideally, data collection targeting European wildcats would be most adequate during the breeding season (in winter), when detection probability is the highest for this species (Kery *et al.*, 2011; Steyer *et al.*, 2013). However, the variety of goals and protocols of the projects available to this study generated high variability in chosen sampling seasons. Therefore, sampling season, duration and survey design varied across study areas (Table 3, Table 4). Overall, data collection spanned between 2009 and 2021, occurring in all seasons, and with different spatial designs (e.g., grids versus lines, 1 versus 2 camera traps per station), camera trapping deployment choices (e.g., camera models and flash types used), and use of lures (Figure 5). Below, I provide a brief description of each survey's protocols.





Figure 5 – Different camera deployment settings: (a) white flash, on trail, in MB; (b) infrared, on trail, in MMNP; (c) use of attractant and white flash, in WJ; and (d) use of infrared, off trail, in SP.



Table 3 – Projects integrated for the modelling of the European wildcat population density. (Reference included when corresponding data has been previously published).

Country	Study area	Project	Person of contact	Reference
Portugal	MtNP	Wildcat population density in NE Portugal: A regional stronghold for a nationally threatened felid	Dr Pedro Monterroso, Gonçalo Matias	(Matias <i>et al.</i> , 2021)
Portugal				
Spain	MNR MNP SANP CNP	 Ecological interactions in Iberian carnivore communities: study methods and effects of climatic factors and game management 	Dr Pedro Monterroso	(Monterroso, 2014)
Spain	SANP	Diez años de conservación del lince ibérico [Ten years of Iberian Lynx conservation]	Dr Pedro Monterroso	(Simón <i>et al.</i> , 2012)
Spain	CNP	Factors for the coexistence of mesocarnivores in National Parks of Mediterranean climate (OAPN 352/2011)	Dr Pablo Ferreras, Dr Pedro Monterroso	
Spain	SP	The Egyptian mongoose in Castilla-La Mancha: distribution, abundance, population trends, effects on its prey and social perception (SBPLY/17/180501/000184)	Dr Pablo Ferreras	
Spain	Crb Pgl SV	Spanish national census and population trends of wildcats	Dr Emilio Virgós	
Spain	MMNP	Coexistence of predators in time	Marc Vilella	
Spain		The population of wildcats in the Eastern Pyrenees	Dr Ferran Sayol	(Sayol <i>et al.</i> , 2018)
	NCAG	Spatial contura, recenture with multiple per	Pau Federico	
Switzerland	NSJM	invasive marks: An application to camera- trapping data of the European wildcat (Felis silvestris) using R package multimark	Maronde, Dr Fridolin Zimmermann	(Maronde <i>et al.</i> , 2020)
Germany	MB	Using camera traps to study the elusive European Wildcat <i>Felis silvestris silvestris</i> Schreber, 1777 (Carnivora: Felidae) in central Germany: what makes a good camera trapping site?	Dr Markus Port	(Wening <i>et al.</i> , 2019)
Germany	BF	Data collected in the Bavarian Forest	Dr Marco Heurich, Maik Henrich	
Italy	EIA	The wildcat in the Venetian Prealps	Marco Catello	
Italy	EIA	Progetto Lince Italia [Lynx project Italy]	Dr Anja Jobin	
Italy	Etn	volcano, Italy: a comparison of density estimation methods	Dr Stefano Anile	(Anile <i>et al.</i> , 2014)
Slovenia	SS	Eurasian lynx (Lynx lynx) monitoring with camera traps in Slovenia in 2018-2019	Dr Miha Krofel, Ursa Flezar	(Fležar <i>et al.</i> , 2019)
Austria	WJ	Ist die Europäische Wildkatze (Felis silvestris) zurück in Österreich? [Is the European wildcat back in Austria?]	Peter Gerngross	(Gerngross, Slotta- Bachmayr, & Hagenstein, 2021)
Albania	PNP	Data collected in Prespa National Park	Dr Christian Fiderer	

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Montesinho National Park (MtNP), Portugal

This survey was performed between October 2019 and March 2020, adopting the protocol described in (Matias, 2020). Briefly, a single camera per trapping station was deployed at 34 locations spaced $1,59 \pm 0,65$ km of each other, following a grid spatial sampling scheme. All cameras were equipped with infrared sensors (models Cuddeback Model H-1453, Moultrie M-990i, and Browning Strike Force HD Pro). Cameras were attached to wooden sticks or tree trunks, at 40–80 cm above ground level and were serviced every 15-20 days. All stations were lured with valerian extract and domestic cat urine, on a wood stick 2m from the camera (Matias, 2020).

Guadiana Valley Natural Park (GVNP), Portugal, Cabañeros National Park (CNP), Spain, Monfrague National Park (MNP), Spain, Sierra de Andújar Natural Park (SANP), Spain, Muniellos Natural Reserve (MNR), Spain, and Peneda-Gerês National Park (PGNP), Portugal

Data collection took place from 2009 to 2013, during which each study area was sampled in two distinct seasons for a period of at least 28 days: breeding (February-April) and non-breeding (July-October) (Monterroso, 2014). The study design described in (Monterroso, Alves, & Ferreras, 2011) was based on a 1 km resolution grid sampling scheme that overlayed each study area. Camera traps were located at alternating grid cell vertices, distanced approximately 1.4 km apart. Between 20 and 50 cameras were placed in areas of easy access and potentially good detection probability. The camera-trap models used were *Leaf River IR5* and *Scout-Guard* deployed with infrared flash and installed on trees at about 0.5–1.0 m off the ground. Scent lures were placed at approximately 2–3m from the camera traps. The attractants used included urine from Eurasian and Iberian lynxes (*Lynx lynx* and *Lynx pardinus*, respectively) and valerian (Monterroso, Alves, & Ferreras, 2011).

Sierra de Andújar Natural Park (SANP), Spain

This survey consisted in a minimum of 4 cameras per Iberian lynx territory, resulting in 1 station/km2 in almost the entire surface occupied by the species. Between March and October 2011, a single camera per trapping station was deployed at 28 locations, selected to maximize lynx detections. All cameras were equipped with infrared sensors (model DLC Covert II). Cameras were attached to wooden sticks or tree trunks, at 40–80 cm above ground level and were serviced every 7-20 days. Lynx urine and live pigeons were used as attractants in a subset of the camera stations (Simón *et al.*, 2012).

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Cabañeros National Park (CNP), Spain

An area of 6000 ha was sampled between February 2012 and April 2014, where 38 to 42 stations were deployed in each survey at an approximate distance of 1.5 km. 1 camera was deployed in each station attached to trees where available, or otherwise on stakes at 0.5 to 1.0 m from the ground. The models used were *SG550V*, *SG570V HCO OutDoor Products*, *USA*, with infrared flash. Iberian lynx urine and valerian extract were used as attractant.

Sierra de Picón (SP), Spain

An approximate area of 600 ha was sampled between February and June 2020, where 46 cameras were deployed at about 0.4km from each other (in the frame of a project aimed at estimating the density of Egyptian mongoose, *Herpestes ichneumon*). Each camera was attached to trees where available, or otherwise on deployed stakes with infrared sensors, at approximately 0.5 - 1.0 m from the ground. The models used were *SR1-BK Spartan (HCO Outdoor Products, Georgia, USA)*. Lure was also deployed: Iberian lynx urine and valerian extract.

Penyagolosa (Pgl), Spain, Sierra de la Virgen (SV), Spain, and Carabaña (Crb), Spain

Data collection occurred between 2019 and 2021 on defined plots between 1700-2100 ha with 12 stations each. Each station was deployed with one camera distanced over 1700 m on average. The cameras were usually placed on trees or, alternatively, on stakes (in areas with low tree cover or to improve the orientation of the camera). Several *BolyGuard* camera models were used with a white flash, 22-30 cm above ground). Iberian lynx urine was used as attractant.

Massis del Montseny Natural Park (MMNP), Spain

Sampling occurred between July 2018 and July 2019 in an area of approximately 150 km². 18 cameras were deployed about 0.8 to 5 km from each other on fauna trails. The models used were *Browning Strike Force HD Pro* and *Cuddeback C*, deployed with white flash (3) and infrared (15) at about 20-50 cm from the ground. No lure was used.

Northern Catalonia (NC) and Alta Garrotxa (NCAG), Spain

Sampling took place between 2013 and 2016 in an area of approximately 24km², and posteriorly between 2017 and 2019. 13 cameras were deployed at an approximate



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distance of 1km on game paths. The model used was *Cuddeback C*, deployed with both white flash and infrared sensors. No lure was used.

Northern Swiss Jura Mountains (NSJM), Switzerland

Field sampling took place in 2016 (February- April) using the study design described by (Maronde *et al.*, 2020). Accordingly, a 2.5km resolution grid was used to place 4 stations per grid cell over an area of 100 km². Each station included 2 camera traps, generating a camera trap density of 1/1.56 km². All camera traps were located on trails in optimal sites for wildcats, based on the researchers and local game wardens' experience, and ensuring the coverage of the whole elevation gradient. The models used included *Cuddeback-Ambush*, *Cuddeback-Capture*, and *Cuddeback-C1*, deployed with white flash and installed approximately 40 to 60 centimetres above ground level. Valerian tincture was used as lure, sprayed in wooden sticks of about 60 cm height (Maronde *et al.*, 2020).

Melsunger Bergland (MB), Germany

Field sampling was carried out in 2017 (June-October) and the study design is described in (Wening *et al.*, 2019). In summary, 25 sampling stations were placed in a 1km resolution grid (1 station per grid cell overlaying the forest). The average distance between stations was 863m (±207m). Two camera traps were installed in each station located on trails (one camera on each side of the trail). The models used were *Cuddeback-Ambush* and *Cuddeback-C1*, deployed with white flash and placed in trees or poles (at approximately 0.30m above ground). No lures were used (Wening *et al.*, 2019).

Bavarian Forest (BF), Germany

Sampling in the Bavarian Forest occurred in 2018 and 2019. A total of 108 cameras were deployed all off trail with an infrared flash, according to a systematic grid. The average distance between cameras was $1052m \pm 163m$ and the model used was *Cuddeback C2*.

Eastern Italian Alps (EIA), Italy

The area was sampled during 2017 and 2020, where stations were defined systematically in a grid. The distance between each station was $2172m \pm 2705m$ where either 1 or 2 cameras were deployed (at a distance of approximately 3-4 m from each



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other in the stations with 2 cameras), which resulted in a total of 78 cameras. The traps were placed on tree trunks with white and infrared flash at about 40-80 cm from the ground. The models chosen for cameras were *Cuddeback, Secam, Browning*, and *Moultrie*. Lure was not used.

Mount Etna (Etn), Italy

Field sampling occurred in 2010 for 120 days (May-September). The survey design is described in (Anile *et al.*, 2014) and consisted of two trapping lines with 9 sampling stations (two camera traps facing each other in each station). The distance between each station was approximately 1351 ± 790 m. The cameras were placed on trails known to be often used by wildcats. The model used was *Sony-DSC-W55*, installed on trees (at 50 ± 10 cm from the ground). No lures were used (Anile *et al.*, 2014).

Southern Slovenia (SS), Slovenia

Sampling took place between 2018 and 2020, from late August until the end of April every year. 318 stations were defined in a 3km resolution grid, taking into account previous knowledge of lynx occurrence in the study area. Each station was equipped with 1 to 3 camera traps, resulting in the deployment of 407 cameras. The camera models chosen were the *Cuddeback X-Change*TM *Color Model 1279* (which was deployed with white or IR flash), the *Cuddeback X-Change*TM *Color Model 1213*, and the *StealthCam STC-G42NG* (which were both deployed with IR). Cameras with white flash were placed on remote locations such as animal paths, natural stone walls, rocky terrain, etc., while cameras with IR were placed at locations which could be frequented by people (forest roads, paths, etc.) to avoid theft (Fležar *et al.*, 2019).

Wachau (WJ), Austria

Sampling took place between 2019 and 2020 in an area of approximately 12 km². 11 camera traps were placed opportunistically on deer crossings, forest roads or other guidelines, using white flash, and at an average distance of 876m \pm 809m. The models used were *Cuddeback Professional, Cuddeback G*, and *Cuddeback Ambush*. Valerian was used as an attractant on wooden sticks in front of the cameras (Gerngross, Slotta-Bachmayr, & Hagenstein, 2021).

Prespa National Park (PNP), Albania

Sampling in Prespa National Park occurred from August 2020 to March 2021 using a 1 km resolution grid. A total of 70 cameras (1 in each station) were deployed all



off trail with an infrared flash, at a height of approximately 50 cm. The model used was Cuddeback C and no lure was deployed.



Table 4 – Sampling details for each of the study areas included. (# cameras per station – number of cameras deployed per station; NA - sampling details were not registered by the project).

Study area	Sampling period	Spatial design	# cameras per station	Inter- station distance (m)	Camera models	Flash type	Lures
MtNP	2020	Grid	1	1578 ± 636	Cuddeback Model H- 1453, Moultrie M-990i, Browning Strike Force HD Pro	Infrared	urine, valerian
GVNP	2009-2010	Grid	1	1006 ± 327	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
PGNP	2010-2011	Grid	1	1028 ± 266	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
CNP	2009-2010	Grid	1	1100 ± 300	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
CNP	2012-2014	Grid	1	873 ± 355	SG550V, SG570V HCO OutDoor Products, USA	Infrared	Urine, valerian
MNR	2010-2011	Grid	1	1088 ± 293	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
SANP	2012	Grid	1	1092 ± 165	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
SANP	2011	Opportunistic	1	1233 ± 1531	DLC Covert II	Infrared	Some stations (urine and pigeons)
MNP	2012-2013	Grid	1	791 ± 277	Leaf River IR5, Scout- Guard	Infrared	Urine, valerian
SP	2020	Grid	1	371 ± 283	SR1-BK Spartan (HCO Outdoor Products, Georgia, USA	Infrared	Urine, valerian
Crb	2020	Grid	1	1461 ± 244	BolyGuard	White	Urine
Pgl	2020	Grid	1	1563 ± 207	BolyGuard	White	Urine
SV	2020	Grid	1	1471 ± 133	BolyGuard	White	Urine
MMNP	2018-2019	Opportunistic	1	1187 ± 326	Browning Strike Force HD Pro, Cuddeback C	Both	None
NC	2013-2016	Grid	1	833 ± 253	Cuddeback C	Both	None
NCAG	2017-2019	Grid	1	1516 ± 1037	Cuddeback C	Both	None
NSJM	2016	Grid	2	787 ± 215	Cuddeback-Ambush, Cuddeback-Capture, Cuddeback-C1	White	Valerian
MB	2017	Grid	2	863 ± 207	Cuddeback-Ambush, Cuddeback-C1	White	None
BF	2018-2019	Grid	1	1052 ± 163	Cuddeback C2	Infrared	NA
EIA	2017-2020	Grid, Opportunistic	1-2	2172 ± 2705	Cuddeback, Secam, Browning, Moultrie	Both	None
Etn	2010	Line	2	718 ± 272	Sony-DSC-W55	White	None
SS	2018-2019	Grid	1-3	680 ± 1006	Cuddeback X-Change Color Model 1279	Both	NA
WJ	2019-2020	Opportunistic	1	876 ± 809	Cuddeback Professional, Cuddeback G, Cuddeback Ambush	White	Valerian
PNP	2020-2021	Grid	1	1269 ± 302	Cuddeback C	Infrared	None

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2.3. Compilation and standardization of the data sets

Standardization of all datasets was vital to allow comparability across different regions. A unified database was created to compile all data sets from the different projects, where all the data (including photographs and effort tables) were organized with the same structure. All putative European wildcat pictures obtained from the different collaborators were organized under a hierarchical folder structure, and each photo's metadata and file organization was extracted using the camtrapR package (Niedballa et al., 2016) in R software v.4.0.3 (R Core Team, 2019). All camera stations' coordinates were converted into the same coordinate system (WGS84, crs = 4326) using the sf R package (Pebesma, 2018) and were visually checked for outlying locations. Effort dates (set, removal, and malfunctioning periods) were converted to the same format (day/month/year) and individually checked for errors, such as the end date being earlier than the start date. Doubtful or inconsistent data (e.g. wrong dates) was not included in the analysis. Important detection variables were identified to account for the variability in survey designs, namely, the sampling season, the deployment of the cameras on or off trail, the model of the cameras used, whether bait was deployed, and the type of flash used (white flash or infrared).

Camera-trapping surveys should be conducted over a short period of time to ensure demographic closure (i.e., closed population assumption) (Karanth & Nichols, 2002; Royle et al., 2009). This assumption is based on the principle that the population at each site does not experience births, deaths, or migration throughout the course of the study, and so it remains constant during this period (Dail & Madsen, 2011). This period is intimately associated with the life history of the study species (Dupont et al., 2019). Hence, a period of 90 days has been recommended for felid species (Brassine & Parker, 2015; Karanth & Nichols, 1998; Karanth & Nichols, 2002). However, this might not be sufficient for species with low detectability or that occur at very low population densities, which sometimes require the number of trapping days to be extended to improve robustness of the results, even though the closure assumption may be violated (Brassine & Parker, 2015; Dupont et al., 2019; Foster & Harmsen, 2012). Therefore, a tradeoff between bias (introduced by the risk of violation of the closure assumption) and precision (achieved with a higher number of captures) is needed to obtain an optimal sampling period (Dupont et al., 2019). (Brassine & Parker, 2015) suggest a period of 130 days for other felid species occurring at low population densities. In the case of the data sets available for this study, both situations occurred: long sampling periods with an

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adequate number of captures; and short sampling periods with very few captures that would not allow further data analysis. To reach that trade-off, shorter sampling periods were defined (primary sampling periods according to Pollock's robust design (Pollock, 1982)) from the original long surveys, to comprise at most 130 days (Brassine & Parker, 2015) (Table 5).

Table 5 - Effort summary. 2053 stations were deployed during a total of 5657 sampling days over 53 surveys. Survey effort varied 5 and 210 cameras/survey (41.64 ± 47.01, mean ± SD) and mean survey length was 100.39 ± 38.09 (range: 30-130). (Survey – period of 130 days, at most, defined for the data analysis; Start/End – dates when sampling started/ended; #Stations - number of sampled stations; #Cameras - number of cameras deployed).

Study area	Survey	Start	End	Sampling season	Sampling time (days)	#Stations	#Cameras
	2009	30/07/2009	05/09/2009	summer	37	39	39
GVNP	2010	03/03/2010	05/04/2010	spring	33	39	39
PGNP	2010	05/10/2010	12/11/2010	autumn	38	35	35
	2011	05/04/2011	12/05/2011	spring	37	35	35
MtNP	2020	09/11/2019	18/03/2020	autumn-winter	130	34	34
	2009	24/09/2009	28/10/2009	autumn	34	44	44
	2010	26/01/2010	26/02/2010	winter	31	44	44
	2012	11/04/2012	19/06/2012	spring	69	60	60
CNP	2013.1	20/02/2013	22/04/2013	spring	61	42	42
	2013.2	15/10/2013	19/11/2013	autumn	35	38	38
	2014	15/01/2014	23/04/2014	winter-spring	98	40	40
SP	2020	01/02/2020	10/06/2020	spring	130	46	46
	2010	24/08/2010	29/09/2010	summer	36	41	41
MINK	2011	02/03/2011	04/04/2011	spring	33	42	42
	2012	21/08/2012	23/10/2012	autumn	63	50	50
WINP	2013	09/01/2013	13/02/2013	winter	35	37	37
	2012.1	29/02/2012	30/03/2012	winter	30	20	20
SANP	2012.2	22/08/2012	16/10/2012	autumn	55	20	20
	2011	01/02/2011	11/06/2011	spring	130	28	28
	2013	15/12/2013	24/04/2014	winter	130	7	7
	2014.1	25/04/2014	02/09/2014	summer	130	7	7
NC	2014.2	03/09/2014	31/12/2014	autumn	120	7	7
	2015	15/06/2015	23/10/2015	summer	130	6	6
	2016	24/10/2015	02/03/2016	autumn-winter	130	6	6
	2017	12/08/2017	20/12/2017	autumn	130	5	5
	2018	21/12/2017	30/04/2018	winter	130	5	5
NCAG	2019.1	01/12/2018	01/04/2019	winter	121	12	12
	2019.2	02/04/2019	10/08/2019	spring-summer	130	6	6
	2018	02/07/2018	09/11/2018	summer-autumn	130	18	18
MMNP	2019.1	10/11/2018	20/03/2019	autumn-winter	130	18	18
	2019.2	22/05/2019	29/09/2019	summer	130	17	17
Crb	2020	19/11/2020	29/01/2021	autumn	71	12	12
Pgl	2020	15/06/2020	15/09/2020	summer	92	12	12
SV	2020	30/05/2020	30/08/2020	summer	92	12	12
MB	2017	26/06/2017	07/10/2017	summer	103	25	50
	2018	07/05/2018	14/09/2018	summer	130	108	108
RF	2019	11/04/2019	19/08/2019	spring-summer	130	106	106



Study area	Survey	Start	End	Sampling season	Sampling time (days)	#Stations	#Cameras
	2017	09/09/2017	17/01/2018	autumn	130	18	18
	2018	01/05/2018	08/09/2018	summer	130	20	20
	2019.1	19/07/2019	26/11/2019	summer-autumn	130	42	42
LIA	2019.2	27/11/2019	05/04/2020	winter	130	44	44
	2020.1	06/04/2020	14/08/2020	spring-summer	130	47	49
	2020.2	15/08/2020	23/12/2020	autumn	130	26	28
Etn	2010	14/05/2010	11/09/2010	spring-summer	120	18	36
\\/	2019	13/11/2019	20/02/2020	autumn-winter	99	8	8
VVJ	2020	21/02/2020	31/05/2020	winter-spring	99	11	11
NSJM	2016	22/02/2016	30/04/2016	winter-spring	68	64	128
	2018	06/08/2018	14/12/2018	autumn	130	147	179
66	2019.1	15/12/2018	24/04/2019	winter	130	122	151
33	2019.2	20/08/2019	28/12/2019	autumn	130	155	210
	2020	29/12/2019	22/04/2020	winter	115	154	210
DND	2020	27/08/2020	02/11/2020	summer-autumn	68	66	66
FINE	2021	08/11/2020	18/03/2021	autumn-winter	130	55	55

2.4. Estimation of European wildcat density through SCR modelling

Field surveys

All surveys with spatial wildcat recaptures were used to generate independent SCR density estimates. These included: GVNP in 2010, MtNP, Pgl, Etn, NSJM, NC in 2014.2, MB, WJ in 2019 and 2020, SS in 2019.1, SP, SANP in 2011, and EIA in 2020.1.

Species and Individual identifications

All camera trapping records of potential wildcats identified were classified based on pelage characteristics according to 3 marking systems (Kitchener *et al.*, 2005; Ragni & Possenti, 1996; Spassov, Simeonovski, & Spiridonov, 1997), and only records compatible with putative wildcats were retained for further analyses. Individual identifications were performed by external examination of pelage patterns (Figure 6), such as number, dimension and shape of spots and stripes on the limbs and body, and individual tags were assigned using *Digikam* software (v.6.4.0). Individual identity was based in a comparative assessment of morphological similarities between different detection records from the right flank, left flank or both, whenever possible (e.g. if individuals show both flanks in the same detection record, or if two cameras were deployed per trapping station) (Johansson *et al.*, 2020). Detection records that caused uncertainty in wildcat identity (e.g., due to poor photo quality) were discarded. Additional





Figure 6 - Individual MB_R2 captured in two different occasions and stations (above), and posterior image enhancement for comparison during individual identification process (below).

procedures were employed to prevent individual misidentification, as suggested by (Choo *et al.*, 2020), including checking the photograph from each new recapture against all previous photographs of the recaptured individual and other individuals and placing photographs side-by-side for comparison to ensure that no individual was counted more than once.

Individual wildcats were assumed to occur in only one study area, unless the minimum distance between trapping stations of neighbouring study areas was lower than three 3 times the diameter of the largest wildcat home range (HR) recorded in literature - 59.78 km² (Oliveira *et al.*, 2018) (Equation 1). This distance allowed accounting for possible explorative behaviour of individuals. Therefore, study areas further than 26.2 km apart were considered independent.

Study site independence distance =
$$3 * diameter_{HR} = 3 * 2 * \sqrt{\frac{59.78}{\pi}} = 26.173 \ km$$

Equation 1 - Study site independence distance calculation, where $diameter_{HR}$ is the diameter of the largest wildcat home range recorded in literature.

Spatial capture-recapture density estimates

All surveys with spatial wildcat recaptures were used to generate independent SCR density estimates using the MLE package *oSCR* v.0.42.0 (Sutherland, Royle, & Linden, 2019) in *R* software v.4.0.3 (R Core Team, 2019). As in any SCR approach, this package assumes that each individual from a population has an activity centre, which can be considered the individual's home range centre during the survey. The individual encounter probability is then expressed as inversely related to the distance between the activity centre of the individual and the trap location (Royle *et al.*, 2013a). The spatial distribution of the activity centres is assumed to be constant, following a homogenous distribution *i* ~ *Uniform(SS)*, where *i* is the activity centre and SS is the state-space (Royle & Young, 2008). SS is the defined area that includes all traps and a buffering area (i.e., including unsampled areas of the survey). The SS should be large enough to comprise all individuals (*N*) that possibly have been detected in the survey (Royle *et al.*, 2013a).

The *oSCR* framework requires two primary data: i) the trap deployment file (TDF), which includes information concerning the effort and locations of the stations of each survey; and ii) the encounter data file (EDF), that contains the individual-specific encounter histories per trapping device (Sutherland et al. 2019). Specifically, the TDF consists of a binary matrix revealing the sampling days when each camera was active (1) or inactive (0), with the station identification and the respective cartesian geographic information (X and Y coordinates). The EDF consists of a matrix disclosing the trapping station and sampling day each identified wildcat was captured, and the respective session. These objects were integrated into list objects that compose the SCR Frame (SF) used by *oSCR*.

Furthermore, the baseline probability of encountering an individual (*p0*) by a trap is a function of the distance between the detector and the individual's activity centre. This function allows us to estimate the average of individual movement rate (sigma, σ) within SS in relation to its activity centre (i.e., the probability of detecting an individual decreases with increasing distance between its activity centre and detector position) (Efford, Borchers, & Byrom, 2009; Royle *et al.*, 2014). As such, a density estimate (D) can be measured as (Equation 2). In this context, a discretized state space (SS) needs to be defined. This is created using trap locations contained in the SF, and by specifying a buffer region and resolution of the discrete surface (Sutherland, Royle, & Linden, 2019). The buffer size was indexed to the mean maximum distance moved (MMDM) by the wildcats in each respective study area (Equation 3) (Royle *et al.*, 2013c), and a



common resolution of 1000m was used, as it corresponds to the minimum wildcat home range described in the literature (1.22 km²; (Oliveira *et al.*, 2018)).

$$D = \frac{N}{SS}$$

Equation 2 - Estimation of density, where D is the density estimate, N is the total number of individuals recorded in the survey, and SS is the defined state-space.

Buffer =
$$3 * \frac{MMDM_{SF}}{2}$$

Equation 3 – State-space buffer distance calculation, where $MMDM_{sF}$ is the mean maximum distance moved by the wildcats captured in the survey

For each SCR Frame, we fitted a set of candidate models including all covariate combinations and also a null model. Detection variables used to model baselined detection probability (p0) included the season of the year when sampling occurred, the placement of the cameras on- or off-trail, the models of the cameras used, whether bait was used, and the number of cameras deployed per station. This depended on the information available for each survey and its variability within the survey design. We integrated the capture histories from each flank as different sessions in the same model, which was coerced to produce the same density estimate (Chutipong, Steinmetz, & Gale, 2021; Matias et al., 2021). Models in each model set were ranked and selected according to Akaike information criteria (AIC) (Akaike, 1973; Burnham & Anderson, 2002), as topranked models are considered to have the highest predictive performance in the set (Fuller et al., 2016). Additionally, the coefficient of variation of each density estimate was generated (Equation 4). In cases where the best model corresponded to a high coefficient of variation density estimate (>0.6), an alternative model corresponding to a lower coefficient of variation density estimate was chosen. Density estimates of different surveys from the same study area were selected according to the coefficient of variation (i.e., the models selected were the ones that generated density estimates with lowest coefficient of variation).

$$coefficient of variation = \frac{SE_D}{D}$$

Equation 4 – Coefficient of variation calculation, where D is the density estimate, and SE_D is the standard error of de density estimate.

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2.5. Mean local abundance modelling and forecasting wildcat density across Europe

We used the RN formulation (Royle & Nichols, 2003) to fit abundance models to our occupancy data from different populations across Europe and posteriorly generate estimates of study area-specific mean local abundance (MLA). A generalized linear model (GLM) approach was fitted under the hypothesis that there is a relationship between density (as provided by *oSCR* estimates) and mean local abundance of wildcat populations across Europe. The exceptions were the cases of NSJM and CNP, for which reference estimates will be used based on prior information collected by these researchers and the higher robustness of their results, respectively, which have led us to believe that those approaches provide estimates closer to real population densities (Ferreras *et al.*, submitted; Maronde *et al.*, 2020). Simultaneously, the RAIs, defined as the capture rates of wildcats, were calculated and tested for its relationship with density. Given the models describing the relationships between density and both the mean local abundance and the relative abundance index have more support than the null model, we may then predict density estimates for populations that did not have enough available information for density estimation through SCR analysis.

Mean local abundance estimation

Local abundances (i.e., the number of animals associated with each station of a certain study area) were estimated in *unmarked* v.1.0.1 (Fiske & Chandler, 2011). The model-fitting function *occuRN* allows estimation of abundance from the presence and absence data of animals without having to uniquely identify the individuals sampled (Royle & Nichols, 2003). The RN model relates the detection probability of the species to the number of individuals available for detection at each site (Fiske & Chandler, 2011). For this purpose, the unmarked frame organizes detection/non-detection data along with the covariates.

Wildcat detections were formatted in a binary occupancy matrix with the respective stations and occasion of encounter (1 for presence and 0 for absence of the species), while detection variables were included in a data frame relating the covariates that vary at the site level with the respective station. These two objects were then integrated into an unmarked frame for each survey.

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For model fitting, different combinations of detection variables were used, when available, creating a set of candidate models for each survey. Detection variables included the sampling season, the placement of the cameras on- or off-trail, the models and the number of the cameras used per station, and whether bait was used or not. The same surveys used to generate density estimates in oSCR were used for estimating local abundance, as for the remaining study areas, all surveys were tested in model sets and posteriorly selected according to the goodness of fit test. A chi-square goodness of fit test was applied to the models with 1000 bootstrapped samples. A p-value of approximately 0.5 was considered a good fit, however, the literature is not clear on a threshold, so all p-values departing from either 0 or 1 were considered as an acceptable fit (Kéry & Royle, 2015). Overdispersion was tested by the c-hat value, which should be close to 1. However literature does not have a solution for c-hat<<1, or when it tends to zero (Mazerolle, 2020; White & Seymour, 2005)). Model sets validated by the goodness of fit were ranked and selected by AIC (Akaike, 1973). For each survey, the model presenting the lowest AIC of the model set was selected, as considered to have the highest predictive performance in the set (Fuller et al., 2016). Whereas, for each study area, the model presenting the goodness of fit p-value closest to 0.5 was selected as the best fit and further used in the estimation of mean local abundances.

For each study area, the *ranef* function of the *unmarked* package was used to obtain the empirical Bayes estimates of abundance at each station. The *bup* function of the same package was applied to these estimates in order to obtain the best unbiased predictor of abundance for each station (Fiske & Chandler, 2011; MacKenzie *et al.*, 2006; Royle, 2006). Mean local abundances for each study area were calculated as the mean best unbiased predictor of abundance estimates.

Relative abundance index calculation

The number of wildcat detections per 100 trap days, i.e., relative abundance index (Equation 5), was calculated for the same surveys used to generate density estimates in *oSCR* and mean local abundances in *unmarked*. The number of trap nights of each survey was considered the total number of days all cameras were active. Detection records were considered independent when the time between consecutive detections was >30 minutes (Rocha *et al.*, 2021).



 $RAI = \frac{detections * 100}{trap \ nights}$

Equation 5 - RAI calculation, where detections is the number of independent detection events.

Assessing the relationships between density and mean local abundance and the relative abundance index

The *glm* function (from the *R Stats* package v.4.0.3 (R Core Team, 2019)) was used to fit a generalized linear model (GLM) describing a logarithmic relationship (i.e., a linear relationship at the logarithmic scale, allowing increased data for smaller values and skewness towards large values) between the density estimates obtained in *oSCR* and both the mean local abundance estimates obtained in *unmarked* and the respective RAI estimates (Table 6). The dispersion of each mean local abundance estimate was included as observation weights of each estimate in the model (Equation 6). Models were fitted with and without the observation weights. Because our data was over dispersed, non-negative, non-integer, we used the quasipoisson family with a log link function (McCullagh & Nelder, 1989; Wedderburn, 1974). However, this family does not provide an AIC value to be used in the model selection process. Therefore, the deviance of each model and corresponding models using the gaussian family were used for model selection (Bolker, 2021). The function *predict.glm* was then used to obtain predicted density estimates for study areas with poor data using their mean local abundance estimates.

weight = $\frac{1}{MLA \text{ confidence interval amplitude}/MLA}$

Equation 6 – Calculation of the mean local abundance estimate weights on the glm model, where weight is the observation weight, and MLA is the estimated mean local abundance.

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Table 6 – GLM models fitted to test both SCR-RN and SCR-RAI relationships. (Family - distribution family used in the model; Model – parameterization of each model; weights – use of observation weight as calculated in Equation 6 in the model)

Family	Model
quasipoisson	d ~ log(mla), weights
quasipoisson	d ~ log(mla)
quasipoisson	d ~ log(rai)
quasipoisson	d ~ 1
gaussian	d ~ log(mla), weights
gaussian	d ~ log(mla)
gaussian	d ~ log(rai)
gaussian	d ~ 1

3. Results

3.1. Estimation of European wildcat density through SCR modelling

Wildcat individual identifications

Of the total 1293 wildcat detections, 92 individuals were identified by the left side, 110 by the right side, and 30 by both sides simultaneously (Table 7, Supplementary Information 1, Supplementary Information 2). Out of the 53 surveys, only 14 presented spatial recaptures, and MNP was the only study area where there were no wildcat captures in any of the surveys.

Table 7 – Wildcat detections and number of individuals identified per survey with SCR (Identifications of surveys with no SCR are in Supplementary information). (Survey – Survey per study area, as defined in Table 5; #Detections – number of wildcat detections; id_R - right side identifications; id_L - left side identifications; id_C - complete identifications, i.e., identification of the left and right flank simultaneously).

Survey	#Detections	#id_R	#id_L	#id_C
GVNP, 2010	17	1	5	0
MtNP	24	4	4	2
CNP, 2012	10	2	2	0
SP	6	1	1	0
SANP, 2011	8	2	2	2
NC, 2014.2	8	0	1	0
Pgl	18	5	3	3
MB	141	15	17	7
EIA, 2020.1	79	2	7	0
Etn	74	10	8	3
WJ, 2019	30	3	3	0
WJ, 2020	36	3	2	0
NSJM	86	12	10	5
SS, 2019.1	139	11	11	0

Spatial capture-recapture density estimates

Survey effort varied between 7 and 151 cameras/survey (49.85 ± 40.10) and survey length was 104.15 ± 28.81 (range: 33-130). Density estimates were obtained for 10 (45.4%) study areas across Europe, including for populations that have never been studied before.

Average spatial captures per individual varied between 0.00 in NC (Spain) and 3.00, also in NC, and averaged 1.51 \pm 0.58. The mean maximum distance moved by



wildcats ranged from 527 m in CNP (Spain) to 6895 m in WJ (Austria) and averaged 2276.17 ± 1845.98 m (Table 8).

Table 8 – Spatial recaptures summary of each survey. (Survey – Survey per study area, as defined in Table 5; avg spatial caps (L) – average spatial captures of the left flank per individual; avg spatial caps (R) - average spatial captures of the right flank per individual; MMDM_L – mean maximum distance moved by wildcats identified on the left flank; MMDM_R – mean maximum distance moved by wildcats identified on the right flank; Buffer – area defined according to Equation 3; State-space – resulting area of inference for density estimates).

Survey	Avg spatial caps (L)	Avg spatial caps (R)	MMDM_L (m)	MMDM_R (m)	Buffer (m)	State-space (km ²)
GVNP, 2010	1.20	1.00	2062	0	3092	173
MtNP	1.75	2.00	2633	3720	4928	489
CNP, 2012	1.00	1.50	0	527	791	80
SP	2.00	1.00	538	0	806	15
SANP, 2011	1.50	1.50	1115	1115	1673	110
NC, 2014.2	3.00	0.00	1196	0	1795	22
Pgl	1.00	1.50	0	1731	2596	81
MB	2.06	2.13	1712	1730	2580	81
EIA, 2020.1	1.00	1.50	0	1298	1947	360
Etn	1.50	1.10	1495	3624	2881	73
WJ, 2019	1.67	1.33	2831	5614	5637	252
WJ, 2020	2.50	1.67	6895	6386	9961	579
NSJM	2.40	2.08	2654	3675	4637	296
SS, 2019.1	1.09	1.09	1289	74	1023	306

In general, null models were the top-ranked models across model sets, except in WJ (Austria), SS (Slovenia), and EIA (Italy), where the baseline detection probability (p0) explained by the camera model (WJ) and the type of flash used (SS and EIA) presented a higher predictive performance (Supplementary Information 3). Sigma estimates varied between 425 ± 194 m in CNP (Spain) and 2574 ± 465 in MtNP (Portugal) and averaged 991 ± 612 m, whereas *p0* estimates varied ranged from 0.002 ± 0.002 in SP (Spain) to 0.042 ± 0.035 in NC (Spain) and averaged 0.017 ± 0.011 (Supplementary Information 4). Average density estimates were 11.3 ± 11.6 individuals/100km² and varied between 1.13 ± 0.44 in MtNP (Portugal) and 33.3 ± 6.2 individuals/100km² in MB (Germany) (Table 9). Three study areas - SP, NC, and CNP - did not fulfil the minimum coefficient of variation threshold, and therefore those estimates were discarded from the SCR analysis (a prediction will be made posteriorly along with the data sets with less information).

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Table 9 – Density estimates of European wildcat for each study area, as obtained from the top-supported spatial capturerecapture models. (Survey – Survey per study area, as defined in Table 5; SE – Standard error; Coefficient of variation – Coefficient of variation of the density estimate, calculated as SE / Density; Model – Parameterization of the top-supported model.)

Survey	Density (individuals/100km ²)	SE	Coefficient of variation	Model
GVNP, 2010	6.481	3.563	0.550	~1
MtNP	1.130	0.437	0.387	~1
Pgl	10.165	5.620	0.553	~1
Etn	28.782	10.745	0.373	~1
NSJM	7.881	1.730	0.219	~1
MB	33.308	6.138	0.184	~1
WJ, 2019	1.816	0.854	0.470	p0~Model
SS, 2019.1	23.245	11.989	0.516	p0~White.flash
SANP, 2011	2.662	1.530	0.575	~1
EIA_2020.1	4.644	2.009	0.432	p0~White.flash

3.2. Mean local abundance modelling and forecasting wildcat density across Europe

Mean local abundance estimates (MLA)

The recorded presence of wildcats varied between 1 occasion in PGNP, 2010 (Portugal) and 132 occasions in MB (Germany), and averaged 24.16 ± 34.34 occasions (Supplementary Information 5).

Out of all study areas, one - BF - did not provide enough independent detections to allow fitting the RN model in unmarked. Overall, null models were the top-ranked models, except where detection probability explained the placement of cameras on- or off- trails showed a higher predictive power (EIA, GVNP, MtNP, SS, and MNR). Other detection covariates, such as the number of cameras deployed per station, the camera models used, and the flash type, only occasionally improved the predictive power of models (SS, WJ, MMNP, and NCAG) (Supplementary Information 6, Table 10).

Mean local abundance estimates (95% confidence interval) varied between 0.083 (0.071 - 0.107) in SANP, 2011 (Spain) and 14.25 (7.833 - 21.667) in NCAG, 2019.2 (also in Spain) and averaged 2.584 ± 4.251 (Table 11).



Table 10 – Best model and respective goodness of fit of each study area. (Survey - Survey per study area, as defined in
Table 5; Model – Parameterization of the top-supported model; Chi-sq - Pearson chi-square statistic; p-value – p-value
assessed from the parametric bootstrap; c-hat - estimate of the overdispersion parameter.)

Survey	Model	Chi-sq	p-value	c-hat
CNP, 2014	~1	6.380E+03	0.380	0.022
EIA_2020.1	~trail	2.640E+25	0.418	0.000
Etn	~1	6.810E+15	0.261	0.000
GVNP, 2010	~trail	8.420E+04	0.581	0.002
MB	~1	6.810E+15	0.261	0.000
MtNP	~trail	5.600E+08	0.625	0.000
NSJM	~1	5.480E+09	0.174	0.000
Pgl	~1	1.370E+04	0.270	0.000
SANP, 2011	~1	4.890E+07	0.236	0.000
SS, 2019.1	~trail+cams	2.520E+16	0.204	0.000
WJ, 2019	~model	1.020E+18	0.270	0.000
Crb	~1	5.340E+06	0.338	0.000
MMNP_2019.1	~model+flash	3.920E+10	0.338	0.000
MNR, 2010	~trail	2.940E+04	0.392	0.001
PGNP, 2011	~1	1.120E+03	0.376	0.004
PNP, 2021	~1	2.260E+07	0.410	0.000
SP	~1	1.440E+02	0.523	0.002
SV	~1	1.370E+04	0.271	0.000
NC, 2015	~1	1.270E+04	0.540	0.000
NCAG, 2019.2	~model	2.230E+14	0.472	0.000

Table 11 - Mean local abundance and respective confidence intervals for each study area. (Survey - Survey per study area, as defined in Table 5; Cl 95% - confidence intervals with a level of confidence of 0.95.)

Survey	Mean local abundance		CI 95%
GVNP, 2010		0.395	0.231 - 1.333
MtNP		0.421	0.265 - 1.588
Pgl		0.108	0.083 - 0.167
Etn		3.034	1.444 - 5.500
NSJM		0.640	0.375 - 1.625
MB		4.023	2.160 - 6.720
WJ, 2019		0.587	0.500 - 1.000
SS, 2019.1		0.636	0.377 - 1.811
SANP, 2011		0.083	0.071 - 0.107
EIA_2020.1		0.134	0.109 - 0.174
CNP, 2014		1.145	0.150 - 3.175
Crb		0.086	0.083 - 0.083
MMNP, 2019.1		1.361	0.278 - 3.500
MNR, 2010		1.094	0.146 - 3.073
PGNP, 2011		0.206	0.083 - 1.083
PNP, 2021		0.601	0.273 - 2.327
SP		10.674	5.130 - 17.130
SV		0.108	0.083 - 0.167
NC, 2015		12.093	5.667 - 19.000
NCAG, 2019,2		14.250	7.833 - 21.667



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Relative abundance index (RAI)

Sampling effort ranged between 458 (NCAG, Spain) and 10868 (SS, Slovenia) trap nights over the considered surveys. NC (Spain) was the survey that presented fewer wildcat independent detection records (n=4), while MB (Germany) presented the highest number of independent detection records (n=141). The average number of wildcat detections over these surveys was 37.25 ± 42.15 detections/survey. Relative abundance indexes varied between 0.104 in SP (Spain) and 6.74 in Etn (Italy), and averaged 1.922 ± 1.920 (Table 12).

Survey	#Trap-nights	#Detections	RAI
CNP, 2014	3810	7	0.184
EIA_2020.1	3856	77	1.997
Etn	1098	71	6.466
GVNP, 2010	988	18	1.822
MB	2550	142	5.569
MtNP	3357	24	0.715
NCAG, 2019.2	458	13	2.838
NSJM	4164	71	1.705
Pgl	946	18	1.903
SANP, 2011	2918	6	0.206
SS, 2019.1	10868	135	1.242
WJ_19	761	24	3.154
Crb	735	38	5.17
MMNP, 2019.1	2120	12	0.566
MNR, 2010	1138	8	0.703
PGNP, 2011	1049	8	0.763
PNP, 2021	5775	28	0.485
SP	5777	6	0.104
SV	726	7	0.964
NC, 2015	786	4	0.509

Table 12 - Relative abundance indexes. (Survey - Survey per study area, as defined in Table 5; #Trap-nights - total number of trap nights all cameras were active; #Detections – number of wildcat independent detection records)

Relationships between density, mean local abundance and the relative abundance index

The quasipoisson logarithmic relationship between density and MLA was the model that presented the least deviance (Table 13). Simultaneously, the corresponding model in the gaussian family was the top-ranked model using the AIC model selection criterion (Table 14). Furthermore, The AIC model rank matches the ascending deviance order of the models from the quasipoisson family (Table 13 and Table 14), which provides a higher degree of confidence that models in the quasipoisson family could be selected according to model deviance. Models including mean local abundance (in the logarithmic scale) as covariate had stronger support than models including RAI (also in



the logarithmic scale) and than the null model. The parameter estimate was $\hat{\beta}_{\log (mla)} = 0.54 \pm 0.13$, and was highly significant (p<0.01; Table 13), suggesting the strong relationship between density and mean local abundance. Likewise, the parameter estimate for the SCR-RAI relationship was $\hat{\beta}_{\log (RAI)} = 0.65 \pm 0.26$ (p<0.05; Table 13), indicating that although with less support, encounter rates also enclose information about underlying density.

Table 13 - GLM model summary results. (Family - distribution family used in the model; Model – parameterization of each model; Deviance – Deviance of each model; SE – standard error; t-value – assessment of the difference relative to the variation of the data; Pr(>|t|) - p-value for the t-test.)

Family	Model	Deviance	Coefficients	Estimate	SE	t-value	Pr(> t)
	d ~ log(mla), weights	36.234 -	intercept	2.657	0.188	14.115	0.000
			log(mla)	0.540	0.134	4.024	0.003
	d ~ log(mla)	54.524 -	intercept	2.642	0.204	12.943	0.000
quasipoisson			log(mla)	0.548	0.179	3.063	0.014
	d ~ log(rai)	59.244 -	intercept	2.030	0.333	6.094	0.000
			log(rai)	0.669	0.261	2.569	0.030
	d ~ 1	109.744	intercept	2.493	0.290	8.601	0.000

Table 14 - Model selection ranked by AIC. (Family - distribution family used in the model; Model – parameterization of each model; df – degrees of freedom; logLik - log-likelihood that maximizes the optimal values of the estimated coefficients; AICc - corrected Akaike Information Criterion; Delta - difference between AIC score for the best model and the model being compared; Weight - predictive power of the model; Cumulative weight - sum of the AICc weights)

Family	Model	df	logLik	AICc	Delta	Weight	Cumulative weight
gaussian	d ~ log(mla), weights	3	-37.654	84.70	0.00	0.57	0.57
	d ~ log(mla)	3	-38.335	86.10	1.36	0.29	0.86
	d ~ log(rai)	3	-39.404	88.20	3.50	0.10	0.95
	d ~ 1	2	-42.068	89.60	4.90	0.05	1.00

Predicted densities based on the best model ($d \sim log(mla)$, weights) varied between 3.79 ± 1.39 individuals/100km² in Crb (Spain) and 59.784 ± 24.831 individuals/100km² in NCAG (Spain), and averaged 24.71 ± 22.06 (Table 15 and Figure 7).



Table 15 - Predicted density results (individuals/100km²) for SCR-RN relationship and the respective area for which the estimate was based (minimum convex polygon). (Survey - Survey per study area, as defined in Table 5; SE – standard error; Coefficient of variation – coefficient of variation of the density estimate, calculated as SE / Density.)

Survey	Predicted density ± SE (individuals/100km ²)	Coefficient of variation	Minimum convex polygon (km²)
Crb	3.79 ± 1.39	0.37	19.28
MMNP, 2019.1	16.83 ± 3.30	0.20	94.32
MNR, 2010	14.96 ± 2.84	0.19	86.82
PGNP, 2011	6.08 ± 1.66	0.27	60.87
PNP, 2021	10.83 ± 2.12	0.20	265.99
SP	51.15 ± 19.50	0.38	8.73
SV	4.29 ± 1.46	0.34	15.65
NC, 2015	54.71 ± 21.66	0.40	2.73
NCAG, 2019.2	59.78 ± 24.83	0.42	49.72



Figure 7 - Logarithmic relationship between density and mean local abundance.

3.3. Wildcat density across Europe

Our combined density results across all study areas ranged between 1.13 ± 0.437 individuals/100km² in MtNP (Portugal) and 59.78 ± 24.83 in NCAG (Spain) (Table 16 and Figure 8). However, most populations show low population densities (<10 individuals/100km²; Figure 9).

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		-		
Method	Study area	Density ± SE (individuals/100km ²)	Coefficient of variation	Density Reference (individuals/100km ²)
SCR	MB	33.308 ± 6.138	0.184	
	Etn	28.782 ± 10.745	0.373	32 ±10 (Anile <i>et al.</i> , 2014)
	SS	23.245 ±11.989	0.516	
	Pgl	10.165 ± 5.620	0.553	
	NSJM	7.881 ± 1.730	0.219	17 (11-25) (Maronde <i>et al.</i> , 2020)
	GVNP	6.481 ± 3.563	0.550	
	EIA	4.644 ± 2.009	0.432	
	CNP	3.800 ± 1.700	0.447	3.8 ±1.7 (Ferreras et al., submitted)
	SANP	2.662 ± 1.530	0.575	6.9 ±0.19 (Gil-Sánchez <i>et al.</i> , 2020)
	WJ	1.816 ± 0.854	0.470	
	MtNP	1.130 ± 0.437	0.387	3.2 ± 1.2 (Matias <i>et al.</i> , 2021)
GLM predict	Crb	3.792 ± 1.390	0.367	
	MMNP	16.831 ± 3.295	0.196	
	MNR	14.960 ± 2.835	0.190	
	NC	54.716 ± 21.658	0.396	13-60 (Sayol <i>et al.</i> , 2018)
	NCAG	59.784 ± 24.831	0.415	
	PGNP	6.075 ± 1.656	0.273	
	PNP	10.828 ± 2.115	0.195	
	SP	51.152 ± 19.498	0.381	
	SV	4.288 ± 1.461	0.341	

Table 16 - Density and mean local abundance estimates obtained for all study areas. (SE – standard error; Coefficient of variation - coefficient of variation of the density estimate, calculated as SE / Density.)



Figure 8 - Density estimates reliably obtained compared to the known wildcat distribution assessed by IUCN (NC, NCAG, and SP study areas excluded due to unexpectedly high standard errors).



Figure 9 - Distribution of the density estimates obtained.

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4. Discussion

We achieved our goals of obtaining density estimates with a single comparable approximation, as well as providing support that metrics obtained from camera trapping data can be useful as density proxies. Furthermore, we were able to obtain density estimates for the first time for populations where data is scarce. This was important to generate new information about European wildcat populations using data that is hard to obtain due to the elusive behaviour of this species and to the fact that they generally occur in low densities.

Camera-trapping was an unquestionably useful tool to assess wildcat population densities across Europe, especially because it is the most adequate to address the limitation of the generally low detection rate for this species (Anile, Amico, & Ragni, 2012; Brassine & Parker, 2015; Gil-Sánchez, Jaramillo, & Barea-Azcón, 2015; Kilshaw *et al.*, 2015).

4.1. Overview of wildcat density estimates across Europe

To our knowledge, most of our density results (70%) were the first ever to be generated for wildcats in the respective study areas. Only in Etn (Italy), NSJM (Switzerland), MtNP (Portugal), and CNP, SANP, and NC (Spain) European wildcat population density studies had already been previously estimated. From these, Etn and NC reference densities are similar to ours (Table 16, (Anile *et al.*, 2014; Sayol *et al.*, 2018)). However, significant density discrepancies are found in NSJM, SANP, and MtNP, with our estimates being systematically inferior to the previously published estimates (Table 16, (Gil-Sánchez *et al.*, 2020; Maronde *et al.*, 2020; Matias *et al.*, 2021)).

Observer bias (i.e., the risk of individual misidentification of animals inherent to each different observer, and its impact on population abundance estimates (Johansson *et al.*, 2020)) might be the main driver of these discrepancies. Indeed, fewer captures and spatial recaptures result in lower estimates of density (Fleming *et al.*, 2021). In the case of MtNP, we were only able to identify 4 individuals from each flank, while (Matias *et al.*, 2021) identified 5 from the left and 9 from the right flank. In the NSJM, although data was also provided by the authors, (Maronde *et al.*, 2020) had access to prior information on wildcat identifications, which increased the number of individuals identified. Furthermore, (Gil-Sánchez *et al.*, 2020), in SANP, achieved a much higher
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number of wildcat detections and therefore identified many more individuals. Despite the general study area of our studies is the same (eastern Sierra Morena), the state-space and year of sampling diverge, which can lead to natural differences in population densities, due to heterogeneity of wildcat density throughout the landscape and temporal dynamics of the population.

Although identification errors tend to overestimate population size relative to the true population size, as observers generally identify more animals than the real capture history (Johansson *et al.*, 2020), our identification approach was a conservative one. Therefore, our results should not be overestimated, as is suggested by comparison with the previously mentioned reference results. It is important to note that all the individual identifications of wildcats were performed by the same observer, which reduces bias that would be introduced by different observers - in case the identifications from previous studies would have been incorporated from projects which had a similar goal.

Additionally, as the buffer size of the sampled area is indexed to the mean maximum distance moved by the wildcats (Royle et al., 2013c), observer bias will therefore influence the extent of the state-space upon which density inferences are drawn. Simultaneously, the individuals encountered, and corresponding spatial recaptures inform the sigma and baseline detection probability parameters, upon which the ability to estimate density relies (Dupont *et al.*, 2021; Efford, 2004; Efford, Dawson, & Borchers, 2009; Royle *et al.*, 2009).

With regard to populations for which no previous wildcat densities had been estimated before, only 3 study areas - NC, NCAG, and SP - show unexpectedly high estimates and standard errors. These inferences should be interpreted with caution as such high estimates may be related to the study design. In the NC and NCAG, very few cameras were deployed (6 and 12, respectively) in an area of approximately 2.73km² and 49.72 km², respectively. As for the SP, much more effort was employed (46 cameras) although also in a small area (approximately 8.73km²). The low number of cameras and small areas sampled (inferior to expected wildcat ranges) may be the main drivers of these unexpected results. Indeed, SP, NC and NCAG study areas revealed the widest confidence intervals in mean local abundance (above 12, in contrast with all the other study areas with confidence intervals below 5). These results suggest that our approach to calculating the estimates weights in the GLM model (Equation 6) might not be sufficient to account for such lack of precision and alternative solutions should be explored.

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As expected, our results show that most wildcat populations occur in low density (Anile et al., 2017; Matias et al., 2021)(Figure 9). However, our density estimates are lower than expected for most European populations (<10 individuals/100km²), and contrast with the estimate of ca. 20 individuals/100km² suggested by (López-Martín et al., 2007) and with other previous studies across Europe: 23-35 individuals/100km² in Switzerland (Kery et al., 2011), 17-25 individuals/100km² in Germany (Heller, 1992), 20-30 individuals/100km² in Italy (Ragni & Seminara, 2006), 10-13 individuals/100km² in Poland (Okarma & Olszańska, 2002), and 16-45 individuals/100km² in Serbia (Dimitrijevic, 1980)). This discrepancy might be explained by our study focusing on many small, isolated, and fragmented populations for which estimates have never been generated due to lack of data, contrasting with the literature studies from populations where wildcat is well known to occur and that use methodologies that require many captures, and, therefore, have more potential to occur in higher densities. Simultaneously, an even more concerning explanation, is that European wildcat populations may have been declining since these early studies, as most of them are over 15 years old.

According to the density-mass allometry (DMA) power law, mean population density decreases with increasing body mass (Belgrano & Reiss, 2011; Blackburn & Gaston, 1999; Damuth, 1981, 1987; Jennings, Oliveira, & Warr, 2007). This relationship has been recently studied for felines (Anile & Devillard, 2020), where an average body mass of 4.30kg for wildcats (Johnson *et al.*, 2017) should result in population densities of roughly 12 to 26 individuals/100km² (Anile & Devillard, 2020). Although density may depend on other natural factors intrinsic to each ecosystem, we may hypothesize that European wildcat populations occurring at much lower densities than predicted by the DMA power law might face a higher risk of extinction and that their genetic diversity may pass through a bottleneck with serious evolutionary consequences (Cohen, Xu, & Schuster, 2012).

Our RAIs ranged between 0.1 and 6.7 and most values were below 1. These values are similar to those obtained in some previous studies (0.5 (Kilshaw *et al.*, 2015), 0.51 (Sarmento *et al.*, 2009), but lower than usually reported across Europe: 2.9 (Anile, Amico, & Ragni, 2012), 1.95 (Maronde *et al.*, 2020), 3.1 (Velli *et al.*, 2015), 6.48 (Anile *et al.*, 2014), 6.43 (Wening *et al.*, 2019)).

Densities in the Mediterranean region (mean 8.88 \pm 8.01 individuals/100km²) tended to be lower than in the Temperate region (mean 14.55 \pm 10.85

individuals/100km²). This is especially noticeable in the Iberian Peninsula, where Mediterranean densities vary between 1.13 ± 0.44 individuals/100km² (in MtNP) and 16.83 \pm 3.30 individuals/100km² (in MMNP), with a mean of 6.14 \pm 4.77 individuals/100km², contrasting with the Temperate densities where the 2 study areas present densities of 6.08 \pm 1.66 individuals/100km² (PGNP) and 14.96 \pm 2.84 individuals/100km² (MNR). The lower Mediterranean estimates in the Iberia peninsula could be explained by the decrease of the main wildcat prey in this region, the European rabbit (Apostolico *et al.*, 2016; López-Martín *et al.*, 2007; Lozano, Moleón, & Virgós, 2006; Monterroso *et al.*, 2020; Oliveira *et al.*, 2018; Sunquist & Sunquist, 2002; Széles *et al.*, 2018), as this has been suggested as an important driver of wildcat's population density in this biome (Monterroso *et al.*, 2009). Despite this trend, the WJ population presented a low-density estimate compared to other populations in the Temperate region. This may illustrate a slow recovery of the population since it has been considered extinct since 1989 (Gerngross, Slotta-Bachmayr, & Hagenstein, 2021; Slotta-Bachmayr, Meikl, & Hagenstein, 2016).

4.2. Relationships between density and mean local abundance and the relative abundance index

We were able to establish a relationship between density and mean local abundance, as well as between density and the relative abundance index, although the SCR-RN relationship had higher support. This approach allowed us to use occupancy data and capture rates, which was very useful for populations with very few wildcat detections or deprived of spatial recaptures, and enabled estimating density predictions for these populations.

The higher support for SCR-RN relationship may arise from the fact that RN abundance models take into account the heterogeneous probability of detecting a species at a given site in its hierarchical approach (Royle & Nichols, 2003; Sollmann *et al.*, 2013). Therefore, MLA estimates, derived from the RN formulation, has higher support for being a more reliable proxy for density than RAI. Even so, (Carbone *et al.*, 2001) and (Rovero & Marshall, 2009) demonstrated that photographic rates can be used to derive estimate densities of elusive mammals under certain circumstances. Additionally, (Gil-Sánchez *et al.*, 2020) explored a different approach by using

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environmental variables to predict wildcat density in a GLM from explicit spatial capturerecapture data.

The limits to the use of camera trapping rates as an index of abundance have been widely debated (Carbone *et al.*, 2002; Jennelle, Runge, & MacKenzie, 2002; Jimenez *et al.*, 2019; O'Brien, Kinnaird, & Wibisono, 2003; Williams, Nichols, & Conroy, 2002a), but they are generally overcome when the indexes are calibrated with estimates of density (O'Brien, 2011; Williams, Nichols, & Conroy, 2002a), as was performed by (Carbone *et al.*, 2001), (Rovero & Marshall, 2009), and also in this study (although only (Rovero & Marshall, 2009) generated photographic rates and density estimates from two independent data collection methods). Under these calibrated conditions, it is reasonable to assume these abundance indexes could serve as density proxies. However, predictions tend to have inherently higher associated uncertainty.

Given these cautious circumstances where results are calibrated, the use of photographic rates is promising and cost-effective for the assessment of animal abundance when alternative methods are not possible (O'Brien, Kinnaird, & Wibisono, 2003). This approach has the potential to be used on a wider range of species, as the occupancy data and encounter rates do not rely on individual identity (Carbone *et al.*, 2001; Rovero & Marshall, 2009). Furthermore, even for species that can be individually identified, datasets poor in the number of captures are common for elusive animals and require the use of simpler approaches (O'Brien, Kinnaird, & Wibisono, 2003; O'Brien, 2011), as was confirmed by our study.

4.3. Large scale integration of different projects

Using a common and collaborative approach allowed us to obtain reliable density estimates for multiple European wildcat populations under a spatial capture-recapture framework, including for populations for which density estimates had never been attempted before. This collaborative initiative that brought together projects with distinct goals was key to obtaining wildcat data across virtually its entire distribution and allowed to produce directly comparable density estimates across multiple populations.

Collaborative initiatives have made it possible to expand knowledge about the European wildcat. (Oliveira *et al.*, 2018) is the first European wildcat multi-population study exploring the sex-specific habitat selection patterns in human-dominated landscapes of Western Europe. Additionally, (Bastianelli *et al.*, 2021) is another project



from the EUROWILDCAT initiative, which has allowed the identification of the most important cause of wildcat mortality at the European scale.

Other initiatives have allowed robust assessments of multiple species at large spatial and temporal scales (Van der Weyde et al., 2021). The Euromammals initiative, involving more than 150 institutes, has pioneered collaborative science in spatial terrestrial mammal ecology by using data stored in a shared database (Urbano, Cagnacci, & 2021). (Khwaja et al., 2019) were able to uncover relationships of occurrence and landscape variables on a broad scale for a highly threatened and understudied mammal, the pangolin (Pholidota: Manidae). These are just examples that highlight the potential of collaborative and integrative approaches to advance our understanding of general principles in ecology and environmental science (Fraser et al., 2013; Steenweg et al., 2017). Nevertheless, data management and the availability of a standardised analytical approach that addresses the challenges of heterogeneous data is extremely important for data quality assurance in such large-scale initiatives (Khwaja et al., 2019; Urbano, Cagnacci, & 2021; Van der Weyde et al., 2021). Particularly, recommendations have been made for the implementation of unified data collection and sharing protocols and also for the review of the shared data through robust technical standards (Urbano, Cagnacci, & 2021; Van der Weyde et al., 2021; Williams et al., 2021).

Moreover, our approach allowed the effective use of by-catch data from projects developed for the study of species other than the wildcat. Although such an approach is not very common, other studies have also successfully integrated by-catch data to generate fundamental ecological knowledge such as population size and occupancy estimates (Edwards *et al.*, 2018; Harihar *et al.*, 2010; Wevers *et al.*, 2021; Williams *et al.*, 2021). This reuse of data extends the potential of camera trapping far beyond its original goals, while also informing wildlife conservation management strategies at a global scale (Edwards *et al.*, 2018; Williams *et al.*, 2021).

4.4. Limitations

The main limitations of the large-scale integration of different projects were mostly associated with variability among projects in relation to sampling design. When there is no coordination between camera studies, the resultant datasets can be fragmented, unstandardized, and difficult to integrate (Meek, 2014; Steenweg *et al.*,

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2017). Additionally, different experimental methodologies can limit the strength of the results (Fraser *et al.*, 2013).

Analytical limitations

The trade-off between achieving the population closure assumption and having enough captures is a challenge, as a wider time frame would have provided more sampled individuals (Brassine & Parker, 2015). In particular, we noted some spatial recaptures were lost across surveys, which would have been useful to improve the MMDMs' accuracy.

As for identifications of wildcats, the main limitation regarded the lack of absolute certainty on the pure wild phenotypes, as the phenotypic continuum between wild and hybrid phenotypes makes it challenging to ensure only pure individuals (Krüger *et al.*, 2009). Wild phenotypes can only be guaranteed through genetic confirmation, which was not performed here. However, by including only photographs where animals were clear and focused, and describing individuals according to marking systems, we are confident that individuals included in the analysis are all potential wildcats.

While the use of the left and right sides as sessions enables the use of all identifications without overestimating density, both sides are not directly associated in cases of complete identifications (i.e., identifications of individuals by both sides simultaneously). Alternative model parameterizations that explicitly integrate the capture probabilities of each flank in the same model, as is the case with *Multimark* (McClintock, 2015) and *SPIM* (Augustine, 2018) have been developed. It is a consensus among authors that analyses where both flanks are integrated, directly or indirectly, will often both reduce bias and improve precision (Augustine *et al.*, 2018; Maronde *et al.*, 2020; McClintock *et al.*, 2013; Meredith, 2018).

The c-hat of the goodness of fit tests for our abundance models was always much inferior to one, but literature only presents alternatives in cases of overdispersion (c-hat>1) (Mazerolle, 2020; White & Seymour, 2005). Although our c-hat values might suggest poor fit of the models, the p-values of the goodness of fit are close to 0.5, indicating the opposite (Kéry & Royle, 2015). These contradicting results might be explained by the fact that we are working with elusive species, which makes data difficult to obtain, and therefore small sample sizes for most study areas. However, to our knowledge, literature does not present any solution to be applied in cases of underdispersed data.



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Methodological limitations

The monitoring of wildcats is particularly difficult due to their elusive nature (e.g., they are nocturnal, prefer dense vegetation cover, and occur at low densities), resulting in low capture rates (Anile, Amico, & Ragni, 2012; Kilshaw *et al.*, 2015). This was particularly evident in this study, as even with the large amounts of data available it was still a challenge to produce reliable densities for some study areas. In order to improve capture rates, some authors have suggested the use of lures to attract more individuals or keep them for longer in the camera's field of view (which was the case in some study areas, see Field methods). However, this might induce a trap-happy behavioural response, with some individuals being captured more often (Kilshaw *et al.*, 2015), thereby biasing density estimates. Other solutions include deploying more cameras to survey larger areas (Kilshaw *et al.*, 2015; Soto & Palomares, 2014), although this is not always possible due to logistic and financial constraints. Camera definitions including flash type, trigger speed, battery life, and camera trap models might also adapted to optimize capture rates (Kilshaw *et al.*, 2015; Meek & Pittet, 2012).

There was also a significant discrepancy between the number of wildcat detections and the number of individuals identified. This happened in cases where the photographs did not have enough quality for a reliable identification of coat patterns, or when it was not possible to be sure if the present wildcat was an individual already identified or a different one. In these cases, a photographic capture is not assigned to any individual identification, and, instead, it is excluded from further SCR analysis. Consequently, despite containing visible wildcat detections, the information of such cases is lost, potentially biasing density estimates (Creel et al., 2003; Sethi et al., 2016). To decrease the gap between detections and identifications, deploying more than one camera in each station (as was done by a few studies included here, see Field methods) is recommended for maximizing sampling of bilaterally asymmetric species, such as the wildcat (Kilshaw et al., 2015; McClintock et al., 2013). Also, identification probability could be optimized by increasing image quality through the use of white flash (sometimes used in protocols here, see Field methods), although this can generate fewer detections because it is more disturbing to animals (Kilshaw et al., 2015; Meek & Pittet, 2012). Additionally, it would be beneficial to have more observers replicate the identification process for all datasets and reach a consensus among identifications performed by all observers for all study areas, in order to achieve a higher certainty degree in



identifications, without compromising the ability to compare estimates (Choo *et al.*, 2020; Foster & Harmsen, 2012).

Unfortunately, beyond the populations where no spatial recaptures were recorded, 3 additional study areas (SP, NC, and CNP) did not generate accurate spatial capture-recapture density estimates due to poor datasets (few spatial recaptures). According to (Efford, Borchers, & Byrom, 2009), spatially explicit capture-recapture methods need more than 20 recaptures for precise estimates of population density. We did not achieve such a recapture rate in any of our populations (Table 8), which might be underestimating the sigma parameter since the MMDM of wildcats recorded by the cameras might be smaller than in reality.

Mean local abundance was not obtained for the BF (Germany), as the 2 wildcat detections in the study area would not allow fitting RN abundance models. Besides, the species is only now recovering after being completely absent from the study area for decades (Beutel *et al.*, 2017)).

Although in NC, NCAG, and SP, density estimates were predicted, it is not prudent to consider them as reliable, as they are unreasonably high, imprecise, and refer to low sampling effort. Even so, other study areas where density was not possible to be estimated due to lack of spatial recaptures, provided reasonable estimates of mean local abundance (as is suggested by the lower coefficients of variation and standard errors) by using the occupancy data and allowed predicting wildcat density. However, we have no means to cross-validate those results.

Temporal variation of data collection

The wide time range of data collection between study areas, due to the data being derived from several projects, results in the estimation of densities for different years, and therefore may not fully represent an up-to-date picture for all European wildcat populations, as there is the possibility that densities have already changed in some study areas.

4.5. Implications for wildcat conservation

Our study has provided new information regarding density estimates of multiple European wildcat populations and we have also highlighted the general low density of most wildcat populations across Europe. Although the wildcat occurs throughout almost

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the whole Europe, most populations are here shown to exhibit very low densities, highlighting the need to bridge the knowledge gap between wildcat distribution and the viability of its populations. This is further supported by the fact that no captures of wildcats were registered in MNP, a large, protected area located on the centre of the assessed wildcat range. Additionally, aside from this study area, we have only included studies where wildcat detections were recorded, thereby becoming apparent the possibility that the scenario could be even worse for areas where the species has not been detected vet. This also holds for large European regions where the detailed distribution of wildcats is still unknown (Lozano, Virgós, & Cabezas-Díaz, 2013; Nowell & Jackson, 1996). Therefore, conservation efforts, which are currently scarce for the European wildcat, should focus on these low-density populations as well as on bridging the knowledge gaps that remain about the ecology of this species. Important steps could be taken to increase the information available. First, address the lack of spatial recaptures and individuals identified. These limitations make it essential for the availability of alternative methods to estimate density in populations with such low capture rates, as was suggested by our approach, and should be applied to the whole European wildcat range. Second, more studies should focus on small, fragmented populations and their connectivity with larger and viable populations, resulting in a finer scale assessment of wildcat distribution across Europe, which might not be as continuously widespread as previously thought. Additionally, it would be of great importance to find the main large scale ecological drivers of wildcat density at the European scale.

4.6. Final considerations

Given some above-mentioned limitations and discrepancies with previously published results, our results will still undergo a posterior refinement for future publication, by including more observers in the identification process and implementing a more robust modelling approach that takes into account the direct association of left and right flanks, the high variability between surveys, and the low capture rate of wildcats. This should involve a Bayesian computationally heavy approach.

This study has shown that collaborative approaches that combine camera-trap data from small-scale datasets are fundamental to generate new and important information about European wildcat populations throughout the species range and should therefore be applied through a unified and standardized protocol in the future.





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Supplementary Information

Supplementary Information 1- Wildcat individual identifications and respective morphological descriptions according to the three marking systems (Kitchener et al., 2005; Ragni & Possenti, 1996; Spassov, Simeonovski, & Spiridonov, 1997).

ID - identification code = [study area code]_[left side identification number]_[right side identification number]. 1 (nose without upper black margin); 2 (nose with upper black margin); 3 (dorsal surface of the ear uniformly coloured); 5 (apex of the ear without formations of brown-black hair); 8 (white areola in the gular region, from few hairs to a large patch, with or without collars); 9 (gular region without markings); 12 (occipital region four longitudinal stripes; four permanent longitudinal stripes, and one median thin and/or evanescent stripe or bar); 13 (occipital region as 12, altered but objectively distinguishable); 15 (orderly, but different from 16, in the scapular region); 16 (scapular region with two parallel longitudinal stripes, plus one intermediate thin or evanescent stripe, flanked or not by rare bars and/or evanescent maculae); 17 (double pattern in the dorsal region: a cephalic half, disorderly or with a longitudinal median band, a caudal half with longitudinal stripes or longitudinal bars and/or maculae lines); 21 (dorsal region with more than one permanent longitudinal median stripe); 22 (dorsal region with permanent longitudinal median stripe flanked or not by rare bars and/or evanescent maculae); 23 (disorderly pattern in the lateral region); 24 (maculae pattern in the lateral region) 25 (the cephalic half of the lateral region with vertical stripes, the caudal half with maculae and/or bars); 28 (caudal region without longitudinal markings or a dorsal longitudinal median evanescent bar on the proximal 1/2-1/4; number, shape and size of black or paler rings are not significant); 29 (dorsal stripe stops at base of tail); 30 (dorsal stripe continues onto tail); 31 (blunt tail tip); 32 (intermediate tail tip); 33 (tail tip tapered to a point); 34 (distinct tail bands); 35 (indistinct or fused tail bands); 36 (no marking on flanks and hindquarters); 37 (> 50% broken stripes/no marking on flanks and hindquarters); 38 (25–50% broken stripes on flanks and hindquarters); 39 (< 25% broken stripes on flanks and hindquarters); 40 (many spots/no marking on flanks and hindquarters); 41 (no spots on flanks and hindquarters); 42 (some spots on flanks and hindquarters); 44 (4 thick stripes on the nape); 45 (intermediate shape and number of stripes on nape); 46 (2 thick stipes on the shoulders); 47 (colour of the muzzle differing from the one of the frontal part); 48 (colour of the muzzle the same with the one of the frontal part), 49 (colour of the upper lip light ochre or grevish), 50 (colour of the upper lip white), 51 (dorsal stripe does not reach tail rings); 52 (dorsal stripe reaches the tail rings without crossing them); 53 (short tail tip when its form is close to square); 54 (long tail tip - when its form is close to rectangle); 55 (two or three dark tail rings); 56 (four to seven dark tail rings); 57 (one to six pale tail rings); 58 (pale tail rings absent); 61 (body stripes not broken); 62 (body stripes are scarcely broken on two or three spots and their separation is just marked); 63 (body stripes are strongly broken on more than three spots and obviously separated from each other); 64 (side stripes contrasting); 65 (side stripes scarcely notable); 66 (side stripes absent); 67 (one or two stripes on foreleg side); 68 (three to five stripes on foreleg side); 69 (without stripes on foreleg side); 70 (one or two stripes on inner side of the foreleg); 71 (dark spot on the armpit); 72 (whole surface of the plantar of the metatarsus is black); 73 (plantar surface of the metatarsus varies from brown to ochre, with a dark spot in the lower part); 74 (white chin); 75 (ochre chin); 76 (grey chin); 77 (one to three, oval-shaped, white spots on the ventral body);

ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
CNP_L1_R1	2 3; 8; 12; 22; 25; 28	31; 34; 39; 41; 44	47; 49; 61; 64; 68; 70; 74
CNP_L2	5; 25; 28	34; 39; 41	47; 51; 57; 62; 64; 68; 70; 72
CNP_L3	5; 12; 22; 25; 28	29; 34; 39; 42; 44	57; 62; 64; 70; 72
CNP_L4	5; 25	39; 41	61; 64; 68
CNP_L5_R4	3; 8; 22; 25	31; 34; 38; 42	53; 55; 57; 62; 64; 68; 71; 72
CNP_R2	5; 22; 25	29; 34; 39; 42	51; 62; 64; 68
CNP_R3	2; 5; 9; 13; 15; 22; 25	29; 32; 34; 39; 45;	47; 49; 51; 53; 55; 57; 61; 64; 68;
		46	70; 72; 75
CNP_R5	2; 5; 9; 12	39; 41; 44	47; 49; 61; 65; 67
SANP_L1_R2	5; 8; 25; 28	32; 34; 39; 42	51; 54; 55; 57; 62; 64; 67
SANP_L2_R3	25	32; 34; 39	55; 57; 64
SANP_R1	5; 8; 22; 25; 28	29; 32; 34; 38; 42	51; 54; 55; 57; 62; 64; 68; 70; 73
GVNP_L1	8; 25	31; 34; 39; 41	47; 53; 55; 57; 62; 64
GVNP_L2	5; 8; 22; 25; 28	29; 33; 34; 39; 41	47; 51; 54; 55; 57; 62; 64; 68; 77
GVNP_L3	5; 8; 22; 25; 28	29; 34; 39; 42	51; 55; 57; 62; 64; 68; 71
GVNP_L4	5; 8; 17; 25; 28	29; 31; 34; 39; 42	47; 51; 53; 55; 57; 61; 64; 68; 70
GVNP_L5	5; 25; 28	29; 34; 38; 41	51; 57; 62; 69; 70
GVNP_L6	5; 8; 23; 28	34; 39; 41	51; 57; 63; 69; 71
GVNP_L7	5; 8; 23; 28	32; 34; 39; 42	51; 54; 55; 57; 62; 64; 68; 70
GVNP_L8	5; 22; 23; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 62; 64; 68
GVNP_R1	5; 8; 22; 25; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 62; 64; 68; 70; 72
GVNP_R2	23	31; 34; 36; 40	47; 53; 57; 62; 64; 69; 70
GVNP_R3	22; 25; 28	29; 32; 34; 39; 41	51; 53; 55; 57; 62; 64; 69; 72



ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
GVNP_R4	22; 25	31; 34; 38; 42	53; 57; 62; 65; 67; 70
GVNP_R5	3; 12; 22; 25; 28	34; 39; 41; 44	51; 55; 57; 61; 64; 69; 71
GVNP_R6	16; 25	39; 44; 46	63; 64; 68
GVNP_R7	12; 25	32; 34; 44	54; 55; 57; 71
GVNP_R8	22; 24; 28	29; 31; 34; 38; 41	51; 54; 55; 57; 64; 69; 71
MNR_L1	2; 5; 9; 22; 23; 28	32; 34; 36; 40; 46	47; 51; 54; 55; 57; 66; 69; 71
MNR_L2	22; 23	34; 38; 42	47; 53; 55; 57;62; 64; 68
MNR_L3_R2	16; 22; 25; 28	29; 31; 34; 46	51; 53; 57; 65; 71
MNR_R1	12; 22; 23; 28	29; 36; 40; 44	51; 53; 57; 65; 68; 71
MNP_L1_R1	2; 5; 8; 22; 25; 28	29; 31; 34; 38; 42	47; 51; 53; 55; 57; 62; 64; 68; 71
MNP_L2	23	34; 38	55; 57; 62; 64; 68; 71
MNP_L3			53; 55; 57; 65
MNP_L4_R2	5; 22; 25; 28	29; 31; 34; 37; 40	51; 53; 55; 57; 65; 69; 70
MNP_R3	8; 22; 25; 28	32; 34; 37; 40	47; 51; 53; 55; 57; 62; 65; 68
MNP_R4	8; 25	32; 34; 37; 40	47; 53; 55; 57; 65; 68; 70
PGNP_L1_R1	3; 9; 12; 22; 25; 28	29; 32; 34; 39; 41; 44	51; 53; 55; 57; 61; 64; 68; 70
PGNP_L2	25		61; 64
PGNP_L3_R2	3; 8; 12; 22; 25; 28	29; 32; 34; 37; 41; 44	51; 53; 55; 57; 62; 64; 68; 71
SP_L1	5; 12; 16; 22; 25	29; 32; 34; 39; 41; 44; 46	51; 53; 55; 57; 62; 64; 69
SP_R1	5; 8; 25		62; 68
MB_L1_R1	2; 5; 25	34; 39; 41	47;57; 62; 64; 68; 71
MB_L2	23	32; 34; 36; 40	47; 49; 54; 55; 62; 65; 68; 71
MB_L3	25; 28	32; 34; 37; 40	47; 51; 53; 55; 57; 62; 65; 69; 76
MB_L4_R10	5; 25	31; 34; 37; 40	47; 53; 55; 57; 65; 69; 71
MB_L5_R6	2; 5; 8; 12; 25	31; 34; 37; 40	47; 53; 55; 57; 65; 69; 71
MB_L6_R13	2; 5; 23	31; 34; 39; 41	47; 53; 55; 57; 63; 65; 69; 70
MB_L7_R2	2; 5; 25	32; 34; 38; 42	47; 49; 3; 55; 57; 62; 64; 68; 70
MB_L8	5; 8; 25; 28	31; 34; 38; 42	47; 51; 53; 55; 57; 62; 64; 68; 70; 73
MB_L9_R8	2; 5; 8; 24	32; 34; 37	47; 53; 55; 57; 63; 67; 70
MB_L10_R5	2; 5; 8; 25	32; 34; 39; 41	47; 49; 54; 55; 57; 62; 65; 68; 70
MB_L11	2; 5; 8; 24	32; 34; 37; 41	47; 49; 53; 55; 57; 64; 68; 70
MB_L12	12; 25	31; 34; 38; 42	47; 54; 55; 57; 63; 64; 67; 70; 73; 74
MB_L13	2; 5; 8; 25	31; 34; 37; 40	47; 53; 55; 57; 62; 65; 68; 70
MB_L14	23	32; 34; 38; 41	47; 53; 55; 57; 62; 65; 69; 70
MB_L15	23	31; 34; 36; 40	47; 53; 55; 57; 66; 69; 71
MB_L16	25	31; 34; 38; 41	47; 53; 55; 57; 62; 65; 69; 71
MB_L17	25	32; 34; 39; 42	47; 49; 53; 55; 57; 62; 64; 67; 70
MB_R3	5; 25	34	55; 57; 62; 64; 67; 70
MB_R4	5; 25	32; 34	47; 53; 55; 65; 71
MB_R7	8; 23	32; 34; 42	47; 49; 53; 55; 57; 64; 67; 70
MB_R9	5; 25	29; 32; 34; 38; 42	47; 51; 54; 55; 57; 63; 64; 67; 71; 73
MB_R11	25	34; 38; 41	47; 62; 69; 71
MB_R12	23	34; 38; 41	47; 55; 57; 62; 64; 69; 70
MB_R14	25	31; 34; 40	47; 53; 55; 57; 61; 65; 69; 71
MB_R15	25	32; 34; 39; 42	53; 55; 57; 62; 64; 67; 70
BF_L1	28	29; 34	51; 55; 57
BF_L2		31; 34	53; 55; 57; 72
Etn_L1_R1	5; 22	31; 34; 41	47; 53; 55; 57; 65; 69; 71; 75
Etn_L2_R2	2; 5; 12; 16; 22; 25; 28	32; 34; 39; 42; 44;	47; 49; 51; 53; 55; 57; 61; 65; 67;

ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
Etn_L3	5; 8; 22; 25; 28	29; 31; 34; 39; 42	47; 49; 51; 53; 55; 57; 61; 67; 71; 72; 74
Etn_L4	2; 5; 23	32; 34; 36; 41	47; 49; 54; 55; 58; 66; 69; 71
Etn_L5	2; 3; 12; 22; 25; 28	32; 34; 39; 42; 44	47; 49; 1; 54; 55; 57; 62; 64; 67; 70; 72
Etn_L6	3; 12; 25; 28	29; 31; 34; 39; 42; 44	51; 53; 55; 57; 62; 64; 67; 70; 73
Etn_L7	2; 5; 25	34	47; 49; 55; 57; 65; 70
Etn_L8_R9	5; 23	31; 34; 36; 41	47; 49; 53; 55; 57; 65; 69; 71
Etn_R3	5; 25; 28	29; 32; 34; 39; 42	47; 49; 51; 54; 55; 57; 62; 65; 67; 71; 73
Etn_R4	1; 5; 25; 28	29; 33; 34; 39; 42	48; 51; 54; 55; 57; 62; 64; 67; 72
Etn_R5	2; 5; 12; 22; 23; 28	29; 31; 34; 36; 41; 44	47; 51; 53; 55; 57; 65; 69; 71; 73
Etn_R6	1; 5; 22; 23; 28	29; 32; 35; 36; 42	48; 49; 51; 53; 55; 57; 65; 67; 70; 72
Etn_R7	2; 5; 22; 23; 28	32; 34; 36; 42	47; 51; 53; 55; 57; 65; 67; 70
Etn_R8	25; 28	32; 34; 39; 42	51; 53; 55; 57; 63; 64; 67; 73
Etn_R10	3; 12; 16; 25	31; 34; 39; 41; 44; 46	53; 55; 57; 62; 65; 69
EIA_L1	5; 8; 25	31; 34; 39; 42	47; 53; 55; 57; 62; 64; 67; 70
EIA_L2	25	31; 34; 39	53; 55; 57
EIA_L3	22; 25; 28	29; 31; 35; 39; 41	47; 51; 53; 55; 57; 62; 64; 69
EIA_L4		32; 34	54; 55; 57; 66
EIA_L5		33; 34	54; 55; 57; 65; 71
EIA_L6	23; 28	34; 38; 42	47; 51; 55; 57; 63; 65; 67
EIA_L7	25	32; 34; 39; 42	54; 56; 57; 62; 64; 67; 70
EIA_L8	23	31; 34; 36; 41	47; 53; 55; 57; 66; 69
EIA_L9	25	31; 34; 39; 41	53; 55; 61; 64; 69; 70
EIA_L10	23	37; 42	63; 64; 67; 70
EIA_L11	28	32; 34; 42	51; 54; 55; 57; 67
EIA_L12	25	34	53; 55; 57; 65; 69; 70
EIA_L13	25	31; 34; 39; 41	53; 55; 57; 61; 65; 69
EIA_L14	25; 28	31; 34; 39; 42	47; 49; 51; 54; 55; 57; 62; 64; 67
EIA_L15	25	39; 42	47; 62; 64; 67
EIA_R1		32; 34	53; 55; 65
EIA_R2	5; 8; 24	31; 34; 37; 42	53; 55; 57; 62; 64; 67; 70
EIA_R3	8	31; 34	47; 53; 55; 57; 64
EIA_R4	25	33; 34	54; 55; 57; 63; 64
EIA_R5	25	31; 34	53; 55; 57; 65
	25	33; 34; 39; 41	47; 50; 54; 55; 57; 62; 65; 69; 70
	25; 28	29; 31; 34; 39; 42	47; 51; 53; 55; 57; 62; 64; 67; 70; 73
EIA_R8	22; 25	34; 39	53; 55;57;62; 65; 69
EIA_R9	25	34; 39	47; 55; 57; 62; 64
EIA_R10	25	00.04.00.44	65
EIA_R11	25	32; 34; 39; 41	54; 55; 57; 62; 64; 69; 70; 72
	20, 20 22: 25	29, 32, 33, 38	<u>31, 34, 33, 37, 03, 04, 70</u> <u>47, 62, 65, 70</u>
	<u>22, 20</u> 5: 25	31· 3/· 20· /1	41, 02, 00, 10 A7: 53: 55: 57: 62: 64: 69: 71
	3. 25	37. 34. 33. 41 37. 3 <u>1</u> . 33. 41	<u>47, 53, 55, 57, 62, 64, 60, 71</u> <u>47, 54, 55, 57, 63, 64, 67, 70</u>
	3. 25	34. 38. 42	<u>47: 55: 57: 62: 64: 67: 71</u>
NC 15	5: 25	34: 39: 41	47.6 1. 64. 68. 70
NC 16	2: 5: 25	31: 34: 39: 41	53: 55: 57: 62: 65: 67
NC L7	28	30: 31: 35: 37: 40	52: 53: 55: 57: 63: 64: 71
NC_L8	3	29; 31; 34	51; 53; 55; 57; 72



ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
NC_L9	3; 8; 25	29; 31; 35; 39; 42	47; 49; 53; 55; 57; 62; 64; 70; 73
NC_L10	5; 8; 25	29; 31; 34; 39; 42	47; 49; 53; 55; 57; 62; 65; 70
NC_R1	5; 22; 25	31; 34; 39; 41	47; 54; 55; 57; 62; 64; 68; 70
NC_R2	5; 25	31; 34; 39; 41	47; 51; 53; 55; 57; 62; 65; 67; 71
NC_R3	5; 25	31; 34; 39; 41	47; 53; 55; 57; 62; 65
NC_R4	5; 25	39; 41	47; 61; 64
NC_R5	5; 25	31; 34; 39; 41	53; 55; 57; 65; 67; 70
NC_R6	5; 23	31; 34; 39	47; 54; 55; 57; 65; 70
NC_R7	5; 25	34; 39; 41	47; 53; 55; 57; 62; 64; 67; 70
NC_R8	5; 25; 28	29; 31; 34; 39; 41	47; 54; 55; 57; 62; 64; 71; 72
NC_R9	25	31; 34; 39; 42	49; 53; 55; 57; 61; 64; 70
NC_R10	23	32; 34; 41	48; 54; 55; 57; 66
NC_R11	25	34; 39; 41	47; 55; 57; 62; 64; 71; 72
MMNP_L1	2; 5; 8; 22; 24	34; 37; 42	47; 53; 55; 57; 63; 64; 67
MMNP_L2	2; 5; 22; 25; 28	29; 33; 34; 39; 42	47;51; 54; 55; 57; 62; 65; 67; 71
MMNP_L3	1; 5; 8; 25	32; 34; 38; 42	48; 53; 55; 57; 63; 64; 67; 70
MMNP_L4_R2	1; 5; 8; 12; 16; 21; 25; 28	29; 31; 34; 38; 41;	48; 51; 53; 55; 57; 63; 64; 69; 71;
		44; 46	73
MMNP_L5	2; 5; 22; 25; 28	32; 34; 39	47; 51; 53; 55; 57; 65; 67
MMNP_R1	5; 22; 25; 28	29; 31; 34; 39; 42	51; 55; 57; 62; 64; 67; 73
MMNP_R3	25	31; 34; 39; 41	53; 55; 57; 61; 64; 69
MMNP_R4	5; 22; 28	29; 34	51; 55; 57; 73
WJ_L1	3; 8; 12; 22; 25; 28	30; 32; 34; 39; 42	47; 51; 54; 55; 57; 62; 64; 67; 70; 73
WJ_L2	1; 5; 8; 25	32; 35; 38; 42	47; 53; 55; 57; 62; 64; 67; 70
WJ_L3	5; 25	31; 35; 39; 41	47; 53; 55; 57; 62; 64; 69; 70
WJ_R1	5; 25	31; 34; 39; 42	47;53; 55; 57; 63; 64; 67; 71; 73
WJ_R2	1; 23	32; 34; 36	47; 54; 55; 57; 66
WJ_R3	1; 5; 8; 22; 25	32; 34	47; 54; 62; 64
WJ_R4	22; 25; 28	29; 31; 34; 39; 41	51; 54; 55; 57; 62; 64; 69; 72
WJ_R5	22; 25; 28	30;31; 34; 38; 42	51; 54; 55; 57; 63; 64; 67; 73
NSJM_L1_R1	2; 5; 8; 25; 28	29; 31; 34; 39; 42	47; 49; 51; 53; 55; 57; 62; 64; 67; 70; 72; 74
NSJM_L2	25	32; 34; 39; 42	47; 54; 55; 57; 62; 64; 67; 70
NSJM_L3	5; 25	31; 34; 39; 42	47; 49; 54; 55; 57; 62; 64; 67; 70; 74
NSJM_L4	25	34; 39; 41	47; 49; 55; 57; 62; 64; 69; 74
NSJM_L5	5; 25	31; 35; 38; 42	47; 49; 53; 56; 57; 63; 64; 67; 70; 74
NSJM_L6	25	32; 34; 39; 42	47; 49; 54; 55; 57; 62; 64; 67; 74
NSJM_L7_R5	2; 5; 25	31; 34; 39; 41	47; 49; 53; 55; 57; 62; 65; 69; 73; 74
NSJM_L8_R6	2; 5; 8; 22; 25; 28	29; 31; 34; 39; 42	47; 49; 51; 53; 55; 57; 61; 64; 67; 70; 73; 74
NSJM_L9_R7	25	29; 31; 34; 39; 41	51; 53; 55; 57; 61; 64; 69; 70; 72
NSJM_L10	12; 25	31; 34; 38; 42; 44	53; 55; 57; 62; 64; 67; 71
NSJM_R2	25	33; 34; 39; 42	47; 54; 55; 57; 62; 64; 67; 70
NSJM_R3	5; 25; 28	31; 34; 39; 41	47; 49; 51; 53; 55; 57; 62;64; 69; 74
NSJM_R4	25	32; 34; 39; 41	47; 54; 55; 57; 62; 64; 69
NSJM_R8	5; 8; 25	30; 31; 34; 38; 42	47; 53; 55; 57; 62; 64; 67; 70; 74
NSJM_R9	3; 8; 25; 28	29;31; 34; 39; 42	47; 51; 53; 55; 57; 62; 64; 67; 70; 74
NSJM_R10	25; 28	29; 32; 34; 39; 41	51; 53; 55; 57; 62; 64; 69; 70
NSJM_R11	25; 28	32; 34; 38; 41	47; 51; 54; 56; 57; 62; 65; 69; 70; 74
NSJM_R12	25; 28	29; 31; 34; 39; 42	51; 53; 55; 57; 62; 64; 67; 70; 72



ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
Crb_L1	5; 25	39	61; 74
Crb_R1	5; 22; 25; 28	29; 35; 39; 41	51; 62; 64; 69; 70; 74
Crb_R2	8; 25	34; 38; 41	55; 57; 63; 64; 69; 72; 74
Crb_R3	5; 25	29; 31; 34; 39; 41	51; 54; 55; 57; 61; 64; 69; 72; 74
Crb_R4	2; 5; 25	29; 31; 34; 39; 41	47; 51; 53; 57; 61; 65; 69; 72
Crb_R5	2; 5; 8; 25; 28	29; 33; 35; 39; 41	47; 51; 54; 55; 57; 61; 64; 69; 72; 74
Crb_R6	25	32; 35; 39; 41	54; 55; 57; 61; 64; 69
Crb_R7	5; 8; 25	39; 41	53; 57; 61; 64; 69; 74
Crb_R8	5; 8; 12; 16; 22; 25; 28	29; 31; 34; 39; 41; 44; 46	51; 53; 55; 57; 62; 64; 69; 71; 72
Pgl_L1_R3	5; 8; 25	31; 34; 39; 41	53; 55; 57; 62; 65; 69; 74
Pgl_L2_R4	22; 25; 28	29; 33; 35; 39; 41	51; 62; 64; 69; 70; 72
Pgl_L3_R5	5; 22; 25; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 62; 64; 69
Pgl_R1	22; 25; 28	29; 33; 34; 39; 42	51; 54; 57; 62; 65;67; 71; 72; 74
Pgl_R2	5; 8; 25; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 62; 64; 69; 70; 74
SV_L1	5; 8	32; 34	54; 55; 65
SV_R1	22; 25; 28	29; 32; 35; 39; 41	51; 54; 55; 62; 65; 69; 70
SV_R2	22; 25; 28	29; 32; 34	51; 55; 57; 65
SS_L1	5; 25	31; 34; 38; 42	47; 53; 55; 57; 63; 64; 67; 71
SS_L2	5; 25	31; 34; 39; 41	47; 53; 55; 57; 62; 64; 69; 70; 74
SS_L3	5; 25	31; 34; 39; 41	53; 55; 57; 62; 64; 69; 70
SS_L4_R3	5; 8; 25; 28	29; 31; 34; 39; 42	47; 51; 53; 55; 57; 62; 64; 67; 70; 72; 74
SS_L5	5; 25	31; 34; 39; 42	53; 55;57; 62; 64; 67; 70
SS_L6	5; 8; 25	31; 39; 41	47; 53; 55; 57; 65; 69; 70; 74
SS_L7	5; 25	31; 34; 39; 42	47; 54; 55; 57; 62; 64; 67; 71; 73; 74
SS_L8_R1	5; 25	31; 34; 39; 41	53; 55; 57; 61; 64; 69; 70
SS_L9	5; 8; 25	39; 42	62; 64; 67; 70
SS_L10	25	34; 39	62
SS_L11	5; 25		70
SS_L12	5; 25	34; 39	55; 57; 62; 64; 70
SS_L13	25	39	62; 65
SS_L14_R16	5; 25	34; 39; 41	61; 65; 69; 70
SS_L15	25	39	61; 65; 71
SS_L16	25	34	53; 55; 57; 62; 64; 70
SS_R1	25; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 61; 64; 69; 70; 73
SS_R2	5; 25	31; 34; 39; 41	47; 53; 55; 57; 61; 65; 69; 70; 74
SS_R4	5; 25	34; 39	47; 55; 57; 62; 65
SS_R5	24	31; 34; 37	53; 55; 57; 63; 64; 70
SS_R6	25	31; 34; 39	53; 55; 57; 61; 64
SS_R7	5; 25	31; 34; 39; 41	47; 53; 55; 57; 62; 4; 69; 70; 73
SS_R8	5; 25	29; 34; 39; 41	47; 51; 55; 57; 61; 5; 69; 71
SS_R9	5; 25	31; 34; 39; 41	53; 55; 57; 62; 64; 69; 70
SS_R10	25	31; 34; 39	53; 55; 57; 62; 70
SS_R11	25	34; 39	47; 55; 57; 62; 64; 67; 71; 73
SS_R12	25	33; 34; 39	54; 55; 57; 62; 64
SS_R13	5; 25	34; 39	47; 61; 64; 70; 74
SS_R14	25	31; 34; 38	53; 55; 57; 63; 64; 71
SS_R15	25	39	61; 65
SS_R17	25; 28	29; 31; 34; 39	51; 53; 55; 57; 62; 73
SS_R18	25	39	62; 65
SS_L23_R22	8; 25; 28	29; 31; 34; 39; 41	47; 51; 53; 55; 57; 62; 64; 69; 70
SS_L18	25	33; 34; 38; 42	54; 55; 57; 63; 64; 67; 70



ID	(Ragni & Possenti, 1996)	(Kitchener et al., 2005)	(Spassov, Simeonovski, & Spiridonov, 1997)
SS_L17_R19	25; 28	29; 31; 34; 39; 41	47; 51; 53; 55; 57; 62; 64; 69; 70
SS_L8_R1	25	31; 34; 39; 41	53; 55; 57; 61; 64; 69
SS_L19	5; 25	31; 34; 39; 42	53; 55; 57; 61; 64; 67
SS_L20	25	31; 34; 39; 42	47; 53; 55; 57; 62; 64; 67
SS_L24	5; 25	39	53; 55; 57; 62; 64
SS_L21	5; 25	32; 35; 39; 41	47; 53; 55; 57; 62; 64; 69; 72
SS_L25	5; 8; 25	31; 34; 39; 41	53; 55; 57; 61; 65; 69; 70
SS_L15	25; 28	29; 32; 35	51; 53; 55; 57; 63; 70; 73
SS_L26	5; 25	31; 34; 39; 41	47; 53; 55; 57; 62; 64; 69; 70
SS_L22	25	34; 38	53; 55; 57; 63; 64
SS_L27	25; 28	31; 34; 39; 41	51; 53; 55; 57; 61; 65; 69; 72
SS_L28	25	33; 34; 39; 42	51; 55; 57; 62; 64; 67; 70; 73
SS_L29_R28	25; 28	30; 31; 34; 39; 41	47; 51; 53; 55; 57; 61; 64; 69; 72
SS_R12	25	34; 39; 41	54; 55; 57; 62; 64; 69
SS_R29	25	31; 34; 39; 41	53; 55; 57; 62; 64; 69
SS_R23	8; 23	34; 36; 41	57; 66; 69; 70
SS_R24	5; 8; 25	31;34; 38; 42	53; 55; 57; 63; 64; 67; 70
SS_R20	25	31; 34	53; 55; 57
SS_R25	25	31; 34; 38	47; 53; 55; 57; 63; 64; 71
SS_R26	25	34; 38	55; 57; 63
SS_R27	25	32; 34; 38; 42	55; 57; 63; 64; 67
SS_R21	25	32; 34; 39; 42	47; 53; 55; 57; 62; 64; 67; 73
PNP_L1	25	31; 34; 39; 42	53; 55; 57; 62; 65; 67
PNP_L2	5; 22; 25	31; 34; 38	53; 55; 57; 62; 64
PNP_L3	25; 28	29; 31; 34; 39; 41	51; 53; 55; 57; 61; 65; 69; 73
PNP_L4	25	39	61; 64
PNP_L5	25	31; 34; 39	53; 55; 57; 61; 64
PNP_L6	22; 25	29; 31; 34	51; 53; 55; 57
PNP_L7	28	29; 34	51; 55; 57
PNP_L8	25; 28	29; 34	51
PNP_R1	25	31; 34; 39	55; 57; 73
PNP_R2	23	34	53; 55; 57; 65
PNP_R3	25	34	53; 55; 57; 65
PNP_R4	25	31; 34	53; 55; 57; 65



Supplementary Information 2 - Wildcat detections and number of individuals identified per survey. (Survey – Survey per study area, as defined in Table 5; #Detections – number of wildcat detections; id_R - right side identifications; id_L - left side identifications; id_C - complete identifications, i.e., identification of the left and right flank simultaneously; SCR - presence of spatial recaptures.

Survey	#Detections	#id_R	#id_L	#id_C	SCR
GVNP, 2009	21	4	2	0	no
GVNP, 2010	17	1	5	0	yes
PGNP, 2010	1	0	0	0	no
PGNP, 2011	6	2	3	2	no
MtNP	24	4	4	2	yes
CNP, 2009	3	1	0	0	no
CNP, 2010	7	0	0	0	no
CNP, 2012	10	2	2	0	yes
CNP, 2013.1	3	1	0	0	no
CNP, 2013.2	2	1	1	1	no
CNP, 2014	7	2	2	1	no
SP	6	1	1	0	yes
MNR, 2010	8	0	2	0	no
MNR, 2011	7	2	1	1	no
MNP, 2012	0	0	0	0	no
MNP, 2013	0	0	0	0	no
SANP, 2012.1	0	0	0	0	no
SANP. 2012.2	2	1	0	0	no
SANP. 2011	8	2	2	2	ves
NC. 2013	7	2	0	0	no
NC. 2014.1	8	0	2	0	no
NC. 2014.2	8	0	1	0	Ves
NC. 2015	4	2	0	0	
NC. 2016	1	0	0	0	no
NCAG. 2017	8	1	1	0	no
NCAG. 2018	7	0	0	0	no
NCAG 2019 1	10	2	5	0	no
NCAG 2019 2	13	4	4	0	no
MMNP 2018	10	1	3	0	
MMNP 2019 1	12	1	2	0	
MMNP 2019 2	5	2	1	1	
Crb	39	8	1	0	
Pal	18	5	3	3	Ves
 SV	7	2	1	0	
MB	1/1	15	17	7	
BE 2018	2	2	0	0	
BF 2019	0	0	0	0	no
FIA 2017	2	0	0	0	no
FIA 2018	2	0	0	0	
ΕΙΑ, 2010 ΕΙΔ. 2019 1	<u> </u>	1	1	0	no
ΕΙΑ, 2019.1	82	7	8	0	
EIA, 2010.2	70	2	7	0	110
EIA, 2020.1	27	2	2	0	yes
EIA, 2020.2	7/	10	8	3	110
W/L 2010	30	3	3	0	yes
W1 2020	36	3 3	<u> </u>	0	yes
	96	3 12	<u> </u>	5	yes
	100	0	0	<u>ບ</u>	yes
SS, 2010 SS, 2010 1	120	0	9 11	2	
SS, 2019.1	27	2 2	6	1	yes
00, 2019.2 66, 2020	3/ 76	3 11	10	ו ס	110
33, ZUZU	10	11	10	3	yes



Survey	#Detections	#id_R	#id_L	#id_C	SCR
Survey	#Detections	#id_R	#id_L	#id_C	SCR
PNP, 2020	11	1	4	0	no
PNP, 2021	27	3	4	0	no



Supplementary Information 3 - oSCR model AIC rank (1 model set for each survey). (Survey – Survey per study area, as defined in Table 5; Model – parameterization of each model; AIC - Akaike Information Criterion; dAIC - difference between AIC score for the best model and the model being compared)

Survey	Model	AIC	dAIC
GVNP, 2010	~1	125.34	0.00
	p0~Trail	127.26	1.92
MtNP	~1	348.57	0.00
	p0~Trail	350.35	1.78
SANP, 2011	~1	120.80	15.22
	p0~Trail	122.59	17.01
	p0~Bait	105.58	0.00
	p0~Trail+Bait	107.58	2.00
NC, 2014.2	~1	65.22	0.00
	p0~Trail	66.84	1.62
	p0~Model	66.43	1.21
	p0~White.flash	66.43	1.21
	p0~Trail+Model	68.12	2.90
	p0~Trail+White.flash	68.12	2.90
	p0~Trail+Model+ White.flash	70.12	4.90
WJ, 2019	~1	215.68	5.94
	p0~Trail	217.12	7.38
	p0~Model	209.74	0.00
	p0~Trail+Model	211.65	1.91
WJ, 2020	~1	443.50	3.08
	p0~Trail	441.63	1.21
	p0~Model	440.42	0.00
SS, 2019.1	~1	413.84	3.01
	p0~Trail	415.83	5.00
	p0~White.flash	410.83	0.00
	p0~ Cams.per.Station	415.61	4.78
	p0~Trail+White.flash	412.83	2.00
	p0~Trail+ Cams.per.Station	417.59	6.76
	p0~White.flash+ Cams.per.Station	411.26	0.43
	p0~Trail+White.flash+ Cams.per.Station	413.26	2.43
EIA_2020.1	~1	612.25	0.00
	p0~Trail	613.08	0.83
	p0~White.flash	614.12	1.87
	p0~Cams.per.Station	613.19	0.94
	p0~Trail+White.flash	615.05	2.80
	p0~Trail+ Cams.per.Station	613.98	1.73
	p0~White.flash+ Cams.per.Station	615.06	2.81
	p0~Trail+White.flash+ Cams.per.Station	615.95	3.70

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Supplementary Information 4 - Parameters estimated for the best model selected of each study area. (Survey – Survey per study area, as defined in Table 5; Model – parameterization of each model; SE – standard error; p0 - Baseline detection probability parameter estimate)

Survey	Model	Density (indiv/100km ²)	Density SE	Sigma (m)	Sigma SE (m)	р0	p0 SE
GVNP, 2010	~1	6.481	3.563	728.063	204.424	0.021	0.016
MtNP	~1	1.130	0.437	2574.212	465.078	0.008	0.003
CNP, 2012	~1	6.152	5.067	425.355	193.924	0.017	0.021
SP	~1	13.679	12.643	470.035	210.812	0.002	0.002
SANP,2011	~1	2.662	1.530	894.679	362.369	0.014	0.010
NC, 2014.2	~1	4.857	4.882	854.492	285.941	0.042	0.035
Pgl	~1	10.165	5.620	538.539	164.608	0.024	0.021
Etn	~1	28.782	10.745	1340.339	351.037	0.004	0.002
NSJM	~1	7.881	1.730	1098.667	85.305	0.016	0.003
MB	~1	33.308	6.138	794.169	50.739	0.018	0.002
WJ, 2019	p0~Model	1.816	0.854	1973.214	401.831	*	*
SS, 2019.1	p0~White.flash	23.245	11.989	500.527	185.770	*	*
EIA_2020.1	p0~White.flash	4.644	2.009	695.229	155.615	*	*

*Baseline detection probability parameters

Survey	Model	Baseline detection probability	Estimate
		parameters	
WJ, 2019	p0~Model	p0.CuddebackAmbush	0.011
		p0.CuddebackAmbush SE	0.007
		p0.CuddebackG	0.014
		p0.CuddebackG SE	0.012
		p0.CuddebackProfessional	0.064
		p0.CuddebackProfessional SE	0.036
SS, 2019.1	p0~White.flash	p0.whiteflash	0.005
		p0.whiteflash SE	0.003
		p0.infrared	0.002
		p0.infrared SE	0.001
EIA_2020.1	p0~White.flash	p0.whiteflash	0.014
		p0.whiteflash SE	0.011
		p0.infrared	0.011
		p0.infrared SE	0.004



Supplementary Information 5 - unmarked frame summaries. (Survey – Survey per study area, as defined in Table 5; #Sites – number of sites sampled; #Observations – number of wildcat occurrences; Obs/sites – number of wildcat observations per site)

Survey	#Sites	#Observations	Sites with at least one detection		Obs/sites
CNP_14	40	7		6	0.175
EIA_20sp	46	44		4	0.957
Etn	18	68		16	3.778
GVNP_10	39	17		9	0.436
MB	25	132		25	5.280
MtNP	34	23		9	0.676
NCAG_19sp	6	12		3	2.000
NSJM	64	54		24	0.844
Pgl	12	2		1	0.167
SANP_11	28	5		2	0.179
SS_19wi	166	120		44	0.723
WJ_19	8	23		4	2.875
BF_18	108	2		2	0.019
Crb	12	4		1	0.333
MMNP_18	18	10		4	0.556
MMNP_19su	17	6		2	0.353
MMNP_19wi	18	12		5	0.667
MNR_10	41	8		6	0.195
MNR_11	42	6		4	0.143
PGNP_10	35	1		1	0.029
PGNP_11	36	4		3	0.111
PNP_20	66	11		7	0.167
PNP_21	55	25		15	0.455
SP	46	6		6	0.130
SV	12	2		1	0.167



Supplementary Information 6 - unmarked models. (Survey – Survey per study area, as defined in Table 5; Model – parameterization of each model; AIC - Akaike Information Criterion; Delta - difference between AIC score for the best model and the model being compared; AICwt - predictive power of the model; cumltvWt - sum of the AIC weights; Chi-sq - Pearson chi-square statistic; nsims - number of bootstrap samples; p-value – p-value assessed from the parametric bootstrap; c-hat - estimate of the overdispersion parameter.)).

Survey	Model	AIC	delta	AICwt	cumltvWt	chi-sq	nsims	p-value	c-hat
CNP_14	~1	106.429				6.38E+03	1000	0.380	0.022
EIA_20sp	~1	325.400	0.000	0.316	0.320	1.23E+26	1000	0.018	0.013
	~trail	327.400	2.000	0.116	0.740	2.64E+25	1000	0.418	0.000
	~flash	326.850	1.450	0.153	0.470	1.19E+26	1000	0.014	0.015
	~cams	326.850	1.450	0.153	0.620	1.19E+26	1000	0.018	0.005
	~trail+cams	327.660	2.270	0.102	0.840	1.10E+26	1000	0.017	0.016
	~flash+cams	328.270	2.870	0.075	0.910	1.15E+26	1000	0.028	0.000
	~trail+flash+	329.340	3.950	0.044	0.960	1.08E+26	1000	0.020	0.001
	cams								
Etn	~1	600.041				6.81E+15	1000	0.261	0.000
GVNP_10	~1	174.290	0.170	0.480	1.000	9.14E+04	1000	0.441	0.004
	~trail	174.120	0.000	0.520	0.520	8.42E+04	1000	0.581	0.002
MB	~1	1032.711				6.81E+15	1000	0.261	0.000
MtNP	~1	268.600	1.310	0.340	1.000	6.04E+08	1000	0.563	0.000
	~trail	267.290	0.000	0.660	0.660	5.60E+08	1000	0.625	0.000
NCAG_19sp	~1	116.480	5.400	0.034	0.970	3.93E+14	1000	0.090	0.000
	~trail	116.690	5.600	0.031	1.000	3.57E+14	1000	0.107	0.000
	~model	111.080	0.000	0.505	0.500	2.23E+14	1000	0.472	0.000
	~trail+model	111.400	0.320	0.430	0.940	2.22E+14	1000	0.436	0.000
NSJM	~1	557.072				5.48E+09	1000	0.174	0.000
Pgl	~1	29.890				1.37E+04	1000	0.270	0.000
SANP_11	~1	67.540	0.000	0.430	0.430	4.89E+07	1000	0.236	0.000
	~trail	69.390	1.850	0.170	0.880	4.90E+07	1000	0.218	0.000
	~bait	68.350	0.810	0.290	0.710	4.96E+07	1000	0.186	0.000
	~trail+bait	70.140	2.600	0.120	1.000	4.97E+07	1000	0.232	0.000
SS_19wi	~1	1304.610	8.070	0.006	0.990	8.18E+16	1000	0.044	0.000
	~trail	1304.430	7.890	0.007	0.990	6.63E+16	1000	0.057	0.006
	~flash	1306.390	9.850	0.003	1.000	7.59E+16	1000	0.037	0.000
	~cams	1297.110	0.570	0.264	0.610	3.17E+16	1000	0.143	0.000
	~trail+flash	1306.270	9.730	0.003	1.000	6.25E+16	1000	0.054	0.006
	~trail+cams	1296.540	0.000	0.351	0.350	2.52E+16	1000	0.204	0.000
	~flash+cams	1298.280	1.740	0.147	0.980	2.95E+16	1000	0.165	0.000
	~trail+flash+	1297.470	0.930	0.220	0.830	2.36E+16	1000	0.256	0.000
	cams								
WJ_19	~1	184.520	0.800	0.250	0.630	1.17E+18	1000	0.078	0.000
	~trail	185.850	2.120	0.130	1.000	1.05E+18	1000	0.078	0.000
	~model	183.730	0.000	0.380	0.380	1.02E+18	1000	0.270	0.000
	~trail+model	184.630	0.900	0.240	0.870	9.77E+17	1000	0.322	0.000
Crb	~1	41.810	0.000	0.535	0.530	5.34E+06	1000	0.338	0.000
MMNP_18	~1	121.780	0.000	0.507	0.510	9.36E+05	1000	0.737	0.000
	~model	123.500	1.720	0.215	0.720	9.89E+05	1000	0.701	0.000
	~flash	123.650	1.870	0.199	0.920	1.01E+06	1000	0.624	0.000
	~model+flash	125.490	3.720	0.079	1.000	9.93E+05	1000	0.715	0.000
MMNP_19su	~1	73.280	0.000	0.310	0.310	1.71E+09	1000	0.165	0.000
_	~model	73.380	0.100	0.290	0.600	1.80E+09	1000	0.149	0.000
	~flash	74.440	1.160	0.170	1.000	1.75E+09	1000	0.166	0.000
	~model+flash	73.910	0.630	0.220	0.830	1.88E+09	1000	0.161	0.000



Survey	Model	AIC	delta	AICwt	cumltvWt	chi-sq	nsims	p-value	c-hat
MMNP_19wi	~1	142.980	5.990	0.029	1.000	6.17E+10	1000	0.087	0.000
	~model	139.780	2.790	0.141	0.970	5.35E+10	1000	0.105	0.000
	~flash	138.570	1.580	0.260	0.830	4.24E+10	1000	0.297	0.000
	~model+flash	136.990	0.000	0.571	0.570	3.92E+10	1000	0.338	0.000
MNR_10	~1	101.430	4.140	0.110	1.000	3.00E+04	1000	0.077	0.219
	~trail	97.290	0.000	0.890	0.890	2.94E+04	1000	0.392	0.001
MNR_11	~1	76.820	0.000	0.710	0.710	1.94E+04	1000	0.141	0.017
	~trail	78.620	1.800	0.290	1.000	1.95E+04	1000	0.112	0.041
PGNP_10	~1	20.440	0.000	0.730	0.730	3.92E+01	1000	0.247	0.700
	~trail	22.380	1.940	0.270	1.000	3.93E+01	1000	0.274	0.766
PGNP_11	~1	56.640	0.000	0.710	0.710	1.12E+03	1000	0.376	0.004
	~trail	58.470	1.830	0.290	1.000	1.12E+03	1000	0.372	0.019
PNP_20	~1	147.913				3.17E+08	1000	0.010	0.629
PNP_21	~1	327.932				2.26E+07	1000	0.410	0.000
SP	~1	29.890				1.44E+02	1000	0.523	0.002
SV	~1	29.890				1.37E+04	1000	0.271	0.000



