

Habitat fragmentation and anthropogenic factors affect wildcat Felis silvestris silvestris occupancy and detectability on Mt Etna

Authors: Anile, Stefano, Devillard, Sebastien, Ragni, Bernardino,

Rovero, Francesco, Mattucci, Federica, et al.

Source: Wildlife Biology, 2019(1): 1-13

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00561

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Subject Editor: Luc Wauters. Editor-in-Chief: Ilse Storch. Accepted 15 May 2019

Habitat fragmentation and anthropogenic factors affect wildcat Felis silvestris occupancy and detectability on Mt Etna

Stefano Anile, Sebastien Devillard, Bernardino Ragni, Francesco Rovero, Federica Mattucci and Mario Lo Valvo

S. Anile, (https://orcid.org/0000-0001-8871-9615)

(stefanoanile@yahoo.it), Cooperative Wildlife Research Laboratory, Southern Illinois Univ., Carbondale, IL 62901, USA. – S. Devillard, Univ Lyon, Université Claude Bernard Lyon, CNRS, Laboratoire de Biométrie et Biologie Evolutive, Villeurbanne, France. – B. Ragni, Dipto di Chimica, Biologia e Biotecnologie, Univ. degli Studi di Perugia, Perugia, Italy. – F. Rovero, Dept of Biology, Univ. of Florence, Sesto Fiorentino, Italy, and: Sezione di Biodiversità Tropicale, MUSE – Museo delle Scienze di Trento, Trento, Italy. – F. Mattucci, Laboratorio di Genetica, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA), Bologna, Italy. – M. Lo Valvo, Dipto STEBICEF, Univ. di Palermo, Palermo, Italy.

Knowledge of patterns of occupancy is crucial for planning sound biological management and for identifying areas which require paramount conservation attention. The European wildcat Felis silvestris is an elusive carnivore and is classified as 'least concern' on the IUCN red list, but with a decreasing population trend in some areas. Sicily hosts a peculiar wildcat population, which deserves conservation and management actions, due to its isolation from the mainland. Patterns of occupancy for wildcats are unknown in Italy, and especially in Sicily. We aimed to identify which ecological drivers determined wildcat occurrence on Mt Etna and to provide conservation actions to promote the wildcats' long-term survival in this peculiar environment. The genetic identity of the wildcat population was confirmed through a scat-collection which detected 22 different wildcat individuals. We analysed wildcat detections collected by 91 cameras using an occupancy frame work to assess which covariates influenced the detection (p) and the occupancy (y) estimates. We recorded 70 detections of the target species from 38 cameras within 3377 trap-days. Wildcat detection was positively influenced by the distance to the major paved roads and negatively affected by the presence of humans. Wildcat occupancy was positively associated with mixed forest and negatively influenced by pine forest, fragmentation of mixed forest and altitude. A spatially explicit predicted occupancy map, validated using an independent dataset of wildcat presence records, showed that higher occupancy estimates were scattered, mainly located on the north face and at lower altitude. Habitat fragmentation has been claimed as a significant threat for the wildcat and this is the first study that has ascertained this as a limiting factor for wildcat occurrence. Conservation actions should promote interconnectivity between areas with high predicted wildcat occupancy while minimising the loss of habitat.

In the current, unprecedented extinction crisis, carnivorans and especially felids, are facing the highest extinction risks among mammals (Cardillo et al. 2004). Threats are even more important for populations on islands (Purvis et al. 2000), that likely suffer from a lack of connectivity with larger mainland source populations. Habitat destruction and fragmentation are the major causes of biodiversity loss worldwide (Krauss et al. 2010). In addition, an increasing human population can severely interfere with and disturb ecological processes (Cardillo et al. 2008, Pimm et al. 2014). In such a context of habitat change, knowledge of patterns of occupancy,

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) http://creativecommons.org/licenses/by/4.0/. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

and their ecological correlates are crucial for planning sound biological management and for identifying areas which require paramount conservation attention for a given species.

Within the family Felidae, the smallest species are understudied (Brodie 2009, Zanin et al. 2014, Anile and Devillard 2015), but efforts to correct this bias are increasing (Macdonald et al. 2010, Anile and Devillard 2018, Ruiz-Olmo et al. 2018). This lack of knowledge about the ecology of small felids might result in overlooking their ecological and conservation requirements, hence leading to an enhanced risk of extinction in the short term. Luckily, with the advent of camera-trapping (O'Connell et al. 2010) an increasing number of studies has been run worldwide to identify environmental and anthropogenic variables critical for determining the occurrence of a variety of felid species (Schuette et al. 2013, Andresen et al. 2014, Lesmeister et al. 2015, Hemami et al. 2018, Penjor et al. 2018, Rovero et al. 2018, Wang et al.

2018), including small ones (Galvez et al. 2013, Singh et al. 2014, Jennings et al. 2015). This approach has improved our knowledge of the ecology of felid species, enabling researchers to identify or predict areas of particular value for conservation purposes, and hence to provide sound management actions with the ultimate goal of increasing the likelihood of the long-term survival of these carnivorous species.

The European wildcat *Felis silvestris* is a small (body mass = 2.4–6.2 kg) (Nowell and Jackson 1996, Macdonald and Loveridge 2010) carnivorous mammal currently listed in the HABITATS directive (European Council Directive 92/43/EEC, Appendix IV of 21 May 1992) and classified by the IUCN as 'Least Concern', but notably with a decreasing population trend (Yamaguchi et al. 2015) throughout most of its range, although wildcat distribution is currently expanding in some countries (Nussberger et al. 2018).

Across Europe five distinct biogeographic groups of wildcat populations were identified (Mattucci et al. 2016) and likely originated during the protracted isolation which occurred in the late Pleistocene—early Holocene due to climate fluctuations. A similar evolutionary patterns explained the main genetic/geographic substructure observed in Italy, with the exception two subpopulations found in the central Italian peninsula that likely resulted from a more recent adaptive processes (Mattucci et al. 2013). Human induced habitat fragmentation, instead, mainly conditioned the genetic clustering of the subspecies in France (Say et al. 2012) and Germany (Steyer et al. 2016) where wildcats split into two main groups during the last century.

The Sicilian wildcat population is therefore considered a distinct unit of conservation (Mattucci et al. 2013) and deserves particular management conservation actions since being isolated from the Italian peninsula precludes any immigration/recolonization process, decreasing the likelihood of long-term persistence (Anile et al. 2014). The main threats to the long-term survival of wildcat populations are loss and fragmentation of suitable habitat, hybridization with domestic cats *Felis catus* (Nowell and Jackson 1996, Macdonald and Loveridge 2010) and human-induced mortality (mainly road kills and poaching; Krone et al. 2008, Devillard et al. 2013, Falsone et al. 2014).

Wildcat populations are usually found at low densities (less than 1/km²; Can et al. 2009, Soto and Palomares 2013, Anile et al. 2014, Gil-Sanchez et al. 2015), most of their activity is nocturnal (Daniels et al. 2001, Germain et al. 2008) and they typically display elusive behaviour (i.e. human avoidance) (Piñeiro et al. 2012). However, the application of camera-trapping to study wildcats has overcome these constraints (Anile et al. 2009), and camera-trapping surveys for wildcats have been used extensively in Spain (Sarmento et al. 2009, Soto and Palomares 2013, Gil-Sanchez et al. 2015), Scotland (Kilshaw and Macdonald 2011, Kilshaw et al. 2014, Littlewood et al. 2014), Turkey (Can et al. 2009), Germany (Beutel et al. 2017), the Netherlands (Canters et al. 2005) and Italy (Velli et al. 2015). Camera-trapping data have been analysed using capture-recapture (CR) (Can et al. 2009, Anile et al. 2012a) and spatially explicit capture-recapture (SECR) models (Anile et al. 2014, Kilshaw et al. 2014, Gil-Sanchez et al. 2015) to estimate wildcat population densities in numerous environments. Interestingly, camera-trapping has also been used in Scotland to estimate wildcat occupancy (McKenzie et al. 2006; % of area occupied while accounting for an imperfect detection process) and to elucidate the role played by environmental variables in determining wildcat occupancy (Kilshaw et al. 2016). Knowing spatial variations in density and occurrence might help in deciphering the impacts of major threats to wildcat populations over their geographical distribution.

Habitat fragmentation has been frequently considered (Nowell and Jackson 1996, Macdonald and Loveridge 2010) as a direct threat to wildcat populations in Europe, but its effect has not been investigated properly (Zanin et al. 2014). The current scientific knowledge on wildcat habitat requirements is mainly based on radio-tracking studies conducted in Germany (Klar et al. 2008, Jerosch et al. 2010, 2017), Spain (Sarmento et al. 2006, Soto and Palomares 2013), Portugal (Monterroso et al. 2009), France (Germain et al. 2008, Beugin et al. 2016) and Scotland (Daniels et al. 2001). Radio-tracking is relatively expensive and invasive as it requires the live-trapping of wildcats (Bizzarri et al. 2010), therefore radio-tracking studies in Italy are rare (Anile et al. 2017) and have not addressed wildcat habitat requirements. According to radio-tracking studies, wildcats prefer forest habitats (Nowell and Jackson 1996, Daniels et al. 2001, Wittmer 2001), mainly deciduous (but see Klar et al. 2008, Lozano 2010). In Mediterranean areas shrub vegetation can also play an important role in the ecology of this species (Lozano et al. 2003, Monterroso et al. 2009). Moreover, open meadows can also be used by wildcats as hunting areas due to the abundance of suitable prey (Silva et al. 2012). Some studies have found that agricultural area can be used by wildcats (Lozano 2010), as long as these areas are linked to forest habitat (Jerosch et al. 2017). Overall, the wildcat is adapted to a wide range of different ecological scenarios and this remarkable capacity for adaptation is also reflected in the plasticity of its feeding behaviour (Malo et al. 2004, Lozano et al. 2006, Apostolico et al. 2015). However, the role of the fragmentation of preferred habitats on the population dynamics and population density, or at least on the occurrence of the wildcat, remains understudied. In addition, habitat fragmentation might also have an effect on the degree of hybridization with domestic cats, which may have strong potential effects on wild carnivores (Morin et al. 2018). Hybridization with the domestic cat is indeed a direct threat to wildcat populations (Nowell and Jackson 1996, Macdonald and Loveridge 2010), that has been widely detected in Europe (Nowell and Jackson 1996, Steyer et al. 2018). Interestingly, a recent study (Beugin et al. 2018) suggests that in fragmented habitat, hybridization should be more common due to the higher presence of domestic cats when compared with continuous and large habitats. This is also supported by the findings of Nussberger et al. (2018) that hybrids were located more frequently at the periphery of the wildcat distribution range where forested habitat might be of lower quality.

In this study, we used camera-trapping data from Mt Etna (Sicily, Italy) to 1) identify ecological drivers and human-induced determinants to estimate wildcat occupancy (ψ) and detection (p); 2) develop a spatially explicit wildcat occupancy model for the entire study area; 3) test the

robustness of this model against an independent dataset of wildcat records and 4) use the results to propose sound conservation actions for the long-term persistence of this unique insular wildcat population in the peculiar ecosystem of the highest active volcano in Europe. Our a priori expectations, based on scientific literature and preliminary observations of wildcat records collected within our study area, were that 1) mixed forest should promote wildcat occupancy whereas pine forest are used less frequently; and 2) fragmentation of the preferred habitat should impact occupancy negatively. Additionally, we also expected that 3) human disturbance (in term of distance to major roads and human presence) should negatively affect wildcat detectability.

Material and methods

Study area

The Etna Regional Park (~590 km²) comprises the ecosystem of Mt Etna, Italy, with an altitude range from 550 up to ~3360 m a.s.l. The landscape is characterized by recent large lava flows and inactive secondary cones of different ages, intermixed with areas dominated by trees (Corsican pine Pinus laricio, different species of oak Quercus pubescens, Quercus ilex, chestnut Castanea sativa, aspen Populus tremulus, European beech Fagus sylvatica and Mt Etna broom Genista etniensis). Forest cover usually lies between 1000 and 2000 m a.s.l. and areas at higher altitude are characterized by low shrub vegetation. The most widespread habitat within the forest cover range consists of large woodland patches intermingled with relatively small open fields, sometimes surrounded or interrupted by lava flows of variable extents (Fig. 1). The climate is typically Mediterranean at the lower altitudes, with warm springs and hot dry summers. Rainfall is concentrated during autumn and winter with, a yearly mean of 1000-1400 mm. Snow cover is common in winter and usually abundant at higher altitudes. Wildcat refuges are widely available in the form of cavities, characteristic of the volcanic soil, which also represent (due to water condensation on the cavity walls) the only available source of water in summer.

The park is divided into four main management units (zone A–D) according to different level of protection/activities. In zone A vehicle access is subject to permission and restricted to unpaved roads used for forest management, sheep farming and tourism. 'Integral reserve' - zone A is subject to more constraints in order to ensure maximum protection of plant and animal species. 'General reserve' zone B where educational activities and regular excursions are permitted. 'Protection area' - zone C, located close to population centres, where eco-friendly activities are encouraged. 'Pre-park area' - zone D where the landscape is dominated by medium-sized traditional agricultural fields, mixed with wooded areas and human activities, should comply with the general purpose of the park. The most remote areas (zone A) of Mt Etna have been declared a World Heritage Site by UNESCO in 2013 (https://whc.unesco.org/en/ list/1427>). The most congested roads within the park serve to reach the two skiing centres located on the southern and north-eastern slope (SP. 92 and 'Mareneve', respectively). Other heavily congested roads, located on the north-western slope of Mt Etna, are the SS. 284 which connects the town of Bronte with that of Randazzo, the SS. 120 which connects the town of Randazzo with that of Maniace, and the 'Quota Mille' which intersects the park at 1000 m a.s.l. on the north-eastern slope (Fig. 1). Currently Mt Etna is almost totally surrounded by unsuitable wildcat habitat with widespread towns and villages, in addition to the close presence of a metropolitan city (Catania). Only a narrow strip (~30 km) of the northern slope is adjacent to the Nebrodi Park (~855 km²) where suitable wildcat habitat is present and wildcats are historically widespread. Unfortunately, this strip is intersected by congested roads where evidence of wildcat

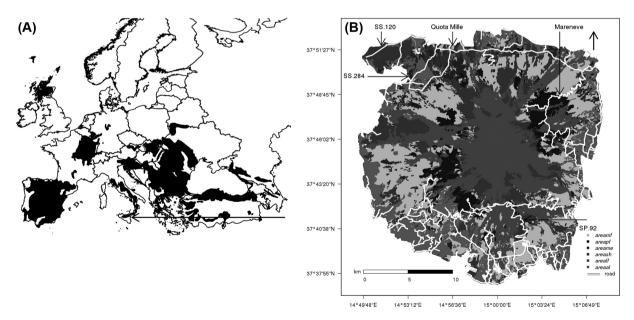


Figure 1. Approximate distribution ranges of the European wildcat *Felis silvestris* for western Europe (A) and Etna Park (Sicily, Italy) (B), where we conducted the camera-trapping study in 2015–2016. Major paved roads (white lines) across the Etna Park and habitat vegetation classes (*areamf* = mixed forest; *areapf* = pine forest; *areame* = meadow; *areash* = shrub; *arealf* = lava flow; *areaal* = agricultural) are indicated.

road-kills (Falsone et al. 2014) have been found, probably reducing dispersal movements of the species between the two parks.

Camera trapping and scat-collection

We deployed seven arrays of camera traps across Mt Etna from 2 July 2015 to 22 December 2015 (3 arrays with 15 cameras and 1 array with 12 cameras) and from 1 April 2016 to 1 July 2016 (2 arrays with 12 cameras and 1 array with 10 cameras), with the aim of surveying the widest presumed suitable area for wildcats (i.e. <2000 m a.s.l.) within the park (Fig. 2), as is usually done in camera trapping surveys on this and other felids (Anile and Devillard 2015, 2018). The discrepancy in the number of cameras used per array is because four cameras (array no. 4) were stolen during the study. However data from two cameras were partially retrieved before the theft. Cameras were located within public areas of the park (i.e. not on private property). We designed in GIS a grid with a cell size of 1 km that we randomly laid over the study area. Within each grid cell in each array, we then placed cameras as close as possible to the cell centroid on suitable sites for wildcat movements, i.e. along unpaved roads (>2 m) and trails (<2 m). This resulted in a mean spacing of 759.9 ± 24.5 m (\pm SE; range = 273-1663) between adjacent cameras, and at a mean elevation of 1415 ± 24.5 m a.s.l. (±SE; range=1075-1874). Cameras were checked twice per week for camera functioning, batteries and data download. We aimed to collate at least 30 functional days at each camera; when cameras were not properly working (e.g. batteries to replace and human alteration such as covering or moving the camera), we accordingly accommodated the 'capture' matrix.

We used 18 digital cameras. We angled cameras slightly downwards $(15 \pm 3^{\circ})$ to obtain a better view of the wildcat's norma dorsalis (part of the coat that is useful for identifying individuals (Anile et al. 2014). Each camera was accommodated in an iron box, locked with a padlock and then tied to a tree (at 50 ± 10 cm from the ground) with a chain. We set cameras with a delay time of 10 min between successive bursts (n = 3) of photos. No lure or bait was used as an attractant. For each camera we measured the width (width) of the road/trail where cameras were placed using a tape measure and the elevation (elevation) by using a GPS. Wildcat identification was conducted according to the coat-colour and marking-system of the European wildcat developed by Ragni and Possenti (1996) and used in previous camera-trapping studies for the same study area (Anile et al. 2014). Following Anile et al. (2014), we also walked transects (n = 97); 1.23 ± 0.06 km mean \pm SE; range = 402-2742 m) four times on a weekly basis between cameras to collect putative wildcat scats (Fig. 2). For each fresh 'putative' wildcat scat, a small portion (~40 µg) was scratched from the surface and immediately stored in a small pipe (capacity ~12 ml) filled with 7 ml of 95% ethanol. Soon after the collection, the scat and the pipe were both stored in a thermic bag filled with replaceable ice. Finally, scat samples were stored at −20°C within four hours of finding. Samples were then genotyped at eleven feline unlinked autosomal microsatellites to ensure the genetic identity of the wildcat population sampled using cameras (Supplementary material Appendix 1).

Covariates

Spatial analysis of habitat covariates were performed using the software QGIS ver. 2.8 Wien (<www.qgis.org>) and its

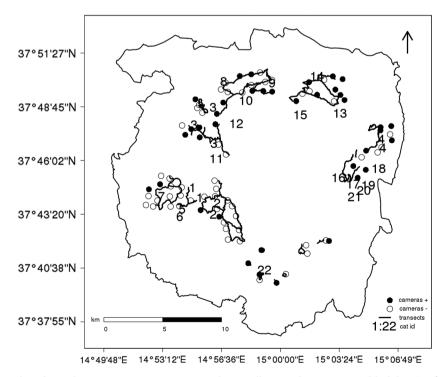


Figure 2. Results of combined sampling, using camera-trapping and scat-collection along transects (black lines), of European wildcat *Felis silvestris* on Mt Etna during 2015–2016. Black points = cameras positive for wildcat; white points = cameras negative for wildcats; numbers = individual genotype detected.

Table 1. Description of covariates used to model the detection (p) and the occupancy (ψ) process of the European wildcat *Felis silvestris* on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016.

Model component	Covariates	Description			
Detection (p)	width	width of the road/trail where cameras were placed			
•	days	camera trap effective working days			
	array	categorical factor indicating each array (1–7)			
	distanceMR	straight distance between each camera and the closest major road			
	RAIh	sum of all events with humans such as bikers, trekkers, forest workers and mushroom collectors			
Occupancy (ψ)	areamf, areapf, areash, areame, arealf, areaal	the area (% of km²) of each habitat class within each circular buffer			
	nclass	number of habitat class			
	npatchesmf, npatchespf, npatchessh, npatchesme, npatcheslf, npatchesal	number of patches per habitat class			
	npatchestot	sum of all patches			
	lengthMR	length of the major roads located within the circular buffer			
	distanceMR	straight distance between each camera and the closest major road			
	elevation	altitude of each camera			

plugins. We expected detection probability (p) to be influenced by the following covariates (Table 1): 1) width (width of the road/trail where cameras were placed): wildcat detection on narrower trails might be enhanced (i.e. a wildcat moving through a smaller detection zone is more likely to be detected than when passing through a larger detection zone (Clare et al. 2015, Bahaa-el-din et al. 2016); 2) days (cameratrap days, i.e. from detection to retrieval or to last photo taken in case the camera malfunctioned): wildcat detections can decrease along with an increase in the effort if a trap-shy response occurs (Wegge et al. 2004); 3) array (a categorical factor created for each array of traps (1-7)): given that we used seven non simultaneous arrays, we expected that all parameters of interest for the detection process could also vary by arrays, hence this detection covariate was acting as a 'random site effect' (Harihar and Pandav 2012, Tan et al. 2017, Penjor et al. 2018); 4) distanceMR (the straight-line distance between each camera and the closest major paved road): wildcat detections might decrease for those cameras located closer to the major roads. Indeed, it has been shown that wildcat ranging behaviour is seriously affected by the presence of such human structures (Klar et al. 2009, Mata et al. 2017, Planillo et al. 2018); 5) RAIh (the sum of all events with humans such as bikers, hikers, forest workers and mushroom collectors): wildcat detections can be negatively influenced by persistent use of the trails by humans (Piñeiro et al. 2012).

Ecological covariates to model wildcat occupancy (ψ) (Table 1) were derived from the land map 'Nature map of the Sicilian region' at the scale of 1:50 000 created in 2008 with a resolution of 1 ha. Map accuracy was screened through extensive ground-truthing. The map is originally composed of 41 layers which we merged into eight main habitat classes (Supplementary material Appendix 2). Specifically, layers were combined into habitat classes according to the current knowledge of wildcat ecology. Previous studies have shown that mixed forest (areamf; 170 km² – 29.3%), mostly composed by deciduous trees, are preferred by wildcats to pine forests (areapf; 42 km² – 7.2%) (Silva et al. 2012, Kilshaw et al. 2016), whereas shrub vegetation (areash; 88 km² – 15.1%) has been found to be crucial

to promoting wildcat occurrence in Mediterranean habitat (Lozano 2010). Additionally, meadows (*areame*; 29 km² – 4.9%) can also be important for wildcats as hunting areas (Klar et al. 2008, Kilshaw et al. 2016). The Etna ecosystem is also characterized by the presence of extensive lava flows (*arealf*; 152 km² – 26.1%) at higher altitudes (>2000) which become irregularly sparse at lower altitudes. Small agricultural lands (*areaal*; 97 km² – 16.6%) can be tolerated by wildcats (Jerosch et al. 2017), whereas lands with persistent human presence (*areahl*; 3.5 km² – 0.5%) are usually avoided (Klar et al. 2008, Silva et al. 2012). In our analysis we did not consider *areahl* and *arearv* (river vegetation; 0.5 km² – 0.08%) as these habitat classes were not represented within our sampling area.

For each camera (Supplementary material Appendix 3) we created a circular buffer with a radius of 750 m (hence we covered an area of ~1.7 km² which corresponds to the minimum home-range for a wildcat in a Mediterranean habitat (Klar et al. 2008, Monterroso et al. 2009) and for each buffer/camera we extracted the following variables: 1) the area (% of km²) of each habitat class (areamf, areapf, areash, areame, arealf, areaal); 2) the number of the habitat classes (nclass) as a proxy for habitat structural complexity; 3) the number of patches per habitat class (npatchesmf, npatchespf, npatchessh, npatchesme, npatcheslf, npatchesal) as a proxy for fragmentation for each habitat class; 4) the number of all patches *npatchestot* as a proxy of overall habitat fragmentation; 5) the length of major paved roads lengthMR (km) located within the circular buffer (Galvez et al. 2013); 6) distanceMR (km, the straight-line distance between each camera and the nearest major roads). As lengthMR and distanceMR are both proxy for disturbance, these two covariates were independently included in occupancy models.

Lastly, we note that our camera trapping sites sampled the habitat classes suitable for wildcat occurrence proportionally to their availability in the whole study area, as their extents within the circular buffers and across the area were correlated significantly (Pearson's correlation coefficient = 0.64; Supplementary material Appendix 4). Candidate covariates for occupancy and detection were screened for collinearity with a threshold for the Pearson's correlation > |0.7| (Silva et al.

2012, Kilshaw et al. 2016); when two covariates were found to be collinear, we included only one covariate of the pairs within occupancy models. For easier model computations covariates were normalized to have mean = 0 and SD = 1.

Occupancy modelling

We used the R package camtrapR (Niedballa et al. 2016) to manage the data (camera records and camera setting deployments), to prepare the 'capture' matrix (i.e. detection 1 versus no detection 0) and the 'occasion' matrix (0 = camera not operational or malfunctioned; 1 = camera operational and working). We then ran single-species, single-season occupancy analysis with the R package unmarked (Fiske and Chandler 2011) in the R environment (<www.r-project. org>). Each occupancy model represented a set of ecological hypotheses that can be tested for the detection (p) and the occupancy (ψ) process, given that model assumptions are respected (Rovero and Zimmermann 2016). Model assumptions for single-season, single species occupancy models are: 1) occupancy is assumed to be constant throughout the survey; 2) detections and sites are independent 3) occupancy and detectability are constant among sites or they can be modelled using covariates. The detection process (p) and the occupancy process (ψ) are then estimated, using maximum likelihood estimations in our case, from a 'capture' matrix, where detection (1) or non-detection (0) of a given species at each site for each occasion, is reported, resulting in an occupancy estimate corrected for imperfect detection (McKenzie et al. 2006).

Although our survey was split into two non-consecutive periods, we used a single-season occupancy model as adult wildcats (we detected only adults) show high home-range fidelity (Daniels et al. 2001), therefore shifts in individual home-ranges between years can be consider minimal (Wang et al. 2018) and changes in occupancy between these two periods were assumed negligible (assumption 1). We pooled five consecutive sampling days into one 'capture' occasion to minimize the risk of non-independence between detections at each site (assumption 2), whereas detections of different individuals at the same site and detections of the same individual at neighbouring cameras (assumption 2) were rarely observed within our dataset. However, we still checked for a spatial autocorrelation signal in wildcat detections by running the Moran's I test (Silva et al. 2012), which may have inflated our occupancy model.

In our first step, we modelled detection (p) while occupancy (ψ) was over-parametrized (e.g. an occupancy model formulation with all habitat classes included as predictors). Therefore, detection was investigated by building all the possible combinations (n = 31) for the above mentioned six covariates) (Karanth et al. 2011) (Table 1). We included a null model $p(.)\psi(areamf+areapf+areame+areash+arealf+areal)$ which represents the null hypothesis (e.g. detection is constant and not influenced by any predictors). We selected the best fitting models among this first set of models using AIC information criteria with a Δ AIC < 2. In our a second step, we ran each of the best detection models (i.e. those ranked within Δ AIC<2) in conjunction with 42 occupancy models (Supplementary material Appendix 5) which reflected a priori, plausible ecological hypotheses about

wildcat occupancy in the study area. Owing to sparse data and to facilitate numerical computations, occupancy models were constrained to a maximum of 6 covariates and with only additive terms. All models with convergence issues were discarded (Supplementary material Appendix 6). Goodness-of-fit for the best model was checked with the function *mb. gof.test* (500 replicates) within the R package *AICcmodavg* (Mazerolle 2016) to test for overdispersion. The relative importance of covariates (*EAICw*) was calculated for each covariate included in those models within the cumulative AIC weight of 0.95 (Kilshaw et al. 2016).

Testing predictions

We also created a grid of 1300 × 1300 m (1.69 km²), which is approximately the minimum home range for a wildcat in a Mediterranean habitat (Monterroso et al. 2009) over the entire study area (grid cells = 402), populated with the covariates included in the top model (the model with the minimum AIC), to spatially predict the wildcat occupancy across Mt Etna. Elevation data were downloaded as GMTED (https://earthexplorer.usgs.gov) and the mean elevation value was extracted for each grid cell. We then tested our wildcat occupancy predictions (predicted occupancy and 95% CI) against an independent (i.e. one record per cell) dataset (Supplementary material Appendix 7) of wildcat presence records to identify which scenario among our predictions was the most congruent with actual data. This dataset was made up of 26 wildcat presence locations (cameras record=7, dead wildcat=6, opportunistic wildcat pictures = 10 and wildcat sightings observed by the first author of this study = 3) collected from 2005 to 2019. Therefore, we used the continuous Boyce index (hereafter, CBI) to compare the predicted values of wildcat occupancy for the entire study area against the predicted values assigned for any wildcat presence location by our top 'best' model (Klar et al. 2008, Clare et al. 2015). This index ranges from -1 to +1 with values close to 0 indicating a random association between predicted occupancy and verified presence locations, whereas positive values describing a useful model (i.e. good agreement between predicted values and verified presence locations) and negative values indicating a model with fewer predicted values than verified presence locations (Hirzel et al. 2006). All results are presented as mean plus standard errors, unless explicitly stated.

Results

We collected 41 putative wildcat scats after walking 478.8 km. Of these, 27 (66%) were successfully genotyped, identifying 22 different wildcats (one wildcat was detected three times, three wildcats were detected twice and the rest once each (Supplementary material Appendix 1 Fig. A1, A2). We accumulated 3377 camera-trap days (37.1 \pm 0.48) from 91 camera traps that worked effectively (Supplementary material Appendix 3) over an area of 62.2 km² (the cumulative sum of the MPC for each array). We obtained 70 wildcat detections from 38 cameras located across the seven arrays (naïve occupancy=0.41; trap-rate=2.07 number of detections/100 trap-days) (Fig. 2), including

Table 2. Model selection for determining the best detection process (*p*) for European wildcat *Felis silvestris* on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016 while the occupancy process (*w*) is kept constant and over parametrized. First four models shown along with the null model for the detection process. Models within 2 AIC are in bold.

Detection process	nPars	AIC	Delta
p(array+distanceMR+RAIh)	16	408.04	0.00
y(areamf+areapf+areame+areash+arealf+areaal) p(days+array+distanceMR+RAIh)	17	408.94	0.90
ψ(areamf+areapf+areame+areash+areal+areaal)	15	409.69	1.66
p(array+distanceMR) $\psi(areamf+areapf+areame+areash+arealf+areaal)$	15	409.09	1.00
p(array+RAIh) ψ(areamf+areapf+areame+areash+arealf+areaal)	17	410.04	2.00
p(.)	8	414.65	6.61
ψ(areamf+areapf+areame+areash+arealf+areaal)			

two detections from one camera (6N) showing a black cat, presumably the same individual. Removing these two detections and the relative camera did not significantly alter our results; further research is needed to classify the identity of this cat (Supplementary material Appendix 8). The Moran's I test did not suggest any spatial autocorrelation signal for wildcat detections (observed = 0.02; expected = -0.01; SD = 0.02; p = 0.10). Collinearity was detected for npatchestot and npatchesmf (Pearson's correlation coefficient = 0.71), which therefore were independently included in our occupancy models. Time-to-first wildcat detection was 17 ± 1.23 days after camera deployment and 28, 60 and 87% of the detections occurred within the first 10, 20 and 30 days after camera deployment, respectively. The first step of model selection identified 4 best detection models (Table 2), which were then combined with the 42 a priori occupancy models. After discarding 123 models due to lack of convergence we successfully ran 45 models (Supplementary material Appendix 6). Of these, only one model was strongly supported (Table 3); p(array+distanceMR+RAI h)ψ(areamf+areapf+npatchesmf+elevation). This model didn't show signs of overdispersion ($\hat{c} = 0.7$; p = 0.834): mixed forest (areamf) had a positive effect on wildcat occupancy (EAICw = 0.95), whereas altitude (*elevation*), number of patches of mixed forest (*npatchesmf*) and pine forest (*areapf*) negatively affected wildcat occupancy (EAICw = 0.90; EAICw = 0.86, EAICw = 0.80; respectively). The remaining covariates (arealf, areash, areame and lengthMR) included in those models within 0.95 AIC cumulative weight poorly influenced wildcat occupancy (EAICw < 0.02). Results of the best model (i.e. the model with the minimum AIC) are shown in Table 4. Although not significant (p = 0.09), RAIh was retained within the most supported model and negatively influenced detection. In contrast, distanceMR positively influenced detection. Estimated values for p and ψ from the best occupancy model were 0.016 ± 0.009 and 0.74 ± 0.03 respectively, so when imperfect detection was not taken into account, naïve occupancy (0.41) was greatly underestimated (45% less than the estimated occupancy). When plotting univariate responses for wildcat occupancy w, we found that it steadily increased when areamf reached the threshold of 15% and decreased when areapf reached the threshold of 50% (Fig. 3). Moreover, wildcat occupancy w decreased when npatchesmf approached the value of 9 and the same was observed for elevation at the threshold value of ~1400 m a.s.l. (Fig. 3). The CBI clearly indicated that the lower confidence limit of our occupancy model was the most congruent scenario for fitting the independent dataset of wildcat presence data (CBI = 0.93), whereas the average occupancy scenario and the upper confidence limit scenario were less well-supported (CBI = 0.70 and CBI = 0.52 respectively). Spatially-explicit predictions of wildcat occupancy for Mt Etna (Fig. 4) for the most congruent scenario (lower confidence limit) showed that the distribution of cells with high predicted wildcat occupancy was highly fragmented, with the majority of these cells located at lower altitudes and mostly on the northern slope of Mt Etna.

Discussion

In our study wildcat presence was confirmed on Mt Etna by DNA analysis, therefore subsequent phenotypic identifications on pictures can be considered reliable. Additionally, by using camera-trapping and an occupancy modelling frame-work, we documented how wildcat occupancy on Mt Etna was driven by a combination of habitat structure and vegetation features. Our basic expectations of the role

Table 3. Model selection results testing for habitat covariates on European wildcat *Felis silvestris* occupancy on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016. First four models shown and models within 2 AIC are in bold. Full model selection is reported in Supplementary material Appendix 6.

Formula	nPars	AIC	Delta	AlCwt	CumltvWt	Rsq
p(array+distanceMR+RAIh) ψ(areamf+areapf+elevation+npatchesmf)	14	394.86	0.00	0.55	0.55	0.50
p(array+distanceMR) ψ(areamf+areapf+elevation+npatchesmf)	15	396.85	1.99	0.20	0.76	0.50
p(width+array+distanceMR+RAIh) ψ(areamf+areapf+elevation+npatchesmf)	13	399.84	4.98	0.04	0.80	0.46
p(array+distanceMR+RAIh) ψ(areamf+areapf+elevation+nclass)	14	399.95	5.09	0.04	0.85	0.48

Table 4. Results of the top 'best' model. p(array+distanceMR+RAIh) $\psi(areamf+areapf+elevation+npatchesmf)$ for describing European wildcat Felis silvestris occupancy on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016.

Model component	β	SE	Z	p(> z)
Detection	·			
parameters (p)				
Intercept	-4.102	0.589	-6.97	0.0000
Array 2	3.329	0.880	3.78	0.0001
Array 3	1.597	0.672	2.38	0.0173
Array 4	1.411	0.637	2.22	0.0267
Array 5	2.288	0.626	3.65	0.0002
Array 6	2.770	0.722	3.84	0.0001
Array 7	3.309	0.905	3.66	0.0002
distanceMR	0.732	0.288	2.54	0.0109
RAIh	-0.506	0.303	-1.67	0.0951
Occupancy				
parameters (ψ)				
Intercept	10.57	5.06	2.09	0.0368
areamf	7.70	3.94	1.95	0.0509
areapf	-2.88	1.61	-1.79	0.0737
npatchesmf	-4.20	2.04	-2.06	0.0394
elevation	-4.14	2.08	-1.99	0.0469

played by environmental variables were supported as mixed forest (*areamf*) contributed to wildcat occupancy positively and pine forest (*areapf*) contributed negatively along with the altitude (*elevation*). Most importantly, we also found that fragmentation of the preferred habitat (*npatchesmf*) negatively influenced wildcat occupancy. The considerable difference, between naïve occupancy and estimated occupancy (estimated occupancy was almost twice the naïve occupancy), was expected because detection probability was quite low as usually found in camera-trapping surveys of felid species (Galvez et al. 2013, Andresen et al. 2014, Penjor et al. 2018, Strampelli et al. 2018).

Pattern of detectability

Distance to major roads (distanceMR) clearly influenced wildcat detectability, making wildcats more detectable in remote areas far away from major roads, but the effect of this covariate on wildcat occupancy was not found. We argue that, rather than the distance from major roads per se, the level of traffic might be a better proxy for disturbance (Klar et al. 2009). Although the effect was not statistically significant (p = 0.09), the detection covariate RAIh (a measure of human disturbance) was retained within the most supported model and negatively influenced wildcat detectability. Wildcats are mainly nocturnal (Daniels et al. 2001, Wittmer 2001, Germain et al. 2008), but daylight movements can also occur (Daniels et al. 2001, Germain et al. 2008) and the contemporary presence of humans along the trails might have induced wildcats to be more 'cautious' when human presence was 'massive' (Piñeiro et al. 2012), similar to bobcats (George and Crooks 2006, Clare et al. 2015), leopards Panthera pardus (Carter et al. 2015) and tigers (Carter et al. 2012).

Pattern of occupancy

We found that mixed forest (areamf) promoted wildcat occupancy, as found for the wildcat population in Scotland (Kilshaw et al. 2016). Forest cover was important for other small felid species, such as bobcats (Clare et al. 2015), kod-kods Leopardus guigna (Galvez et al. 2013, Schuttler et al. 2016) and caracals Caracal caracal (Singh et al. 2014). Forest cover has been frequently found to be an important habitat feature for wildcats (Klar et al. 2008, 2012, Jerosch et al. 2010, Lozano 2010, Beugin et al. 2016, 2018, Beutel et al. 2017), although it seems that when rabbits Oryctolagus cuniculus are present, wildcats tend to be less forest-dependent

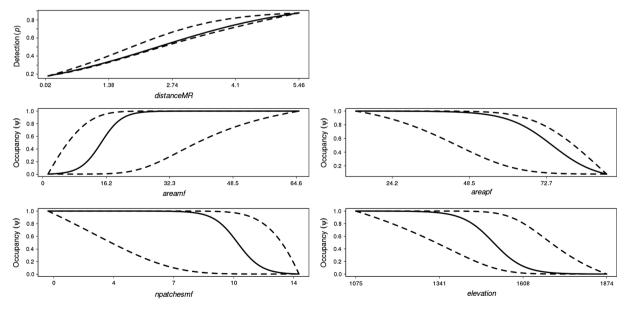


Figure 3. Predictions from the 'best' model $p(array+distanceMR+RAIh)\psi(areamf+areapf+elevation+npatchesmf)$ for describing European wildcat *Felis silvestris* occupancy on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016. Top-left panel shows the relationship between wildcat detectability and distance from main road (*distanceMR*). The other panels show the relationship between wildcat occupancy and the covariates *areamf*, *areapf*, *elevation* and *npatchesmf* (the other covariates in the model where held at their mean values).

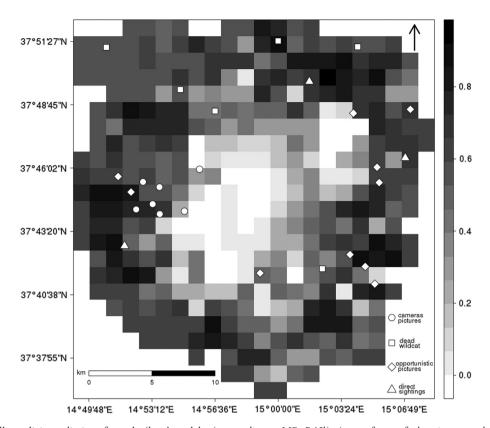


Figure 4. Spatially explicit predictions from the 'best' model. $p(array+distanceMR+RAIh)\psi(areamf+areapf+elevation+npatchesmf)$ for describing European wildcat Felis silvestris occupancy on Mt Etna (Sicily, Italy) from data collected using camera traps in 2015–2016 and from the most congruent scenario (lower estimates) for fitting the independent dataset of European wildcat presence (black square = camera-trapping records; black points = dead wildcats; black triangle = opportunistic photographs; black diamonds = sightings) collected on Mt Etna.

(Monterroso et al. 2009, Lozano 2010, Silva et al. 2012, Lozano et al. 2013).

The impact of habitat fragmentation on felid species has often been claimed, although direct evidence of its effects is rare (Zanin et al. 2014, Galvez et al. 2017). Habitat fragmentation is considered one of the most severe threats for wildcat (Macdonald and Loveridge 2010, Lozano and Malo 2012) and our study, to the best of our knowledge, is the first to find direct evidence that fragmentation (*npatchesmf*) of the preferred habitat (areamf) negatively affects wildcat occupancy. Moreover, as fragmentation of mixed forest (npatchesmf) also negatively impacts wildcat occupancy, our study confirms the pivotal role of mixed forest (mainly deciduous such as Quercus sp., Castanea sativa and Fagus sylvatica, but also the particular local habitat of wooded patches populated by Genista etniensis in our case) as even a minimal amount of this habitat promoted wildcat occupancy on Mt Etna. The critical role of habitat fragmentation for wildcat conservation also emerged when considering that hybrids were mostly located at the periphery of the local wildcat distribution area where, reasonably, habitat fragmentation should be more pronounced and thus wildcats were less abundant (Nussberger et al. 2018). Additionally, female wildcats prefer to establish their home ranges inside forest patches rather than at the periphery as did males (Beugin et al. 2016, Oliveira et al. 2018), thus displaying avoidance of fragmented habitats, similar to that of female jaguars (Conde et al. 2010). Considering this recent evidence in its entirety, we suggest more studies are needed to better understand the effects of habitat fragmentation on wildcat ecology.

In line with our basic expectations, wildcat occupancy decreased in pine forests (areapf), especially when this habitat was the most predominant, but see Klar et al. (2008) and Lozano (2010) for contrasting results. Pine forests are usually avoided by wildcats (Sarmento et al. 2006, Martin-Diaz et al. 2017), or at least, used less frequently as they represent a less suitable habitat in terms of abundance of prey (Lozano and Malo 2012). Wildcat occupancy was also negatively affected by altitude (elevation) and, congruently with Say et al. (2012), in our study wildcat occupancy levelled off at ~1800 m a.s.l. probably because long-lasting thick snow cover may have hindered wildcat movements (Mermod and Liberek 2002) and hence habitat above this altitude was less suitable for wildcats.

Despite being a Mediterranean area, the importance of scrub (Lozano et al. 2003, Monterroso et al. 2009, Lozano 2010) for wildcats was not supported by our data. It is likely that the shelter provided by this habitat (Lozano et al. 2003) is largely overwhelmed by the almost ubiquitous natural cavities typical of the volcanic soil, which offer a safe shelter for wildcats throughout our study area. Likewise, meadows did not promote wildcat occupancy in our study area. Meadows (as depicted on the map we used to derive our occupancy covariates) were usually very small $(0.11\pm0.02\,\mathrm{km^2})$, not very widespread (39 cameras out of 91 hosted this habitat class) and isolated (*npatchesme* per camera = 1.23 ± 0.14),

Table 5. List of camera-trapping studies on the European wildcat *Felis silvestris* across Europe. * indicates this study. Trap-rate is expressed as number of detections for 100 trap-days.

Study	Country	Naive occupancy	No. of #cameras	Trap-rate	Trap-days	Baited/not baited
Anile et al. 2009	Italy (Mt Etna)	0.66	18	2.9	824	baited and not baited
Anile et al. 2010	Italy (Mt Etna)	0.63	11	4.02	671	not baited
Anile et al. 2012a, b	Italy (Mt Etna)	0.66	18	2.9	1080	not baited
Anile et al. 2012b	Italy (Mt Etna)	0.72	18	4.07	1080	baited
Anile et al. 2014	Italy (Mt Etna)	0.88	18	6.48	1080	not baited
Anile and Devillard 2018*	Italy (Mt Etna)	0.41	91	2.07	3377	not baited
Velli et al. 2015	Italy	0.5	20	3.1	819	baited
Can et al. 2009	Turkey	0.3	40	1.8	1200	not baited
Beutel et al. 2017	Germany	0.34	46	0.06	31107	not baited
Sarmento et al. 2009	Spain	0.01	186	0.02	6127	baited
Soto and Palomares 2013	Spain	0.07	166	0.4	5761	baited
Gil-Sanchez et al. 2015	Spain	0.2	64	1.23	4278	baited
Kilshaw and MacDonald 2011	Scotland	0.55	20	0.5	1460	baited and not baited
Littlewood et al. 2014	Scotland	0.04	356	0.28	7499	baited
Kilshaw et al. 2016	Scotland	0.04	526	0.17	49031	baited

so it is very likely this habitat did not influence wildcat occupancy in our study area. Future studies on wildcats in the unique ecosystem of Mt Etna are needed; in particular, home-range estimation through the use of GPS collars would better elucidate wildcat habitat requirements.

Comparison with other camera-trapping studies

Although we recognized that comparisons among raw metrics, such as naïve occupancy and trap-rate, can be biased (Sollmann et al. 2013, Anile and Devillard 2015) and thus have to be taken with great caution, we observed a general decrease (range naïve occupancy = 0.66-0.88; range traprate = 2.9-6.48) when comparing our results to those of previous surveys from the same study area (range naïve occupancy = 0.66-0.88; range trap-rate = 2.9-6.48) (Anile et al. 2009, 2010, 2012a, b, 2014) (Table 5). Even if a different sampling design likely affected this comparison as previous studies used fewer camera locations (range = 11-18) to cover smaller areas (range = 6.6-10.9 km²) and with less effort (range trap-days = 671-1080), in the current study we also sampled the majority of these previous camera locations and obtained only a few detections (n = 8 at only four cameras). We suspect this decreasing trend in either naïve occupancy and trap-rate might truly corresponded to a decrease in wildcat population density, at least compared to the last survey performed in 2010. Although previous data are not available, rabbits were much more widespread and abundant in the recent past than when we observed them during the current study (29 detections at only 3 cameras). This likely reduction in the abundance of rabbits (the wildcat's preferred prey) (Malo et al. 2004, Lozano et al. 2006) in the entire Etna Park, as well as in the smaller study area sampled during previous surveys, has probably driven this decrease in wildcat detection (Lozano and Malo 2012, Littlewood et al. 2014). Future analyses are required to evaluate whether a decrease in wildcat population density has really occurred and so our findings here should be considered preliminary. With regards to other similar camera-trapping studies, although again different sampling designs have to be taken into consideration (i.e. in the current study we did not use any lure or bait), our results were generally higher or similar in terms

of both naïve occupancy and trap-rate (Table 5). From the current study Mt Etna is still confirmed a stronghold for the Sicilian wildcat population, despite the fact that a decreasing trend in population density might have occurred.

Conclusions

We suggest that the maintenance of large patches of mixed forest would be a good practice to promote long-term population viability of wildcats on Mt Etna. Additionally, improving the connectivity between the largest patches of mixed forest (Klar et al. 2012) and reducing the impact of traffic on critical roads by employing appropriate wildcat mitigation structures, such as fences, tunnels and viaducts (Klar et al. 2009), are management actions that should favour wildcat survival. During our survey four cameras were stolen and this prompted us to reduce our cameratrapping effort. We also detected other illegal activities like unauthorized vehicle accesses and a large presence of feral pigs in some areas of the park. Moreover, the numerous illegal human-caused fires that afflict our study area during summer are likely to be a major threat for the wildcat as they increase the loss and the fragmentation of suitable wildcat habitat. A radical change in forest fire prevention, along with more stringent and concrete surveillance of this protected area is therefore needed to ensure the viable persistence of this wildcat population. Moreover, cooperation between adjacent natural parks (e.g. Nebrodi Park, Alcantara Park and the Etna Park) to sustain wildcat conservation actions at the regional level is strongly recommended. A camera-trapping project across the largest regional parks (e.g. Etna, Nebrodi and Madonie) and suitable connective corridors would be a step forward for the conservation of the Sicilian wildcat population.

Acknowledgements – We thank all the people who kindly shared with us their wildcat pictures shot on Mt Etna. Alisia Schiff kindly and Clay Nielsen reviewed and edited the English of this manuscript. During the writing of this study, Prof. Bernardino Ragni passed away. He was the supervisor of SA during his PhD-project on wildcats and an always present mentor during the successive years of collaboration. This study is dedicated to him, without his

support this study (as well as previous ones) would not have been possible. SA thanks all the officers of Etna Park (particularly Dr Michele Leonardi and Dr Rosa Spampinato), their hard work made this study feasible. SA also thanks Dr Luigi Piccinini and Maurizio Pennisi from the 'Ripartizione Faunistico Venatoria di Catania' for providing the cameras used in this study. We also thank Subject Editor Dr Luc Wauters for the helpful suggestions which greatly improved this manuscript. Lastly, we all thank Marisa Mazzaglia (former president of Etna park) for supporting this wildcat research without any hesitation.

Funding - This research was funded by the Etna Park.

References

- Andresen, L. et al. 2014. Use of site occupancy models for targeted monitoring of the cheetah. J. Zool. 292: 212–220.
- Anile, S. and Devillard, S. 2015. Study design and body mass influence RAIs from camera trap studies: evidence from the Felidae. – Anim. Conserv. 19: 35–45.
- Anile, S. and Devillard, S. 2018. Camera-trapping provides insights into adult sex ratio variability in felids. – Mammal Rev. 48: 168–179.
- Anile, S. et al. 2009. Camera trapping the European wildcat (*Felis silvestris silvestris*) in Sicily (southern Italy): preliminary results.
 Hystrix Ital. J. Mammal. 20: 55–60.
- Anile, S. et al. 2010. Estimation of European wildcat population size in Sicily (Italy) using camera trapping and capture–recapture analyses. – Ital. J. Zool. 77: 241–246.
- Anile, S. et al. 2012a. Population density estimation of the European wildcat (*Felis silvestris*) in Sicily using camera trapping. – Wildl. Biol. Pract. 8: 1–12.
- Anile, S. et al. 2012b. A non-invasive monitoring on European wildcat (*Felis silvestris silvestris* Schreber, 1777) in Sicily using hair trapping and camera trapping: does scented lure work? – Hystrix Ital. J. Mammal. 23: 45–50.
- Anile, S. et al. 2014. Wildcat population density on the Etna volcano, Italy: a comparison of density estimation methods. J. Zool. 293: 252–261.
- Anile, S. et al. 2017. Home-range size of the European wildcat (*Felis silvestris silvestris*): a report from two areas in central Italy.
 Mammalia 82: 1–11.
- Apostolico, F. et al. 2015. Long-term changes in diet and trophic niche of the European wildcat (*Felis silvestris silvestris*) in Italy. Mammal Res. 61: 109–119.
- Bahaa-el-din, L. et al. 2016. Effects of human land-use on Africa's only forest-dependent felid: the African golden cat *Caracal aurata*. Biol. Conserv. 199: 1–9.
- Beugin, M. P. et al. 2016. Female in the inside, male in the outside: insights into the spatial organization of a European wildcat population. Conserv. Genet. 17: 1405–1415.
- Beugin, M. P. et al. 2018. Contrasted hybridization patterns between two local populations of European wildcats in France. bioRxiv. doi: 10.1101/342576.
- Beutel, T. et al. 2017. Spatial patterns of co-occurrence of the European wildcat Felis silvestris silvestris and domestic cats Felis silvestris catus in the Bavarian Forest National Park. – Wildl. Biol. 1–8
- Bizzarri, L. et al. 2010. Live capture and handling of the European wildcat in central Italy. Hystrix Ital. J. Mammal. 21: 73–82.
- Brodie, J. F. 2009. Is research effort allocated efficiently for conservation? Felidae as a global case study. Biodivers. Conserv. 18: 2927–2939.
- Can, O. E. et al. 2009. The wildcat *Felis silvestris* in northern Turkey: assessment of status using camera trapping. Oryx 45: 112–118.
- Canters, K. J. et al. 2005. The wildcat (*Felis silvestris*) finally recorded in the Netherlands. Lutra 48: 67–90.

- Cardillo, M. et al. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biol. 2: 909–914.
- Cardillo, M. et. al. 2008. The predictability of extinction: biological and external correlates of decline in mammals. Proc. R. Soc. B 275: 1441–1448.
- Carter, N. H. et al. 2012. Coexistence between wildlife and humans at fine spatial scales. Proc. Natl Acad. Sci. USA 109: 1–6.
- Carter, N. et al. 2015. Impacts of people and tigers on leopard spatiotemporal activity patterns in a global biodiversity hotspot. – Global Ecol. Conserv. 3: 149–162.
- Clare, J. D. J. et al. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. – J. Wildl. Manage. 3: 469–480.
- Conde, D. A. et al. 2010. Sex matters: modeling male and female habitat differences for jaguar conservation. – Biol. Conserv. 143: 1980–1988.
- Daniels, M. J. et al. 2001. Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat. J. Appl. Ecol. 38: 146–161.
- Devillard, S. et al. 2013. How reliable are morphological and anatomical characters to distinguish European wildcats, domestic cats and their hybrids in France? J. Zool. Syst. Evol. Res. 52: 154–162
- European Council Directive 1992. The Habitats Directive, Appendix IV.
- Falsone, L. et al. 2014. The European wildcats (Felis silvestris silvestris) as reservoir hosts of Troglostrongylus brevior (Strongylida:crenosomatidae) lungworms. Vet. Parasitol. 205: 193–198.
- Fiske, I. And Chandler, R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. – J. Stat. Softw. 43: 1–23.
- Galvez, N. et al. 2013. Forest cover outside protected areas plays an important role in the conservation of the vulnerable guina *Leopardus guigna*. – Oryx 47: 251–258.
- Galvez, N. et al. 2017. A spatially integrated framework for assessing socioecological drivers of carnivore decline. J. Appl. Ecol. 55: 1393–1405.
- George, S. L. and Crooks, K. R. 2006. Recreation and large mammal activity in an urban nature reserve. Biol. Conserv. 133: 107–111
- Germain, E. et al. 2008. Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. J. Zool. 276: 195–203.
- Gil-Sanchez, J. M. et al. 2015. Strong spatial segregation between wildcats and domestic cats may explain low hybridization rates on the Iberian peninsula. Zoology 118: 377–385.
- Harihar, A. and Pandav, B. 2012. Influence of connectivity, wild prey and disturbance on occupancy of tigers in the human-dominated western Terai arc landscape. PLoS One 7: e40105.
- Hemami, M. R. et al. 2018. Using ecological models to explore niche partitioning within a guild of desert felids. – Hystrix Ital. J. Mammal. 29: 216–222.
- Hirzel, A. H. et al. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199: 142–152.
- Jennings, A. J. et al. 2015. Diversity and occupancy of small carnivores within oil palm plantations in central Sumatra, Indonesia. – Mammal Res. 60: 181–188.
- Jerosch, S. et al. 2010. Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): implications for its conservation. J. Nat. Conserv. 18: 45–54.
- Jerosch, S. et al. 2017. Spatial organisation of European wildcats (Felis silvestris silvestris) in an agriculturally dominated landscape in central Europe. – Mammal. Biol. 82: 8–16.
- Karanth, U. K. et al. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. – J. Appl. Ecol. 48: 1048–1056.

- Kilshaw, K. and Macdonald, D. W. 2011. The use of camera trapping as a method to survey for the Scottish wildcat. Scottish Natural Heritage Commissioned Report. No. 479.
- Kilshaw, K. et al. 2014. Detecting the elusive Scottish wildcat *Felis silvestris silvestris* using camera trapping. Oryx 49: 207–215.
- Kilshaw, K. et al. 2016. Mapping the spatial configuration of hybridization risk for an endangered population of the European wildcat (*Felis silvestris silvestris*) in Scotland. – Mammal Res. 61: 1–11.
- Klar, N. et al. 2008. Habitat selection models for European wildcat conservation. – Biol. Conserv. 141: 308–319.
- Klar, N. et al. 2009. Effects and mitigation of road impacts on individual movement behaviour of wildcats. – J. Wildl. Manage. 73: 631–638.
- Klar, N. et al. 2012. Between ecological theory and planning practice: (re-)connecting forest patches for the wildcat in lower Saxony, Germany. Landsc. Urban Plan. 105: 376–384.
- Krauss, J. et al. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett. 13: 597–605.
- Krone, O. et al. 2008. Endoparasite spectrum of wild cats (*Felis silvestris* Schreber, 1777) and domestic cats (*Felis catus* L.) from the Eifel, Pfalz region and Saarland, Germany. Eur. J. Wildl. Res. 54: 95–100.
- Lesmeister, D. B. et al. 2015. Spatial and temporal structure of a mesocarnivore guild in Midwestern North America. – Wildl. Monogr. 191: 1–61.
- Littlewood, N. A. et al. 2014. Survey and scoping of wildcat priority areas. – Scottish Natural Heritage Commissioned Report No. 768.
- Lozano, J. 2010. Habitat use by European wildcats (*Felis silvestris*) in central Spain: what is the relative importance of forest variables? Anim. Biodivers. Conserv. 33: 143–150.
- Lozano, J. and Malo, A. (2012). Conservation of the European wildcat (*Felis silvestris*) in Mediterranean environments: a reassessment of current threats. In: William, G. S (ed.), Mediterranean ecosystems. Nova Science Publishers, pp. 1–31.
- Lozano, J. et al. 2003. Importance of scrub–pastureland mosaics for wild-living cats occurrence in a Mediterranean area: implications for the conservation of the wildcat (*Felis silvestris*). Biodivers. Conserv. 12: 921–935.
- Lozano, J. et al. 2006. Biogeographical patterns in the diet of the wildcat, *Felis silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. J. Biogeogr. 33: 1076–1085.
- Lozano, J. et al. 2013. Monitoring European wildcat *Felis silvestris* populations using scat surveys in central Spain: are population trends related to wild rabbit dynamics or to landscape features? Zool. Stud. 52: 16.
- Macdonald, D. W. and Loveridge, A. J. 2010. The biology and conservation of wild felids. Oxford Univ. Press.
- Macdonald, D. W. et al. 2010. Dramatis personae: an introduction to the wild felids. – In: Macdonald, D. W. and Loveridge, A. (eds), Biology and conservation of wild felids. Oxford Univ. Press, pp. 3–58.
- Malo, A. F. et al. 2004. A change of diet from rodents to rabbits (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? J. Zool. 263: 401–407.
- Martin-Diaz, P. et al. 2017. Integrating space and time in predator—prey studies: the case of wildcats and rabbits in SE Spain.

 Mammal. Biol. 88: 114–122.
- Mata, C. et al. 2017. Small-scale alterations in carnivore activity patterns close to motorways. Eur. J. Wildl. Res. 63: 64
- Mattucci, F. et al. 2013. Genetic structure of wildcat (*Felis silvestris*) populations in Italy. Ecol. Evol. 3: 2443–2458.
- Mattucci, F. et al. 2016. European wildcat populations are subdivided into five main biogeographic groups: consequences of Pleistocene climate changes or recent anthropogenic fragmentation? Ecol. Evol. 6: 3–22.

- Mazerolle, M. J. 2016. Aiccmodavg: model selection and multi-model inference based on (Q)AIC (c). R package ver. 2.1-0. https://cran.r-project.org/package=AICcmodavg.
- McKenzie, D. I. et al. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.

 Academic Press.
- Mermod, C. P. and Liberek, M. 2002. The role of snowcover for European wildcat in Switzerland. – Zool. Jagdwiss 48:17–24.
- Monterroso, P. et al. 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. J. Zool. 279: 27–35.
- Morin, D. J. et al. 2018. The truth about cats and dogs: landscape composition and human occupation mediate the distribution and potential impacts of non-native carnivores. Global Ecol. Conserv. 15: e00413
- Niedballa, J. et al. 2016. R package ver. 0.99.2 camtrapR: an R package for efficient camera trap data management. Methods Ecol. Evol. 7: 1457–1462.
- Nowell, K. and Jackson, P. 1996. Status survey and conservation action plan wild cats. Burlington Press.
- Nussberger, B. et al. 2018. Range expansion as an explanation for introgression in European wildcats. – Biol. Conserv. 218: 49–56.
- O'Connell, A. F. et al. 2010. Camera traps in animal ecology: methods and analyses. – Springer Science & Business Media.
- Oliveira, T. et al. 2018. Females know better: sex-biased habitat selection by the European wildcat. Ecol. Evol. 8: 9464–9477.
- Penjor, U. et al. 2018. Identifying important conservation areas for the clouded leopard *Neofelis nebulosa* in a mountainous landscape: inference from spatial modeling techniques. – Ecol. Evol. 8: 4278–4291.
- Pimm, S. L. et al. 2014. The biodiversity of species and their rates of extinction, distribution and protection. – Science 344: 987–998.
- Pińeiro, A. et al. 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildl. Res. 39: 532–539.
- Planillo, A. et al. 2018. Carnivore abundance near motorways related to prey and roadkills. J. Wildl. Manage. 82: 319–327.
- Purvis, A. et al. 2000. Predicting extinction risk in declining species. – Proc. R. Soc. B 267: 1947–1952.
- Ragni, B. and Possenti, M. 1996. Variability of coat-colour and markings system in *Felis silvestris*. Ital. J. Zool. 63: 285–292.
- Rovero, F. and Zimmermann, F. 2016. Camera-trapping for wildlife research. Pelagic Publishing.
- Rovero, F. et al. 2018. Co-occurrence of snow leopard *Panthera uncia*, Siberian ibex *Capra sibirica* and livestock: potential relationships and effects. Oryx doi: 10.1017/S0030605317001685.
- Ruiz-Olmo, J. et al. 2018. Breeding pattern of wildcat *Felis silvestris* (Schreber, 1777) studied in captivity in the iberian peninsula. Hystrix Ital. J. Mammal. 29: 202–210.
- Sarmento, P. et al. 2006. Space and habitat selection by female European wildcats (*Felis silvestris silvestris*). Wildl. Biol. Pract. 2: 79–89.
- Sarmento, P. et al. 2009. Spatial colonization by feral domestic cats *Felis catus* of former wildcat *Felis silvestris silvestris* home ranges.

 Acta Theriol. 54: 31–38.
- Say, L. et al. 2012. Distribution and spatial genetic structure of European wildcat in France. – Anim. Conserv. 15: 18–27.
- Schuette, P. et al. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biodivers. Conserv. 158: 301–312.
- Schuttler, E. et al. 2016. Habitat use and sensitivity to fragmentation in America's smallest wildcat. Mammal. Biol. 86: 1–8.
- Silva, A. P. et al. 2012. Wildcat occurrence in Scotland: food really matters. Divers. Distrib. 19: 232–243.

- Singh, R. et al. 2014. Population and habitat characteristics of caracal in semi-arid landscape, western India. J. Arid Environ. 103: 92–95.
- Sollmann, R. et al. 2013. Risky business or simple solution relative abundance indices from camera-trapping. Biol. Conserv. 159: 405–412.
- Soto, C. A. and Palomares, F. 2013. Surprising low abundance of European wildcats in a Mediterranean protected area of southwestern Spain. – Mammalia 78: 57–65.
- Steyer, K. et al. 2018. Low rates of hybridization between European wildcats and domestic cats in a human-dominated landscape.

 Ecol. Evol. 8: 2290–2304.
- Steyer, K. et al. 2016. Large-scale genetic census of an elusive carnivore, the European wildcat (*Felis s. silvestris*). Conserv. Genet. 17: 1183–1199.
- Strampelli, P. et al. 2018. Habitat use responses of the African leopard in a human-disturbed region of rural Mozambique. Mammal. Biol. 89: 14–20.
- Tan, C. K. W. et al. 2017. Habitat use and predicted range for the mainland clouded leopard *Neofelis nebulosa* in peninsular Malaysia. – Biol. Conserv. 206: 65–74.

Supplementary material (available online as Appendix wlb-00561 at <www.wildlifebiology.org/appendix/wlb-00561>). Appendix 1–8.

- Velli, E. et al. 2015. Non-invasive monitoring of the European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three different monitoring techniques and evaluation of their integration. – Eur. J. Wildl. Res. 61: 657–668.
- Wang, T. et al. 2018. Living on the edge: opportunities for Amur tiger recovery in China. – Biol. Conserv. 217: 269–279.
- Wegge, P. et al. 2004. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim. Conserv. 7: 251–256.
- Wittmer, H. U. 2001. Home range size, movements and habitat utilization of three male European wildcats (*Felis silvestris* Schreber, 1777) in Saarland and Rheinland-Pfalz (Germany). Mammal. Biol. 66: 365–370.
- Yamaguchi, N. et al. 2015. Felis silvestris. In: IUCN Red list of threatened species. Ver. 2015.3.1. <www.iucnredlist.org>.
- Zanin, M. et al. 2014. What we (don't) know about the effects of habitat loss and fragmentation on felids. Oryx 49: 96–106.