Mammal Research
https://doi.org/10.1007/s13364-022-00627-5

ORIGINAL PAPER

Show me your tail, if you have one! Is inbreeding depression occurring in wildcats (*Felis silvestris silvestris*) from Italy?

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Received: 24 September 2021 / Accepted: 22 February 2022
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Abstract
Knowledge of genetic diversity is important to wildlife conservation because genetically depleted populations experience an increased risk of extinction. Mammalian carnivores are characterized by small and fragmented populations and low dispersal, so that genetic erosion can lead to the fixation of deleterious genes relatively quickly, leading to morphological abnormalities. Kinked tails and cowlicks are indicative of inbreeding depression and have been described in two wild cat species so far, the puma (*Puma concolor*) and the cheetah (*Acinonyx jubatus*). Here we report the first records of morphological abnormalities in five populations of the European wildcat (*Felis silvestris silvestris*) in Italy by using (1) camera-trapping and (2) necropsy of road-killed individuals assessed through genetic analysis. We collected 24,055 trap-nights from 251 cameras and recorded 566 wildcat detections, from which we identified 148 wildcats. Among these, 11 individuals had a kinked tail and four displayed brachyuria, whereas three wildcats from Sicily had cowlicks on the thorax. We recovered 28 road-killed wildcats and two of them (from Sicily and Friuli Venezia Giulia) had a kinked tail. Among these, one female with a kinked tail had a male foetus with a kinked tail, which proved that this characteristic was genetically inherited. We are unsure why brachyuria or cowlicks were not detected across all monitored wildcat populations, given we found kinked tails throughout Italy. The frequencies at which we have detected these abnormalities in wildcats are far lower than reports from Florida panthers (*Puma concolor*). Future research is needed to verify whether these abnormalities are also associated with low genetic diversity or other morphological defects which might lower fitness. We recommend a nationwide effort, using these techniques within a standardized sampling design, to further understand the status of the wildcat in Italy.

Keywords Brachyuria · Cowlicks · Inbreeding depression · Genetic diversity · Wildcats · Kinked tails

Communicated by: Jeremy Herman

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Introduction

Carnivoran populations are suffering globally due to human exploitation of natural ecosystems and also direct exploitation of carnivorans, which have threatened wildlife populations (Dirzo et al. 2015; Ripple et al. 2019; Brodie et al. 2021) that may be characterized by reduced genetic variability. These populations are more affected by stochastic events (Azizan and Paradis 2021), which is a great concern (Hedrick & Kalinowski, 2000; Luque et al., 2016) given the higher frequency of extreme weather conditions and increasing climate extremes (Maxwell et al. 2019). This scenario can be even worse for smaller carnivoran species, which are incapable of dispersing over large distances (Macdonald et al. 2018) or threatened by increased road-kill mortality (Bastianelli et al. 2021). In these cases, such species can become locally threatened, even though their population densities might not be too low to raise concerns (Miller-Butterworth et al. 2021). The largest wild cat species (e.g. tigers *Panthera tigris* and lions *Panthera lion*) have been greatly impacted by humans, mainly due to competition for food (Dirzo et al. 2015; Ripple et al. 2016, 2019; Bogoni et al. 2020) and retaliatory killing following conflict with humans, including direct killing of people (Dhanwatey et al. 2013; Anile and Devillard 2020). However, populations of smaller cat species populations can also be severely affected by human disturbance (Dickman, 2015; Fleschutz et al., 2016), while also being largely understudied when compared to larger species (Macdonald and Loveridge 2010; Anile and Devillard 2020; Marneweck et al. 2021). Nevertheless, ecosystem services provided by small cats are essential for any ecosystem by regulating the distribution and abundance of a variety of prey species (Williams et al. 2018).

Kinked tails, which appear as abnormal deviations/turns of the tail with respect to its normal central axial development (i.e. the character is determined by fusion and dysmorphology of the tail vertebrae) (Farkas and Chapman 2009), were first described in domestic cats (*Felis catus*) in Asia, where the frequency of this character is particularly high (Darwin 1868). Kinked tails can occur anywhere along the length of the tail (Ernest et al. 2014) and with three modalities (minor/medium/extreme) currently recognized (Xu et al. 2016) and where there is also a reduction of the tail length accompanying the kink (i.e. leading to brachyuria — the loss of part or the entirety of the tail) (Beddington et al., 1992).

Shortened tails are found in at least five different breeds of the domestic cat (Lyons 2015), suggesting that at least three different independent events have led to the fixation of this character in the domestic cat (Xu et al., 2016). Whether kinked tails and brachyuria are also associated with diminished fitness is controversial (Pimm et al. 2006b, a; Ernest et al. 2014; Xu et al. 2016), although it is evident this condition is caused by an unusual development of the tail but is possible that other important parts of the body, such as internal organs, may be affected (e.g. cryptorchidism and atrial septal defects) (Farkas and Chapman 2009; Johnson et al. 2010; Terio et al. 2018). Given the tail is of paramount importance for the normal execution of several behaviours (e.g. locomotion, thermoregulation, and communication), which are connected to a healthy body condition (Xu et al. 2016), knowledge of any abnormalities of the tail is important for anticipating potential negative health impacts in cat populations.

Another abnormality frequently observed is the cowlick, which appear as small regions (i.e. few cm^2) of the coat where the hairs grow in clockwise or counter-clockwise directions and against the prevalent direction of hair growth in the surrounding area, providing a clear whirled appearance (Kerk et al., 2019; O'Brien, 2003). This particular trait was detected at a very high frequency (more than 90%) in Florida panthers (*Puma concolor*) before the introduction of individuals from the Texas population (Darrell & Lacy, 2000; Johnson et al., 2010). Interestingly, when cowlicks are present on the front of the head in humans (*Homo sapiens*), they are associated with the FG syndrome (Unger et al. 2007), a rare disease caused by mutations found on the X chromosome, which, although not lethal, can greatly impair affected individuals.

Evidence of wild cat populations showing low levels of genetic diversity (Hedrick and Kalinowski 2000) are accumulating across the world (Azizan & Paradis, 2021), from small cats like the Andean mountain cat (*Leopardus jacobita*) (Cossíos et al. 2012) to larger cats like the cheetah (Terio et al. 2018) and the lion (Trinkel et al., 2010); these studies reported clear signs of inbreeding depression. Puma (*Puma concolor*) populations in Florida (Roelke et al. 1993; Pimm et al. 2006a; Kerk et al. 2019) and California (Ernest et al. 2014) had kinked tails, cowlicks, and other associated abnormalities at alarming frequencies (Johnson et al. 2010). Both abnormalities were associated with a reduced genetic richness in affected individuals (Ernest et al. 2014) and independent studies conducted on both populations documented a sharp reduction in the occurrence of such characters after the introduction of new individuals from a different population (Darrell and Lacy 2000; Johnson et al. 2010; Gustafson et al. 2017).

The European wildcat (*Felis silvestris silvestris*) — hereafter wildcat — is a small felid species currently listed as "Least Concern" in the IUCN Red List of Threatened Species™, although its populations are highly fragmented with increasing evidence that hybridization with the domestic cat occurs and threatens the species (Yamaguchi et al. 2015). In addition, wildcat population densities are usually extremely low (Soto and Palomares 2013; Gil-Sanchez et al. 2020; Matias et al. 2021) even when considering the ecological laws underpinning population density regulation (Anile & Devillard, 2020). Wildcats also face threats from livestock, feral pigs, and human disturbance (Anile et al., 2019, 2021). Taken together, this evidence indicates that wildcats deserve increased conservation actions and support from wildlife agencies.

Studies of wildcat genetics have mainly assessed the rate of introgression with domestic cats, population structure, and divergence times among populations (Mattucci et al. 2013, 2019; Witzenberger and Hochkirch 2014; Senn et al. 2019; Howard-McCombe et al. 2021). In Italy, wildcats did not experience a historical bottleneck (Mattucci et al. 2013) and genetic diversity is relatively high (Mattucci et al. 2016), but see Randi and Ragni (1991) for discordant results. However, the genetic structure of wildcats indicated a persistent (~5000 generations) low level of gene flow among populations, and hence local episodes of genetic drift/erosion were possible (Mattucci et al. 2016).

We report the first records of kinked tails, brachyuria, and cowlicks across five different Italian wildcat populations, which represent different ecological functional units (Boitani and Powell 2012), as assessed by visual inspection of camera-trapping images and necropsy on road-killed wildcats, whose species identification was confirmed via genetic analysis. To our knowledge, this is also the first study that has documented the occurrence of such abnormalities in wildcats, hence providing a benchmark for future studies.

Materials and methods

Study area

Our sampling surveys took place in Italy, including the regions of Sicily, Basilicata and Apulia (southern), Umbria (central), and Friuli Venezia Giulia (north) (Fig. 1). Extensive descriptions of the study areas located in Sicily (Etna Regional Park), Apulia (Gargano National Park), and Friuli

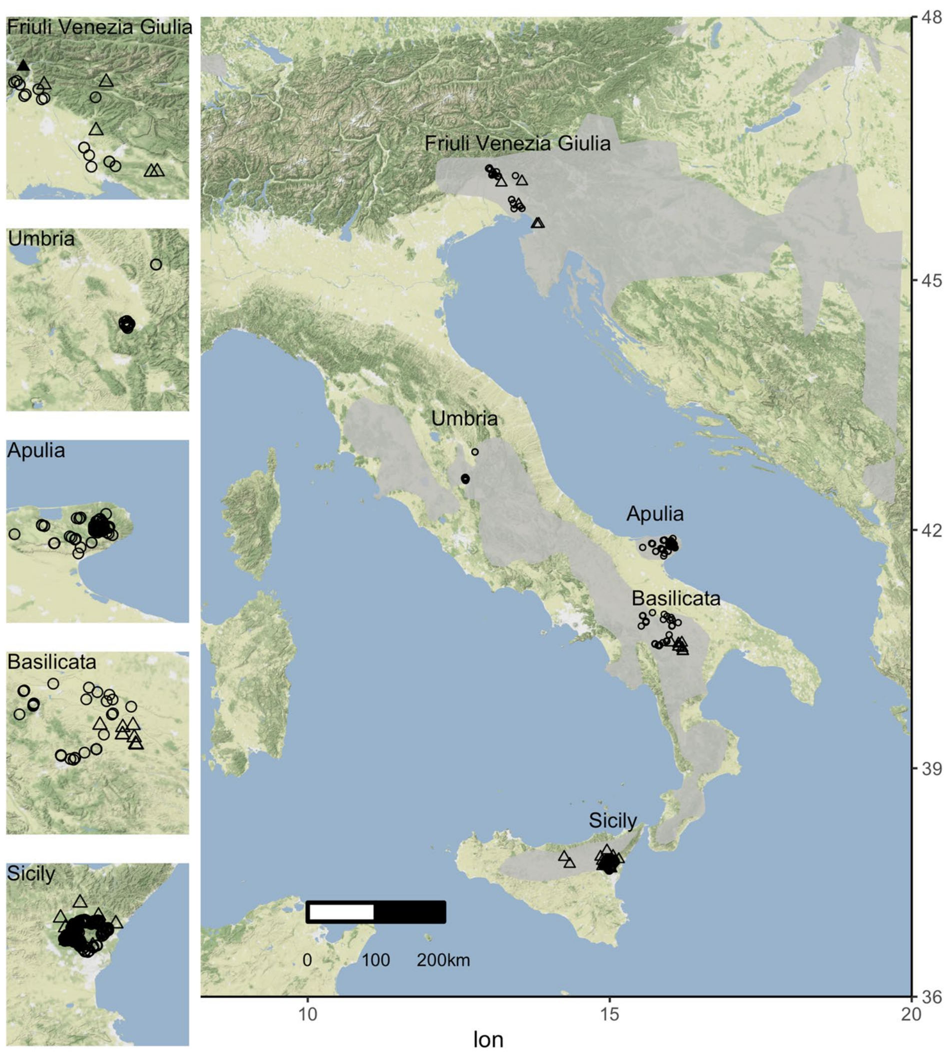

Fig. 1 Locations of the cameras used to survey the four wildcat populations in Italy (points) and of the road-killed wildcats (triangles) analysed in the current study. European wildcat distribution range across the Italian peninsula is shown in light grey

Venezia Giulia are provided elsewhere (Anile et al. 2019; Franchini et al. 2019; Filacorda et al. 2021; Gaudiano et al. 2021). In Basilicata region, a variety of habitats (e.g. forests, rocky formations, creeks and ponds, and agricultural areas) were sampled in the province of Potenza, between the Basento, Bradano, and Ofanto rivers. The sampling area in Umbria region was relatively small (7 km^2), consisting of two sites ~ 40 km apart, located in a low (< 1000 m) mountain range (Martani mountains) mainly populated by oaks *Quercus* sp.; this region represents a stronghold for wildcat conservation in Italy (Ragni et al. 1994).

Camera-trapping

Wildcats were detected through either opportunistic surveys (Gaudiano et al. 2021), species-specific surveys (Anile et al. 2009, 2010, Anile et al., 2012a, Anile et al., 2014, Anile et al., 2019, Anile et al., 2021), or a continuing citizen science project. We used a variety of camera brands and models (e.g. film and digital cameras from different manufacturers). In addition, some species-specific surveys used a lure (*Valerian officinalis* tincture), though with unsatisfactory results (Anile et al. 2009, 2012b). We identified individuals as domestic cat, wildcat, or hybrid (putative when genetic analysis for a given individuals was not available, i.e. camera-trapped individuals); all images were examined by a single experienced researcher (SA) to minimize the bias associated with multiple observers (Alexander et al. 2020; Johansson et al. 2020). Cats were considered to belong to the wild species if (i) they had the typical coat marking system described by Ragni and Possenti (1996); or (ii) they did not exhibit any evident anomalous features (e.g. large white area over the body or the typical *caudalis* of the domestic cat — with a stripe, well defined or not, going throughout the tail), which suggest introgression with the domestic cat (Kitchener et al., 2005). Putative hybrids (Velli et al. 2015) were not considered further.

During two of the surveys conducted in Sicily, the genetic status of the population was also assessed via genetic analysis of the scats collected through systematic sampling (Anile et al., 2014, 2019). Domestic cats or hybrids were not detected, either via cameras or genetic analysis, providing support for the congruency between the protocol developed by Ragni and Possenti (1996), and further refined by Kitchener et al. (2005), and genetic analysis (Kilshaw et al. 2010; Devillard et al. 2013; Ballesteros-Duperon et al. 2014; Senn et al. 2019). However, one domestic cat was detected via camera-trapping during a subsequent survey (Anile et al. 2012b).

Necropsy

Cats subjected to necropsy were collected as road-kills through opportunistic sampling in each region except Apulia and Umbria. Routine necropsy procedures are fully described elsewhere (Falsone et al. 2014) and for each cat, a sample of muscle tissue was taken and further processed for genetic analysis (Mattucci et al. 2013) to confirm genetic status (i.e. wildcat, domestic cat, or hybrid). Each carcass was also inspected for coat markings (Ragni & Possenti, 1996), while standard biometric measures were also recorded (e.g. nutritional status, weight, and the lengths of the body, of the tail, and of the hind foot). To be consistent with the camera-trapping protocol, hybrids, as determined via genetic analysis, were not considered further.

Results

We collected over 24,055 trap-nights from 251 cameras and we recorded 556 wildcat detections at 135 cameras, leading to the identification of 148 wildcats (Table 1). Individuals with kinked tails were observed in all study regions across the populations, whereas brachyuria was detected only in Basilicata and Puglia and cowlicks were detected only in Sicily (Table 1).

Among these cats, 11 had a kinked tail (Fig. 2; Online Resource 1 and 2), two had a very short tail (i.e.

Table 1 Summary of the results from camera-trapping surveys of wildcats from five regions of Italy. The number of road-killed wildcats is also reported in column N and F.V.G. = Friuli Venezia Giulia. Cameras indicates the number of sampling sites, cameras + indicates the number of sampling sites with wildcat detections, event is the number of wildcat detections obtained, and n.wildcat indicates the number of individual wildcats identified. K, B, and C indicate the numbers of wildcats with a kinked tail, brachyuria, or cowlicks, respectively; the frequency (%) for a given abnormality across the populations is reported beside the number of wildcats

Region	Start–end monitoring period	Cameras/cameras +	Trap-days	Events/n.wildcat	N	K	B	C
Sicily	11/04/06–10/12/18	118/75	10,441	348/91	12	8/7.7	0	3/2.9
Basilicata	23/05/10–20/07/21	36/26	7587	106/30	9	2/5.1	3/1.1	0
Apulia	29/09/13–10/05/19	61/30	1747	47/12	0	0/0	1/0.1	0
F.V.G	28/08/12–20/09/21	16/14	2259	35/9	7	1/6.2	0	0
Umbria	15/04/17–20/09/21	20/20	4333	130/6	0	2/33	0	0
Total	11/04/06–20/09/21	251/135	24,055	566/148	28	13/22.8	4/7	3/1.7

Fig. 2 Kinked wildcats from camera-trapping (**a** = Sicily; **b** = Basilicata)

approximately less than one-third of the normal length observed in wildcats), one had a tail which was half of the normal length, and one had no tail at all (i.e. the whole tail was apparently missing) (Online Resource 3 and 4). In addition, three cats from Sicily had a cowlick in the dorsal portion of the thoracic region (Fig. 3).

We necropsied 28 wildcats from Sicily, Basilicata, and Friuli Venezia Giulia. Only one female from Sicily and one male from Friuli Venezia Giulia had a kinked tail. The tail kink of the male from Friuli Venezia Giulia was located at the distal tip (Fig. 4a). The kink-tailed female from Sicily was pregnant with two foetuses; the male foetus, but not the female foetus, also had a kinked tail. Here, the kink of the adult female was located at the centre of the tail (Fig. 4b), whereas the kink of the male foetus was located at the base of the tail (Fig. 5). Mean and standard error of the mean (s.e.m.) of the body, tail, and hind foot lengths were 73.9 ± 3.2, 26.3 ± 1.2, and 11.3 ± 0.4 cm, respectively.

Fig. 3 Three Sicilian wildcats showing the cowlicks on the dorsal portion of the thoracic region

Discussion

We used camera-trapping and necropsies on road-killed wildcats, which were genetically confirmed to show no evidence of recent hybridization (Mattucci et al. 2013), to investigate the occurrence of morphological abnormalities across five wildcat populations in Italy. In addition, we documented how the kinked-tail trait was likely transmitted via genetic inheritance from an affected individual to its offsprings. This observation also provides evidence that the kinked-tail trait can be found in both sexes, although it might occur at different frequencies (Benirschke et al. 1981). Wildcats with kinked tails were detected across the populations at a relatively similar frequency (5–7%); we consider the 33% value observed in Umbria was likely an outlier due to small sample sizes.

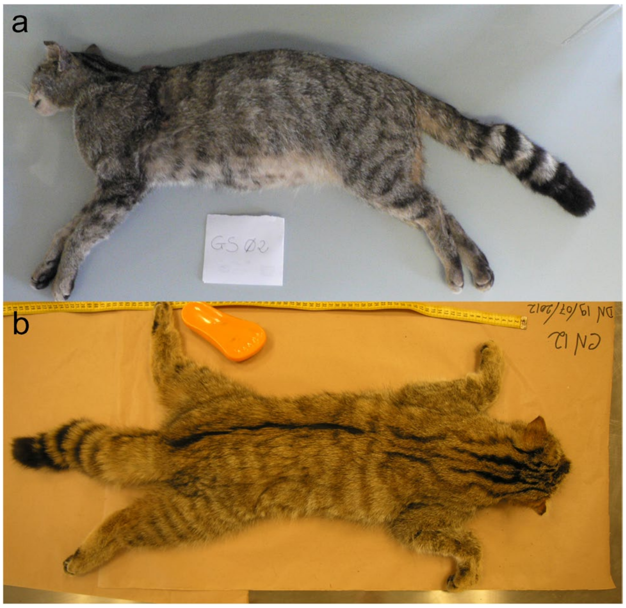

Fig. 4 Kinked tails in road-killed wildcats (**a** = Sicily; **b** = Friuli Venezia Venezia Giulia)

Fig. 5 The two foetuses from the female wildcat with a kinked tail (Fig. 4b) from Sicily (Mt. Etna); the male showing a kinked tail

Interestingly, some of these abnormalities appear to be population-specific. For example, cowlicks were detected only in Sicily, an island with no gene flow with other wildcat populations (Mattucci et al. 2016). Relative to other wildcat populations in Italy, the Sicilian population had the lowest: (i) number of alleles per locus (3.6); (ii) allelic richness (2.1); and (iii) heterozygosity, either observed (0.46) or expected (0.50) (Mattucci et al., 2013). Given these findings, the genetic status of the Sicilian wildcat population is more typical of a cat species classified by the IUCN Red list of Threatened Species™ as Critically Endangered, like the Asian cheetah (*Acinonyx jubatus* spp. *venaticus*), or Endangered, like the Andean mountain cat *Leopardus jacobita* and the Iberian lynx (*Lynx pardinus*) (Azizan and Paradis 2021). Alternatively, the detection of such abnormalities might be related to the local set-up of cameras in this study area, given the surveys conducted in Sicily always focused on wildcats. Thus individuals were more likely to be located at the centre of the image and at a relative short distance with a white flash; these features might have enhanced the detection of cowlicks when inspecting photographs.

Similarly, none of the road-killed wildcats in the Basilicata region had any abnormalities, but three camera-trapped individuals were affected by brachyuria (one total and two — most likely siblings — partial) and two had kinked tails. Two potential, and likely concurrent, explanations may have caused this apparent contradiction: (1) overlap between the areas surveyed with cameras and where the road-kills were collected (Falsone et al. 2014) (south of the region around the Regional Park of Gallipoli Cognato) was extremely low, hence we may have sampled two different sub-populations within the same region; and (2) temporal overlap between camera surveys and collection of road-kill was extremely low, hence we may have sampled the same population during different time periods. We also detected two wildcats (one male and the other undetermined) with a kinked tail, via a citizen camera-trapping project from the Umbria region, providing further evidence that the kinked-tail trait is also found in this wildcat population. Furthermore, we are aware of some road-killed wildcats with kinked tails collected in central Italy by Prof. Bernardino Ragni and his team, but we did not have access to this historical dataset.

We are unsure why brachyuria or cowlicks were not detected across all monitored wildcat populations, given we found kinked tails throughout Italy. However, the fixation of a particular phenotypic trait in isolated cat populations is not uncommon. For example, pseudomelanism was detected at relatively high frequency (~37%) only in the tiger population of the Similipal Tiger Reserve, India (Sagar et al. 2021). Likewise, melanism in servals (*Leptailurus serval*) is frequent only around the moorland of the Aberdares and Mt. Kenya (Grimshaw et al. 1995) and it was detected in margays (*Leopardus wiedii*) only in two localities from Colombia and Chile (González-Maya et al. 2018). Similarly, albinism in the fishing cat (*Prionailurus viverrinus*) was observed only in the Haor Basin area in Bangladesh (Giordano et al. 2013) and erythristic leopards (*Panthera pardus*) are reported only from India and South Africa (Pirie et al. 2016).

We have not yet investigated further whether individuals with kinked tails among the road-kill dataset also have a lower genetic diversity, or any defects of the atrial septa in the heart (Johnson et al., 2010). No road-killed wildcats with kinked tails had any apparent morphological abnormalities in the heart, although detection of this kind of abnormality would require more detailed necropsy.

Hence, we recommend researchers conduct more thorough necropsies on wildcats in Italy to fill this gap. Likewise, we could not ascertain if wildcats with brachyuria had a lower fitness, although we note these individuals were not detected throughout the years. Given that our camera-trapping surveys in both Apulia and Basilicata spanned several years, this finding might suggest a lower survival of these individuals.

In general, the frequencies at which we detected these abnormalities in wildcats are far lower (1.7%, 7%, and 22.8% for cowlicks, brachyuria, and kinked tails) than reports (90% and 81% for kinked tails and cowlicks, respectively) from Florida panthers (Johnson et al. 2010). Regardless, our findings urgently call for extensive investigation into the genetic associations with these abnormalities, with greater collaboration among conservation agencies, universities, and stakeholders throughout Italy (Karanth 2016). If the association between these abnormalities and reduced genetic diversity were confirmed, it would be then extremely important to identify their causes. Multiple factors can increase the genetic erosion in a wild cat population. For example, when populations are too fragmented, dispersal is inhibited (Kenney et al. 2014), leading to local extirpations and population bottlenecks. Alternatively, male wildcats may not disperse if population densities are too low (Anile and Devillard 2020), similar to findings for the leopard (Fattebert et al. 2015). In addition, dispersal capacity is correlated to body size (Bowman et al. 2002) and hence wildcats in Italy may be faced with another threat.

In conclusion, we recommend a standardized sampling protocol to better link genetics and morphometrics (i.e. via camera-trapping surveys coupled with scat collection followed by genetic analysis) in Italian wildcats. Even though such a sampling protocol would require a profound commitment to field work over large areas for achieving satisfactory results (Anile et al. 2014, 2019), the number of genotyped individuals ($n=32$) is promising. In addition, there is a lack of a national plan based on the best scientific knowledge and expertise for monitoring wildcats in Italy. However, the recent establishment of the Eurowildcat network (https://eurowildcat.org/; accessed 25/02/2021), which aims to improve wildcat conservation and collaboration, has built the basis for a pragmatic, science-based cooperative effort across countries. This network will surely contribute to a more standardized approach across scientific disciplines for fostering the conservation of wildcats in Italy and across Europe (Bastianelli et al. 2021).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13364-022-00627-5.

Acknowledgements SA and SF thank Ettore Randi and Federica Mattucci from the ISPRA for kindly assessing the genetic status of the wildcats collected and used in this study. SA thanks Marisa Mazzaglia, former president of the Etna Regional Park, for supporting the wildcat research project without any hesitation. SA also thanks Dr. Michele Leonardi and Dr. Rosa Spampinato (Etna Park officers) for supporting his research throughout the years. Dr. Luigi Piccinini and Maurizio Pennisi from the "Ripartizione Faunistico Vena-toria di Catania" kindly provided the cameras used in this study. The wildcat project on Mt. Etna was funded by Etna Park in 2015–2016 and 2018. SA is also extremely graceful to the citizen scientists which are collaborating to the wildcat camera-trapping project "Piccoli Fototrappolatori Indipendenti." The comments of two anonymous reviewers have improved this study.

Funding The wildcat project on Mt. Etna was funded by Etna Park in 2015–2016 and 2018.

Data availability Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no competing interests.

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