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Monitoring distribution, density and introgression in European wildcats in Switzerland

Beatrice Nussberger [a,b,*], Stefan Thomas Hertwig [c,d], Tobias Roth [e,f]

[a] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland
[b] Wildtier Schweiz, Winterthurerstrasse 92, CH-8006 Zurich, Switzerland
[c] Natural History Museum Berne, Bernastrasse 15, CH-3005 Berne, Switzerland
[d] Institute of Ecology and Evolution, University of Berne, Baltzerstrasse 6, CH-3012 Berne, Switzerland
[e] Department of Environmental Sciences, Zoology, University of Basel, Vesalgasse 1, CH-4051 Basel, Switzerland
[f] Hintermann & Weber AG, Austrasse 2a, CH-4153 Reinach, Switzerland

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ABSTRACT

Monitoring the population dynamics of elusive hybridizing species in human-dominated landscapes helps conservation and management of these species. This is particularly relevant when wild species are potentially threatened by hybridization with a domestic species, as is the case for European wildcats and domestic cats. We estimated the occupancy of European wildcats in 2010 and in 2020, based on genetic analysis of single hairs, systematically collected at 121 1 km^2 sites, evenly distributed across the Jura (4307 km^2). We mapped the current density of European wildcats in Switzerland based on a spatial capture recapture model using data from 246 1 km^2 sites, evenly distributed across the Jura, the Plateau and the Prealps. We estimated the level of admixture between European wildcats and domestic cats in Switzerland in 2010 and 2020. The proportion of occupied sites in the Swiss Jura doubled from 15 % to 31 % within ten years. The current wildcat population size in Switzerland is estimated to be around 1100 individuals. Gene flow from domestic cats into the wildcat gene pool increased from 0.02 to 0.03 migrants per generation between 2010 and 2020. The results suggest that the European wildcat distribution in Switzerland expanded to regions of increased human presence and thus presumably also of increased domestic cat presence. In this context, the threat of introgression of domestic genes becomes more relevant. Thus, continued monitoring of population dynamics using molecular tools is recommended. Long-term systematic genetic survey of population dynamics proves to be an important tool to manage elusive hybridizing mammals.

1. Introduction

Monitoring the population dynamics of elusive, hybridizing species in a human-dominated landscape supports conservation and management of these species. Distribution, density, and admixture are dynamic and interdependent population parameters. For example, changes in distribution and local density can influence hybridization level (Johannesen et al., 2006; Garcia et al., 2011; Ren et al., 2012; Quilodrán et al., 2019). A growing population can lead to increased density within the current range. Territorial, solitary species often demonstrate negative density-dependent dispersal, that is, individuals tend to disperse away from regions with higher density of conspecifics to regions with lower density (Quilodrán et al., 2019). This behavior may favor an expansion of the species range, especially if suitable habitat is available for colonization outside of densely populated regions. During such colonization processes, density of the dispersing species may be particularly low at the edge of the range. Low densities of conspecifics may promote hybridization with a more abundant, closely related species.

In conservation, hybridization is seen as a potential threat, especially hybridization between wild and domestic species (an important example of anthropogenic hybridization; Allendorf et al., 2001). Domestic species may carry traits that are less adapted for optimal survival in the wild, compared to wild populations (Saetre et al., 2004; Tymchuk et al., 2007; Marsden et al., 2016; Gehring et al., 2019). Although maladaptive

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* Corresponding author at: Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.

E-mail addresses: beatrice.nussberger@ieu.uzh.ch, beatrice.nussberger@wildtier.ch (B. Nussberger), stefan.hertwig@unibe.ch (S.T. Hertwig), t.roth@unibas.ch, roth@hintermannweber.ch (T. Roth).

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domestic traits are expected to be selected against in natural settings, domestic animals are usually more numerous than their wild counterparts, who are therefore at risk of extinction through genetic swamping (Rhymer and Simberloff, 1996; Ellstrand et al., 1999; Allendorf et al., 2001; Field et al., 2008). Wild-domestic hybridization is of particular conservation concern since domestic species are abundant and widely distributed around the world, including regions outside the range of their wild progenitors. Some domestic species, like cats and dogs, are free-ranging or feral and proliferate, which may increase the frequency of hybridization events.

For conservation and management of the European wildcat (*Felis silvestris* Schreber, 1777), we undertook long-term, systematic monitoring of three population parameters: distribution, density, and hybridization with domestic cats (*Felis catus* Linnaeus, 1758). The European wildcat is a widespread (Yamaguchi et al., 2015) yet protected species in Europe, through the Bern Convention (Appendix II, 1979) and the European Habitat Directive 92/43/EEC (EUROP, 1992). The species is potentially threatened by hybridization with the domestic cat, and the potential for subsequent loss of genetic integrity (Yamaguchi et al., 2015; Capt, 2022). An increase in wildcat presence has been reported in several regions of Europe, e.g. Germany (Mueller et al., 2020; von Thaden et al., 2021) and France (Say et al., 2012). The density of wildcats has been studied locally across the species distribution and varies between 0.1 and 0.4 ind/km^2, with some, rare, outliers outside of this range (synthesis in Matias et al., 2021). The level of admixture between wildcats and domestic cats is also well documented in Europe, with hybridization rates ranging from 0.03 in Central Germany to 0.21 in the Iberian Peninsula, or even complete admixture in Scotland (synthesis in Tiesmeyer et al., 2020).

Former range dynamics in Switzerland, from the Neolithic to the beginning of the 21st century, have previously been described (Schauenberg, 1970, Eiberle, 1980, Sommer and Benecke, 2006, Nussberger et al., 2007, Weber et al., 2010); while wildcats were present in the Jura and the Plateau region during the Neolithic, they disappeared from Switzerland during the first half of the 20th century due to habitat loss and persecution, only recolonizing the Jura after their legal protection in 1962. Estimates of wildcat density have been determined in two small regions of the northern Jura mountains (genotypic wildcats at Blauen: Kéry et al., 2011, phenotypic wildcats in the region of Moutier-Delémont: Maronde et al., 2020) and admixture level was previously assessed once in Switzerland (Nussberger et al., 2014b). Nevertheless, to our knowledge, data quantifying distribution, density and hybridization together, over different time frames and over a large geographical range, applying a systematic, replicable monitoring method are still lacking.

The aim of this study is to provide a systematic assessment, at a national level, of the long-term population dynamics of an elusive species in a human-dominated landscape. We report the current distribution of European wildcats, their density, and level of admixture with domestic cats in Switzerland, and discuss the changes in these three population parameters over a ten-year period.

2. Materials and methods

The “Swiss wildcat monitoring project” was launched by the Federal Office for the Environment in 2008, to assess systematically the national, long-term population dynamics of the European wildcat, specifically, the distribution, density, and level of admixture with domestic cats in Switzerland. The first survey was carried out during the winters of 2008/09 and 2009/10 (hereafter “survey 2010”), and the second survey during the winters of 2018/19 and 2019/20 (hereafter “survey 2020”).

For survey 2020, non-invasive hair samples were collected at 246 sites of 1 km^2. Sites were sampled systematically, evenly spaced across a 5 × 5 km grid and included all 121 sites sampled in survey 2010. Cat hairs were genotyped to determine the individual's mitochondrial DNA, admixture level and individual genetic signature. Based on the data collected at sampling site-level, we modeled the occupancy of wildcats across the study area using generalized linear models. Individual recognition allowed the use of individual-based spatial capture-recapture models (CRM) to map the density and estimate population size. Finally, the level of admixture with domestic cats was assessed using two approaches: the proportion of hybrid individuals in the wildcat population and the amount of gene flow from domestic cats to wildcats at a population level.

2.1. Study area

The study area contained three biogeographic regions: the Jura (4307 km^2), a woody, hilly region with agricultural land and small towns, the Plateau, a flat, human-dominated landscape, and the Prealps, a mountainous region (Fig. 1). All officially reported plausible wildcat sightings were limited to the core of the Jura region until the start of the project in 2008 (Nussberger et al., 2007). For this reason, we assumed that wildcats were absent elsewhere in Switzerland at that time. Thus, sampling during survey 2010 was restricted to the Jura region, west of the A3 highway, and a small western part of the Plateau adjacent to the Jura region. Here, we refer to this part of the study area as the “Swiss Jura”. However, after 2010, a few sporadic occurrences of genetically confirmed wildcats were documented outside of this range. Thus, for survey 2020, sampling was expanded further east. The study area is assumed to cover the entire distribution range of wildcats in Switzerland.

Sampling sites were plots of 1 km^2, evenly distributed on a grid of 5 × 5 km covering the study area (Suppl. Mat. 1). Sites with $<$10 ha forest or with $>$20 % human settlements were excluded a priori, since wildcats are known to avoid urbanized areas (Parent, 1975; Klar et al., 2008) and we thus expected to find mostly domestic cats at these sites. Woods within 200 m of settlements were not considered as forest for the same reason. The total number of sampling sites was limited for logistical reasons, we therefore reduced sampling effort in regions where we could reasonably expect reduced wildcat occurrence, that is at high altitude, and in the study area outside the Swiss Jura (Nussberger et al., 2007; Nussberger and Maronde, 2021).

Accordingly, we sampled 50 % of the sites in which $>$90 % of the surface was $>$1000 m.a.s.l. in the Jura and none in the Prealps. Further, only 50 % of the potential sites on the Plateau and Prealps were sampled. Regular sampling in the year 2010 took place at 121 sites: 100 in the Jura and 21 on the Plateau. In the year 2020, there were 246 regular sampling sites: 120 sites in the Jura, 99 in the Plateau and 27 in the Prealps (Fig. 1).

2.2. Sample collection

To collect hair samples noninvasively, a team of 87 trained fieldworkers (mostly gamekeepers and hunters) placed three wooden lure-stick-hair-traps within each sampling site of 1 km^2, at least 50 m inside the forest, along a game path, maximizing the coverage of different regions within the square-kilometer and keeping a minimum distance of 100 m between sticks. The sticks were baited with approx. 12 sprays of valeriane tincture (Valerianae tinct, Art. 25-6151-13 1LT GID, Haenseler, Herisau Switzerland), a known cat attractant (Monterroso et al., 2011). They were sampled and rebaited every two weeks, at least five times in total (i.e., five sampling occasions). Hairs from each stick and collection date were stored separately in antistatic plastic bags containing a 5 g silicagel Tyvek packet (Dry & Safe GmbH), in a freezer at −80 °C until further analysis.

2.3. Genetics

From the 810 hair-sample-bags collected, we selected samples with a hair bulb for genetic analysis (detailed protocol described in Nussberger et al., 2014a) and excluded a priori the hairs which obviously came from other species, such as roe deer. We quantified the cat-specific DNA

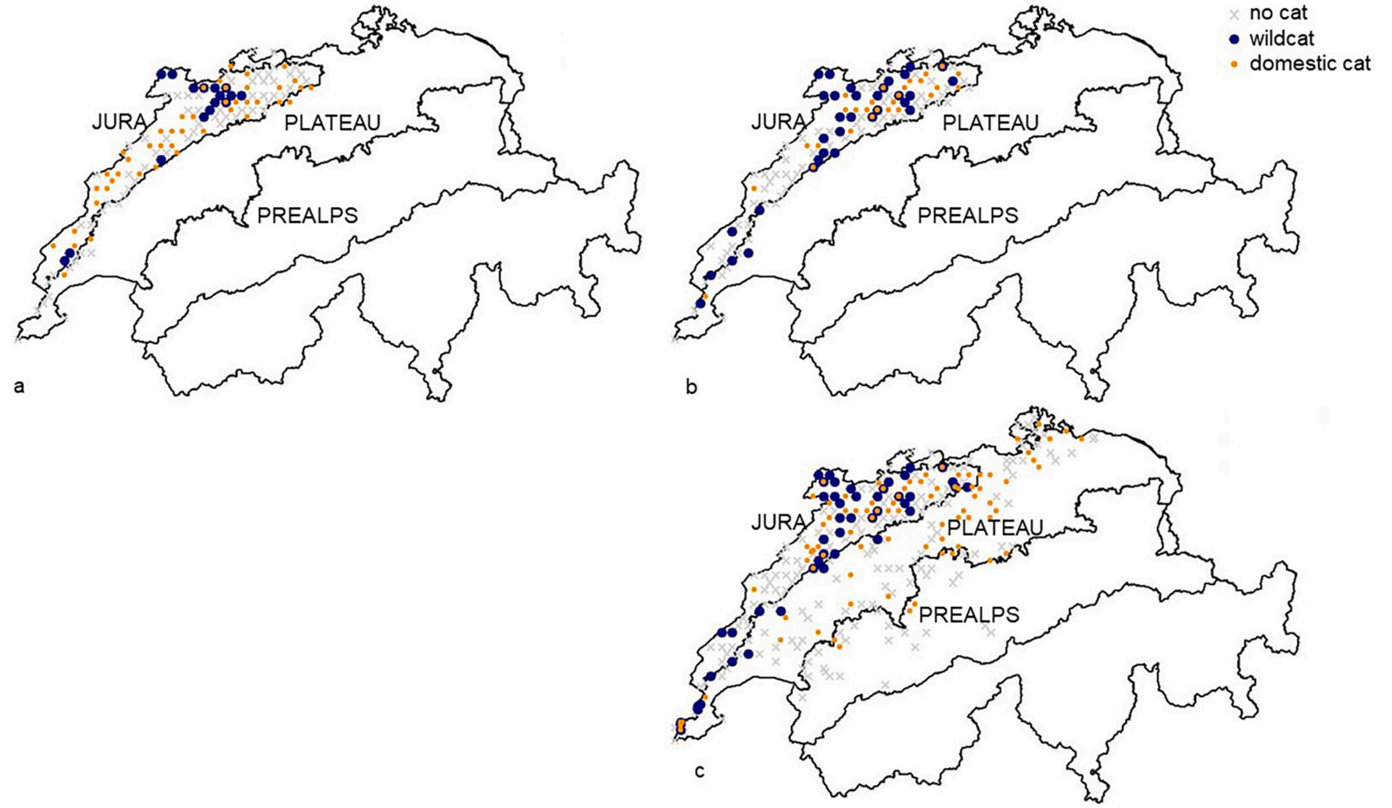

Fig. 1. Sampling sites for the occupancy model in the survey 2010 (a) and in the survey 2020 (b), as well as for the density model 2020 (c). Crosses: sites without detected cat presence. Small orange dots: sites with domestic cat occurrence. Large blue dots: sites with wildcat occurrence.

available in each of the 1362 single hairs using quantitative real-time PCR. Of these, 513 hairs yielded enough DNA and generated reliable genetic data, at least concerning the mitochondrial DNA-type of the individual.

We used a 96.96 Fluidigm single nucleotide polymorphism (SNP) genotyping array chip to genotype single hairs, following the protocol of Nussberger et al. (2014a). The chip contained genetic markers to determine mtDNA-type (wildcat or domestic cat haplotype) and nuclear DNA markers with high F_{st}-values between wild- and domestic cats used to assess individual admixture level (wildcat, backcross into wildcat, F1- or F2-hybrid, backcross into domestic cat, domestic cat), as well as markers on the Y chromosome for sex determination (Nussberger et al., 2013, 2014a). We used the software NewHybrids (Anderson and Thompson, 2002) to estimate individual admixture level. The posterior probability of each individual belonging to the six admixture categories above is estimated with a Bayesian clustering algorithm, based on the observed and expected allele frequencies at the nuclear DNA markers. We used the software Gimlet (Valière, 2002) for individual recognition. Different mtDNA-haplotype signatures and sex – determinated through presence or absence of alleles at the Y-markers – were used as preliminary sorting categories for individual recognition. The amount of gene flow from domestic cats into wildcat populations was assessed using the software BayesAss 3.0.4 (Wilson and Rannala, 2003).

2.4. Occupancy 2010–2020

We applied a generalized linear model (GLM) with a binomial distribution to the presence or absence of wildcats per sampling site. We used median altitude, proportion of forest, and the proportion of settlement at sampling sites as predictor variables. Based on this model we predicted wildcat occurrence across the potential wildcat habitat in the Swiss Jura (i.e., all square kilometers with at least 10 ha forest and not >20 % settlement). Occurrence was defined as the presence of a wildcat-mtDNA-haplotype, identified from at least one sampling occasion, from at least one of the three sticks at a sampling site. Occupancy was defined as the proportion of sites with predicted wildcat occurrence compared to all potential sites within the Swiss Jura. The estimates are based on the data from the 121 regular 1 km^2-plots from the Jura and western Plateau, sampled both in 2010 and 2020.

The detection probability of wildcat occurrence was defined as the probability of detecting evidence of a wildcat-mtDNA-haplotype from at least one of the three sticks, and at least one of five sampling occasions in the field. The detection probability was estimated using a site-occupancy model that also accounted for differences in sampling effort between sampling sites (MacKenzie et al., 2002), and was estimated separately for the first and second survey.

2.5. Distribution, density and population size 2020

To model the current distribution and density, and to estimate population size in Switzerland, we used individual-based spatial capture-recapture models (CRM), as described by Kéry et al. (2011) and implemented in the R-package oSCR (Sutherland et al., 2019). CRM estimate the density of a species based on individual site data, by accounting for both the probability to detect an individual and the size of individual activity centers. In our model we used the mean altitude, the proportion of forest, and the proportion of settlement as explanatory variables for density. The linear and quadratic terms of the X and Y coordinates were also included in the model as predictor variables, to better account for regional differences in density. Density is here defined as the number of individual activity centers per square kilometer.

To estimate the size of activity centers, we collected complementary data on larger surfaces with a known wildcat presence, where the probability of detecting several wildcat individuals repeatedly was thus maximized. Indeed, as wildcat home ranges are usually larger than 1 km^2 (e.g. approx. 3 to 10 km^2, Nussberger and Maronde, 2021), using only the 246 1 km^2 sampling sites, distributed across a 5 × 5 km grid, the estimation of individual activity centers was impossible (that is, the model would have been overparametrized), due to a low number of individual spatial recaptures within their activity range. Thus, we collected a set of complementary data from larger adjacent surfaces, covering 29 km^2 in total (15 km^2 in Ajoie, 13 km^2 in Yverdon and 2 km^2 in Kerzers, these three areas representing the north and the south of the Swiss Jura, as well as the Plateau). On each 1 km^2-site within these complementary surfaces, the same systematic sampling method was applied as for the regular sampling sites. Further, 35 additional 1 km^2-sampling sites outside the regular 5 × 5 km grid were monitored in 2020. The sites were chosen opportunistically, where presence of wildcats was strongly suspected based on sightings, or where there was a particular interest in knowing if a wildcat was present or not. This increased the total amount of data with documented wildcat presence or absence, thus allowing to estimate the size of the activity centers. Note, that by including the complementary data we assumed that the estimated size of the activity centers in complementary data areas were representative for the whole study area. However, the complementary data were not used to estimate the wildcat density and, thus, the densities in the areas where complementary data were sampled did not have to be representative of the entire study area.

In the CRM, size of activity centers and average detection probability were estimated for regular and complementary studies together, that is, using the 246 regular 1 km^2-sampling sites from the Jura, the Plateau and the Prealps, as well as the larger adjacent surfaces covering 29 km^2 and the 35 additional sampling sites.

3. Results

3.1. Occupancy 2010–2020

Within the 121 1 km^2-sites that were sampled in both 2010 and 2020, wildcat presence was detected in 13.2 % of these sites in 2010 and 27.3 % in 2020 (Fig. 1, Suppl. Mat. 1). Based on the site-occupancy models that accounted for imperfect detection and that considered the entire study area of the Swiss Jura, occupancy (proportion of occupied potential wildcat habitat) was 0.15 (CI: 0.09–0.24) in the first survey and 0.31 (CI: 0.23–0.42) in the second, which represents a doubling of occupied area in the Swiss Jura. The detection probability of wildcats was similar in both surveys. In the first survey it was 0.33 (95 % confidence interval 0.21–0.46), in the second survey 0.31 (0.24–0.4). This means that, for example, in the second survey we were able to detect wildcat presence in 84 % of sites in which wildcats are truly present (CI 75 %–92 %). Indeed, with five sampling occasions and a detection probability of 0.31 per sampling occasion, per site, the probability of missing a wildcat presence at one site is $(1–0.31)^5 = 0.16$, or 16 %, thus the probability of detecting the presence 100 %–16 % = 84 %.

Wildcats occurred mainly in the sites with a high proportion of forest (Table 1, positive slope for this parameter in all models). This relationship was strong and significant ($p = 0.021$) in survey 2010, but weaker and no longer significant in 2020 ($p = 0.468$).

In 2010, wildcat presence was restricted to the core biogeographical region of the Jura, no wildcats were detected on sites located on the Plateau (Fig. 1 a). In 2020, wildcat presence was still mostly limited to the Swiss Jura (Fig. 1 b). The wildcat occurrences observed during survey 2020 on the Plateau were all adjacent to the Jura (Fig. 1 b and c). No wildcats were detected in the Prealps (Fig. 1 c).

3.2. Distribution, density and population size 2020

Based on the spatial capture-recapture model, the highest densities of wildcats were found in low-lying areas of the Jura with a high proportion of forest (Table 1, Fig. 2). The median elevation of the 1 km^2-sites with wildcat presence was 591 m.a.s.l. (min. 390, mean 666, max. 1186 m.a.s.l.). On average, an individual was encountered 1.5 times and at 1.2 spatial locations.

We found between 0 and 4 wildcats per 1 km^2 sample site. Across all regular sample sites, the average number of wildcats per km^2 (±SE) was 0.23 ± 0.66. The density of domestic cats was twice as high with 0.47 ± 1.01 individuals per km^2. The density of wildcats in the Jura was on average 0.39 ± 0.85 per km^2, higher than the average observed over all sample sites from the Jura, the Plateau and the Prealps together. The average density of domestic cats in the Jura was similar to the value for the entire study area with 0.49 ± 1.07 individuals per km^2.

Wildcat population size in the study area was estimated to be about 1100 individuals in 2020. The 95 % confidence interval was 513–13,066 individuals, the 80 % confidence interval was 713–3060 (Fig. 3).

3.3. Admixture 2010–2020

At the population level, gene flow from domestic cats into the wildcat population was 0.03 (0.02–0.04 95 %-CI) migrants per generation in 2020, and 0.02 (0–0.04 95 %-CI) migrants per generation in 2010. Gene flow from wildcats into the domestic cat population was 0.003 (0–0.006) in 2020 and 0.006 (0–0.02) in 2010.

The proportion of hybrids in the wildcat population in 2020 was 15 %. We identified 68 individuals carrying wildcat genes based on their nuclear DNA. From these, ten also carried between 25 and 75 % domestic genes and were thus considered to be hybrids (3 backcrosses into wildcats, 4 F1, 1 F2, 2 backcrosses into domestic cats). The proportion of hybrids increased to 23.5 %, if the six individuals that were wildcats based on their nuclear genes but carried a domestic mtDNA-haplotype were also considered as hybrids. In 2010, the proportion of hybrids was 21 %; we identified 19 individuals with nuclear wildcat genes, of which four were hybrids (4 backcrosses into wildcats). This proportion increased to 37 % when the three nuclear wildcats carrying domestic mtDNA-haplotypes were included as hybrids (Nussberger et al., 2014b). In addition, we found 121 domestic cat individuals in 2020 (versus 56 in 2010).

Based on mtDNA and Y-chromosome markers, hybrids were descendants from both the reproduction between wildcat females and domestic cat males and the opposite pairing (individual genotypes shown in Suppl. Mat. 2). For example, two of the four F1-hybrids detected in 2020 had a domestic father.

Table 1
Occupancy and density of wildcats explained by three descriptive variables of the sampling sites. Occupancy (Occ.) is indicated for the surveys 2010 and 2020 in the Jura region (Jura), density is indicated for the survey 2020 in the Jura, the Plateau and the Prealps (all). Slope, standard error (SE) and *P*-value for occurrence are based on a generalized linear model with a logit-link function, whereas for density, these data are based on a spatial capture-recapture-model considering detection probability (statistically significant P-values are highlighted in bold).

Variable	Slope Occ.	Slope Occ.	Slope Density	SE Occ.	SE Occ.	SE Density	P-value Occ.	P-value Occ.	P-value Density
Year (dataset)	2010 (Jura)	2020 (Jura)	2020 (all)	2010 (Jura)	2020 (Jura)	2020 (all)	2010 (Jura)	2020 (Jura)	2020 (all)
Altitude (effect by 100 m)	−0.036	−0.012	−0.595	0.134	0.097	0.158	0.786	0.900	**<0.001**
Proportion of forest (effect per 1 %)	3.535	0.728	1.669	1.528	1.004	0.759	**0.021**	0.468	**0.028**
Proportion of settlement (effect per 1 %)	−0.672	−1.467	−6.956	5.102	3.263	6.036	0.895	0.653	0.249

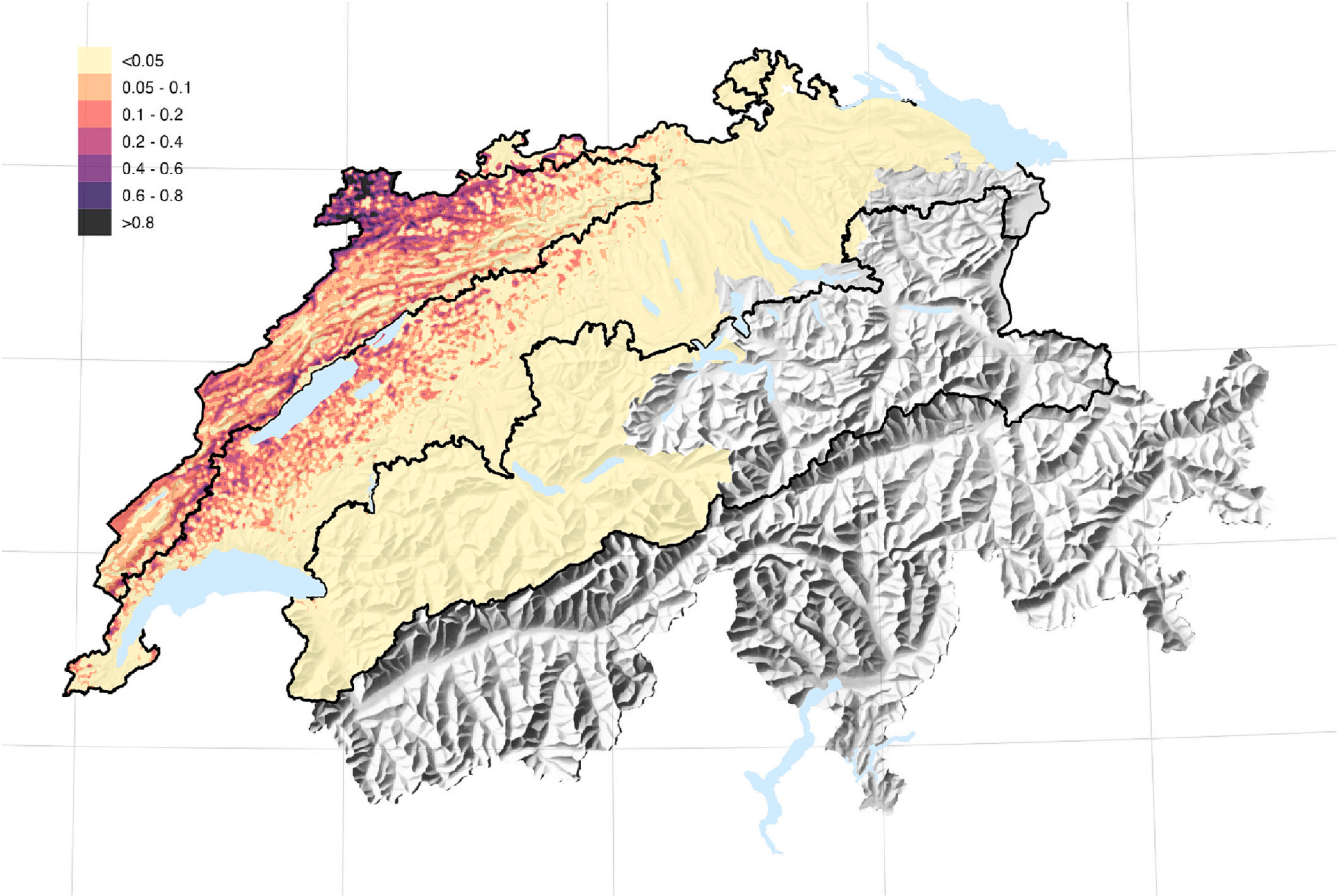

Fig. 2. Modeled density of wildcats in 2020, representing the current distribution of the species in Switzerland. The map shows the estimated number of wildcat activity centers per square kilometer: the darker the color, the more abundant the wildcat.

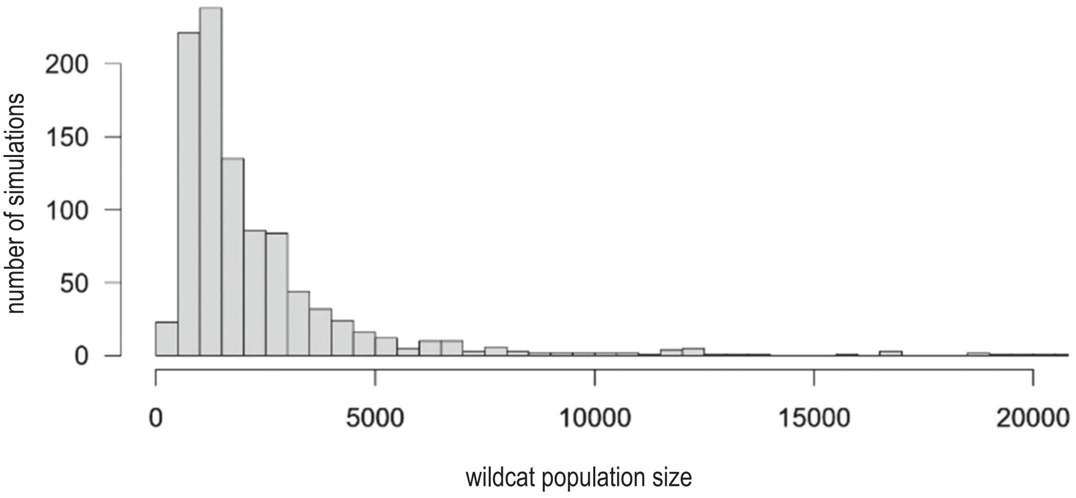

Fig. 3. Distribution of number of simulation outcome for wildcat population size. Simulations were iterated 1000 times, based on the CRM for survey 2020.

4. Discussion

We report a doubling in the occurrence of wildcats in the Swiss Jura within ten years. We provide a countrywide map predicting wildcat range and density within a given habitat, using a spatial capture-recapture model that links the densities of individual wildcat activity centers to specific habitat parameters: proportion of forest, proportion of settlement and altitude. Finally, we observed that gene flow from domestic cats to wildcats was higher in 2020 than in 2010.

4.1. *Distribution*

Wildcats doubled their occupancy of the Swiss Jura within 10 years. Our results suggest that wildcats are currently expanding their range from the Jura into the Plateau, towards a more human-dominated landscape. In 2010, additional sampling sites at the south-west and north-east edges of the known Swiss distribution were surveyed using the standardized monitoring protocol: 18 sites in the canton of Geneva and 14 in Basel-Landschaft. From these 32 additional sites, wildcat presence was detected at only one site in Basel-Landschaft (2′598’000 long. 1′248’000 lat., Weber et al., 2009, 2010), which supports our findings of an expansion. A similarly fast range expansion was observed during the nineteen-sixties in the Belgium wildcat population (Parent, 1975), although it was not quantified based on systematically collected presence/absence data. A range expansion occurring over the last few decades has also been proposed in Germany, although an undetected previous presence could not be excluded (Mueller et al., 2020). Range expansions might be explained by prey abundance and accessibility, combined with habitat and climate conditions becoming increasingly favorable to wildcats. Parent (1975) proposed improved habitat quality following the two world wars (no restocking of forest clearance led to more rodents and reduced human presence) as a driver of range expansion.

In the mid-20th century, wildcats were almost extinct in Switzerland, with recorded presence at its lowest (Eiberle, 1980). A remnant presence may have persisted in the Jura region of the cantons Vaud, Neuchatel and Berne. The range expansion of wildcats in Switzerland following its protection in 1962 was limited, at least until 1980 (Eiberle, 1980). Harsh winter conditions with heavy snow may have limited wildcat presence, and abundant rainfall may have limited reproduction success through low juvenile survival (Eiberle, 1980; Mermod and Liberek, 2002). Nowadays, wildcats may benefit from climate change; milder winters allow better access to their preferred prey, i.e., small rodents (Germain et al., 2009), and less precipitation in summer increases juvenile survival (Eiberle, 1980). Additionally, in Switzerland, changes in forestry management may favor wildcat presence; spruce forests are gradually being replaced by temperate mixed forests and structural diversity in forests has increased in recent decades (Swiss National Forest Inventory running since 1981, Brändli et al., 2020).

Overall, wildcats seemed to prefer habitats with a higher proportion of forest and avoid those with a high proportion of settlements (Berberat, 2021), as previously described (Parent, 1975; Klar et al. 2012). Our data confirm that they can also cope with habitats with a lower proportion of forest, which is in line with the observation that wildcats can live in agriculturally-dominated landscapes, if sufficient shelter is available (Eiberle, 1980; Jerosch et al., 2017; Jerosch et al., 2018). In the Swiss Jura, the preference for forested habitat was significant in our survey 2010. Ten years later, while the probability of occurrence doubled, this trend was no longer significant within the Swiss Jura, suggesting a delayed occupation of habitats with lower forest cover, usually correlating with a more human-dominated landscape. Interestingly, when considering the entire study area, i.e., including the Plateau and Prealps, the preference for more forested areas was again significant in both the CRM and the GLM for the 2020 dataset (Table 1 and Suppl. Mat. 3 Table 1). This supports the hypothesis of a preference for forests when space is available and flexibility in habitat choice when the occurrence of congeners in preferred habitat increases.

These findings highlight the importance of continuous wooded vegetation as migration corridors and stepping-stones in densely human-dominated landscapes (Parent, 1975; Jerosch et al., 2018), to favor further wildcat expansion, through the Plateau and into existing suitable habitat in the Prealps not yet colonized.

4.2. Density and population size

Generating a national density map is a powerful tool for management, outperforming estimations of overall or regional density values, as the map reveals geographic differences across a large area (Fig. 2). Nevertheless, we estimated an overall density of wildcats in Switzerland, to compare with values from populations in other countries. We found a mean value of 0.23 individuals per km^2, which is within the range reported by other studies from northwestern continental populations (synthesis in Matias et al., 2021). For example, this value is slightly lower than in Sicily (Italy) 0.28 ± 0.1 wildcat/km^2 (Anile et al., 2012) and in the northeast of Italy 0.35 ± 0.1 wildcat/km^2 (Fonda et al., 2022), but slightly higher than in Andalousia (Spain) 0.02 to 0.17 wildcat/km^2 (Gil-Sánchez et al., 2020). Our findings are also in the range of values reported from two smaller regions of Switzerland: 0.29 wildcat/km^2 (SE 0.06) in the Blauen (Kéry et al., 2011) and 0.26 (0.17–0.36) wildcat/km^2 in the region between Delémont and Moutier (Maronde et al. 2020).

The current population size of European wildcats in Switzerland was estimated to be around 1100 individuals. This is higher than the estimate from ten years earlier, where population size was estimated to be a few hundred individuals (Weber et al., 2010). However, the confidence interval for the population size was large. This was not surprising for a model that considered several explanatory variables and was applied to a large sampling area. The model accounts for a high number of uncertainties. There is uncertainty around the correlation between the number of sites with proof of presence and the number of sites in which wildcats were present. Indeed, it is unlikely that every wildcat presence in a given area will be detected for several reasons, e.g., the cat did not use the exact path on which sampling was done, the cat did not leave enough DNA for genetic testing, sampling method failure, etc. In addition, we could reasonably sample only a small part of the entire study area, which contributes significantly to increased levels of uncertainty. Nevertheless, the estimated population size is still a sufficiently exact value to be used in conservation policy, e.g., to help evaluate the status of the wildcat in the national Red List of endangered species (Capt, 2022).

In both surveys 2010 and 2020, we had more sites with domestic cat presence than wildcat presence (44 domestic cat-sites versus 16 wildcat-sites in 2010, 84 vs 57 in 2020) and we detected more domestic cat individuals than wildcat individuals (19 wildcats versus 56 domestic cats in 2010, 68 versus 121 in 2020), despite avoiding sampling urban areas where we expected most of the domestic cats to occur. Based on the 2020 monitoring data presented here, we observed quite strong spatial segregation between wildcats and domestic cats: the co-occurrence of wildcats and domestic cats was found in only 3 % of the surveyed plots, whereas in 20 % of the plots, exclusively wildcats were observed, and in 25 % of the plots, only domestic cats were reported. An analysis of the differences between habitat characteristics at the sampling sites with and without wildcats and domestic cats confirmed that wildcats avoided human infrastructures, whereas domestic cats are found in areas with more settlements and less forest cover (Berberat, 2021).

4.3. Admixture

Gene flow increased from 0.02 to 0.03 domestic cat migrants into the wildcat population per generation. This can be explained by an increased proportion of first-generation hybrids in the second survey, whereas in the first survey, hybridized individuals were generally second or even third generation backcrosses. A greater occurrence of first-generation hybrids is in accordance with a growing, expanding population (Nussberger et al., 2018). Gene flow may seem low, but even low amounts of introgression could lead to a loss of genes that are unique to wildcats (Quilodrán et al., 2020). Introgression can increase within short timeframes, as shown in Scotland, where substantial introgression has probably occurred within one century (Howard-McCombe et al., 2021).

In the case of hybridizing species, it is crucial to implement a monitoring program based on genotype data, evaluated in the context of the gene pool. Hybrids can share phenotypic traits with both parental species (Krüger et al., 2009; Hertwig et al., 2009; Senn et al., 2019). Even if in some cases it is possible to recognize a hybrid sensu lato, based only on the phenotype, it remains impossible to assess the precise admixture level of this hybrid (e.g. F1 or backcross). Assessing the proportion of “hybrid” versus “non-admixed” individuals is not sufficient to evaluate gene flow within hybridizing species at the population level, since the admixture level within a hybrid sensu lato can vary massively. It makes sense to monitor gene flow by pooling data from genotyped individuals to estimate a theoretical rate of migrants per generation between the hybridizing populations (Wilson and Rannala, 2003).

It is likely that hybridization events will increase in frequency if there is continued expansion of wildcats into areas of high domestic cat presence, e.g., into urbanized areas and areas where continuity of natural forest habitats is disrupted (Beugin et al., 2019). Although the number of hybrids ($n = 10$) is too small for statistically sound conclusions, it is interesting to note that in the survey 2020, hybrids tended to be more frequent at low elevation and high settlement rates (altitude $p = 0.067$, proportion of settlement $p = 0.207$, proportion of forest $p = 0.635$), according to a CRM for hybrids similar to the model described for wildcats (Suppl. Mat. 3 Table 2).

4.4. Conclusions

Our results show that mesocarnivores such as wildcats can reestablish a large range and increase in number fairly rapidly, even in a human-dominated landscape. This may be explained by legal protection, availability of suitable habitat, in sufficient quantity, and appropriate climatic conditions. Thus, the wildcat might be considered as a beneficiary of species and habitat conservation efforts, and of climate change. Based on these findings, it was possible to downgrade the Red List category of this species in Switzerland (Capt, 2022). Such a rapid resurgence of a species formerly on the brink of extinction has also been observed in recent years in other European mammals, e.g., wolves, beavers, or otters (Capt, 2022). Nevertheless, expansion into a more human-dominated landscape, with fragmented remaining habitat may be accompanied by an increase in anthropogenic hybridization events, assuming a higher density of domesticated species in close vicinity of human settlements. Thus, further conservation efforts are still needed.

The non-invasive genetic monitoring of an elusive species at large-scale, as we presented here for European wildcats, is a valuable conservation tool.

The advantage of genetic monitoring is high accuracy and reproducibility of the results. Genotypic data allow us to 1) unambiguously identify individuals, 2) quantify individual hybridization level beyond the three potential phenotypic categories: wild, hybrid or domestic, and 3) determine the amount and the direction of the gene flow between the cat populations. In addition, genetic samples can be collected in the field at a large-scale simultaneously and do not need to be stratified for logistical reasons, e.g., as for limited number of camera-traps. The downside of genetic monitoring is that genetic analyses are expensive, requiring collection and analysis of DNA-samples. Not all cats leave hairs on lure-sticks and not all hairs yield enough DNA for genetic analysis. However, cats do not need to leave hairs each time they pass close to a lure-stick, since the applied model corrects for imperfect detection. If costs are not a limiting factor, an interesting approach would be to combine genetic sampling with phenotypic capture through camera-traps, maximizing detection probability (Velli et al., 2015). On the other hand, the different precision of these approaches to determine hybridization level and individual recognition could be challenging for data evaluation, especially for assessing the level of gene flow with the domesticated species.

Estimating reliable trends in population dynamics is an important tool for sound conservation decisions. For species at risk from hybridization, monitoring the population dynamics of both the focal wild species and the species that act as a source of alien domestic genes is essential, as both contribute to hybridization dynamics. In Switzerland, wildcat monitoring is only at its beginning, with these first two surveys within ten years. It should be pursued long-term, especially since it has been demonstrated that the species is currently expanding into human-dominated and fragmented landscapes, where domestic cats are predicted to have a particularly dense presence. As the expansion of wildcats into areas where they are outnumbered by domestic cats may potentially favor hybridization, it will be crucial to monitor the future evolution of distribution, density, and admixture level of European wildcats.

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CRediT authorship contribution statement

BN: Study design, Writing, Review & Editing.
SH: Resources, Review.
TR: Study design, Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Supplementary Material available

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