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Spatial patterns of co-occurrence of the European wildcat *Felis silvestris silvestris* and domestic cats *Felis silvestris catus* in the Bavarian Forest National Park

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After persecution and a long period of extinction in parts of central Europe, the European wildcat is currently increasing its range, also to areas deemed unsuitable for this species. This range expansion facilitates close contact with domestic cats, which can reach high population densities even in protected areas. We provide unambiguous evidence that the European wildcat is present in the Bavarian Forest National Park. We assessed the frequency of domestic cat occurrence, and analyzed the distributions of the two felid subspecies with regard to residential areas, forested habitat, elevation and protected areas, and analyzed their spatial overlap. Camera traps installed in the national park detected six putative wildcats in 2008–2015 at elevations between 800 and 1100 m a.s.l. Genetic analysis of material obtained from hair traps with valerian-treated lure sticks confirmed the presence of three wildcat individuals in early 2015. The number of wildcat events detected increased slightly in recent years and wildcats were detected closer to shrub cover and the forest edge. Of the domestic cat events, 90% were within 1.1 km of residential areas, but some moved up to nearly 3 km into the national park. Ranges of wildcats and domestic cats broadly overlapped. All but one camera trap that recorded wildcats also recorded domestic cats, and some camera traps recorded domestic cats but no wildcats. Domestic cats were the fifth most often detected mammal species in the protected area. To avoid a negative impact of domestic cats on wildcats through hybridization, which might already occur, and considering the ecological impact of predation by domestic cats, we recommend a buffer zone of 1 km surrounding the national park, where domestic cats should not be allowed outdoors.

Populations of the European wildcat *Felis silvestris silvestris* Schreber 1777, once widely distributed across Europe, decreased dramatically in central Europe owing to persecution and habitat loss over the past two centuries (Piechocki 1990, Nowell and Jackson 1996, Driscoll and Nowell 2010). However, in some regions, including Germany and adjacent areas, the species currently seems to be expanding its range (Driscoll and Nowell 2010, Hartmann et al. 2013, Nussberger et al. 2014).

Domestic cats pose a threat to wildcats as hybridization of the two subspecies is possible, and this has led to high rates of introgression in several regions, especially when wildcat densities are low (e.g. Scotland: Hubbard et al. 1992, Beaumont et al. 2001; Hungary: Pierpaoli et al. 2003). Domestic cats spend most of their time close to human settlements (Barratt 1997, Biró et al. 2004, Kays and DeWan 2004, Goszczyński et al. 2009, Thomas et al. 2014), whereas wildcats avoid residential areas (Klar et al. 2008) and prefer large and richly structured forests with old trees, shrubs, and perimeters of open areas for resting, hiding and hunting (Piechocki 1990, Mölich and Klaus 2003, Biró et al. 2004, Klar et al. 2008, Jerosch et al. 2010). Therefore, a spatial separation of domestic cats and wildcats would be expected in landscapes with high forest cover.

Both subspecies avoid harsh winter conditions (George 1974, Piechocki 1990, Woods et al. 2003, Germain et al. 2008, Goszczyński et al. 2009, Thomas et al. 2012) and wildcat distribution is limited by a closed snow cover of more than 20 cm depth over a period of 100 days because locomotion becomes difficult and prey hide under the snow (Piechocki 1990). Therefore, in Bavaria, an elevation of 800 m a.s.l. is considered the limit for an all-season wildcat habitat (Klar 2009). However, global warming could potentially lead to range expansions towards higher altitudes,

as has been found for several other taxa (La Sorte et al. 2014, Sauer et al. 2011).

In the Bavarian Forest National Park, the last known wildcat was shot during World War I (Piechocki 1990) and since then, there has been no unambiguous proof of wildcat presence in the park or its surroundings. A chronology of the history of the wildcat in the Bavarian Forest can be found in the Supplementary material Appendix 1. Control measures for domestic cats in the national park were stopped at the end of the 1980s (Bavarian Forest National Park unpubl. data). However, they can be a serious threat to wildlife (Mitchell and Beck 1992, Woods et al. 2003) and are of relevant concern in protected areas (Wierzbowska et al. 2012); therefore, their populations have to be monitored carefully. The aims of this study were to document the presence of the wildcat in the Bavarian Forest National Park and to determine the detection frequency of domestic cats. We also analyzed the habitat use and spatial overlap of wildcats and domestic cats in the park, focusing on potentially different spatial behavior towards residential areas, forested habitat and elevation. We hypothesized that both subspecies would select elevations lower than 800 m a.s.l. in winter (Klar 2009) and structurally rich forests and that domestic cats would be found close to human settlements, which would be avoided by wildcats.

Material and methods

Study area

The Bavarian Forest National Park covers an area of 240 km² in Germany in the Bohemian Forest Ecosystem and borders the Šumava National Park in the Czech Republic (Heurich et al. 2015). Elevations range from 650 m a.s.l. in valleys to 1453 m a.s.l. at Mount Rachel. Average annual temperature is 6°C in valleys and 3°C at the top of the ridges; annual precipitation is 1000–1300 mm in valleys and 2000 mm at high elevations. In valleys, snow cover lasts up to five months; at high elevations, snow cover can reach a depth of up to 3 m and lasts up to seven months. Valleys are dominated by lowland spruce forests (*Soldanello – Piceetum bazzanietum*), slopes are dominated by mixed mountain forests (*Luzulo – Fagion* and *Asperulo – Fagetum*), and high elevations are dominated by mountain spruce forests (*Soldanello – Piceetum barbilophozietosum*) (Heurich et al. 2010). A massive bark beetle outbreak led to openings and high amounts of dead wood covering 6500 ha (Lausch et al. 2013).

Lure stick hair traps

We installed ten rough, wooden sticks ($5 \times 5 \times 200$ cm) treated with valerian oil as hair traps for genetic proof of wildcat presence (Steyer et al. 2013). These lure sticks were set near camera trap sites where putative wildcats had been previously photographed. Lure sticks were checked weekly from November 2014 to December 2014 and from February 2015 to April 2015. After inspection and removal of any hair present, we flamed the lure sticks and re-treated them with valerian oil as described in Steyer et al. (2013). Collected hair samples were kept in zip-lock bags filled with silica gel until processing.

Genetic analyses

DNA from collected hair samples was analyzed by haplotype sequencing of 14 variable microsatellites, a marker in the mitochondrial control region and a sex marker in the zink-finger region (Steyer et al. 2013) to identify the species, differentiate wildcats from domestic cats, and identify individuals. For microsatellite analyses, we conducted three PCR replicates and calculated error rates and consensus genotypes as described in Steyer et al. (2016). Genotypes with more than 3 loci missing out of 14 were excluded from further analyses. Sequences were processed in Geneious 7.1.8 (Biomatters) and compared to our internal cat haplotype database comprising > 3000 control region sequences from European wildcats (<www.wildtiergenetik.de>).

Microsatellite genotypes of identified wildcats were assigned to potential source populations using Structure software (Pritchard et al. 2000) ver. 2.3.3, with a total of 123 reference genotypes: 33 from domestic cats, 24 from wildcats reintroduced in Bavaria, 11 from zoo animals, and 55 from wildcat hair-trapping studies across Germany. Settings were as described in Steyer et al. (2013). Runs were replicated ten times and averaged using the software Clumpp (Jakobsson and Rosenberg 2007).

Camera traps

To obtain information on the distribution of wildcats and domestic cats in the national park, we used data from 27 camera traps set for monitoring Eurasian lynx (Weingarth et al. 2012). Cameras for annual lynx monitoring are distributed systematically in a grid that covers the entire national park. Each grid cell is 2.7×2.7 km and every second grid cell has a camera-trap site. Trap sites are located along forest roads and hiking trails, and each site comprises two passive infrared-triggered whiteflash-cameras (Cuddeback Capture) facing each other at a distance of 5–10 m, but turned slightly away from each other to avoid photographing only the flashes (Weingarth et al. 2012). Cameras were installed 70 cm above the ground, and the delay between two photographs was 30 s. Cameras were operated from November 2008 to June 2009, from September 2009 to May 2012, and thereafter each year from September to January until January 2015. Camera traps were checked every two months. Based on the wildcat pelage characters as described by Ragni and Possenti (1996) and Müller (2011a), we assigned cat photographs to either 'potential wildcats' or 'domestic cats'. We counted the number of wildcat and domestic cat events, with a cat event defined as all wildcat or domestic cat activities captured in photographs within 5 min per camera trap site. We used all data from all seasons to analyze the habitat of wildcats and domestic cats and to calculate the overall camera-trap capture rates for both subspecies. A day was considered as a trap day when at least one of the two cameras per trap site was functional. We also used the data between September and January from all seasons to determine whether there was a variation in the number of cat events over the years.

To determine the minimum number of photographed individual wildcats in the national park, we used all data from lynx monitoring and data from 19 additional camera-trap sites installed for other purposes. The additional camera trap sites included 16 sites from the annual lynx monitoring that are also operated outside of the season for other monitoring purposes, and three sites with only one infrared camera each (Reconyx HC500, HC600 and RC55) that were installed only for a few days in March 2013 (one camera) and in February and March 2015 (two cameras) for other monitoring purposes (e.g. observing animals at a carcass). Wildcat individuals were identified by two independent observers according to individual coat patterns, such as shape and number of stripes and tail bands (Ragni and Possenti 1996, Müller 2011b). In most cases, both cameras took a photo, and we thus had photographs of both sides of the animal. Sometimes, however, an animal was photographed from only one side. The animal could still be identified if that individual had already been photographed from both sides. But if a single photograph showed an individual that we had not yet identified, we considered only such photographs that showed the left side of an animal for individual identification to ensure that we did not count one individual as two different individuals.

Analysis of habitat use

For the analysis of habitat use, we used only photographs from the lynx monitoring project (Weingarth et al. 2012) between 2008 and 2015. We subdivided all cat events into days with snow and days without snow using snow data from the weather station Waldhäuser (945 m a.s.l.) as a proxy for camera trap sites on slopes and at high elevations and snow data from the weather station Taferlruck (772 m a.s.l.) as a proxy for camera trap sites in the valleys. A day with snow was defined as a day with at least 1 cm snow cover. There were 488 days with snow and 758 days without snow at the weather station Waldhäuser and 478 days with snow and 768 days without snow at the weather station Taferlruck.

We analyzed the influence of the following habitat variables (Table 1): shrub cover, elevation, distance to forest edge, distance to residential areas and distance to winter enclosures. Winter enclosures for red deer encompass a 50–60 ha fenced area with a central feeding place. After the rutting period in October when the first snow falls, deer move into the enclosures. The enclosures are opened in the beginning of May after the flush of ground vegetation, and the animals can again range freely in the park and its surroundings. Because of the fodder in the enclosures, we expected a high rodent abundance there, which in turn could attract cats (Möst et al. 2015).

Elevation and shrub cover were calculated (see Ewald et al. 2014 for computational details) from full-waveform LiDAR data collected across the national park with a Riegl 680i laser scanner (350 KHz, nominal point density 30–40 points per m², altitude 650 m; collected by Milan Flug GmbH in June 2012; Latifi et al. 2015). Land-use data for distance to forest edge, distance to residential areas, and distance to winter enclosures were taken from the Authorative Topographic-Cartographic Information System (ATKIS) (Bayerisches Landesamt für Digitalisierung, Breitband und Vermessung) and a mapping of habitat types based on visual interpretation of aerial photographs. GIS analyses were done in ArcGIS 10.2 (ESRI, Inc.). We assessed the extent of collinearity between explanatory variables; absolute values of the Pearson correlation coefficient were < 0.6 for all pairs of explanatory variables, which is below the recommended threshold of 0.7 (Dormann et al. 2013).

In the analysis, individual camera traps were used as sample units. The number of cat events was summed for wildcats and for domestic cats, separately for days with snow and days without snow, and modeled for each subspecies and snow condition separately. The logarithm of the number of days a photo trap was active under a particular snow condition (i.e. with snow or without snow) was included as a model offset. Because of the low number of wildcat events on days with snow, we did not model this type of event. Explanatory variables were standardized to have a zero mean and a standard deviation of one (see Table 1 for original means and standard deviations).

For each subspecies, we followed the same modeling strategy. All models accounted for over-dispersion by using a negative binomial family. First, we tested for spatial autocorrelation in the residuals with Moran's I for distances up to 15 km. If significant spatial autocorrelation was found, we accounted for this by using generalized linear mixed models with an exponential spatial correlation structure, i.e. the correlation in the residuals between camera traps is modeled to decline exponentially with the distance between camera traps (Dormann et al. 2007). For this, all camera traps were assigned to the same group, i.e. there are no separate independent random effects for each camera trap. All analyses were done with R ver. 3.2.2 (<www.r-project.org>). GLMMs were fitted with package mgcv ver. 1.8-7 (Wood 2006).

Results

We obtained nine hair samples at two lure stick sites between February and March 2015 (Fig. 1). Eight of the hair samples

Table 1. Definition of the explanatory variables, including descriptive statistics (mean and standard deviation) of these variables in the data set. See text for details of how variables were calculated.

Variable	Description	Unit	Mean (SD)
Distance to residential areas	distance to human settlements > 5000 m²	m	1453 (± 912)
Elevation	height above sea level	m a.s.l.	856 (± 132)
Distance to winter enclosures	distance to winter enclosures	m	3395 (± 2160)
Distance to forest edge	distance to non-forest areas > 1 ha	m	911 (± 676)
Shrub cover	percentage of shrub cover in a circle of 10 m radius	%	11 (± 8)

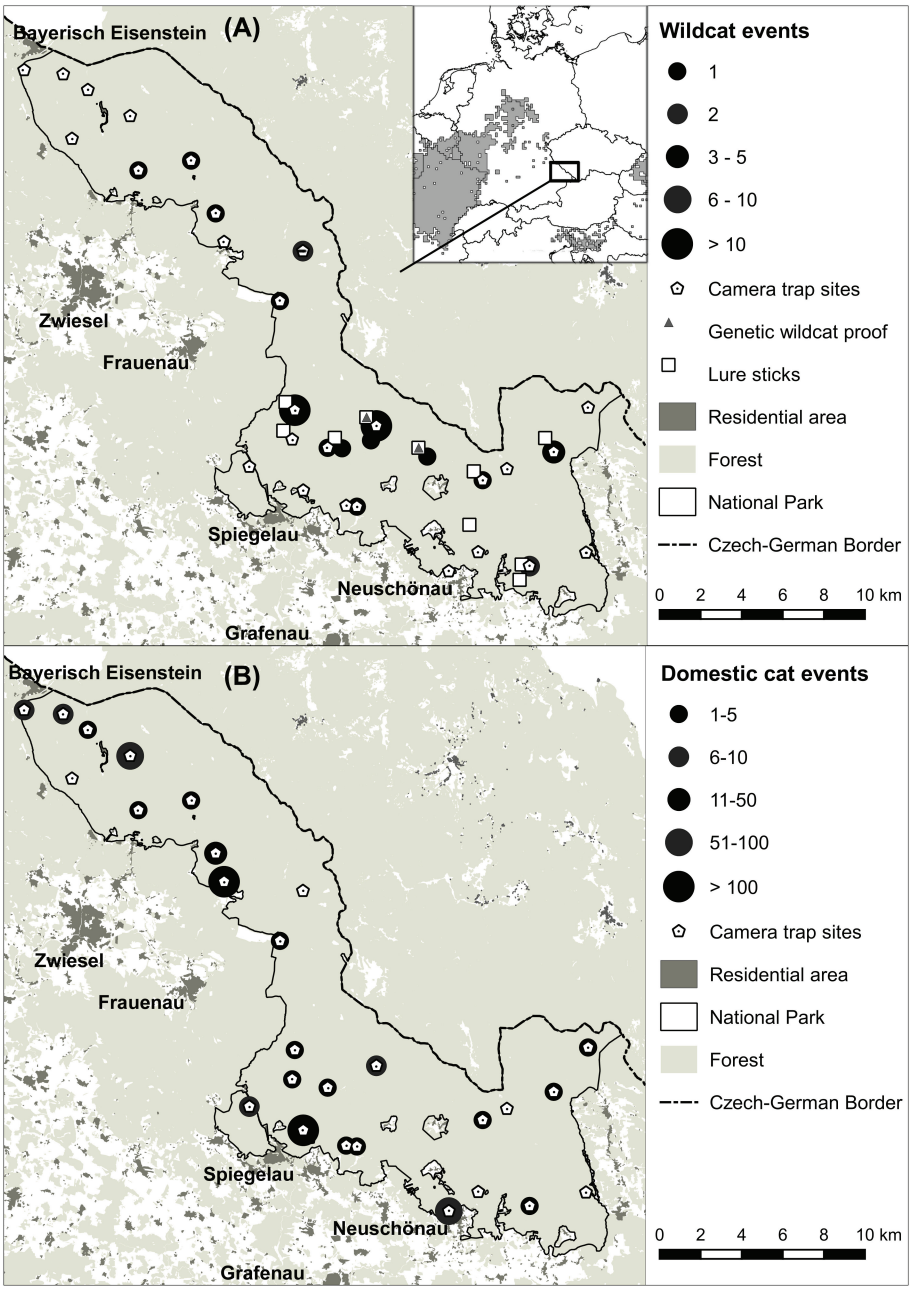

Figure 1. Locations of cat activity recorded between November 2008 and March 2015. (A) Wildcats. All wildcat events during *Lynx* camera-trap monitoring and additional camera-trap monitoring are shown as well as the distribution of the regular camera-trap sites, locations of lure sticks that provided genetic proof of wildcat presence and locations of all other lure sticks. The gray area on the inset shows the known wildcat distribution (European Environment Agency 2015). (B) Domestic cats. Shown are the domestic cat events and the locations of the camera-trap sites during the regular lynx camera trap monitoring.

were from wildcats based on haplotypes of the mitochondrial control region: haplotype FS03 was found in two samples, haplotype FS04 was found in five samples, and haplotype FS22 was found in one hair sample (Supplementary material Appendix 2 Table A4). One sample could not be analyzed because of poor quality. Genotypes were obtained for three samples and identified three different individuals (two males and one female, Supplementary material Appendix 2 Table A2). One of the three samples showed high allelic drop-out (K150055, Supplementary material Appendix 2 Table A3), but was identified as a separate individual because of its clear allelic separation from other individuals and a unique mitochondrial haplotype. All individuals were genetically assigned to the central German wildcat population, and no evidence for admixture with domestic cats was found (Fig. 2).

Based on the distinct coat markings of wildcats in all photographs, we identified at least six different wildcats from 35 events between May 2010 and March 2015. In the entire period from November 2008 to March 2015, there were 44 wildcat events; between September and January during the lynx camera trap monitoring from 2010 to 2014,

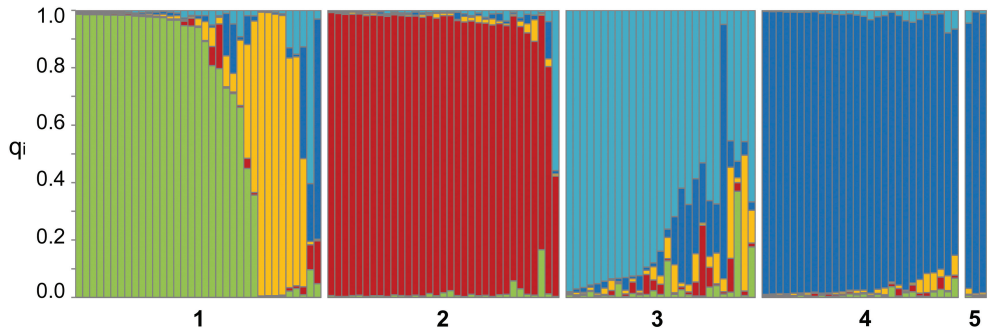

Figure 2. Bayesian clustering of wildcats found in the study area (5) to reference populations (1 = reintroduced wildcats in Bavaria plus captive animals in zoos, 2 = domestic cats, 3 = wildcats from the Western German lineage, 4 = wildcats from the Central German lineage. Each individual is represented by a single vertical bar. Colors are according to the posterior individual proportions of membership (q_i) to each one of possible clusters.

the number of wildcat events slightly increased over time (Table 2).

Wildcat events (44 total) were camera trapped at 16 sites, but 26 events were at only two sites between 800 and 950 m a.s.l. (Fig. 1A, Supplementary material Appendix 2 Fig. A2). No photographs of wildcat events which were captured during the regular lynx camera trapping, but 11 photographs of wildcat events captured by additional traps showed a closed snow cover. One event was in 2014 at 1101 m a.s.l., but most of the events were in early 2015 between 816 and 952 m a.s.l. Some wildcats were camera trapped in winter with snow cover of up to 40 cm (Supplementary material Appendix 2 Table A1). The wildcat events nearest to residential areas were 1 km distant, but 50% of all wildcat events were more than 2.5 km away from residential areas (Fig. 1A).

Domestic cat events (830 total) were camera trapped at 23 sites (Fig. 1B). Ninety percent of all domestic cat events on days without snow were within 1.1 km to residential areas; on days with snow within 0.38 km to residential areas. The domestic cat events farthest from residential areas were at distances of 2.9 km on days without snow and 2.58 km on days with snow. Domestic cats were camera trapped at 15 of the 16 sites where wildcats were camera trapped. We found a high variation in domestic cat events between September and January over time (Table 2).

In total, cameras were active for 31 107 trap days, resulting in 0.06 wildcat captures/100 trap days and 2.67 domestic cat captures/100 trap days. For habitat analysis, we obtained 1432 cat photographs and 849 cat events between November 2008 and January 2015. Most cat events were on days without snow (790 domestic cat events; 19 wildcat events) and only a few were on days with snow (40 domestic cat events; 0 wildcat events).

Only the model for domestic cats without snow showed significant spatial autocorrelation in the residuals. The distribution of domestic cats could be explained to a larger extent than that of wildcats (adj. R^2 of 0.3 versus 0.1). Domestic cat events were more frequent near residential areas and near winter enclosures. By contrast, wildcat events increased with distance to forest edge and with denser shrub cover. Neither subspecies responded significantly to elevation (Table 3).

Discussion

Our analysis of photographs from camera traps and hair from lure sticks confirmed the occurrence of at least six wildcats in the Bavarian Forest National Park up to 1102 m a.s.l. Domestic cats were recorded at distances of up to 2.9 km from residential areas, which broadly overlapped the wildcat distribution. Wildcats preferred forest edges and high shrub cover, whereas domestic cats more often used areas close to residential areas and winter enclosures.

We assumed that any wildcats found in the Bavarian Forest National Park would be derived from wildcats reintroduced

Table 2. Number of cat events between November 2008 and March 2015 used for habitat analysis, trend analysis, and determination of wildcat individuals. Data for habitat analysis were taken from all lynx monitoring seasons, data for trend analysis were taken from all lynx-monitoring seasons between September and January, and data for wildcat individual determination were taken from all lynx-monitoring seasons and additional camera traps.

	Habitat analysis		Trend		Individual determination
Year	Domestic cats	Wildcats	Domestic cats	Wildcats	Wildcats
2008	0	0	0	0	–
2009	75	0	75	0	–
2010	194	1	40	0	1
2011	188	4	137	1	4
2012	74	4	27	2	4
2013	42	3	42	3	4
2014	255	7	255	7	20
2015	2	0	2	0	11

Table 3. Results of the GLMM model for domestic cats and GLM model for wildcats on days without snow (negative binomial family with log link). Domestic cats: adj. $R^2 = 0.297$, scale estimate = 1.3212, n = 27; wildcats: adj. $R^2 = 0.095$, scale estimate = 1.835, n = 27. Boldface indicates significant values.

	Domestic cats		Wildcats	
Variable	Estimate ± SE	p-value	Estimate ± SE	p-value
Intercept	2.106 (0.258)	<0.001	−7.791 (0.462)	<0.001
Distance to residential areas	**−1.732 (0.412)**	**<0.001**	0.440 (0.471)	0.361
Distance to winter enclosures	**−0.560 (0.259)**	**0.042**	−0.925 (0.567)	0.118
Distance to forest edge	−0.171 (0.375)	0.653	**0.838 (0.366)**	**0.033**
Elevation	0.648 (0.347)	0.076	−0.421 (0.469)	0.380
Shrub cover	−0.287 (0.270)	0.300	**0.647 (0.307)**	**0.047**

to northern Bavaria (Worel 2001, Supplementary material Appendix 1), which originate from breeding lines and form largely separate clusters distinct from the autochthonous wildcat clades found in Germany (Fig. 2). It was surprising that our genetic analyses of the three positively identified wildcat individuals indicated a close genetic proximity to the native central German population that occurs mainly in Thuringia and Hesse, but also in northern Bavaria, such as the Spessart (Steyer et al. 2016). While we certainly cannot exclude the possibility of reintroduction origin from the legal reintroductions or from illegal actions, or accidental escapes from zoos, the genetic data point to a natural dispersal from expanding populations in the north. In the Šumava National Park, one putative wildcat was camera trapped in 2011 (Pospíšková et al. 2013), but there is no proof or other hints of wildcat presence in that area (L. Bufka pers. comm.) or in the German surroundings of the national parks (J. Thein pers. comm.). We should mention that wildcats were unofficially reintroduced several times in the past, but it is unlikely that these cats survived (Supplementary material Appendix 1). Information about the connectivity to other wildcat populations obtained from monitoring and lure-stick trapping extended to areas outside of the national park is needed.

In keeping with the results of other studies (Mölich and Klaus 2003, Klar et al. 2008, Jerosch et al. 2010), our habitat modelling showed that wildcats in the national park prefer a denser shrub layer and stay inside the forest. Although wildcats prefer deadwood and open habitats (e.g. watercourses) inside the forest (Mölich and Klaus 2003, Klar et al. 2008), we were not able to include such areas as variables in the model because we recorded only 19 wildcat events. Besides, the national park is relatively open due to an earlier bark beetle outbreak, and such open areas and deadwood are present nearly everywhere, which favors small mammals and facilitates hunting success.

The genetically confirmed wildcats in our study occurred at maximally 870 m a.s.l. Regular wildcat activity captured only by camera trap photographs was observed at 952 m a.s.l. in summer and in winter, and wildcats were camera trapped even when the snow at the weather stations was 30–40 cm deep. The highest site where a putative wildcat was camera trapped was at 1102 m a.s.l. in winter (the photograph showed a closed snow cover, but there was no snow at the weather station Waldhäuser and no data available for Taferlruck). In the Jura Mountains, wildcats have been observed at elevations up to 1200 m a.s.l., and they move between elevations depending on the snow cover (Mermod and Liberek 2002). Wildcats in the Bavarian Forest National Park might also migrate between areas inside as well as outside the national park that are climatically more favorable and that have less snow than the camera trap sites. The increase in wildcat events over the course of our study could be explained by the relatively little snow in the national park during the last two winters and the trend of decreasing snow cover of 0.6 days per year due to relatively mild winters (Bavarian Forest National Park unpubl. data, Supplementary material Appendix 3).

Like wildcats, domestic cats are also influenced by weather conditions (George 1974, Woods et al. 2003, Germain et al. 2008, Goszczyński et al. 2009, Thomas et al. 2012), which could explain the increased presence of domestic cats under snow-free conditions (790 domestic cat events compared to 40 events when snow was present). However, we found also a high variation in domestic cat events between September and January (Table 2) that is difficult to fully explain. Weather conditions appear to be the explanation for the much higher number of domestic cat events on days without snow than on days with snow, but not for the high variation in domestic cat events over the years (Table 2). For example, even though the first closed snow cover with more than 5 cm snow over more than three days occurred in both 2011 and 2012 at the beginning of December, and overall, there was much more snow in 2011 than in 2012 (Supplementary material Appendix 3), there were 137 domestic cat events in 2011 but only 27 in 2012 (Table 2). Another explanation for the high variation in domestic cat events could be changes in the number of individual domestic cats passing a trap station, but this cannot be verified because we did not count individual domestic cats. Distance to residential areas had a significant effect on the detection of domestic cats; 90% of the domestic cat events occurred within 1.1 km from human settlements. Domestic cats were, however, present at nearly all camera trap sites, even up to almost 3 km from residential areas, albeit less often. With such a range distance from the nearest settlements, domestic cats could potentially cover the entire national park area. The wildcat events closest to residential area were about 1 km distant. Most wildcat detection sites spatially overlapped with domestic cat presence, and domestic cats were much more often camera trapped than wildcats (2.67 domestic cat events/100 trap days, 0.06 wildcat events/100 trap days). Therefore, hybridization with domestic cats is a potential major threat to wildcats (Hubbard et al. 1992, Nowell and Jackson 1996, Beaumont et al. 2001, Pierpaoli et al. 2003, Hertwig et al. 2009), especially because hybridization could occur with only limited

spatial overlap between the two cat subspecies (Germain et al. 2008). Furthermore, introgressive hybridization might have a stronger effect on small wildcat populations than on larger populations (Nussberger et al. 2014).

According to camera monitoring results, domestic cats are the fifth most frequently encountered mammalian species in the national park (Seibold and Shao 2014). Such an intense presence within approximately 1 km around residential areas raises concerns about the effects of domestic cat predation on protected species within the national park, especially considering that this zone covers 32% of the park area. Some domestic cats were found almost 3 km from residential areas; this zone covers 76% of the park area. The most important prey of domestic cats are small mammals (69%), birds (24%), and amphibians and reptiles (5%) (Woods et al. 2003). Through feeding by humans, domestic cats can reach up to 3000-fold higher densities than wildcats, and this can severely affect prey populations (Baker et al. 2008, Sims et al. 2008). Since domestic cats were frequently camera trapped in the Bavarian Forest National Park, we assume that they negatively affect the function of the park as a protection area, as found in Poland by Wierzbowska et al. (2012). Our results underline that domestic cats pose threats to the conservation goals of the national park, first through a high predation impact on 32% of the park area and secondly through potential hybridization with the small wildcat population. Similar to Lilith et al. (2008) and Thomas et al. (2014), we recommend a buffer zone of at least 1 km surrounding the park in which domestic cats are not allowed outdoors as a precautionary measure. Additional research on the predatory effects of domestic cats are needed to support this recommendation.

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References

Baker, P. J. et al. 2008. Cats about town: is predation by free-ranging pet cats *Felis catus* likely to affect urban bird populations? – Ibis 150 (Suppl. 1): 86–99.

Barratt, D. G. 1997. Home range size, habitat utilisation and movement patterns of suburban and farm cats *Felis catus*. – Ecography 20: 271–280.

Beaumont, M. et al. 2001. Genetic diversity and introgression in the Scottish wildcat. – Mol. Ecol. 10: 319–336.

Biró, Z. et al. 2004. Home range sizes of wildcats (*Felis silvestris*) and feral domestic cats (*Felis silvestris f. catus*) in a hilly region of Hungary. – Mamm. Biol. 69: 302–310.

Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. – Ecography 30: 609–628.

Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.

Driscoll, C. and Nowell, K. 2010. The IUCN red list of threatened species. Ver. 2014.3. – <www.iucnredlist.org> accessed 5 March 2015.

European Environment Agency 2015. Conservation status of habitat types and species (Article 17, Habitats Directive 92/43/EEC). – <www.eea.europa.eu/data-and-maps/data/ds_resolveuid/DAT-15-en> accessed 20 Sep 2016.

Ewald, M. et al. 2014. LiDAR remote sensing of forest structure and GPS telemetry data provide insights on winter habitat selection of European roe deer. – Forests 5: 1374–1390.

George, W. G. 1974. Domestic cats as predators and factors in winter shortages of raptor prey. – Wilson Bull. 86: 384–396

Germain, E. et al. 2008. Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. – J. Zool. 276: 195–203.

Goszczyński, J. et al. 2009. Activity and exploration range of house cats in rural areas of central Poland. – Folia Zool. 58: 363–371.

Hartmann, S. et al. 2013. Potential barriers to gene flow in the endangered European wildcat (*Felis silvestris*). – Conserv. Genet. 14: 413–426.

Hertwig, S. et al. 2009. Regionally high rates of hybridization and introgression in German wildcat populations (*Felis silvestris*, Carnivora, Felidae). – J. Zool. Syst. Evol. Res. 47: 283–297.

Heurich, M. et al. 2010. National parks as model regions for interdisciplinary long-term ecological research: The Bavarian Forest and Šumavá National Parks underway to transboundary ecosystem research. – In: Long-term ecological research. Springer, pp. 327–344.

Heurich, M. et al. 2015. Country, cover or protection: what shapes the distribution of red deer and roe deer in the Bohemian Forest ecosystem? – PloS ONE 10: e0120960.

Hubbard, A. L. et al. 1992. Is survival of European wildcats *Felis silvestris* in Britain threatened by interbreeding with domestic cats? – Biol. Conserv. 61: 203–208.

Jakobsson, M. and Rosenberg, N. A. 2007. CLUMPP. A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. – Bioinformatics 23: 1801–1806.

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.

Kays, R. W. and DeWan A. A. 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. – Anim. Conserv. 7: 273–283.

Klar, N. 2009. Anwendung eines Habitatmodells für die Wildkatze im Freistaat Bayern. Im Auftrag der Bayerischen Landesanstalt für Wald und Forstwirtschaft (LWF): Abschlussbericht pp. 1–13.

Klar, N. et al. 2008. Habitat selection models for European wildcat conservation. – Biol. Conserv. 141: 308–319.

La Sorte, F. A. et al. 2014. Range-wide latitudinal and elevational temperature gradients for the World's terrestrial birds: implications under global climate change. – PLoS ONE 9: e98361

Latifi, H. et al. 2015. Forest inventories by LiDAR data: a comparison of single tree segmentation and metric-based methods for inventories of a heterogeneous temperate forest. – Int. J. Appl. Earth Obs. 42: 162–174.

Lausch, A. et al. 2013. Spatio-temporal infestation patterns of *Ips typographus* (L.) in the Bavarian Forest National Park, Germany. – Ecol. Ind. 31: 73–81.

Lilith, M. et al. 2008. Roaming habits of pet cats on the suburban fringe in Perth, Western Australia: what size buffer zone is needed to protect wildlife in reserves? – Aust. Zool. 34: 65–72.

Mermod, C. P. and Liberek, M. 2002. The role of snowcover for European wildcat in Switzerland. – Z. Jagdwiss. 48: 17–24.

Mitchell, J. C. and Beck, R. A. 1992. Free-ranging domestic cat predation on native vertebrates in rural and urban Virginia. – Virginia J. Sci. 43: 197–207.
Mölich, T. and Klaus, S. 2003. Die Wildkatze in Thüringen. – Landschaftspflege Naturschutz Thüringen 40: 126–129.
Möst, L. et al. 2015. Creating a landscape of management: unintended effects on the variation of browsing pressure in a national park. – For. Ecol. Manage. 338: 46–56.
Müller, F. 2011a. Körpermerkmale als Unterscheidungskriterien zwischen wildfarbenen Hauskatzen (*Felis s. catus*) und Wildkatzen (*F. silvestris silvestris*, Felidae) aus Mitteleuropa. – Beiträge Jagd- Wildforschung 36: 359–368.
Müller, F. 2011b. Zur individuellen Variabilität von Körpermerkmalen, insbesondere des Fell-Zeichnungsmusters bei adulten Wildkatzen (*Felis s. silvestris*, Felidae) aus Mitteleuropa. – Beiträge Jagd- Wildforschung 36: 351–358.
Nowell, K. and Jackson, P. 1996. Wild cats: status survey and conservation action plan. – IUCN Gland.
Nussberger, B. et al. 2014. Monitoring introgression in European wildcats in the Swiss Jura. – Conserv. Genet. 15: 1219–1230.
Piechocki, R. 1990. Die Wildkatze. – A. Ziemsen Verlag, Wittenberg Lutherstadt.
Pierpaoli, M. et al. 2003. Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. – Mol. Ecol. 12: 2585–2598.
Pospíšková, J. et al. 2013. Nové nálezy *Felis silvestris* v České republice (Carnivora: Felidae). – Lynx 44: 139–147.
Pritchard, J. K. et al. 2000. Inference of population structure using multilocus genotype data. – Genetics 155: 945–959.
Ragni, B. and Possenti, M. 1996. Variability of coat-colour and markings system in *Felis silvestris*. – Ital. J. Zool. 63: 285–292.
Sauer, J. et al. 2011. Low mountain ranges: summit traps for montane freshwater species under climate chance. – Biodivers. Conserv. 20: 3133–3146.
Seibold, H. and Shao, S. 2014. Analysis of the camera trap data to evaluate the association between activity patterns of park visitors and animals. – Unpubl. Stat. Consulting Rep. Dept of Statistics, Ludwig Maximilian Univ. of Munich, p. 5.
Sims, V. et al. 2008. Avian assemblage structure and domestic cat densities in urban environments. – Divers. Distrib. 14: 387–399.
Steyer, K. et al. 2013. Hair trapping with valerian-treated lure sticks as a tool for genetic wildcat monitoring in low-density habitats. – Eur. J. Wildl. Res.59: 39–46.
Steyer, K. et al. 2016. Large-scale genetic census of an elusive carnivore, the European wildcat (*Felis s. silvestris*). – Conserv. Genet. 17: 1183–1199.
Thomas, R. L. et al. 2012. Spatio-temporal variation in predation by urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. – PloS ONE 7:e49369.
Thomas, R. L. et al. 2014. Ranging characteristics of the domestic cat (*Felis catus*) in an urban environment. – Urban Ecosyst. 17: 911–921.
Weingarth, K. et al. 2012. First estimation of Eurasian lynx (*Lynx lynx*) abundance and density using digital cameras and capture–recapture techniques in a German national park. – Anim. Biodivers. Conserv. 35: 197–207.
Wierzbowska, I. A. et al. 2012. Free-ranging domestic cats reduce the effective protected area of a Polish national park. – Mamm. Biol. 77: 204–210.
Wood, S. 2006. Generalized additive models: an introduction with R. – Chapman and Hall/CRC.
Woods, M. et al. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. – Mamm. Rev. 33: 174–188.
Worel, G. 2001. Vom langen Atem. Die Wiederansiedlung der Wildkatze. – In: H. Grabe and G. Worel (eds), Die Wildkatze. Zurück auf leisen Pfoten. Buch & Kunstverlag Oberpfalz, Amberg, pp. 91–100.

Supplementary material (available online as Appendix wlb-00284 at <www.wildlifebiology.org/appendix/wlb-00284>). Appendix 1–3.