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Using camera traps to study the elusive European Wildcat *Felis silvestris silvestris* Schreber, 1777 (Carnivora: Felidae) in central Germany: what makes a good camera trapping site?

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Abstract: Camera traping is a widely used method to study the abundance and population density of elusive terrestrial animals. To make full use of this method, it is necessary to obtain high photographic capture rates of the target species. We examine what characteristics of camera trapping sites are associated with high photographic capture rates of European Wildcat *Felis silvestris silvestris*. We measured Wildcat capture rates across 25 camera trapping sites located in a 20km² study area within an unprotected low mountain range forest in central Germany. We measured the distance of each trapping site to the forest boundary, to the next watercourse, and to the next human settlement, and broadly defined the type of forest structure the site was located in. None of these site characteristics, however, predicted wildcat photographic capture success. We also examined the degree of human disturbance at the site, measured as the photographic capture rate of humans (including vehicles). Wildcats were detected at similar rates on dirt or gravel roads (heavily used by humans) as on soft-surfaced paths or logging trails (less frequently used by humans), and the degree of human disturbance across sites did not affect wildcat capture success. We, therefore, suggest that trail features such as course, curvature and width, or vegetation density along the trail are more important determinants of Wildcat capture success than habitat characteristics. We conclude that for European Wildcats, as for many larger felids, forest roads provide suitable camera trapping sites and that Wildcats are fairly tolerant towards human traffic on these roads.

Keywords: Capture rate, habitat selection, human disturbance, trapping success.

German Abstract: Der Einsatz von Fotofallen ist eine gängige Methode, um die Abundanz und Populationsdichte heimlicher Säugetierarten zu untersuchen. Um diese Methode voll ausschöpfen zu können, ist eine gründliche, auf die zu untersuchende Tierart abgestimmte Auswahl der Fotofallen-Standorte nötig. Die vorliegende Studie untersucht die Fotofrequenz der Europäischen Wildkatze (Felis silvestris silvestris) an 25 Fotofallen-Standorten in einem 20 km² großen Untersuchungsgebiet in einem Wirtschaftswald des deutschen Mittelgebirges. Sie geht der Frage nach, welche Charakteristiken von Fotofallen-Standorten mit einer hohen Fotofrequenz der Europäischen Wildkatze einhergehen. Gemessen wurden die Entfernung des Fotofallen-Standorts zum Waldesrand, zum nächsten Wasserlauf und zur nächsten menschlichen Siedlung. Außerdem wurde der Habitattyp des Fotofallen-Standortes grob bestimmt und der Grad des durch den Menschen verursachten Störung am Fotofallen-Standort als die Foto-frequenz von Menschen (einschließlich Fahrzeugen) gemessen. Wildkatzen wurden in ähnlichen Häufigkeiten auf Forst- und Waldwegen fotografiert wie auf Fußpfaden und Rückewegen. Jedoch hatte keine der von uns gemessenen Variablen einen Einfluss auf die Häufigkeit, mit der Wildkatzen fotografiert wurden. Auch der Grad der durch den Menschen verursachten Störung wirkte sich nicht nicht auf die Häufigkeit aus, mit der Wildkatzen fotografiert wurden. Diese Ergebnisse legen nahe, dass Forst- und Waldwege für die Wildkatze ebenso gute Fotofallen-Standorte darstellen, wie für viele größere Katzen. Zudem scheint die Wildkatze relativ tolerant zu sein gegenüber Störungen durch Menschen und Fahrzeuge auf diesen Wegen.

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GEORG-AUGUST-UNIVERSITÄT GÖTTINGEN

BUND FRIENDS OF THE EARTH GERMANY

INTRODUCTION

The past few decades saw a comeback of some previously rare or locally extinct large and medium-sized carnivores in central Europe (Chapron et al. 2014; Boitani & Linnell 2015; Thiel-Bender 2015). One of these species is the European Wildcat *Felis silvestris silvestris* Schreber 1777, even though in comparison to large mammalian carnivores such as Wolf *Canis lupus*, Lynx *Lynx lynx*, and Brown Bear *Ursus arctos*, its comeback was more secretive in nature.

The European Wildcat is a small (app. 3–6 kg), solitarily-hunting, and predominantly nocturnal felid, which in size and appearance is similar to domestic cat *Felis catus* (Piechocki 1990; Kitchener et al. 2005; Thiel-Bender 2015; Image 1). The species was once widely distributed across central Europe. Within the last two centuries, however, its population experienced a radical decline owing to human persecution, habitat loss, and hybridization with domestic cats (Piechocki 1990; Nowell & Jackson 1996; Beaumont et al. 2001; Pierpaoli et al. 2003; Oliveira et al. 2008; Klar et al. 2009; Macdonald et al. 2010; Hartmann et al. 2013). Today, Wildcats are distributed in fragmented populations ranging from Scotland to the Near East, and from Belarus to Portugal (Yamaguchi et al. 2015). Even though wildcat populations are still threatened and/ or declining in some areas of Europe, particularly on the Iberian Peninsula and in Scotland, the species is currently expanding its range in several European countries (e.g., France: Say et al. 2012; Germany: Thiel-Bender 2015, Steyer et al. 2016).

Until recently, Wildcats in Germany were considered to be distributed in two isolated populations, a central German population and a western population, the latter presumably extending into France (Birlenbach & Klar 2009). A recent large-scale genetic census carried out between 2007 and 2013 suggests that these formerly separated populations are now connected such that the species appears to be continuously distributed across large parts of western and central Germany (Steyer et al. 2016). Moreover, 44% of Wildcat samples were obtained from locations outside the previously known Wildcat distribution. These results illustrate that German Wildcats are currently regaining large parts of their historic range. Estimates of Wildcat population density, however, are often lacking, particularly from the newly colonized areas.

A frequently applied method for wildcat population monitoring is the use of valerian-treated lure sticks (Hupe & Simon 2007; Steyer et al. 2013), which enable the collection of hair samples for genetic analyses. An important advantage of this method is that samples can be sexed and their taxonomic status (i.e., Wildcat, domestic cat, or hybrid) can be determined reliably. In addition, samples can be genotyped, allowing for DNA-based individual identification of the sampled animals. This information can then be used for abundance estimations based on capture-recapture approaches (Kéry et al. 2011). For capture-recapture models to produce reliable abundance estimates, however, a sufficiently large number of genotyped samples are required, rendering the lure-stick method an expensive sampling method.

Another widely applied method for monitoring elusive animals is the use of camera traps (O'Conell et al. 2010; Rovero & Zimmermann 2016). If individual animals can be identified on camera trap images, this method, too, can be used for abundance estimations based on capture-recapture models (Zimmermann & Foresti 2016). This method is a common tool for abundance estimation of striped and spotted felids such as Tiger *Panthera tigris* (Karanth 1995), Jaguar *P. onca* (Harmsen et al. 2017), and European Lynx (Pesenti & Zimmermann 2013), and was also applied to estimate the abundance and population density of Wildcats (Can et al. 2011; Anile et al. 2014; Kilshaw et al. 2015; Velli et al. 2015). Just like any other sampling method used to carry out capture-recapture analyses, this method, too, requires a sufficient number of samples (in this case, identifiable images) for reliable abundance estimation. Yet, in comparison to the lure-stick method, camera traps have the advantage that once the initial costs of purchasing the cameras are paid, any sample 'collected' by the cameras (i.e., any image taken) comes at a low cost. To make full use of this advantage, it is necessary to make a sensible choice of trapping sites, in other words, to choose trapping sites that maximize the capture success of the target species.

The present study examines trapping site characteristics for the study of European Wildcats in a central European low mountain range, i.e., what site characteristics are associated with high photographic capture rates of European Wildcats. A first important factor that comes into mind when choosing a suitable camera trapping site is habitat. Habitat selection is comparatively well-studied in European Wildcats (Okarma et al. 2002; Lozano et al. 2003; Hötzel et al. 2007; Klar et al. 2008; Monterroso et al. 2009; Jerosch et al. 2017) and a number of habitat preferences of European Wildcats were identified. First of all, even though recent studies demonstrated that Wildcats can use significant proportions of open, agriculturally-dominated landscape

Image 1. Camera trap image of a European Wildcat *Felis silvestris silvestris,* taken in November 2016 in the Melsunger Bergland. © University of Göttingen Lynx Project.

(Jerosch et al. 2017; Götz et al. 2018), in central Europe, the Wildcat is traditionally described as a species bound to forests (Piechocki 1990; Nowell & Jackson 1996; Hötzel et al. 2007; Klar et al. 2008). Within forests, radio tracking studies revealed that Wildcats spend more time close to the forest boundary and seem to be attracted also by watercourses, meadows, and open areas within the forest (Klar et al. 2008), presumably because these habitats are characterized by higher prey population densities. A preference for such ecotone habitats was also revealed by snow tracking in the Polish Carpathian Mountains (Okarma et al. 2002). Moreover, Wildcats seem to prefer wind-throw areas and young succession stages with dense undergrowth while coniferous stands tend to be avoided (Okarma et al. 2002; Hötzel et al. 2007). Lastly, human infrastructure, such as roads or villages, are also usually avoided by Wildcats, though beyond a certain distance (ca. 200m to roads and single houses, ca. 900m to villages) human infrastructure does not seem to affect wildcat ranging pattern (Klar et al. 2008). Taking these habitat preferences into account, we should thus expect the photographic capture rate of Wildcats to increase when camera trapping sites are located (i) closer to open areas within forests or to the forest boundary, (ii) closer to watercourses, and (iii) further from human settlements. We should also expect (iv) more Wildcats to be camera trapped at sites located within preferred habitats such as wind-thrown areas, and (v) fewer Wildcats at sites located within the less-preferred habitats such as coniferous stands.

To examine whether the photographic capture rate of Wildcats is affected by the above habitat characteristics and/ or the proximity to human settlements, we analyzed data collected over a period of three months at 25 camera trapping sites within a 20km² study area in central Germany. This study area is located within an unprotected forest that is used for timber production and recreation activities such as hiking, mountain biking, and hunting. Because our trapping sites varied to the extent they were exposed to human disturbance (including vehicles), we also examined whether the photographic capture rate of Wildcats was affected by the degree of human disturbance at the sites.

STUDY AREA

The study area was located in a low mountain range known as Melsunger Bergland, approximately 20km southeast of the city of Kassel in central Germany (Fig. 1). The study area is almost completely covered by forest, consisting of approximately 40% broad-leaved forest, 30% mixed forest, and 30% coniferous forest. The forest is broken up only by the village of Kehrenbach (with a population of 320 inhabitants) and its surrounding fields, located approximately in the centre of the study

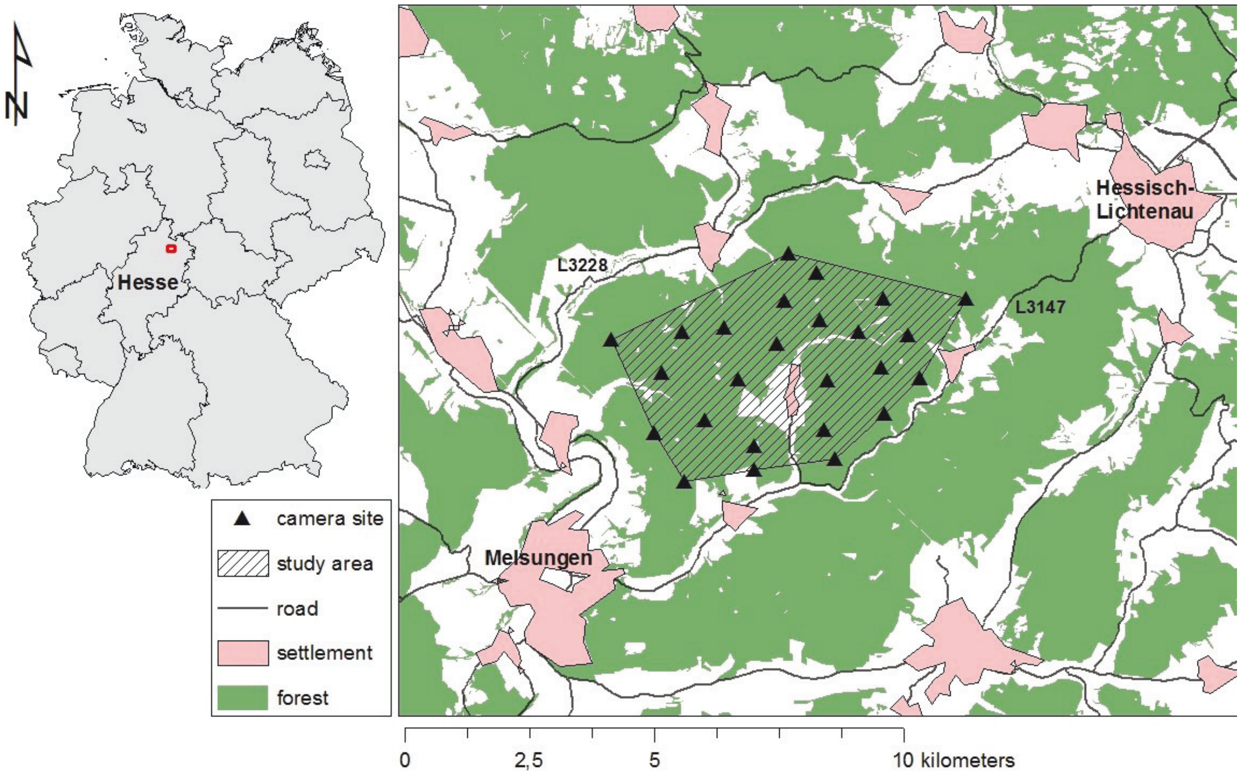

Figure 1. The left-hand image shows a schematic map of Germany with the federal state of Hesse in the center. The right-hand image shows the study area located in the north of Hesse (indicated by a red square on the left-hand image).

area, as well as by a small road (leading to the village) in the south of the study area. Even though the forest is used for timber production and recreation activities, it supports a diverse community of animal species, including large mammals such as Roe Deer *Capreolus capreolus*, Red Deer *Cervus elaphus*, Wild Pig *Sus scrofa*, European Badger *Meles meles*, and Red Fox *Vulpes vulpes*. Moreover, a small population of Eurasian Lynx started to recolonize the area since 2009 (Denk 2016).

The elevation of the study area ranges between 300m in the valley of the river Fulda in the west and 500m in the east. With an annual mean precipitation of 676cm and average temperatures from 0.2°C in January to 17.7°C in July, the Melsunger Bergland is located in the transition zone between Atlantic and continental climate with mild and humid winters.

METHODS

Camera trap placement

The study was carried out between 26 June and 8 October 2017 as part of a project aimed at estimating Wildcat population density in the area (Werner & Port in preparation). Cameras were placed at 25 trapping sites within the forest, one site located in every cell of a 1kmx1km grid (omitting only the village of Kehrenbach and its surrounding fields). The minimum convex polygon encompassing all stations amounted to 20km² with an average (±SD) distance between camera sites of 863m (±207m). Sites were located either along forest roads (n=9) or forest trails (n=16).

All cameras used were Cuddeback® camera traps (Cuddeback Digital, Green Bay, USA) of the models Ambush® and C1®. These are heat- and motion-triggered cameras that record colour images both at day and night using a white flash. We installed two camera traps per station, one on each side of the road or trail, to obtain images of both flanks of a passing animal. Cameras were set up 3.2–22.1 m apart from each other along the road to avoid overexposure of images by the flash of the opposite camera. Delay time between successive images was set to the shortest time frame possible (1–60 s, depending on camera type and time of day). Camera traps were secured inside metal boxes, locked with a padlock or cable lock, and attached to a tree or a pole approximately 30cm above ground. Camera traps were checked every four weeks to replace batteries and SD cards and to clear the areas in front of the cameras of overgrowing vegetation.

Habitat characteristics

To define habitat characteristics of our trapping sites and the proximity to human infrastructure, we used aerial images of the study area and forest management data generously provided by HessenForst, the forestry management unit of the German federal state of Hesse. Geographic data were processed using ArcMap 10.5.1 (Esri, Inc., Redlands, CA, USA).

To determine the distance between the trapping site and the closest forest boundary, we used aerial images. As forest boundary, we defined any 'outer' forest boundary (usually to villages, fields, or roads; Fig. 1), or any boundary to clearings within the forest with a minimum area of 20mx20m. Likewise, we measured the distance of our trapping sites to the closest watercourse (creek, pond, or ditch) with a permanent water body. Lastly, to determine the distance between the trapping site and human settlements, we measured the distance to the closest house with regular human activity (excluding, for example, barns or similar buildings).

We classified the habitat of our trapping sites based on the type of forest stand the cameras were located in. We distinguished broadly between three categories of forest structure that were found to predict Wildcat ranging patterns in previous studies (Okarma et al. 2002; Hötzel et al. 2007). Owing to the small number of trapping sites, a finer subdivision of forest structure types does not appear functional. These three categories were defined based on the dominating type of tree (broad-leaved, mixed, or coniferous) and the following four succession stages (Smith et al. 1997): (1) stand initiation: the earliest succession stage, consisting of young trees with a diameter at breast height (DBH) of usually <7cm, (2) stem exclusion: a succession stage consisting of trees in early development, with DBH<20cm, (3) understorey reinitiation: the stand developed a stratification with canopy, midstorey, and understorey, with older trees reaching a DBH between 21cm and 50cm, and (4) old growth: the stand reached its development climax and is multi-aged and multi-layered with a dense vegetation and a relatively high percentage of dead wood. Stands of this succession stage were rare in the study area and no trapping site was located in it.

In this way, and partially following the classifications used by Hötzel et al. (2007), we defined the following three forest structure types:

(1) Wind-throw/ stand initiation: Areas that experienced a recent disturbance, either by storm damage or clear-cutting, and are now naturally or artificially regenerating. Bushes such as blackberry and dead wood create a dense ground cover (Image 2e).

(2) Mixed/ broad-leaved forest in the succession stages of stem exclusion and older: a very broad category that characterizes large parts of the study area. Mixed and broad-leaved forest were not further distinguished since their understorey structure is similar (Image 2a).

(3) Pure coniferous stands in the succession stage stem exclusion or old: this category usually consists of even-aged, dark stands, usually of Spruce *Picea* trees with poor understorey (Image 2c).

Human disturbance

The degree of human disturbance at the trapping site was measured as the number of camera trap images showing humans and/ or vehicles (e.g., bikes, cars, trucks). In compliance with the data protection policies of the German federal state of Hesse, these images were deleted afterwards.

Wildcat detection and data analyses

The response variable in our analyses was the number of independent Wildcat detections that occurred at a trapping site. As a Wildcat detection, we defined any Wildcat recorded after at least five minutes passed since the last recorded Wildcat. Wildcats captured simultaneously by both cameras at a site were counted as only one detection. Moreover, images of a female with kittens were counted as one detection. In general, we included all recordings of wild-living cats that showed morphologic features characteristic for Wildcats (Kitchener et al. 2005; Kilshaw et al. 2015; Thiel-Bender 2015). We would have excluded images of wild-living cats that showed features characteristic for domestic cats (e.g., white paws, white spots on flanks, pointed tail tip), though no such individuals were recorded during our study.

Since it is difficult to distinguish Wildcats from hybrids based on camera trap images (but see Kilshaw et al. 2015), however, we cannot exclude the possibility that our sample of wild-living cats contained some hybrids as well, though we note that the degree of hybridization is low (3.9%) in German Wildcats (Steyer et al. 2016).

We examined the relationship between our response variable (number of Wildcat detections) and the various site characteristics (distance to forest boundary, distance to water, distance to settlement, forest structure, human disturbance) using general linear models (GLMs) with log link function and negative binomial error structure. In order to avoid overfitting of our models, we ran two separate models: a first model contained the 'habitat characteristics', distance to forest boundary, distance to water, distance to settlement, and forest structure

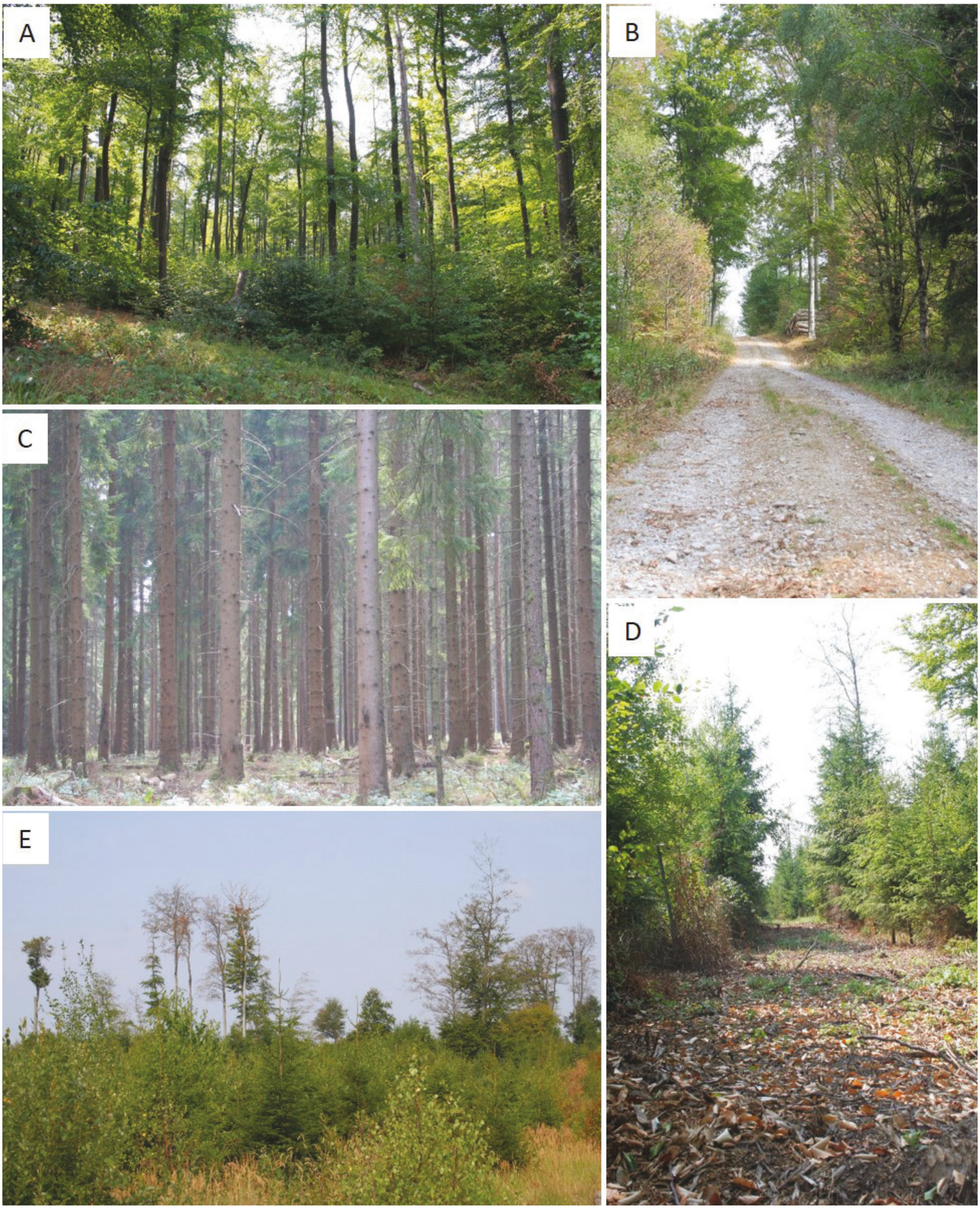

Image 2. Trapping location types and habitat types: A - broad-leaved forest typical for the study area; B - a typical forest road; C - coniferous stand; D - example of a forest trail; E - a wind-thrown area regrowing for approximately 10 years. © M. Port.

as explanatory variables. A second model contained all predictors found to significantly affect the number of Wildcat detections in the first model, as well as the degree of human disturbance measured at the trapping sites. To account for the possibility that Wildcat records differed between sites located on forest roads and sites located on forest trails, this model contained the location of the site (road, trail) as a further predictor. To account for differences in camera operation times between sites, both models contained camera operation time (in days) as an offset term. Analyses were performed in R (R Core Team, 2016, Vienna, Austria) using the package "Mass".

RESULT

Trapping success

Even though several cameras malfunctioned over the course of the study, at least one camera per site operated for 99–105 days (day=24h). Only at one site both cameras broke down during the same time period, such that this site had only 86 recording days. In total, our cameras operated for 2,552 trapping days (defined as the number of sites multiplied by the number of days during which at least one camera per site was operational).

We recorded a total number of 164 Wildcat detections (including possible hybrids), resulting in a capture rate of 6.43 records per 100 trap days. The number of Wildcat records across sites ranged between 1 and 14 detections (mean=6.56, SD=4.69). At least one Wildcat was recorded at each of our 25 sites.

Habitat characteristics

Trapping sites were located between 0m and 577m away from the next forest boundary (mean=226.88m, SD=170.03m), between 1m and 629m away from the next watercourse (mean=352.44m, SD=194.35m), and between 461m and 1,475m away from the next human settlement (mean=934.32m, SD=344.6m). Eleven sites were located within wind-throw areas/ stand initiations (forest structure type 1), 11 sites in broad-leaved or mixed forest areas of succession stages 2 or older (forest structure type 2), while only three sites were located in coniferous stands (forest structure type 3). None of the habitat characteristics had a significant effect on the number of recorded Wildcats (Table 1). On average, only 4 (SD=2) Wildcats were detected in coniferous stands, whereas on average 6.45 (SD=5.12) and 7.36 (SD=4.8) Wildcats were detected in wind-throw areas and mixed or broad-leaved forest stands, respectively, but this difference was statistically not significant.

Human disturbance

The number of human detections ranged between 0 and 1058 (mean=152.84, SD=262.2) and was on average markedly higher at the nine sites located on forest roads (mean=371.7, SD=358.99) than at the 16 sites located on trails (mean=42.93, SD=51.48). On average, 7.4 (SD=5.01) Wildcats were recorded on forest roads, while on average 6 (SD=4.55) Wildcats were recorded on trails. This difference was statistically not significant (Table 2).

Table 1. Results of the general linear model relating Wildcat capture rate to habitat characteristics. Forest structure type "Windthrow/ stand initiation" is used as the baseline level and is represented by the intercept.

	β	SE	z	p	95% CI	
Intercept	-2.99	0.75	-3.95	<0.001	-4.52	-1.43
Distance water	0.001	0.001	1.06	0.29	-0.001	0.003
Distance forest boundary	0.0004	0.001	0.34	0.74	-0.002	0.003
Distance village	-0.0002	0.0005	-0.4	0.69	-0.001	0.0009
Broad leaved/ mixed stand	0.1	0.38	0.27	0.79	-0.69	0.91
Coniferous stand	-0.71	0.56	-1.25	0.21	-1.81	0.42

Table 2. Results of the general linear model relating Wildcat capture rate to location type and human disturbance. Location type "forest trail" is used as the baseline level and is represented by the intercept.

	β	SE	z	p	95% CI	
Intercept	-2.84	0.2	-14.33	<0.001	-3.22	-2.44
Location: forest road	0.09	0.35	0.25	0.8	-0.6	0.8
Human disturbance	0.0004	0.0006	0.53	0.59	-0.0009	0.0018

The degree of human disturbance at the site had no effect on the number of Wildcat records.

DISCUSSION

This study examined whether characteristics of camera trapping sites, such as the distance of the site to the nearest forest boundary or the forest structure type the site was located in, predicted the photographic capture success of European Wildcats. Even though the number of Wildcat records ranged between 1 and 14 detections per site across 25 studied sites, none of the site characteristics examined in our study had a significant effect on the number of recorded Wildcats.

Habitat characteristics

Radio tracking studies of Wildcats revealed that they avoid the proximity of human infrastructure, such as settlements and roads, but only within a critical distance. This distance is reported as approximately 900m to settlements by Klar et al. (2008) and as approximately 500m by Hötzel et al. (2007). The minimum distance of our trapping sites to the nearest village was 461m, and 44% of sites were located more than 900m away from the next settlement. It is thus unsurprising that in our study the (generally large) distance of the trapping sites from human settlements did not affect Wildcat capture success.

Both radio tracking and snow tracking studies revealed that Wildcats strongly prefer ecotone habitats, such as forest boundaries, clearings within the forest, or riparian areas (Okarma et al. 2002; Hötzel et al. 2007; Klar et al. 2008), presumably because these habitats are characterized by high prey population densities, particularly of small rodents. For example, Hötzel et al. (2007) often found Wildcats hunting in open areas at night, whereas they occurred in sheltered forest areas during the day. Okarma et al. (2002) found a large fraction of Wildcat tracks along forest edges. Given these strong preferences of Wildcats for forest boundaries and riparian areas, it is perhaps surprising that the distance of our trapping sites to such habitats did not predict Wildcat capture success. This is not due to a lack of variation in these variables—the distance of our sites to forest boundaries and to watercourses varied greatly, ranging between 0m and 577m for forest boundaries, and between 1m and 629m for watercourses. The most likely reason why our study did not have similar results to those of radio tracking or snow tracking studies is the markedly different methodology. For example, radio collars can usually deliver several locations of an animal per day. In this way, they can draw a dense and detailed picture of animal ranging patterns. Likewise, snow tracking can also provide detailed insights into how frequently different habitat types are used by the animals (Okarma et al. 2002). In contrast, camera traps can only record animal movements at the location they are installed. Because the main aim of our survey was to estimate Wildcat population density (Werner & Port in preparation), we followed previous sampling designs and placed our cameras along human-made forest routes (roads and trails) as we presumed that Wildcats, like many other felids, would preferably use such trails (Karanth 1995; Di Bitetti et al. 2006; Harmsen et al. 2010; Weingarth et al. 2015). Forest trails yield the best capture success if they are used by individuals of the target species regularly and repeatedly, for example, because they connect preferentially used areas of an individual's home range (e.g., areas preferentially used for hunting or resting).

If this is the case, however, the capture success of the trapping site is not necessarily related to habitat characteristics of that site (other than the trail itself). For example, a site located within a coniferous stand, a habitat presumably less preferred by Wildcats, but that is located at a trail connecting two preferred hunting grounds, might still yield higher capture probabilities than a site located close to the forest boundary (a preferred habitat). For presumably the same reason, our study did also not detect any effect of the forest structure type surrounding the camera site. These results are in agreement with findings from three Neotropical felids—the photographic capture success of Jaguars, Puma *Puma concolor*, and Ocelot *Leopardus pardalis* depended only on features of the trail where camera traps were installed, but not on habitat characteristics such as altitude or distance to water (Harmsen et al. 2010).

A number of other variables that were not measured in the present study may affect Wildcat capture success. An important variable is the distribution and population density of prey. Researchers carrying out camera trap studies, however, do not usually have information on prey distributions and population densities, and can only base their choices of trapping sites on habitat characteristics likely associated with high prey abundance, in our case, for example, wind-throw areas (Niethammer & Krapp 1982). This is the approach we took in the present study but, as reported above, none of the studied site characteristics had a significant effect on Wildcat capture success. It is also possible that the abundance of potential competitors such as Red Foxes affects Wildcat ranging pattern and, as a consequence, trapping success at particular sites. Lastly, it is possible that we obtained different results at different times of the year. Our study was carried out in summer when the forest floor and some of the logging trails are covered by dense herbaceous vegetation. At this time of the year, Wildcats may use forest roads more often than in winter when ground vegetation is less dense. Likewise, females might be detected less often on forest roads in spring when they have dependent offspring and prefer areas with dense vegetation cover (Piechocki 1990; Jerosch et al. 2017). Any recommendation on the choice of camera trapping sites in European Wildcats (and other species) should thus take into account possible seasonal changes in ranging patterns. It would be interesting to compare results of the present study with results of prospective future studies carried out at different times of the year and/ or in areas with different population densities of Wildcats and their competitors.

Human disturbance

Photographic capture frequencies of Wildcats were similar on forest roads and on forest trails, despite the fact that forest roads were more extensively used by humans, including cars and trucks. Moreover, the degree of human disturbance, measured as the photographic capture rate of humans (including vehicles) at the site, did not affect Wildcat capture success. In fact, one of the highest capture frequencies of Wildcats (14 detections) occurred at a site with the highest frequency of human captures (1,058 images of humans). These results are largely in agreement with findings on other felids. For example, Ocelots preferred human-made dirt roads over animal trails, both in the Pantanal wetlands of Brazil (Trolle & Kéry 2005) and in northern Argentina (Di Bitetti et al. 2006). Moreover, Ocelots, Jaguars, and Pumas in Belize preferred wider trails over narrower trails (Harmsen et al. 2010). Finally, similar to the present study, the photographic capture rate of Bobcats *Lynx rufus* in Virginia (Kelly & Holub 2008) and of Eurasian Lynx in central Germany (Schröder 2016) was not affected by the amount of human traffic at the site. These results are easily explained by the fact that most human traffic takes place during the day and thus does not interfere with the predominantly nocturnal activity of Wildcats and other felids. They are, however, somewhat in contrast to the perception of the Wildcat as a secretive animal that avoids any human presence (Piechocki 1990). Instead, our results suggest that in areas where Wildcats are not persecuted by humans (as in our study area), they are more tolerant towards human disturbance than commonly thought.

What makes a good camera trapping site?

We started this article by asking "What makes a good camera trapping site?" for the study of European Wildcats in a central European low mountain range. Unfortunately, we cannot provide a conclusive answer to this question as none of the site characteristics examined in our study affected the photographic capture success of Wildcats. We, however, photo-captured at least one Wildcat at all of our sites (100%) and obtained a capture rate of 6.43 detections per 100 trap days. This capture rate is similar to the capture rate obtained by Anile et al. (2014) (6.48 detections/ 100 trap days) and at least twice as high as the capture rate of any other camera trapping study of European Wildcats (Can et al. 2011; Kilshaw et al. 2015; Velli et al. 2015). These results suggest that either Wildcat population density in the study area was particularly high and/ or that most, if not all, of our trapping sites were suitable for detecting Wildcats by means of camera trapping. Nevertheless, there is a large variation with respect to the trapping success across sites: at some sites as many as 13 (three sites) and 14 (two sites) Wildcats were detected, whereas at five sites only a single detection occurred. Clearly, therefore, some sites yielded higher capture rates than others. We suggest that differences in capture success are more closely related to features of the trail at which cameras were installed (Trolle & Kéry 2005; Di Bitetti et al. 2006; Harmsen et al. 2010), for example, course, curvature, and width of the trail, or the density of the vegetation along the trail, rather than to the habitat characteristics examined in the present study.

Still, there are at least two conclusions we can draw from the present study. A first conclusion is that human-made dirt or gravel roads are as suitable as camera trapping sites for the rather small-bodied European Wildcat as they are for many of her larger relatives. A second conclusion is that the extent of human traffic along these roads does not affect Wildcat capture success and that even roads heavily used by humans and vehicles can still make suitable camera trapping sites for the study of European Wildcats.

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