Rise and fall of a Eurasian lynx (*Lynx lynx*) stepping-stone population in central Germany

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Abstract

After having been extinct for approximately 200 years, the Eurasian lynx (*Lynx lynx*) is currently being reintroduced in several European countries. However, it still occurs in several local, isolated populations. Given the patchy distribution of its forest habitat within a human-dominated landscape, the formation of population stepping-stones, i.e., small lynx occurrences between source populations, has been suggested an important mechanism for the expansion of lynx in central Europe. We studied the population history of such a stepping-stone population, which emerged approximately 60 km southwest of a larger reintroduced population in central Germany. We also examined migrations of lynx between the source population and the stepping-stone. At the beginning of our study in autumn 2014, our study population consisted of a minimum number of six resident individuals of both sexes that successfully reproduced in the area. However, over the course of only a single year, this subpopulation declined to only a single resident male as a consequence of death and emigration. In the 4 years after this decline, the subpopulation did not recover due to the absence of female dispersal into the area. Our study illustrates the vulnerability of small, isolated populations to stochastic demographic events and suggests that constraints on female dispersal are a major reason for the slow expansion of lynx in central Europe. To promote the expansion of lynx, active population management will be required, involving the translocation of females to reinforce existing stepping-stone populations or to create new ones.

Keywords Eurasian lynx · Dispersal · Habitat fragmentation · Connectivity · Stepping-stone · Camera trapping

Introduction

The Eurasian lynx (*Lynx lynx*) was once widely distributed across central Europe, but it became extinct in this area during

the nineteenth century due to habitat loss and human persecution (Breitenmoser and Breitenmoser-Würsten 2008). To bring back one of Europe's largest carnivores, several European countries have carried out reintroduction programs since the 1970s (Breitenmoser and Breitenmoser-Würsten 2008; Chapron et al. 2014; Linnell et al. 2009; Wölfl et al. 2001). Many of these programs have successfully reintroduced lynx at the local scale, i.e., they have managed to establish demographically stable populations in the area of reintroduction. However, an expansion of lynx beyond these areas has so far been limited (Müller et al. 2014; Schnidrig et al. 2016; Zimmermann et al. 2007).

In Germany, lynx are currently living in three isolated populations: the Bohemian-Bavarian population, the Harz Mountain population, and the Vosges-Palatinian population (Chapron et al. 2014). The first lynx population on German territory was established in the Bavarian Forest (south-east Germany) and originates from lynx reintroduced in two adjacent national parks (Bavarian Forest National Park in the early 1970s, and Šumava National Park, Czech Republic in the

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1990s). This population is thus part of a larger, transnational population expanding into the Czech Šumava Mountains (Bufka and Cervený 1996; Müller et al. 2014; Wölfl et al. 2001) and northern Austria. A second population was established in the Harz Mountains (central Germany), following the reintroduction of 24 captive-bred Eurasian lynx (9 males, 15 females) between 2000 and 2006 (Anders and Sacher 2005). Lastly, since 2016, lynx are being reintroduced in the Palatinate Forest (western Germany; Huckschlag 2018). All three German lynx populations are currently isolated from each other by at least 280 km (approximate distance of the Harz population to both the Bavarian Forest and the Palatinate Forest populations). Moreover, all three populations are also isolated from other lynx populations in Europe (Chapron et al. 2014). An exchange of individuals between these populations is currently not taking place, and much potentially suitable habitat between these populations (Kramer-Schadt et al. 2005) has yet not been colonized.

While the population in the Bavarian Forest has been stagnating for several years (Heurich et al. 2018; Müller et al. 2014), and reintroduction is continuing in the Palatinate Forest, the Harz population is currently the only German lynx population which is expanding its range. This population has recently been estimated at 55 independent individuals, which have colonized the entire 2200 km² area of the Harz Mountains (Middelhoff and Anders 2018). Moreover, the population has established four population propagules (each consisting of a single reproducing female), located up to 30 km west and northwest of the Harz Mountains. Lastly, a significant and particularly promising range expansion of the Harz population occurred in 2010, when Harz lynx founded a small subpopulation approximately 60 km southwest of the Harz Mountains. This subpopulation is mostly located in the north of the German federal state of Hesse and is hereafter referred to as the Northern Hessian Subpopulation (NHS). First recorded dispersal into the area occurred in autumn 2009, when a radio-collared male from the Harz Mountains settled in northern Hesse (Denk 2010). Snow tracking soon revealed a second individual in the area, and already in the following year, reproduction was recorded for the first time. Since then, random sightings of lynx, including females with kittens, suggested a growing subpopulation in northern Hesse (Mueller et al. 2020). This subpopulation constituted an important stepping-stone, from which other suitable habitat patches further south could potentially be reached. However, it was long unclear how large the NHS was, and how frequently an exchange of individuals occurred between this subpopulation and the source population in the Harz Mountains.

To answer these questions, we have been carrying out annual opportunistic camera trapping surveys (Breitenmoser et al. 2006; Reinhardt et al. 2015) of the NHS since autumn

2014. Like many other striped or spotted felids (Harmsen et al. 2017; Karanth 1995; Maffei et al. 2005), Eurasian lynx can be discriminated from each other based on their unique coat patterns (Pesenti and Zimmermann 2013; Weingarh et al. 2015). We used this information to estimate the minimum number of recognizable lynx individuals present in our study area in each year and, combining data collected over the past 5 years, to sketch the individual histories of all individually known lynx living in that area. Because we presumed the Northern Hessian Subpopulation to be small, we did not use a more systematic camera trapping approach aimed at estimating lynx population density. Moreover, we analyzed data on migrations of lynx into and out of our study area between 2009 and 2019. Collectively, these data informed us of the approximate size of the NHS, its population history (births, deaths, immigrations, emigrations, disappearances), and the connectivity between the NHS and the source population in the Harz Mountains. We used this information to discuss the importance and viability of small population stepping-stones, like the one in Northern Hesse, for the dispersal of lynx in Germany.

Methods

Main study area

The area in which we studied the northern Hessian lynx subpopulation is located predominantly in the north of the federal state of Hesse (Germany; 51° 11' 51" N, 9° 43' 16" E), approximately 60 km south-west of the Harz Mountains. The area is located within a low mountain area, known as the North Hesse Highlands (Nordhessisches Bergland), with elevations ranging from 120 to 753 m above sea level. With an annual mean precipitation of 676 cm and average temperatures from 0.2 °C in January to 17.7 °C in July, the North Hesse Highlands are located in the transition zone between Atlantic and continental climate with mild and humid winters. The area consists of a mixture of woodlands, with an approximate forest cover of 40% (Hessisches Statistisches Landesamt 2016), and agricultural landscape (approximately 45%). European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) dominate forest vegetation and are complemented by *Pinus*, *Quercus*, and *Larix*. 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*, red fox *Vulpes vulpes*, and European wildcat *Felis silvestris silvestris*. With approximately 127 people/km², human population density is lower than the average population density in Hesse (297 people/km², Hessisches Statistisches Landesamt 2019).

Camera trapping of the Northern Hessian subpopulation

In order to test and establish the methodology of camera trapping in northern Hesse, we carried out a pilot study from November 2014 to October 2015, in which we surveyed an approximately 610 km² study area (Fig. 1). This initial study area covered the area in which the majority of random sightings of lynx were reported in previous years. Owing to a limited number of cameras available, we further divided this study area into three smaller subareas of 194 km², 224 km², and 192 km². In each subarea, we operated 40 cameras at 20 trapping sites for the duration of four months (area 1: Nov 2014–Feb 2015, area 2: Mar 2015–Jun 2015, area 3: Jul 2015–Oct 2015). Because our pilot study yielded the highest photographic capture rate of lynx during winter and early spring, in subsequent years, we restricted camera trapping to an approximately 5-month period from November to March (see Table 1 for details). In the trapping seasons of 2015–2016 and 2016–2017, we operated 80 cameras at 40 trapping sites in a 630 km² study area that was largely identical with the area sampled during our pilot study (Fig. 1). Owing to new random sightings of lynx in spring 2017, which were reported only a few kilometers southeast of our study area, we extended our study area toward the southeast, such

that in the 2017–2018 trapping season, we covered an area of 908 km² (Fig. 2). In this area, we operated 100 cameras at 50 sites. Finally, in the 2018–2019 trapping season, we further extended our study area to 1153 km² (Fig. 1). This last extension was carried out to check for the possibility of lynx occurrence in the northeast of the federal state of Hesse, an area that was previously not sampled. In this last season, we operated 75 cameras at 68 sites. Unlike in previous years, the majority of sites were employed with only a single camera. The number of potential trap days per trapping season, defined as the number of sites times the number of days cameras were set up, is given in Table 1.

During our pilot study, we used 30 Cuddeback® camera traps (Cuddeback Digital, Green Bay, USA) of the models Ambush® (18 cameras) and Attack® (12 cameras). These cameras are heat- and motion-triggered cameras that record colour photographs at day and night using a white flash. In addition, we employed 10 Reconyx HC 500 cameras. These cameras operate with infrared flash. They record colour photographs at day and black and white photographs at night. From trapping season 2015–2016, all cameras used were white-flash cameras of the models Cuddeback® Ambush®, Attack®, and C1®.

All trapping sites were located either at forest roads (dirt or gravel roads used for forest management) or forest trails (e.g.,

Fig. 1 Map of the study areas. **a** The location of the study areas in the area of northern Hesse. **b** The location of the study area against the background of the forest distribution in Germany. The large green spot northeast of the study area depicts the area of the Harz Mountains

Table 1 Overview of study periods, sampling effort, and lynx detections

Study period	Area (km ²)	Sites	Time period	Days	Potential trap days	Effective trap days	Lynx detections	Detections identifiable	Capture rate ^a	Successful sites
Pilot period 1	194	20	01.11.2014–28.02.2015	120	2400	2088 (87%)	57	35 (61%)	2.73	12 (60%)
Pilot period 2	224	20	08.03.2015–30.06.2015	115	2300	2042 (89%)	37	28 (76%)	1.81	12 (60%)
Pilot period 3	192	20	08.07.2015–30.10.2015	115	2300	2300 (100%)	3	2 (67%)	0.01	2 (10%)
W 2015/2016	630	40	19.11.2015–31.03.2016	134	5360	5158 (96%)	68	57 (83%)	1.32	12 (30%)
W 2016/2017	630	40	01.11.2016–31.03.2017	151	6040	5744 (95%)	86	71 (83%)	1.5	20 (50%)
W 2017/2018	908	50	01.11.2017 – 31.03.2018	151	7550	7217 (96%)	50	42 (84%)	0.69	24 (48%)
W 2018/2019	1153	68	01.11.2018–31.03.2019	151	10268	9094 (89%)	78	72 (92%)	0.86	11 (16%)

^a Capture rate is given as detections per 100 effective trap days

hiking or logging trails). With the exception of trapping season 2018–2019 (see above), we installed two camera traps per station, one on each side of the road or trail, to obtain pictures of both flanks of a passing animal. Cameras were set up between 3.1 and 20.8 m apart from each other along the road to avoid overexposure of photos through the flash of the opposing camera. Delay time between successive photographs was set to the shortest time frame possible (1–45 s, depending on camera type and time of the day). Camera traps were secured inside metal boxes, locked with a padlock or cable lock, and attached to a tree or a pole approximately 30 cm above ground. Camera traps were checked every 4 weeks to replace batteries and SD cards.

For comparisons of photographic capture success across seasons, we measured photographic capture success as photographic capture rate (Rovero and Marshall 2009), which we define as the number of independent lynx photographs (detections) per 100 effective trap days. The number of effective trap days per season is defined as the number of sites at which at least one camera was operating (Rovero and Marshall 2009; Weingarth et al. 2012). Consecutive lynx photographs at the same site were deemed independent (i.e., counted as detection) when there was at least a 5-min interval between them (Middelhoff and Anders 2018; Weingarth et al. 2015). Simultaneous photographs of both cameras at a site were counted as only one detection.

Identification and sexing of lynx

In Eurasian lynx, five types of coat patterns can be distinguished (Thüler 2002). In the Harz population, the vast majority of individuals belong to type 3, a type of coat pattern characterized by only few spots, restricted mainly to the legs. Lynx exhibiting this type of coat pattern are more difficult to discriminate than lynx

showing other types of coat pattern (e.g., large or small spots across the whole body). For this reason, identification of lynx was carried out by two observers independently (MP + FS, MP + AH, or MP + TLM), using the following protocol:

Each observer was asked independently to rate the lynx shown on the photo as either an already known individual or as a yet unknown individual. If observers were unsure about the identity of the lynx, they were asked to rate the photo as “uncertain,” though they were instructed to avoid this rating if possible. A photo was given an identification number (ID, indicating a yet unknown lynx), or was classified as an already known individual, if both observers agreed on their assessment of the photo. Otherwise, the photo was discarded from analysis. Individuals could be sexed based on camera trap images if genitals were clearly visible, or if females were photographed together with their kittens.

Monitoring data to reconstruct long-distance dispersal

The Hessian Agency for Nature Conservation, Environment and Geology (HLNUG) is responsible for the monitoring of lynx according to the European Union Habitats Directive (Council Directive 92/43/EEC) within the German federal state of Hesse. The Harz National Park (HNP) is responsible for the monitoring of lynx in the neighboring states of Lower Saxony and in Saxony Anhalt, including the largest part of the Harz Mountains. As part of their responsibility, the HLNUG and HNP collect data on occurrences of lynx, including random sightings, genetic evidence (collected e.g., at lynx kills or from fecal samples), and lynx found dead (in which case a pathological examination is being commissioned). In addition, the HNP has been operating camera traps to monitor lynx in the Harz Mountains and the areas containing population

Fig. 2 a The photographic capture rate of lynx (defined as detections per 100 effective trap days) during each trapping season. b Mean ($\pm$ SD) photographic capture rates during winter months (Nov–Mar, where most of our sampling occurred) across the 5 years of our study

propagules since 2014 (Anders and Middelhoff 2016; Middelhoff and Anders 2018), and has radio-collared 23 lynx between 2008 and 2019. Several of these individuals have been migrating from or into the Harz Mountains (e.g., Anders et al. 2012). We use data collected by the HLNUG and HNP to reconstruct immigrations into our study area in northern Hesse and emigrations out of our study area. We are particularly interested in long-distance dispersal events, which we define as any dispersal event between the Northern Hessian Subpopulation and any other spatially distinct (sub-)population. We examine only events where both starting point and end-point are known, and either starting point or end-point was located in northern Hesse. A dispersal event was defined as being terminated in northern Hesse if the individual either died there, or established a home range (being defined as continued presence in the same area for at least half a year, Zimmermann et al. 2005, Reinhardt et al. 2015). These data inform us of the rates of immigration and emigration into and

out of our study population, and hence, the connectivity of our study population with other lynx populations in Germany.

Results

Photographic capture success

Owing to theft and camera failure, cameras did not operate during all potential trap days. The number of effective trap days per season ranged between 2042 during our pilot study and 9094 during trapping season 2018–2019 (Table 1). The number of lynx detections during winter seasons (where most of our sampling occurred) ranged between 50 and 86 detections per season, and was the highest during winter 2016–2017 (Table 1). Across winter seasons, photographic capture rate ranged between 0.69 and 2.73 detections per 100 effective trap days (Table 1). Photographic capture success was the highest during our pilot study in winter 2014–2015, and showed a declining tendency in later years (Fig. 2a). The proportion of “successful” trapping sites, i.e., sites at which at least one lynx detection per season occurred, ranged between 0.3 and 0.6 (Table 1). It was the highest during our pilot study (0.6) in winter 2014–2015, and the lowest in the winters of 2015–2016 (0.12) and 2018–2019 (0.11), when only a fraction of our study area was inhabited by lynx (see below). Within our 5-month sampling period from November to March, the majority of detections occurred in February and March (Fig. 2b).

Identification of lynx

Between 61 and 92% of the lynx images taken each year (or study period) could be used for identification (mean = 78%, Table 1). The proportion of images that could be used was the lowest during period 1 of our pilot study (61%), and increased during later years (Table 1). Images that had to be discarded were images where at least one observer rated the lynx shown on the image as “uncertain” (see methods). Usually, these photos were blurry, overexposed, or had important body parts for identification missing. There was not a single case where the two observers disagreed in their ratings (i.e., one observer rating the photo as showing individual A, whereas the other observer rated it as showing individual B).

Lynx individuals and their individual histories

Over the course of our pilot study from November 2014 to October 2015, we detected an overall number of seven individually distinguishable lynx individuals. However, two of these seven individuals were detected only once: One individual was a resident female (B1061w) that was already known from random monitoring data, and that had most of its home range north of our study area. The status of the other

individual (R1010x) remained unclear. It may have been a disperser (*sensu* Zimmermann et al. 2005), and was not considered part of the resident NHS.

Another individual (B1035x) was detected only two times in December 2014, yet this individual could be identified on an image (kindly provided by Mr. Walter Liese) randomly taken in the same area in March 2014. Following Zimmermann et al. (2005), this individual had likely established a definitive home-range in the area, and was thus considered part of the resident subpopulation. All other individuals were detected at least six times over a period of at least 7 months (see the “Appendix” section for details).

Four of the six resident individuals could be sexed based on camera trap images (three individuals) or after physical capture by the HNP (B1037w). Two of these four individuals were males (B1036m, B1025m), and two individuals were females (B1037w, B1061w). The remaining two individuals (B1035x, B1038x) were presumably also females (see the “Discussion” section). During our pilot study, therefore, the northern Hessian subpopulation consisted of at least six resident individuals, at least two of which were males, and at least two of which were females.

During the second half of the year 2015, however, this population went through a dramatic decline. In autumn 2015, both resident females (B1037w, B1061w) died of sarcoptic mange. Moreover, since trapping season 2015–2016, we could no longer detect individuals B1035x and B1038x. In fact, over the course of this season, 53 of 57 identifiable lynx detections belonged to only a single individual (B1036m). Two detections in November 2015 showed B1025m, yet since December 2015, this individual, too, could no longer be detected in our study-area. In January 2016, surprisingly, B1025m was detected by a camera trap in the Harz Mountains (51° 41' 19" N, 10° 26' 47" E), 66 km north-east of its last known occurrence in northern Hesse. Two further detections in March 2015 showed a yet unknown male individual (B1009m), which, however, only briefly passed through our study area and continued its journey north into the Harz Mountains (O. Anders, unpubl. telemetry data). For most of trapping season 2015–2016, therefore, the NHS consisted of only a single male (B1036m, Fig. 3).

In trapping season 2016–2017, we detected B1036m, as well as a so far unknown individual (B1039m). This individual migrated into Northern Hesse from the Harz Mountains. It was last detected in the Harz Mountains as a juvenile in its mother's territory in January 2016. At the time of its first detection in northern Hesse in October 2016, B1039m was approximately 18 months old. It was mostly detected in the southern parts of our study area, south of B1036m's home range (whom we detected exclusively in the northern parts of our study area). B1039m stayed until January 2018 (last detection in Northern Hesse, Fig. 3). After January 2018, i.e., after being resident in Northern Hesse for at least 16 months, it migrated back into the Harz Mountains, where it was detected in June 2018.

After B1039m's dispersal, B1036m was, once again, the only remaining resident lynx individual in the NHS. We detected B1036m at a regular basis until the end of March 2018, when trapping season 2017–2018 terminated. However, we could no longer detect B1036m in trapping season 2018–2019. In fact, between November 1 and December 24, 2018, not a single lynx detection occurred across 68 camera trapping sites. It was only after December 24 that two new individuals appeared in our study area (Fig. 3), both of them males: one radio collared male (B1009m) already passed through our study area in March 2015 (see above). Since then, it was occasionally detected at the southern edge of the Harz Mountains, but in winter 2018, it migrated back to northern Hesse. This individual was detected 25 times until the end of the trapping season 2018–2019. It died from pneumonia and malnourishment in June 2019. The other individual (B1064m) was a male of so far unknown origin. Until the end of trapping season 2018–2019, it was detected 49 times. While B1009m appeared to have taken over parts of B1036m's former home range, B1064m was mostly detected in the south of our study area, at many of the same trapping sites where B1039m was detected until January 2018.

Long-distance dispersal

Ten long-distance dispersal events were recorded between 2009 and 2019. Since we only examine dispersal events where both origin and end-point of the event were known (see the “Methods” section), we dismissed the case of B1064m, because we do currently not know where this individual originated from. Some of these dispersal events are already mentioned in the previous section. All dispersal events are listed in Table 2. Six events originated in the Harz Mountains and ended in our study area; four events originated in our study area and ended in the Harz Mountains (or one of the population propagules). All ten dispersal events involved male individuals; not a single female was recorded to disperse from the source population into our study area (or the other way around). Assuming an even sex ratio at the age of dispersal, this observed mal bias is unlikely to be a random deviation from an underlying unbiased dispersal process, i.e., a dispersal process where males and females are equally likely to disperse between (sub-)populations (Binomial distribution: $\Pr(x = 0|10; p = 0.5) = 0.001$). Even if we count the repeated dispersals of individuals B1009m and B1039m only once (resulting in eight observed dispersal events), the observed dispersal pattern was likely not created by a sexually unbiased dispersal process ($\Pr(x = 0|8; p = 0.5) = 0.004$).

Discussion

Our study shows the vulnerability of small, isolated populations to stochastic demographic events (Lande 1988; Roughgarden

Fig. 3 Resident lynx individuals detected over the 5-year study period

1975; Shaffer 1981), and provides us with important insights into the population dynamics and connectivity of such small population stepping-stones of Eurasian lynx in a human-dominated landscape. Using data from repeated camera trapping surveys carried out between November 2014 and March 2019, we described the individual histories of nine individually distinguishable Eurasian lynx individuals in a small population stepping-

stone in the North of the federal state of Hesse, central Germany. This stepping-stone emerged approximately 60 km southwest of the source population in the Harz Mountains and represented a promising first step for the successful dispersal of lynx in central Germany. However, during our 5-year study period, the Northern Hessian Subpopulation went through a complete turnover of individuals: none of the six individuals we detected at the

Table 2 Long-distance dispersal

Time	Individual	Direction	Sex	Fate
Nov 2009	B1032m	Harz - > Hesse	Male	Unknown
Oct 2012	LL039m	Harz - > Hesse	Male	Dead, road accident
Dec 2015	B1025m	Hesse - > Harz	Male	Last record: 18.05.2018
Oct 2014	B1028m	Hesse - > Hils ¹	Male	Unknown
Mar 2016	B1009m	Hesse - > Harz	Male	See below
Oct 2016	B1039m	Harz - > Hesse	Male	See below
Aug 2017	LL145m	Harz - > Hesse	Male	Dead, cause unknown
Nov 2017	LL131m	Harz/ Solling ¹ - > Hesse	Male	Dead, road accident
Jun 2018	B1039m	Hesse - > Harz	Male	Dead, road accident
Dec 2018	B1009m	Harz - > Hesse	Male	Dead, pneumonia

Individuals are indicated with their photo-ID (starting with B), or, if a photo-ID was not available, with their genetic ID (starting with LL)

¹ Hils and Solling are propagules of the Harz population, located approximately 30 km northwest and west, respectively, of the Harz Mountains. During our study period, each propagule consisted of only a single reproducing female

onset of our study was still present when this study ended. A particularly serious event mainly responsible for this turnover was a population decline already in the first year of our study, when five of the initially six resident individuals either died (two individuals), dispersed (one individual), or disappeared for unknown reasons (two individuals). In the 4 years that followed, the population did not recover from this dramatic decline, mainly due to the absence of female dispersal into our study area.

Size, sex ratio, and stability of the Northern Hessian subpopulation

We presume the six individuals we detected at the beginning of our study are the minimum number of lynx individuals comprising the NHS at that time. Owing to the small size of the study population, we did not carry out capture-recapture analyses to estimate population size (Borchers and Efford 2008; Otis et al. 1978), yet with the exception of a potential disperser (L1010x) and an individual living predominantly north of our study area (B1061w), we detected all individuals at a highly regular basis (see the “Appendix” section), particularly since trapping season 2015–2016, suggesting that we detected all resident individuals within our study area. It is possible, however, that there might have been individuals living outside our study area, particularly at the beginning of our study, such that the NHS was, in fact, larger than described here.

Two of the six adult individuals we detected in trapping season 2014–2015 could be sexed as males, and two individuals could be sexed as females. The available evidence suggests that the remaining two individuals were likely also females. In early spring 2015, two detections could be sexed as females (one because the individual was photo-captured with offspring and one because genitals were visible), but in both cases, the individual identification of the animal was not possible. One of these detections occurred in an area where we previously detected B1035x, the other detection occurred approximately 13 km southeast, in an area where we regularly detected B1038x. Both photos did not show B1037w (which was easily recognizable due to its radio-collar), and both photos did most likely not show B1061w either (which had its territory mainly north of our study area). We conclude, therefore, that at the beginning of our study, the NHS consisted of at least two resident males, and at least three (more likely four) resident females. Yet despite this favorable sex ratio, our study population collapsed only a few months later due to the death or disappearance of all known and presumed females.

Population history and connectivity

In the 4 years after the population decline, until the end of our study, the NHS did not recover. During these 4 years, the number of resident individuals observed in our study area was never larger than two resident males. Moreover, while dispersing males

from the Harz Mountains regularly reached our study area, during the past 9 years, not a single female was observed to overcome the approximately 60 km between the Harz Mountains and our study area. This result is perhaps not surprising, because dispersal is male-biased in the majority of mammals, i.e., males more frequently leave their natal group or territory than females, and/or disperse over larger distances than females (Greenwood 1980; Lawson-Handley and Perrin 2007). With respect to dispersal distance, this is also true for Eurasian lynx. In Poland (Schmidt 1998), Switzerland (Zimmermann et al. 2005) and Scandinavia (Samelius et al. 2012), males dispersed over larger distances than females, though the male bias was not very pronounced in Switzerland (Zimmermann et al. 2005), yet despite sex-biased dispersal, in the Swiss Jura Mountains, one of the populations studied by Zimmermann et al. (2005), some females dispersed over distances larger than 60 km. In the Bialowieza region of Poland, one female was even observed to disperse 120 km. So why do females from the Harz Mountains not disperse to northern Hesse?

The answer to this question is likely to be found in the degree of habitat fragmentation, which is presumably much higher between the Harz Mountains and northern Hesse than within the Swiss Jura Mountains or within the Bialowieza region. It has been suggested previously that Eurasian lynx may have limited ability to cross unfavourable habitat (Samelius et al. 2012; Zimmermann et al. 2007), and our study suggests that this is particularly true for the sex less prone to dispersal, i.e. females. In line with this suggestion, in the more strongly fragmented Swiss Alps (Schnidrig et al. 2016), female lynx were not observed to disperse distances larger than 40 km (Zimmermann et al. 2005). Likewise, in cougars (*Puma concolor*) living in fragmented habitats, males did disperse over substantially larger distances than females (Sweaner et al. 2000), and in a tiger (*Panthera tigris*) population in Chitwan National Park, Nepal, only males have been observed to cross larger areas of unfavourable habitat (Smith 1993). Even if females occasionally disperse to northern Hesse, our study suggests that these long-distance dispersals are too rare to compensate adverse demographic events (female mortality, failed reproduction).

The decline of the Northern Hessian Subpopulation was further accelerated by the emigration of males from our study area. In several territorial mammals, dispersing individuals establish so-called transient home ranges (Beier 1995; Hinton et al. 2015; Smith 1993; Zimmermann et al. 2005), i.e., home ranges that are used for some time during dispersal, but that are later abandoned in search of a better home range. In Eurasian lynx, such transient home ranges are usually only maintained a few months (Zimmermann et al. 2005). Following Zimmermann et al. (2005), we thus classified both B1025m and B1039m as resident (rather than dispersing or transient) individuals, and their dispersal should consequently be classified as secondary dispersal. In contrast to natal dispersal, secondary dispersal is defined as dispersal occurring after the initial dispersal from the natal

territory or social group (Lawson-Handley and Perrin 2007). Secondary dispersal is common in several species of primates (Pusey and Packer 1987), rodents, (Nunes 2007) and carnivores (Waser 1986). The majority of these species, however, are group living, and where males undergo secondary dispersal in these species, they usually do so in the attempt to improve their reproductive opportunities in the target group (Port et al. 2012; Van Horn et al. 2003). By contrast, male secondary dispersal is rare in solitary mammals, and we are unaware of any reports of secondary dispersal in Eurasian lynx (but see Schmidt 1998). We suggest, however, that the same proximate causes responsible for secondary dispersal in group living species, poor reproductive opportunities, might have also triggered B1025m's and B1039m's secondary dispersal.

Management recommendations

Population biologists and conservationists have long known that the viability of small animal populations is highly susceptible to stochastic demographic events (e.g., Boyce and Boyce 1988; Shaffer 1981), and our study provides an empirical example for this susceptibility. In addition, the collapse of the northern Hessian subpopulation provides a case study indicating that the expansion of lynx in Germany, and other central European countries might suffer from serious setbacks without active population management. It has already been discussed that founding few large populations might be insufficient to create continuously distributed, demographically and genetically stable lynx populations in central Europe (Kramer-Schadt et al. 2005; Schnidrig et al. 2016; Zimmermann et al. 2007). It has thus been suggested that, in addition to large-scale reintroduction programs, population stepping-stones of only a few individuals should be created to facilitate dispersal of individuals between (sub-)populations (Kramer-Schadt et al. 2011; Linnell et al. 2008; Schnidrig et al. 2016; Thiel-Bender and Heider 2017; Zimmermann et al. 2007). One possibility to create such stepping-stones is the translocation of individuals from established populations, a management action that has successfully been implemented to promote the expansion of lynx in the Alps (Schnidrig et al. 2016). In these cases, individuals of both sexes have been translocated, either to found a new subpopulation (Northeast Switzerland, Ryser et al. 2004) or to reinforce an already existing occurrence of lynx (Kalkalpen National Park, Austria, Schnidrig et al. 2016). We suggest making use of this management option also in Germany or other regions with isolated lynx occurrences. Moreover, our data suggest that in areas already populated by resident males (such as northern Hesse), or regularly visited by male dispersers, the translocation of few females might be sufficient to create a viable stepping-stone, because these females should induce male dispersers to settle in the area, or prevent males already present from leaving the area again (see also: Thiel-Bender and Heider 2017). Once established, genetic exchange between the stepping-stone and the source population, and potentially, other nearby

(sub-)populations, may likely be maintained by the natural dispersal of males. We suggest that any translocation of individuals should be accompanied by close monitoring and the commitment to reinforce the stepping-stone if necessary. In this way, a possible collapse of a still growing stepping-stone population (as in northern Hesse) could be prevented, allowing it to grow to a demographically viable population size where further intervention is no longer needed.

Conclusion

Our study provides an example for the vulnerability of small, isolated subpopulations of Eurasian lynx to stochastic demographic events. Such subpopulations function as important stepping-stones for the expansion of lynx in central Europe. To prevent them from getting extinct, active population management may be required, such as the translocation of individuals. In areas regularly visited by male dispersers, the translocation of few females may be sufficient to reinforce the stepping-stone.

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Appendix

Table 3 Number of detections per individual

Individual	Sex	Number of detections							Fate
		Pilot P1	Pilot P2	Pilot P3	W 2015/16	W 2016/17	W 2017/18	W 2018/19	
B1036m	M	19	7	2	53	53	35	169	Disappeared, unknown
B1037w	F	3	10					13	Dead, sarcoptic mange
B1061w	F	1						1	Dead, sarcoptic mange
B1035x	F ?	2						2	Disappeared, unknown
B1038x	F ?	11	3					14	Disappeared, unknown
B1025m	M		5		2			7	Last record: 18.05.2018
B1010x	?		1					1	Unknown
B1009m	M				2			25	Dead, pneumonia
B1039m	M					18	7	25	Dead, road accident
B1064m	M							47	Alive, last record: Dec 2019

A question mark means that the sex of the individual was not known. “F ?”, indicates that the sex of the individual could not be determined with certainty, but that the individual was likely a female.

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