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Robust monitoring of the Eurasian lynx *Lynx lynx* in the Slovak Carpathians reveals lower numbers than officially reported

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Abstract The Eurasian lynx *Lynx lynx* population in the Carpathian Mountains is considered to be one of the best preserved and largest in Europe and hence is a source for past and current reintroduction projects in central Europe. However, its status in Slovakia has been reported to the European Commission on the basis of hunters´ reports and expert estimates that have never been validated by a robust scientific approach. We conducted the first camera-trapping surveys to estimate the density of Eurasian lynx in Slovakia by means of spatial capture–recapture models in two reference areas during 2011–2015. We estimated population density per 100 km^2 of suitable lynx habitat (posterior SD) as 0.58 ± SD 0.13 independent individuals (adults and subadults) in the Štiavnica Mountains and 0.81 ± SD 0.29 in Veľká Fatra National Park and surroundings. These are the lowest densities estimated using spatial capture–recapture models so far reported for the species, suggesting the lynx population in Slovakia is below carrying capacity. We suspect that low densities may be attributable to undetected human-caused mortality. Our results imply that official game statistics are substantially overestimated. Moreover, the lynx population in Slovakia may not be at favourable conservation status as required by the EU Habitats Directive. We therefore call for a thorough assessment of the density and trend of the Slovak Carpathian lynx population, and the establishment of a scientifically robust monitoring system.

Keywords Camera trapping, capture–recapture, Carpathians, favourable conservation status, *Lynx lynx*, population density

Introduction

The population of Eurasian lynx *Lynx lynx* in the Carpathian Mountains is considered to be one of the best preserved and largest in Europe (Kaczensky et al., 2013). It was the source of lynx for several reintroduction projects between the 1960s and the 1990s (Breitenmoser et al., 2000; Breitenmoser & Breitenmoser-Würsten, 2008). Although some of the re-established populations prospered initially, most of them have since stagnated or even declined, and suffer from inbreeding (Breitenmoser-Würsten & Obexer-Ruff, 2003; Sindičić et al., 2013). Reinforcement is recommended as a genetic remedy to assure their long-term viability (Schnidrig et al., 2016).

Many of the translocated individuals came from Slovakia, which encompasses c. 17% of the Carpathians and is considered to be a potential source for reinforcements and further reintroductions (Sindičić et al., 2013; Schnidrig et al., 2016). The removal of individuals, even for conservation purposes, requires adequate monitoring of the source population (IUCN/SSC, 2013). Although Slovakia has been a member of the European Union since 2004 and is therefore obliged by Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (the Habitats Directive) to monitor, assess and report on the conservation status of protected species, to date there has been no robust monitoring system for large mammals, including the lynx. Reporting to the European Commission has been on the basis of expert estimates of 300–400 lynx in Slovakia, and the population's conservation status is categorized as unfavourable–inadequate (Černecký et al., 2014). In contrast, official game statistics based on hunters' reports estimated there were 1,668 lynx in Slovakia in 2014 (NLC, 2015). In neither case were these official figures validated by a scientific approach.

Population densities can be estimated reliably from various types of data, including telemetry and snow tracking (Breitenmoser & Breitenmoser-Würsten, 2008). However, camera trapping combined with capture–recapture analysis has become a widely used approach for elusive but individually distinguishable species such as the Eurasian lynx (e.g. Weingarth et al., 2012; Pesenti & Zimmermann, 2013; Zimmermann et al., 2013; Avgan et al., 2014). To obtain the first robust data from the Carpathian Mountains of

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Slovakia we conducted camera-trapping surveys in two reference areas. The main goals of our study were to (1) apply this methodology in Slovakia to estimate lynx population density by spatial and non-spatial capture–recapture models, (2) compare our results with other estimates of lynx density, and (3) provide baseline data for ongoing lynx monitoring.

Study areas

We monitored lynx in two contrasting reference areas: Štiavnica Mountains Protected Landscape Area (IUCN Category V), near the periphery of occupied lynx range, and Veľká Fatra National Park (IUCN Category II), within the core area of the Carpathian population (Hell & Slamčka, 1996). Štiavnica is the largest volcanic complex in Slovakia, at 180–1,009 m altitude (Fig. 1). Two thirds of the Protected Landscape Area's 776 km^2 are covered by deciduous and mixed forest; the remainder is a fragmented mosaic of meadows and agricultural land around human settlements, with a mean density of 63 persons per km^2 (MPRV SR, 2014). Veľká Fatra National Park is located c. 26 km north of Štiavnica. Mixed and coniferous forests cover 90% of its 665 km^2, with alpine meadows above the timberline. Human settlements are located on the periphery of the Park and the mean density is 10 people per km^2 (MPRV SR, 2014). The topography is largely mountainous, at 400–1,592 m altitude. Both areas are included in the Natura 2000 network of protected areas of the EU Habitats Directive (49.7% of the Protected Landscape Area and 72.7% of the National Park).

Several Carnivora besides lynx are present in both areas, including brown bears *Ursus arctos* and wildcats *Felis silvestris*, and grey wolves *Canis lupus* are present in Veľká Fatra. Three species of native ungulates are common: red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. There are also introduced fallow deer *Dama dama* and mouflon *Ovis musimon* in Štiavnica, and Alpine chamois *Rupicapra rupicapra* in Veľká Fatra. Timber harvesting and hunting are permitted across most of both areas.

Methods

Pilot surveys

To enhance the probability of photographing and identifying lynx during capture–recapture surveys, we conducted pilot surveys of 1.5–2.5 years' duration in each study area. The choice of study areas and camera-trap sites was based on information resulting from snow tracking as well as from observations (e.g. lynx sightings, tracks, prey remains) provided by our monitoring network of four rangers and 90 registered hunters/foresters in Štiavnica and six rangers and 70 hunters/foresters in Veľká Fatra. Beginning in 2011 in Štiavnica and 2013 in Veľká Fatra, various models of digital camera were deployed throughout the year along forest roads, hiking paths, game trails and mountain ridges, as well as at lynx marking sites and kills (Zimmermann et al., 2007).

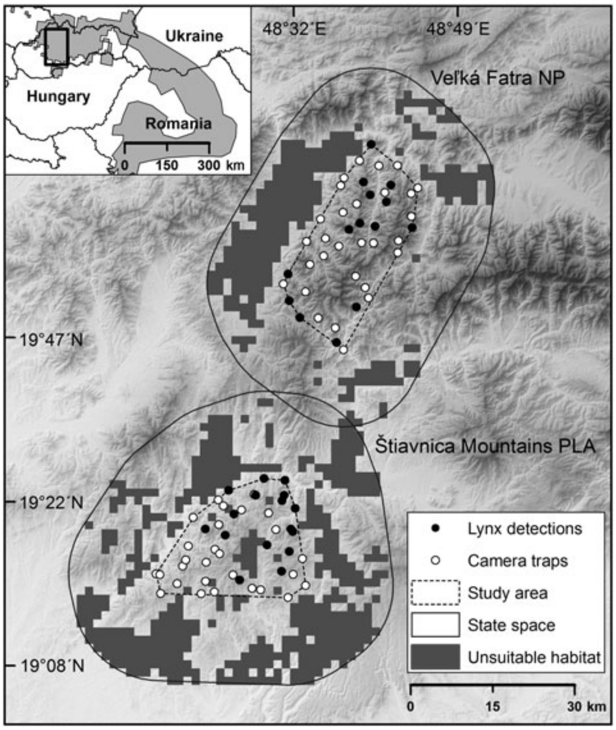

Fig. 1 Location of camera-trap stations in (a) Štiavnica Mountains Protected Landscape Area (PLA) and (b) Veľká Fatra National Park (NP) in the Carpathian Mountains of central Slovakia. Mean convex polygons were enlarged by buffers of 16 and 14 km, respectively, resulting in state-spaces in which we distinguished unsuitable (shaded) from suitable habitat fragments for the Eurasian lynx *Lynx lynx*. The shaded area in the inset shows the lynx's distribution in the Carpathian Mountains (Kaczensky et al., 2013).

Capture–recapture surveys

Winter and early spring, before and during the lynx mating season, has been identified as the best period to conduct systematic camera trapping because of biological (i.e. high lynx activity), logistical (i.e. reduced human disturbance), and environmental factors (Zimmermann & Foresti, 2016). Given the limited availability of cameras, in Štiavnica we used an adjacent block sampling design (Karanth & Nichols, 2002): the western portion of the study area was surveyed during 6 January–6 March, and the eastern block during 16 March–14 May 2014. In Veľká Fatra we surveyed the whole study area simultaneously during 4 December 2014–2 February 2015.

We used a 2.5 × 2.5 km grid to distribute cameras, placing them in every second cell (Zimmermann et al., 2013). We excluded cells with unsuitable lynx habitat, such as agricultural land, human settlements and alpine meadows (15.6% of Štiavnica, 5.2% of Veľká Fatra), and placed cameras in adjacent cells (Weingarth et al., 2012). A total of 44 cells in Štiavnica and 43 in Veľká Fatra were thus selected.

In each selected cell a camera station was established, consisting of a pair of cameras (M-880 infrared, Moultrie, Alabaster, USA; Ambush white flash, Cuddeback, Green Bay, USA) positioned to obtain images of both flanks of animals passing between them. Camera stations were located where lynx activity was recorded during the pilot surveys and at other locations considered to have most potential to obtain images of lynx. Because of their multiple disadvantages, no attractants were used to entice animals to camera traps (Zimmermann & Foresti, 2016). Each camera was protected in a metal box secured to a tree with steel cable and camouflaged using netting, branches, lichen or other material. Cameras, set to detect motion 24 hours per day, were checked every 7–14 days, depending on weather conditions, to download data, replace batteries, clear snow or debris and readjust camera positioning as necessary.

Identification of individuals

We followed the procedure described in Zimmermann & Foresti (2016) to distinguish individual lynx. Photographs of insufficient quality for confident identification were excluded from further analysis. An individual was identified as male if its scrotum was visible and as female if it was accompanied by one or more juveniles or, more rarely, if the genital area was clearly visible.

Statistical analyses

We divided each 60-day survey into 12 sampling occasions of 5 consecutive days each. Multiple records of the same individual at the same location during the same sampling occasion were treated as a single capture event (Zimmermann et al., 2007; Weingarth et al., 2012; Avgan et al., 2014). Juveniles accompanying their mothers were excluded from analysis because of their high mortality and dispersal rates (Zimmermann et al., 2007). We tested whether sampled populations were closed, using *CloseTest* (Stanley & Burnham, 1999; Stanley & Richards, 2004).

Lynx densities were estimated by means of spatial capture–recapture analysis using the SPACECAP package (Singh et al., 2010) in *R v. 1.1.0* (R Development Core Team, 2013). SPACECAP uses capture histories in combination with spatial locations of captures under a unified Bayesian modelling framework to compute density (Royle et al., 2009a,b). Three required input files were prepared: (1) lynx capture details; (2) trap deployment dates when specific cameras were active; and (3) potential home-range centres. For the SPACECAP analysis we used the M_o (null) model, half-normal detection and Bernoulli's encounter process. We ran the model with three Monte Carlo Markov chains with 80,000 iterations, a burn-in of 40,000 and a thinning rate of 3. Bayesian analysis of the model was conducted using data augmentation by increasing the data set with 100 all-zero encounter histories (Royle et al., 2007).

We assessed model adequacy in SPACECAP by following the procedure described in Braczkowski et al. (2016). To find the minimum buffer width for which density estimates began to stabilize, we created a series of state-spaces with buffers of 2–24 km around the minimum convex polygon encompassing all camera traps (Pesenti & Zimmermann, 2013). The total area of this minimum convex polygon was 431.9 km^2 in Štiavnica and 489.1 km^2 in Veľká Fatra. Spatial density estimates decreased with increasing buffer width, stabilizing at a width of 16 km in Štiavnica and 14 km in Veľká Fatra; these buffer widths were retained in the subsequent analyses. The state-space was thus described as a grid of 1,131 equally spaced potential home-range centres (1.5 × 1.5 km) in Štiavnica and 1,066 in Veľká Fatra, corresponding to areas of 2,544.75 and 2,398.5 km^2, respectively (Fig. 1).

To compare our results with earlier studies we also estimated abundance and density based on conventional capture–recapture models, using *MARK 5.1* (White & Burnham, 1999). The CAPTURE module tests several models that differ in their assumed sources of variation in encounter probability, including constant encounter probability (M_o), variation among individuals (M_h), variation across occasions (M_t) and responses to previous encounters (M_b). Subsequently, the best model can be selected from a set of eight closed-population models (M_o, M_h, M_t, M_b, M_{bh}, M_{th}, M_{tb} and M_{tbh}; Otis et al., 1978). To obtain the effective sampled area we applied two measures, the mean maximum distance moved (MMDM) and ½MMDM, often used in studies of elusive felids as a buffer around the mean convex polygon encompassing all camera-trap sites (Pesenti & Zimmermann, 2013). We used the delta method to calculate variance of density estimates (Karanth & Nichols, 1998).

For both spatial and non-spatial capture–recapture analyses, lynx densities were estimated per 100 km^2 of suitable habitat. Proportions of suitable and unsuitable habitats were derived from CORINE Land Cover 2012 (Copernicus Programme, 2012) with resolution of 100 × 100 m in *ArcMap 10.3* (ESRI, Redlands, USA). All types of forest (deciduous, coniferous and mixed), together with shrub and grasslands, were considered suitable habitat for lynx, whereas agricultural land and human settlements were excluded (Fig. 1). For spatial capture–recapture analyses, potential activity centres within (1) and outside (0) fragments of suitable lynx habitat were provided directly in the input matrix of potential home-range centres. We identified 711 centres (1,599.75 km^2) within fragments of suitable lynx habitat in Štiavnica, and 820 (1,845.0 km^2) in Veľká Fatra. Similarly, for non-spatial capture–recapture analyses we excluded unsuitable habitat from the effective sampled area.

Results

Pilot surveys

In Štiavnica a total of 186 photographic records of lynx were obtained during 2011–2014 from 14 of 69 camera locations (20.3%). We discarded 32 (17.2%) photographs because they were of insufficient quality. Fifteen independent individuals (adults and subadults) and eight juveniles were identified (5 female, 10 male, 8 unknown). In Veľká Fatra during 2013–2014 a total of 37 photographs of lynx were obtained from 8 of 31 locations (25.8%), of which 12 (32.4%) were discarded. We identified six independent individuals and two juveniles (2 female, 4 male, 2 unknown).

Capture–recapture surveys

All cameras were active throughout the whole 60-day period in both areas except one station in Štiavnica that was stolen. Trapping effort was therefore 99.6% (2,630 effective trap days) in Štiavnica and 100% in Veľká Fatra (2,580 trap days). A total of 18,653 photographs were obtained in Štiavnica and 9,089 in Veľká Fatra, of which 269 (1.4%) and 100 (1.1%), respectively, were of lynx (Table 1). Four photographs of lynx in each area were excluded from analyses because they were of insufficient quality (1.5% of lynx photographs in Štiavnica and 4.0% in Veľká Fatra). Non-target wildlife species accounted for 64.6% (n = 12,040) of photographs in Štiavnica and 69.9% (n = 6,354) in Veľká Fatra. The red deer was the most frequently detected species in both areas (Table 1). Empty images (i.e. no visible animals or people) accounted for 24.3% (n = 4,527) of all photographs in Štiavnica and 17.2% (n = 1,567) in Veľká Fatra.

During the capture–recapture surveys there were 30 lynx detections at 16 of 44 camera stations (36.4%) in Štiavnica, including seven independent individuals (3 female, 4 male), and 20 detections at 14 of 43 camera stations (32.6%) in Veľká Fatra, representing seven individuals (2 female, 3 male, 2 unknown). The closure test supported the assumption of population closure in Veľká Fatra ($\chi^2 = 4.97$; df = 8; P = 0.76) but not in Štiavnica ($\chi^2 = 25.59$; df = 10; P = 0.00434).

In Štiavnica, the posterior mean baseline encounter rate λ_o (posterior SD) was 0.101 ± SD 0.028 and the posterior mean movement parameter σ (posterior SD) was 6.42 ± SD 0.86 km. In Veľká Fatra, the figures were 0.033 ± SD 0.012 and 5.47 ± SD 1.74 km, respectively. Resulting mean posterior densities (posterior SD) were 0.58 ± SD 0.13 independent lynx per 100 km^2 of suitable habitat in Štiavnica and 0.81 ± SD 0.29 in Veľká Fatra (Table 2). Bayesian P values were 0.57 and 0.52, respectively, suggesting model adequacy. Both the Geweke (values between −1.6 and 1.6) and Gelman–Rubin (shrink reduction factors for key parameters all < 1.1) diagnostics indicated convergence for all models run in SPACECAP.

The model selection procedure in CAPTURE (MARK) rated the M_o model as the most appropriate and M_h as the next best model in Štiavnica and Veľká Fatra. We used the M_h model for abundance estimates for both study areas because of its robustness. As the heterogeneity model M_h (jackknife) indicated ill-conditioned data, we had to rely on M_h (Chao). The mean capture probability (p) under M_h (Chao) was 0.241 in Štiavnica and 0.214 in Veľká Fatra. The respective non-spatial capture–recapture abundance estimates were 9 ± SE 3.74 independent lynx in Štiavnica and 7 ± SE 0.54 in Veľká Fatra. In Štiavnica, MMDM and ½MMDM were 6.4 ± SE 1.30 km and 3.2 ± SE 0.65 km, respectively, and in Veľká Fatra the corresponding values were 8.0 ± SE 1.30 km and 4.0 ± SE 0.65 km. The resulting density estimates in Štiavnica were 1.11 ± SE 0.47 independent lynx per 100 km^2 of suitable habitat using MMDM, and 1.49 ± SE 0.64 using ½MMDM. The corresponding figures in Veľká Fatra were 0.61 ± SE 0.10 independent lynx per 100 km^2 of suitable habitat using MMDM, and 0.84 ± SE 0.09 using ½MMDM (Table 3).

Discussion

Camera-trapping surveys with capture–recapture analysis are an efficient option for monitoring elusive species such as the lynx (e.g. Rovero & Zimmermann, 2016). Our estimates of lynx population density based on spatially explicit capture–recapture models are the lowest reported so far for the Eurasian lynx. In the north-western Swiss Alps, posterior mean densities (posterior SD) of 1.47 ± SD 0.25 and 1.38 ± SD 0.23 individuals per 100 km^2 of suitable habitat were estimated (Pesenti & Zimmermann, 2013), and in Ciglikara Nature Reserve, Turkey, density (posterior SD) was estimated to be 4.2 ± SD 2.0 individuals per 100 km^2 (Avgan et al., 2014). Similarly, our density estimates based on non-spatial capture–recapture are among the lowest reported in similar habitats. The north Jura Mountains of Switzerland and the Bavarian Forest in Germany were found to have 1.13 and 0.9 lynx per 100 km^2 of suitable habitat and all habitat, respectively (Zimmermann et al., 2007; Weingarth et al., 2012).

Our results may represent a population low, as lynx abundance and density may fluctuate over time, depending on ecological (e.g. prey base) and human-induced (e.g.

TABLE 1 Species detected during capture–recapture surveys for the Eurasian lynx *Lynx lynx* in Štiavnica Mountains and Veľká Fatra National Park, Slovakia (Fig. 1), during 2014–2015, with number of photographs, percentage of total photographs in each area, and percentage of photographs of non-target (NT) species.

	Štiavnica (2014)			Veľká Fatra (2014/15)		
Species	No. of photographs	%	%NT	Photographs	%	%NT
Ungulates						
Red deer *Cervus elaphus*	3,836	20.57	31.86	3,475	38.23	54.68
Wild boar *Sus scrofa*	2,372	12.72	19.70	870	9.58	13.68
Roe deer *Capreolus capreolus*	1,691	9.07	14.04	374	4.12	5.90
Fallow deer *Dama dama*	117	0.63	0.97			
Mouflon *Ovis musimon*	61	0.33	0.51			
Chamois *Rupicapra rupicapra*				13	0.14	0.20
Large carnivores						
Eurasian lynx *Lynx lynx*	269	1.44		100	1.10	
Brown bear *Ursus arctos*	23	0.12	0.19	160	1.76	2.52
Grey wolf *Canis lupus*				38	0.42	0.56
Other carnivores						
Red fox *Vulpes vulpes*	1,723	9.24	14.31	1,192	13.11	18.76
Badger *Meles meles*	950	5.09	7.89	52	0.57	0.82
Wildcat *Felis silvestris*	466	2.50	3.87	10	0.11	0.19
Martens *Martes* sp.	437	2.34	3.63	60	0.66	0.94
Domestic cat *Felis catus*	81	0.43	0.67			
Domestic dog *Canis familiaris*	51	0.27	0.42	13	0.14	0.21
Steppe polecat *Mustela eversmanii*	2	0.01	0.02			
Other species						
Brown hare *Lepus europaeus*	135	0.72	1.12	91	1.00	1.42
Red squirrel *Sciurus vulgaris*	79	0.42	0.66	1	0.01	0.02
European hedgehog *Erinaceus europaeus*	16	0.09	0.13			
Hazel grouse *Bonasa bonasia*				5	0.06	0.10
People	1,817	9.74		1,068	11.75	
Empty images	4,527	24.27		1,567	17.24	
Total	18,653			9,089		

hunting, poaching) factors. For example, 3-fold changes in lynx density were observed in the Swiss Jura Mountains (Zimmermann et al., 2009, 2015), and 1.6-fold in the northwestern Alps (Zimmermann et al., 2014, 2016). However, as our results are the first robust estimates of lynx density in Slovakia we cannot assess population trends or fluctuations until the surveys are repeated in the future.

There are several other factors that may account for the relatively low lynx densities in our study areas, including technical (e.g. camera-trap failures), conceptual (e.g. population closure violation, suboptimal sampling period), ecological (e.g. lower carrying capacity, habitat alteration or fragmentation, inbreeding, reduced fitness and interspecific competition) and human–related factors (human-induced mortality). Here we discuss the most relevant issues.

The large number of empty images we obtained is probably attributable to the high sensitivity of infrared cameras to moving objects (e.g. birds, snow) rather than equipment failures. Our cameras worked well throughout the 5,210 trap days of our two surveys and we achieved an effective trapping effort of 99.8%. For comparison, previous studies of the Eurasian lynx carried out using the same methodology achieved 84–99.6% in Switzerland (Zimmermann et al., 2016), 98% in Germany (Weingarth et al., 2012) and 99% in Turkey (Avgan et al., 2014).

Violation of the population closure assumption in Štiavnica may have been influenced by the longer duration of the survey because of the adjacent block sampling design, which may explain the high proportion of lynx detected only once. However, all detected individuals had already been identified during the pilot survey and we have no evidence of immigration during the capture–recapture survey. Juveniles start dispersal in early spring, but they were not included in our estimates. Although our survey in Štiavnica covered a 4-month period and ended slightly later in the year (mid May) compared to the Veľká Fatra survey and other capture–recapture studies of lynx (e.g. Pesenti & Zimmermann, 2013), we do not think that this could have had a strong impact on mean density estimates.

Another reason for low lynx densities could be that the Slovak Carpathians may have a lower carrying capacity than other study sites. However, the Slovak Carpathians are thought to provide excellent conditions for lynx because they have a high proportion of forest cover (the main habitat

TABLE 2 Posterior summaries of the SPACECAP parameters for the camera-trapping surveys in Štiavnica Mountains and Veľká Fatra National Park, Slovakia (Fig. 1), during 2014–2015, with area of suitable habitat, numbers of suitable and unsuitable centres, area of state-space, encounter rate (λo), movement parameter (σ), estimated mean lynx population size, and estimated mean density per 100 km^2 of suitable habitat.

	Štiavnica (2014)	Veľká Fatra (2014/2015)
Suitable habitat (km^2)[1]	1,599.75	1,845.0
No. of suitable/unsuitable centres	711/420	820/246
State-space (km^2)[2]	2,544.75	2,398.5
Encounter rate, $\lambda 0$ (mean ± SD)	0.101 ± 0.028	0.033 ± 0.012
Movement parameter, σ, km (mean ± SD)	6.42 ± 0.86	5.47 ± 1.74
Estimated lynx population size (mean ± SD)	9.26 ± 2.02	15 ± 5.27
Estimated density, lynx per 100 km^2 suitable habitat (mean ± SD)[3]	0.58 ± 0.13	0.81 ± 0.29

[1] Suitable habitat was determined from all types of forest (deciduous, coniferous and mixed) together with shrub and grasslands; agricultural land and human settlements were excluded.

[2] Both state-spaces were described as a grid of equally spaced (1.5 × 1.5 km) potential home range centres, within and outside suitable habitat fragments.

[3] Density was calculated by dividing the estimated population size by the area of the state-space within suitable habitat.

of lynx in Europe; Breitenmoser & Breitenmoser-Würsten, 2008). Wild ungulate populations are at a historical maximum, causing substantial browsing damage to forests and crops (Konôpka & Kaštier, 2014). We therefore consider it unlikely that lynx density in our study areas was limited by carrying capacity compared to other European ecoregions at the same latitude.

Low lynx densities may also be a result of human-induced mortality. In general, the main causes of mortality in adult Eurasian lynx in human-dominated landscapes, even protected areas, are anthropogenic (von Arx et al., 2004; Andrén et al., 2006), particularly vehicle collisions and poaching (Stahl & Vandel, 1999; Schmidt-Posthaus et al., 2002; Magg et al., 2016; Sindičić et al., 2016). During our study there was apparently a high population turnover. Although we detected 23 individuals (15 adult, 8 juvenile) during the pilot survey in Štiavnica in 2011–2014, only 20% were recaptured later. The mean persistence of lynx in Štiavnica was only 12.7 months (range 2–23 months). Of the eight individuals (6 adult, 2 juvenile) we identified in Veľká Fatra during the pilot survey, only three were detected during the capture–recapture survey. We know of two lynx in Štiavnica and one in Veľká Fatra killed by vehicles during our study. Considering the occurrence of apparently orphaned lynx in Slovakia (39 known cases during 2001–2015; B. Tám, Bojnice Zoo, pers. comm.), as well as lynx killed illegally (7 known cases during 2001–2014, of which one was detected in Štiavnica; E. Gregorová, Bojnice Zoo, pers. comm.), we suspect a high rate of adult mortality in the population. In our view, undiscovered anthropogenic mortality is the most likely explanation for the observed low lynx densities and high population turnover.

Official game statistics in Slovakia purport to show strong lynx population growth following the cessation of hunting in 2000, reaching 1,668 individuals in 2014 (NLC, 2015; Fig. 2). However, the veracity of these figures and validity of the methodology used to collect these data, particularly for wide-ranging species such as large carnivores, have been called into doubt by numerous authors (e.g. Hell & Slamečka, 1996; Okarma et al., 2000). Hunters report numbers of game species in hunting grounds throughout Slovakia, which are then simply summed at the National Forest Centre to derive estimates of abundance. However, these numbers are guesstimates based on lynx sightings, tracks and prey remains recorded sporadically by hunters throughout the year. Moreover, hunting grounds are considerably smaller (mean = 26 km^2) than lynx home ranges (e.g. median = 283 km^2 for males and 185 km^2 for females in similar habitats of the Swiss Jura Mountains; Breitenmoser-Würsten et al., 2007), which results in multiple counting of the same individuals, and subsequent overestimation of population size. According to official game statistics in both state-spaces there were 52 lynx in Štiavnica and 104 in Veľká Fatra, at densities of 3.3 and 5.6 per 100 km^2, respectively (i.e. 6–7 times higher than our spatial capture–recapture estimates).

The reports of 300–400 lynx made by the Slovak authorities to the European Commission on the status of species protected by the Habitats Directive (Černecký et al., 2014) for the periods 2004–2006 and 2007–2012 were not based on scientifically robust data, as no systematic monitoring was implemented (Kaczensky et al., 2013; Černecký et al., 2014). Contrary to the declaration of Černecky et al. (2014), the approach did not include any modelling and we believe that it may simply be a repetition of old expert estimates (e.g. Salvatori et al., 2002; von Arx et al., 2004) based on lynx sightings, track counts, unspecific surveys, inquiries, and known mortality. Using the mean lynx density we calculated by means of spatial capture–recapture (0.70 individuals per 100 km^2 of suitable habitat) we estimate there are c. 197 ± SE 56 independent lynx in the 28,090 km^2 of occupied range (Kaczensky et al., 2013) in Slovakia.

Our results indicate not only that lynx abundance in Slovakia is likely to be markedly lower than officially reported, but that the population may not be at favourable conservation status as required by the EU Habitats Directive. The thresholds for favourable conservation status at national level were defined as density of ≥ 1 individuals

TABLE 3 Lynx abundance and density per 100 km² of suitable habitat in Štiavnica Mountains and Veľká Fatra National Park estimated by means of the non-spatial heterogeneity model M_h (Chao). The effective sampled area was restricted to suitable lynx habitat fragments within the areas formed by the minimum convex polygons (MCP) encompassing all camera-trap sites enlarged with two buffer widths: mean maximum distance moved (MMDM) and ½MMDM.

	Štiavnica (2014)		Veľká Fatra (2014/2015)	
Method	MMDM	½MMDM	MMDM	½MMDM
MCP (km^2)	431.9	431.9	489.1	489.1
Abundance (mean ± SE)	9 ± 3.74	9 ± 3.74	7 ± 0.54	7 ± 0.54
Buffer, km (mean ± SE)	6.4 ± 1.30	3.2 ± 0.65	8 ± 1.30	4 ± 0.65
Suitable habitat (km^2)	812.3	603	1,145.3	837
Density, lynx per 100 km^2 suitable habitat (mean ± SE)	1.11 ± 0.47	1.49 ± 0.64	0.61 ± 0.10	0.84 ± 0.09

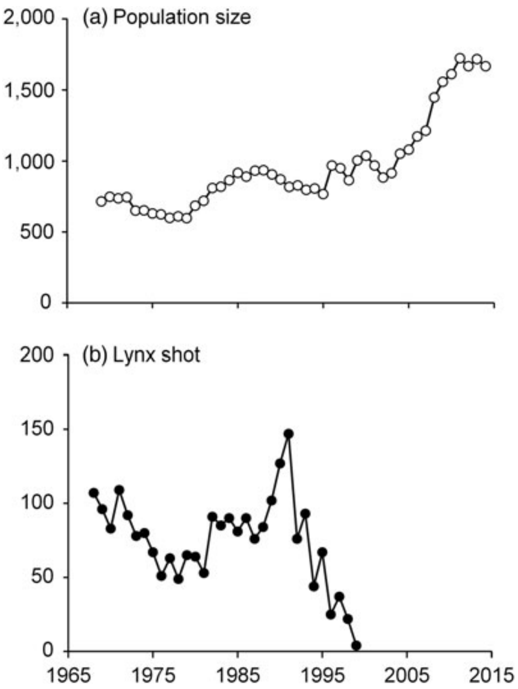

FIG. 2 (a) Lynx population size based on hunters' reports (e.g. lynx sightings, tracks and other field signs) from all hunting grounds throughout Slovakia, and (b) numbers of lynx legally shot during 1968–2014 according to official game statistics in Slovakia (after NLC, 2015).

per 100 km² of main forest habitat, and population size of ≥ 250 individuals in Slovakia (Kropil, 2005).

Although Slovakia reported having 300–400 lynx, the overall conservation status was declared to be unfavourable–inadequate because there were insufficient data to assess lynx range, population and habitat (Černecký et al., 2014). If a species is not at favourable conservation status, the responsible authorities are obliged to implement appropriate measures to improve the status of the species. Such actions should include implementation of a conservation programme based on a thorough understanding of population status and dynamics, including controlling factors and main threats and human dimensions such as attitudes and conflicts (Rigg et al., 2011). Other actions could aim to raise awareness of the species among hunters, foresters and the general public, involve interest groups in the monitoring and conservation of the species, and improve law enforcement for species and habitat protection.

Our results are the first robust estimates of lynx abundance and density in Slovakia. We do not know if they are representative of the whole population or the long-term mean density. However, as our study took place in comparatively well-managed protected areas, we assume our results are more likely to be above than below average for the population. We therefore call for continuous assessment of the density and trend of the Slovak Carpathian lynx population, and the establishment of a scientifically robust monitoring system. Beyond the opportunity to improve monitoring, we hope that renewed international interest in the lynx population in Slovakia will help raise awareness of the species and ensure that it has a higher priority on the agenda of wildlife managers, conservationists and researchers.

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Author contributions

The study was conceived and designed by JK, PS, UB, CB-W, FZ, RR and RK. Fieldwork was coordinated by JK and RR, assisted by PS, TI and BT. JK, PS, FZ and DF performed statistical analyses. RK supervised the work of JK and PS. The article was written by JK, PS, UB, FZ and RR.

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Biographical sketches

Jakub Kubala's research focuses on lynx ecology. Peter Smolko's work is focused on predator–prey relationships in large mammals. Fridolin Zimmermann coordinates monitoring of large carnivores in Switzerland and is an expert in camera trapping. Robin Rigg has led work on large carnivore conservation and research at the Slovak Wildlife Society since its founding in 1998. Branislav Tám is curator of ungulates, elephants and carnivores at Bojnice Zoo. Tomáš Iľko has studied the pelage of the Carpathian lynx. Danilo Foresti specializes in monitoring and habitat modelling. Christine Breitenmoser-Würsten is programme coordinator and administrative director of KORA and co-chair of the IUCN SSC Cat Specialist Group. Rudolf Kropil's research focuses on mammal and bird ecology. Urs Breitenmoser is director of KORA and co-chair of the IUCN SSC Cat Specialist Group.