Biodivers Conserv
DOI 10.1007/s10531-015-0986-5

ORIGINAL PAPER

Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas

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Received: 9 February 2015 / Revised: 2 August 2015 / Accepted: 10 August 2015

Abstract A tool commonly used in wildlife biology is density estimation via camera-trap monitoring coupled with capture–recapture analysis. Reliable regional density estimations of animal populations are required as a basis for management decisions. However, these estimations are affected by the session design, such as the length of the monitoring session, season, and number of trap sites. This method is regularly used to monitor Eurasian lynx (*Lynx lynx*) which mostly occupy the forested mountain ranges in Central Europe. Here we used intensive field sampling data of a major Central European lynx population to investigate (1) the optimal monitoring session length considering the trade-off between population closure and number of recaptures for density estimates, (2) the optimal time window within the year considering the stability of density estimates, detection probability, recapture number, and reproduction, and (3) the number of trap sites and trap spacing required to achieve robust density estimates. Using two closure tests, we found that 80 days are the minimum to ensure adequate data quality. A spatially explicit capture–

Communicated by David Hawksworth.

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recapture model revealed the best monitoring period to be late summer to early winter. Based on our results, we recommend for similar management units of comparable size ($\sim$300 km^2) and similar recapture numbers to sample for at least 80 days in autumn with traps spaced about every 2.5–3 km. Our results also indicated that stable density estimates could still be maintained when the sampling area is enlarged to 760 km^2 with trap spacing every 5–6 km if session lengths are increased.

Keywords *Lynx lynx* · Spatially explicit capture–recapture model (SECR) · Camera traps · Forested areas · Mountainous areas · Density estimates

Introduction

Camera traps are a successful non-invasive monitoring tool for abundance and density estimates of elusive species (Noss et al. 2012; Trolle et al. 2008) and emerged to a mainstream tool particularly for visually recognizable felids, such as tiger (*Panthera tigris*) (Karanth and Nichols 1998), ocelot (*Leopardus pardalis*) (Trolle and Kéry 2003), jaguar (*Panthera onca*) (Silver et al. 2004; Sollmann et al. 2011), and lynx species (Garrote et al. 2011; Heilbrun et al. 2006; Kelly and Holub 2008; Laass 1999; Zimmermann and Breitenmoser 2007).

Closed non-spatial capture–recapture models and *ad hoc* methods such as mean-maximum-distance-moved methods are commonly used for abundance and density estimates (Foster and Harmsen 2012). A basic assumption of these models is a demographic and geographic closure of the population, i.e., a static population size over the study period. However, this is not fulfilled in most studies because study areas have hard boundaries and are of artificial construction, but populations are permanently driven by immigration, emigration, natality, and mortality. For small study areas, density estimates with spatially explicit capture–recapture (SECR) models (Efford et al. 2004; Royle and Gardner 2010) have proven to be more robust (Sollmann et al. 2012). SECR density estimates are, unlike estimates from closed non-spatial capture–recapture models, unbiased in terms of edge effects, temporary emigration, and incomplete detection (Kéry and Schaub 2012) because they incorporate spatial population models with individual movement models. However, adequate data quality, i.e., the number of recaptures, is still essential for unbiased estimates (Sollmann et al. 2012).

During the last century, the Eurasian lynx [*Lynx lynx* (Linnaeus, 1758)] has been extinct in vast parts of Central Europe. Since the 1970s, populations have expanded again owing to reintroduction (Breitenmoser et al. 2000; Cop and Frkovic 1998; Festetics 1981; Müller et al. 2014; Wotschikowsky et al. 2001). The Eurasian lynx has become an attractive symbol of wilderness and nature and has become the focus of conservation and the flagship species of many protected areas (Caro and O'Doherty 1999). In protected areas, threatened species like the Eurasian lynx (EU Habitats Directive, Annex II and IV, fauna and flora) are safeguarded, and the population status, including density estimates, survival or reproduction, must be reported (Linnell et al. 2007, 2008; Nilsen et al. 2011). However, data for such reports are difficult to obtain as the Eurasian lynx is solitary, crepuscular, wide ranging [122–1000 km^2; (Herfindal et al. 2005; Linnell et al. 2000; Magg et al. in press)], well camouflaged, and therefore difficult to observe directly in its mostly forested habitat.

Although systematic camera-trap monitoring is usually more cost efficient than radio telemetry (Gil-Sánchez et al. 2011) or live trapping (De Bondi et al. 2010), the financial effort of acquiring and maintaining camera traps is still a limiting factor. This and the applicability of SECR models require a judiciously selected study design to obtain adequate data quality. Criticisms have arisen regarding the lack of standardized sampling protocols for camera traps, specifically regarding monitoring parameters, e.g., minimum size and shape of the study area (Foster and Harmsen 2012; Maffei and Noss 2008; Tobler and Powell 2013). In the current study, we identified and investigated three important adjustable parameters, namely the length and season of the monitoring session and the number of trap sites required for robust estimates.

The challenge of the study entailed finding the tradeoff between an efficient monitoring session length and adequate data quality (recaptures) for reliable estimations. Zimmermann et al. (2013) recommend camera-trap monitoring of Eurasian lynx in the Swiss Alps during winter, because they assume a higher probability of detection owing to canalization of trails induced by snow height and that males and females with kittens cover wider areas during the mating season (Breitenmoser and Breitenmoser-Würsten 2008). Furthermore, the number of trap sites implies a trade-off between monitoring efficiency and coverage of the study area for adequate data quality. Wegge et al. (2004) found that increasing the trap spacing above 1 km underestimates tiger populations. Dillon and Kelly (2008) underline that population density estimates are negatively correlated with distance between cameras. Sollmann et al. (2012) showed that SECR models perform well if the extent of animal movement is at least half the distance between trap sites.

Specifically, we addressed the following three points: (1) the length of an efficient and systematic monitoring session that fulfills the criteria of population closure and adequate data quality to obtain robust density estimates with SECR (*S-length*), (2) the time of year in which the target criteria for camera-trap monitoring of Eurasian lynx in a low-mountain range area are most favorable (*S-season*), and (3) the spacing of trap sites needed in the study area to reach monitoring efficiency and still achieve stable density estimates (*Tr-sites*, a list of abbreviations is given in Table 1).

Material and methods

Sampling data

We used data sampled in the Bohemian Forest, specifically in the Bavarian Forest National Park (BFNP, 240 km^2) in southeastern Germany and the adjacent Šumava National Park

Table 1 List of abbreviations

Abbreviation	Description
BFNP	Bavarian Forest National Park
SNP	Šumava National Park
MMDM	Mean maximum distance moved
MCP	Minimal convex polygon
SECR	Spatial explicit capture-recapture
$S\text{-}length_{CT}$	Session length—results closure tests
$S\text{-}length_{RC}$	Session length—sufficient recaptures (>20)
$S\text{-}length_{MR}$	Session length—maximum recaptures
Tr-sites	Number and spacing of trap sites
g_d	Detection probability per half trap spacing
CV_d	Coefficient of variation of the density estimate

(SNP, 690 km^2) in the Czech Republic (Fig. 1). The study areas cover elevations between 568 and 1456 m a.s.l. and are dominated by mixed mountainous forests composed of mainly Norway Spruce (*Picea abies*), followed by European Beech (*Fagus sylvatica*), and of minor importance Silver Fir (*Abies alba*) (Bässler et al. 2009); large areas have been affected by windthrows and spruce bark beetle attacks (*Ips typographus*) (Lausch et al. 2013). The area is covered in snow for an average of 5–6 months, with maximal snow heights from January to March, with 32–143 cm snow in the study years (2009–2012; Wetterstation Waldhäuser).

The lynx population of the cross border region of the Czech Republic and Germany has its origin in the reintroduction of 17 lynx (11 males, 6 females) between 1982 and 1987 on Czech territory (Wölfl et al. 2001). Today the size of the Bohemian—Bavarian population is estimated with 50 individuals (Chapron et al. 2014). The BFNP and the adjacent SNP form the core area of this lynx population (Cervený et al. 2002; Müller et al. 2014). Since 2009 systematic camera trapping regularly reports a number of 10–16 lynx individuals which are older than 2 years (independent) and reproduction. GPS telemetry of nine lynx between 2005 and 2012 in the area, offered mean home range sizes of 122 km^2 (*SD* $\pm$ 40.5) for females and 435 km^2 (*SD* $\pm$ 128.4) for males (MCP 95) (Magg et al. in press). Snow tracking data in the area obtained daily movement distances up to 15–20 km for lynx individuals. The main prey species of the lynx in the area is roe deer (*Capreolus capreolus*), which is assumed to occur in low densities (1–5 animals/km^2) (Heurich et al. 2012; Möst et al. 2015). The snow height in winter forces roe deer to migrate to lower elevations outside of the national parks (Cagnacci et al. 2011).

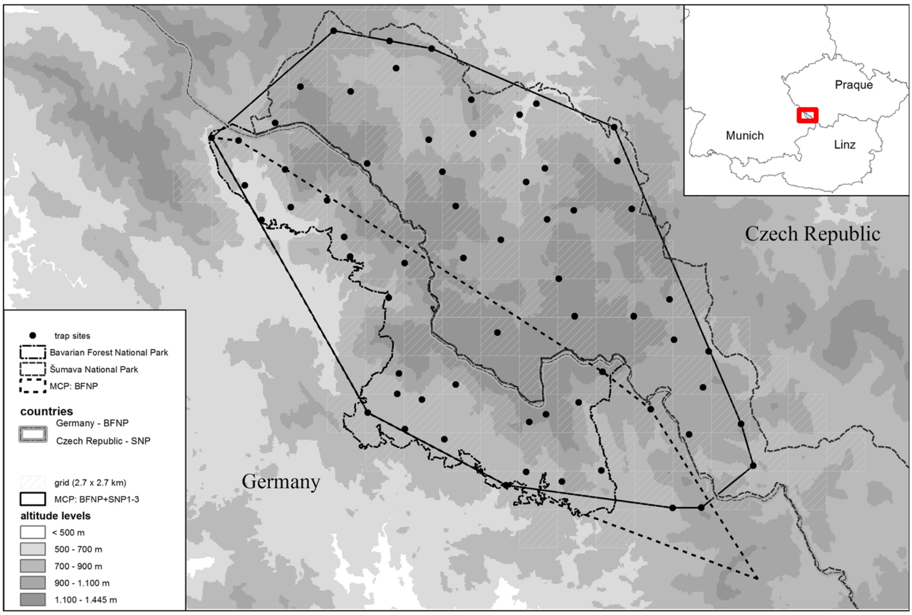


Fig. 1 Study area consisting of the two adjacent national parks—the Bavarian Forest National Park (BFNP) in Germany and the Šumava National Park (SNP) in the Czech Republic. *S-length* and *Tr-sites* data were collected in both national parks, and *S-season* data were collected only in the BFNP

Monitoring design

Sites were selected spatially to maximize detection probability per lynx individual (Blanc et al. 2013; Carbone et al. 2001; Pesenti and Zimmermann 2013; Tobler and Powell 2013) within every second square of a 2.7 × 2.7 km grid (Fig. 1), which we adapted from Laass (1999). To find trap sites with a high probability of detecting lynx, we took advantage of available telemetry data of lynx and roe deer, snow tracking and prey site data of the area, and suggestions of experts (Weingarth et al. 2012b). The setting reduced the risk of gaps that can include a lynx home range (Parmenter et al. 2003; Wilson and Anderson 1985), which comprises approximately 122 km^2 for females (Herfindal et al. 2005), and it assured at least four to five sites per average female home range (Dillon and Kelly 2007; Karanth et al. 2002; Tobler and Powell 2013). The sites were located mostly on forest paths and roads (73.6 %); other sites were located on official hiking trails (21.1 %) and game paths (5.3 %). The camera traps have been maintained every 4 weeks during the whole year, except during snow fall when the routine was reduced to 2 weeks (Weingarth et al. 2012b).

We used the white flash camera trap model Cuddeback Capture™ (Green Bay, WI, USA) during the study, with two opposing cameras installed on each site. The delay between images was set at 30 s, and the cameras functioned 24 h/day (Weingarth et al. 2012a).

In the area of the BFNP, the camera traps operated continuously for 2.5 years from the beginning of November 2009 until the end of April 2012 ($BFNP_{total}$, Table 2). The survey $BFNP_{total}$ included three lynx-years (2009, 2010, 2011), which are defined as from 1st May until 30th April of the following year, as most juveniles are born in May and begin to separate from the mother in April of the following year (Weingarth et al. 2012b; Zimmermann et al. 2005). The cross-border monitoring of the BFNP and SNP area was conducted in three consecutive winter seasons between 2009 and 2012 ($BFNP + SNP_{1-3}$, Table 3). A monitoring session began when a minimum of 50 % of the camera traps were installed in the field; the remainder were installed within the next few days. Lynx individuals identified on the images were classified in status levels, i.e., juvenile, independent, or unknown, and when possible in sex classes, e.g., if the genital area was visible or if kittens (with a female) were present (Weingarth et al. 2012b). One trapping event was defined as 5 min, i.e., if a lynx was detected several times on one site within 5 min, only one event was counted. Lynx clearly recognized as juveniles within their first lynx-year were included in the analysis as proof of the presence of their mother (Zimmermann et al. 2004).

Data analysis

We selected two indicators of a suitable design—demographic closure and number of recaptures—to test a suitable length of monitoring sessions (*S-length*). For the selection of the best season and trap spacing for the monitoring session (*S-season and Tr-sites*), we defined the following target criteria: (a) We chose the number of recaptures as a quantitative measure of data quality. The recaptures were defined as the total number of detections minus the number of different animals detected (Murray Efford, personal communication). Linkie et al. (2008) propose that a higher number of recaptures decrease the coefficient of variation of the abundance estimate. Accordingly, as density fluctuations and low precision of estimates are not desirable in terms of reliability and thus management derivations, (b) we included the coefficient of variation of the density estimate (CV_d). Elusive felids generally have low detection probabilities (Foster and Harmsen 2012;

Zimmermann et al. 2013), but the increase of the detection probability is worthwhile to enable an adequate estimator selection. (c) We calculated the detection probability (g_d) at the distance of half of the average trap spacing per grid size respectively. Thereby we deployed the detection function which is inserted in the SECR model to display the effects on the detection probability. (d) We also used detection of juveniles as a criterion for reproduction.

The analysis was done using package secr (Efford 2015) in R 3.0.1 (R Development Core Team 2013). During the analysis from point 1–3 (*S-length*, *S-season* and *Tr-sites*), we used monitoring session variants with closed SECR -models (maximum likelihood) (Borchers and Efford 2008; Efford 2004; Royle 2009) by creating moving windows, i.e., time frames representing the monitoring session length of n days (window size) were shifted x days (sequence). Again during the analysis of the three points, we defined one trapping occasion as 5 days according to earlier studies of rare felids (Karanth and Nichols 1998), and also Eurasian lynx (Zimmermann et al. 2006). Trap sites were sometimes spatially shifted to improve detection success; this generally occurred at the beginning of each lynx-year (May). Therefore, we cut off or marked moving windows that included the transition of two successive lynx-years.

For specifying the models, we chose the proximity detector type 'count' (Efford 2015), which sums all capture events per occasion. The resulting vector of event counts per occasion was treated as a realization of a Poisson process in the subsequent SECR model fit.

SECR models with maximum likelihood comprise a state model, which depicts the species home ranges in the study area and an observation model. The observation model contains the measurement of detection probability (g_d), which is no longer constant but is a function that links the detection probability to the distance of the camera-trapping site (detector) from the individuals home range centroid (activity center) (Borchers and Efford 2008; Efford 2015).

As the difference between half-normal and exponential detection functions is negligible (Efford et al. 2009) and as we did not include covariates, we followed the default half-normal detection function throughout the analysis [$g(d) = g_0 \times exp(-d^2/2\sigma^2)$] (Efford 2015; Tobler and Powell 2013). Individual home ranges were assumed to be stable over the monitoring session length and in general circular. Each individual has an independent activity center, and these centers are randomly distributed (Poisson process), whereas each detection is an independent event.

For the analysis of (1) *S-length,* we used sliding windows of size 20–120 days (sequence 10 days) to test for closure in demography of BFNP + SNP_{1-3}. In this way, closure tests of Otis et al. (1978) and the overall test of Stanley and Burnham (1999) were carried out. We evaluated the measurements regarding (i) the demographic population closure ($S\text{-}length_{CT}$), which is one of the basic assumptions of closed capture–recapture models (Otis et al. 1978) and (ii) the number of recaptures with the minimum required number of >20 recaptures ($S\text{-}length_{RC}$) for robust estimations with the closed SECR models of Efford et al. (2009), and the maximum number of recaptures ($S\text{-}length_{MR}$) (Harmsen et al. 2011; Tobler and Powell 2013). For the analysis, we filtered the data by excluding time frames of two lynx-years, as the changes during the optimization of trap sites at the beginning of every lynx-year would bias the estimations.

For the analysis of (2) *S-season,* an appropriate model had to be selected. The available models include variances in detection probabilities per individual at the activity center (g_0) and are based on the classic closed capture–recapture models (M_0, M_b, M_t, M_h and their combinations) of Otis et al. (1978). In order to rank the models, we cut out 17 time-overlapping sliding windows of length *S-length*$_{RC}$ of BFNP$_{total}$, shifted by 50 days, fitted them by numerically maximizing the likelihood, and ranked them by the best fitting model [lowest Akaike Information Criterion (AIC) value]. The model that indicates constant detection probability $g_0 \sim 1$ (M_0) per individual, per trapping occasion, and per detector was ranked best and used for the SECR analysis. Models which indicate behavioral response due to the white flash camera were ranked low in the model selection process.

In order to exclude lynx individuals outside that range, a buffer of convenient width needed to be defined. Therefore, we evaluated variants in width within the same 17 time-overlapping sliding windows as in the model selection process. In consideration of the consistency of the density value, which remained constant >12 km, a buffer width of 15 km was selected. This is similar to that used by Pesenti and Zimmermann (2013) for estimating Eurasian lynx density in Switzerland.

With the evaluation of criteria such as stability and consistency of CV_d, detection probability g_d, number of recaptures, and documentation of reproduction (juvenile status) with the dataset of BFNP$_{total}$, we were able to decide which period of the year is most adequate for the camera-trapping session.

As the spacing of trap sites can influence density estimates, we evaluated the influence of the spacing and consequently the number of trap sites with the same criteria as in *S-season* within the recommended minimum-sized study area for Eurasian lynx (>760 km^2) (Zimmermann et al. 2013). In order to derive *Tr-sites* for our study area, we subsampled trap sites using a grid filter approach. We overlaid grids with defined cell sizes of 2500, 3000, 5000, and 7000 m within the study area of BFNP + SNP$_{1-3}$. For each grid cell, we counted trap sites; in the case of multiple sites, one site per cell was randomly chosen. From these, we estimated density with the M_0 ($g_0 \sim 1$) model in monitoring session length *S-length*$_{RC}$ and *S-length*$_{MR}$ and evaluated the target criteria (a–d) listed above. Our aim is to offer an appropriate spacing of trap sites under the priority of stable density estimates with SECR (Tables 2, 3).

Results

During the entire monitoring, we obtained 750 lynx images, representing 276 lynx events on 14,322 effective trap nights for BFNP$_{total}$ (Table 4) and 352 events on 24,486 effective trap nights for BFNP + SNP$_{1-3}$ (Table 5). Six lynx images could not be assigned to an individual and were therefore excluded from the analysis.

With regard to (1) *S-length,* we found that closure tests alone were not appropriate for approaching the adequate length of a camera-trapping session. Both closure tests would enclose a short *S-length*$_{CT}$ of 30 days (Stanley and Burnham) and 40 days (Otis) to reach a maximal chance (>90 %) of demographic closure. In contrast, *S-length*$_{RC}$ resulted in

Table 2 Sampling effort of the total German session

Session name	Sampling time (lynx-year)	MCP study area (in km^2)	Number trap sites	Potential trap nights	Lynx events
BFNP$_{total}$	IX 2009–IV 2010 (2009)	311	31	5123	46
	V 2010–IV 2011 (2010)	313	31	11,232	98
	V 2011–IV 2012 (2011)	313	31	11,346	132

Table 3 Sampling effort per cross-border (Germany + Czech Republic) session

Session name	Winter season—(lynx-year)	MCP study area (in km^2)	Number trap sites	Potential trap nights	Lynx events
BFNP + SNP$_1$	2009/2010 (2009)	750	57	8437	124
BFNP + SNP$_2$	2010/2011 (2010)	780	62	8625	92
BFNP + SNP$_3$	2011/2012 (2011)	775	66	9445	136

Table 4 Results obtained by the total German session

Session name	Lynx-year	Number of lynx status independent + unknown	Number of lynx status juvenile	Effective trap nights (in %)	Individual not recognisable (per event)	Trap nights per event
BFNP$_{total}$	2009	7 + 3	6	4667 (93.6)	1	101.46
	2010	13 + 1	3	4540 (94.7)	4	46.32
	2011	16 + 2	4	5115 (86.9)	–	38.75

Table 5 Results obtained per cross-border (Germany + Czech Republic) session

Session name	Lynx-year	Number of lynx status independent + unknown	Number of lynx status juvenile	Effective trap nights (in %)	Individual not recognisable (per event)	Trap nights per event
BFNP + SNP$_1$	2009	12 + 8	9	7794 (92.4)	–	62.35
BFNP + SNP$_2$	2010	18	6	8014 (92.9)	–	85.26
BFNP + SNP$_3$	2011	18 + 5	4	8678 (91.9)	1	63.81

80 days (session length, recaptures) at a minimum for a 75 % chance of reaching the recommended number of recaptures of at least 20 (dashed line in Fig. 2). *S-length*$_{MR}$ comprised 120 days (session length, maximum recaptures).

For (2) *S-season* with *S-length*$_{RC}$ = 80 days, the best combination for our target criteria was reached in late summer to late autumn (Fig. 3). The M_0 model showed a decrease of the coefficient of variation (CV_d) and a slim range from the end of July to the end of November, and the lowest CV_d from the end of August to the beginning of November. Detection probability g_d was highest from week 38 to week 48, with the smallest range up to week 45. With the M_0 model, the remainder of the year did not reach $g_d > 0.1$ (mean). Recapture numbers >10 were achieved from week 29 to week 46, and >20 recaptures were achieved from week 35 to week 45 (Fig. 3).

For *S-length* with *S-length*$_{MR}$ = 120 days, a stabile course for CV_d was generally observed. The detection probability g_d showed a general increase, with a maximum from week 41 to week 45, decreasing afterwards for the M_0 model. The number of recaptures was adjudged to be >10 for the whole time frame, >20 from week 23 to week 45, and highest (>40) from week 30 to week 38.

Within *Tr-sites,* the number of successful trap sites decreased within *S-length*$_{RC}$ = 80 days and *S-length*$_{MR}$ = 120 days as predicted with the increase of the nearest neighbor distance (Fig. 4a, b). The box plot of CV_d with *S-length*$_{RC}$ showed a

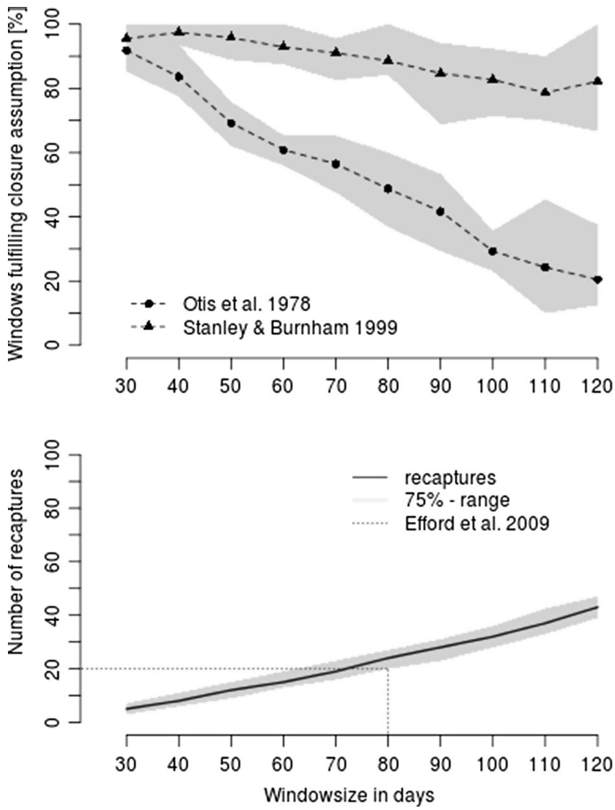


Fig. 2 *Top* Optimal monitoring session length (*S-length*). Window size fulfilling closure assumption. The *points* and *triangles* indicate the number of overall closure tests (Xc) (Otis et al. 1978; Stanley and Burnham 1999) with value >0.05 in % per window size. The proportion of significance (*closed windows*) to all tested windows is given. The range is measured with a reduced amount of data, shifted by 10 days over BFNP + $SNP_{1-3.}$ *Bottom* Number of recaptures. The bottom and top of the range (*gray shading*) indicate the 25th and 75th percentiles respectively; the horizontal line indicates the median of the recapture numbers of BFNP + SNP_{1-3}

slight increase starting at distance 4 km, and was highest at distance 5.5 km. With $S\text{-}length_{\mathrm{MR}}$, the box plot increased very slightly starting at distance 3.5 km. The mean of the detection probability per half-trap spacing g_d remained at >0.1 with $S\text{-}length_{RC}$, with one slightly lower exception at 5.5 km. The mean value of $S\text{-}length_{\mathrm{MR}}$ did not decrease below 0.1 and had its maximum at a distance of 5 km with $g_d > 0.2$. As to be expected, the number of recaptures in both $S\text{-}length_{\mathrm{RC}}$ and $S\text{-}length_{\mathrm{MR}}$ decreased with a reduction in the number of successful trap sites. Generally, fluctuations within CV_d and g_d were relatively low.

Discussion

We used our dataset to evaluate optimal parameters for Eurasian lynx monitoring with standardized methods in forested low-mountain ranges. We showed that the number of recaptures is overall a crucial variable for consistent lynx density estimates. The minimum

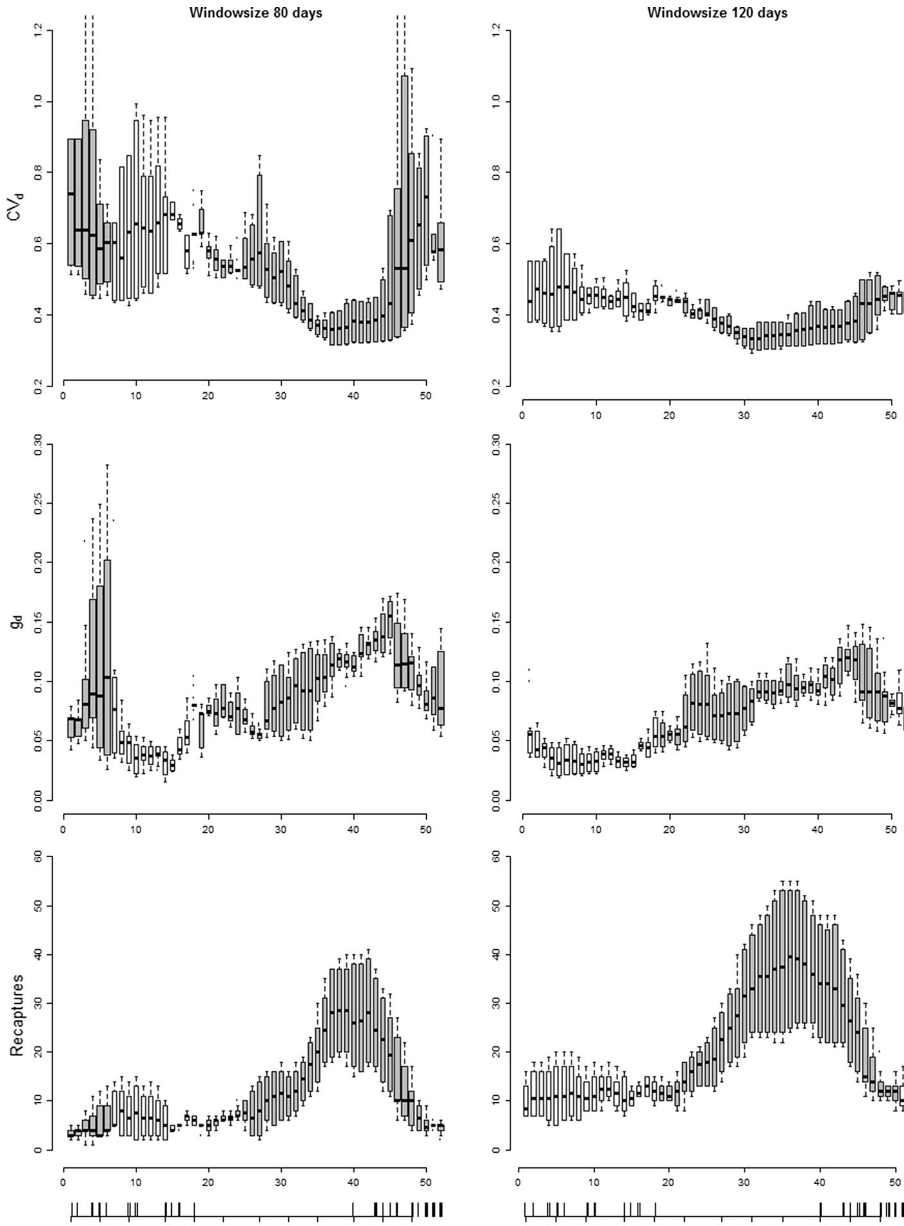


Fig. 3 Optimal seasonal time window (*S-season*). Values of the target criteria CV_d, detection probability (g_d), recaptures, and detected juveniles estimated with $\mathrm{BFNP_{total}}$, with closed SECR including M_0 ($g \sim 0$) model. The sliding window span ranges from $S\text{-}length_{\mathrm{RC}} = 80$ days to $S\text{-}length_{\mathrm{MR}} = 120$ days with the session length plotted per calendar week. Windows covering two lynx-years are in *white*

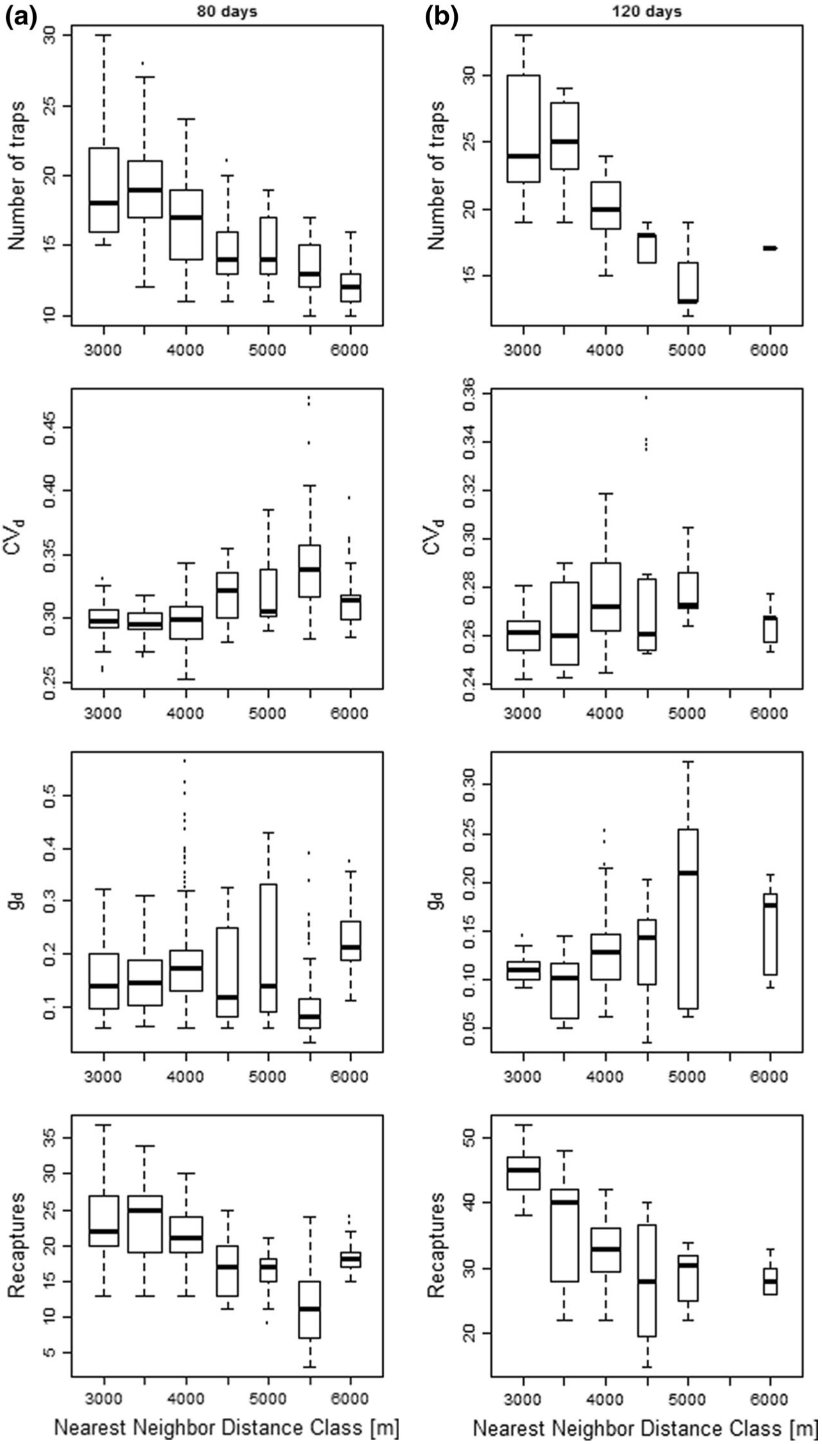
monitoring session period to ensure adequate data quality was 80 days assuming comparable recapture numbers. The best time of the year for the camera-trapping session was from late summer (beginning of September) until the beginning of winter (mid-November).

The evaluation of variants of nearest-neighbor distances showed a robust density estimate with smaller distances, higher numbers of trap sites, and shorter session lengths, and with larger distances and longer session lengths.

At the beginning of a new camera trap study in an unknown research area, two approaches are possible. First, one can predict the species density and detection probability in the area and conduct simulations with artificial camera trap data to obtain an appropriate study design. A problem of this approach is the unknown number of recaptures a field study would reach, which could result in low detection rates. This is, for instance, linked with the success rate of the trap sites in the field. To narrow a probable range of detection rates a sensitivity analysis could be conducted beforehand to support the decision making. But the seasonal variability would not be considered in this approach. The second approach would be to monitor with camera traps for as long as possible and to optimize based on the generated data.

Swiss alpine monitoring studies of Eurasian lynx have used a session length of 60 days (study area 790 km^2) based on long-term positive experience in capturing high numbers of individual lynx and recapture rates of 23 individuals/67 recaptures in 2009/2010 (Pesenti and Zimmermann 2013); this number of recaptures is higher than we obtained in our study, i.e., maximally 40 recaptures within 80 days. These higher recapture rates in the Swiss Alps were most likely achieved because of higher lynx densities and different habitat characteristics, such as steep slopes, which force individuals to use specific paths. In both the alpine study and our study, the camera-trap sites were chosen based on available telemetry data and additionally the trap success is in a comparable high range. Tobler and Powell (2013) recommend a session length of up to 120 days for jaguar (*Panthera onca*), which occur in low densities and whose detection probabilities are low, based on simulations to increase precision and decrease confidence intervals. Other studies of elusive felids, such as tigers, even sampled 6–14 months to increase the number of individuals captured (Karanth 1995; Kawanishi and Sunquist 2004). In our opinion, the risk of low recapture numbers should be minimized, and the avoidance of low recapture numbers should be weighted higher than test results for demographic closure, which can be heavily biased owing to small sample sizes with the consequence that the model cannot present reliable estimates if insufficient data are available (Noss et al. 2012; Tobler and Powell 2013).

Closed SECR models do not assume geographic closure, but demographic closure is still required, i.e., the population size remains constant within the time frame of the session. We opine that we cannot be absolutely sure about gains and losses, which influence the population extent and composition. Real demographic closure cannot be assured, but can only be approximated by avoiding in particular birthing months (May/June). The robustness of closure tests established to determine demographic closure (Otis et al. 1978; Rexstad and Burnham 1991) have been discussed controversially (Foster and Harmsen 2012). Capture–recapture models were originally constructed for large sample sizes of, e.g., birds and insects (Krebs 1999). Since studies of elusive species, such as the Eurasian lynx, have low sample sizes (only 10–20 individuals), the difficulty in obtaining reliable estimates is clear (Otis et al. 1978; White 1982). Closure tests with small sample sizes are considered to provide little evidence (Kawanishi and Sunquist 2004) and are limited in their ability to distinguish between insufficient closure and behavioral changes affecting detection probabilities (Soisalo and Cavalcanti 2006). In our opinion, the existing closure tests are not appropriate for revealing robust values with small recapture numbers as in our study. We agree with Harmsen et al. (2011), who emphasize that the session length is a trade-off between a time frame short enough not to violate the closure


(a)
80 days
(b)
120 days
Number of traps
CV$_d$
g_d
Recaptures
3000
4000
5000
6000
Nearest Neighbor Distance Class [m]

◀**Fig. 4** Number of trap sites (*Tr-sites*). Target criteria (*CV_d, g_d, recaptures)* with decreasing number of trap sites per nearest neighbor distance within BFNP + $SNP_{1–3}$ for **a** *S-length*$_{RC}$ = 80 days and **b** *S-length*$_{MR}$ = 120 days as session length. *Box plot* classes were chosen with 500 m

assumption and a sufficient amount of data to assure reliable and robust estimates. The definition of "sufficient" data is still problematic as there are no real thresholds. In the absence of species-specific benchmarks, we followed the plausible recommendation of Efford et al. (2009) of at least 20 recaptures. We are aware that precision increases with increasing recapture numbers, and attempts should be made to increase the numbers.

For Eurasian lynx in mountainous areas with habitat conditions and species densities similar to those in our study area, we recommend a session length of at least 80 days. Better would be 100–120 days, which would take into account the possible decrease in recaptures owing to population dynamics and possible changes in detection probability. Studies in unknown research areas, which cannot rely on field knowledge of the area, such as telemetry, snow tracking, or prey data, should primarily not expect high trap success rates (>50 %) within the first monitoring sessions, which in turn results in low recapture numbers.

In our analysis of (1) *S-length* and (3) *Tr-sites,* we analyzed the area of two national parks (BFNP + SNP_{1-3}) comprising around 750 km^2. In our analysis of (2) *S-season,* we analyzed the data of only one national park ($BFNP_{total}$) comprising 240 km^2. According to Lehnert et al. (2013), most national parks in mountainous areas of Central Europe are >100 km^2, with a maximum size of 200–300 km^2. Thus, our study area BFNP + SNP_{1-3} lies in the upper 29 % of national park sizes, and even the size of $BFNP_{total}$ can be described as a representative of that of a national park in Central Europe. The study area size of $BFNP_{total}$ lies between that of a mean female home range in the area [122 km^2 (MCP 95)] and a that of a mean male home range (Tobler and Powell 2013), and thus in the lower range of the recommended study area size (Zimmermann et al. 2013).

We used closed SECR models to analyze the time frame of 2.5 years; such models have been assessed as being more robust with decreasing trap array size (Marques et al. 2011; Sollmann et al. 2012). Four of five criteria showed the most stable and highest values from week 35 (late August) to week 50 (beginning of November). However, the affected national parks of the study area have a very high interest in detecting juveniles. If we also take the juveniles into consideration, the best time frame for the monitoring session would start later, i.e., in October (week > 40), as we did not detect juveniles earlier in the year. The detection ends in late April, when juveniles disperse. Female lynx keep their kittens in dens during the first months after birth (May/June–August/September). In the late summer months, the kittens start to join their mother on excursions and later during hunting. By October, the kittens are able to keep up with their mother, even on long excursions, and dens are no longer needed. Therefore, considering all criteria, we recommend camera-trap sessions between mid/late September and the beginning of December.

Blanc et al. (2013) timed their monitoring session of Eurasian lynx in the French Jura Mountains outside the assumed subadult dispersal period (February–April). According to camera-trap data in our study area, the dispersal period of subadults starts in late January, is highest during April/May, and lasts until the end of summer. The risk of immigrating floaters in lynx studies is present all year long, but most likely increases during pre-mating season (December/January) and mating season (February/March) as males from other areas search for mates. In their analysis of long-term telemetry data in their alpine study area, Pesenti and Zimmermann (2013) did not find a significant effect of season on lynx space use in the Swiss Alps and thus monitored from December until January and accordingly from December until February (Zimmermann et al. 2013). In our study, we observed a decline in detection probability within this time period, which do not favor these months for monitoring in our study area. The snowy season in our region usually begins at the end of November or even mid-December. During the snow season, the camera control effort can double or even triple because of the snow height, snow-covered cameras, and shorter battery life. Snow can also lead to trap failure, which can result in underestimation or overestimation (Foster and Harmsen 2012). Therefore, late summer until the beginning of winter is a better season for monitoring as it is more efficient and the risk of losing data is lower (Weingarth et al. 2012b). There might be technical or formal reasons that the monitoring can only be carried out during the winter or spring months. Therefore, we recommend extending the session length as the variance of the CV_d and g_d is reduced with 120 days as session length, rather than 80 days (Fig. 2). Still, our recommendation for camera-trap sessions between mid/late September and the beginning of December are the best choice for our study area and comparable areas.

In (3) *Tr-site*, the relatively highest CV_d and the widest range were reached over all nearest-neighbor distance variants when the number of trap sites was lowest (Fig. 4a, b). This can be explained by the reduced number of input data of captures and recaptures available for the model calculation. Trap-site spacing is dependent on the movement of individuals of the species and on the size and shape of the study area (Rovero et al. 2013). Two recent studies provide contrasting views on trap spacing. On the one hand, the jaguar density estimates of Tobler and Powell (2013) remained stable with their SECR simulations until the distance between trap sites achieved a larger radius than that of a mean home range. As with jaguars female lynx home ranges are smaller than these of males, in our study area about 350 %. Due to this heterogeneity females consequently have the chance to be detected by fewer traps (Sollmann et al. 2011). With 122 km^2 as the mean female home range size in the study area, this would mean a maximum spacing of 6.2 km between trap sites taking Tobler and Powell (2013) into consideration. This underlines our results which indicate optimal trap spacing between 3 and 6 km, considering the criteria of a low and stable CV_d and a preferably high detection probability. For the conditions in both our study areas (BFNP, BFNP + SNP), we agree with Noss et al. (2012), who emphasize that the number of trap sites should ensure multiple detections per animal home range, thus increasing the likelihood of a large number of recaptures. In this case, we can assume a positive effect on individual detection probability (Harmsen et al. 2010; Larrucea et al. 2007).

We included detection probability (g_d) in the half-trap spacing and achieved relatively high values of g_d with larger grid sizes, especially with *S-length*$_{\mathrm{MR}}$. Therefore, we hypothesize even higher values of detection probability as we approach the animals' centroid of the circular imaginary home ranges.

Our data indicated that a session length of even 120 days offers the possibility of enlarging the study area by increasing the grid size to 5–6 km without unstable parameters such as CV_d and g_d. This would be of interest if we consider the potential of monitoring a larger area with the same number of cameras, thereby saving material costs. For further analyses Karanth and Nichols (2002) offer several randomized sampling methods with grid and block approaches to test additional types of sampling regimes. These analyses may offer more flexible monitoring protocols to researchers which are constrained in either space or time and still ensure robust density estimates.

In order to conduct a similar analysis as ours, it is necessary to obtain a highly resolving dataset of an individual recognizable species as a baseline, as we for instance sampled two consecutive years. The moving window is a very efficient method which can also be applied on already existing data to get variance of the results. Obtaining highly resolving data means a lot of effort, which not many projects are able to achieve. As our study area is a common representative of a low mountain range in Central Europe, we see our study as solid reference for future monitoring of Eurasian lynx.

Conclusion

Our results revealed two possible scenarios for *Tr-sites* dependent on the size of the study area. First, for BFNP (MCP $\sim$ 313 km^2), we assume a high risk of not reaching the required number of 20 recaptures for a reliable estimate of density with a reduced number of camera-trap sites. Therefore, we recommend a spacing of 2.5–3 km for consistent results for study areas that size, similar recapture numbers and accordingly, home range sizes. We also recommend this spacing for new lynx monitoring projects with the goal of density estimations in areas with unknown numbers of lynx to ensure sufficient recaptures numbers.

Second, we assume a spacing of 5–6 km for study areas of the size BFNP + SNP (MCP $\sim$ 760 km^2). However, this scenario presumes extensive knowledge of the status quo and the preconditions in the area, such as approximate density numbers and movement patterns of the species.

Our results can be applied to other Central European low mountain ranges with a similar setting (prey resources, climate and topographical conditions etc.). Additionally lynx are on the rise in several European countries (Chapron et al. 2014; Müller et al. 2014) especially such as Germany, Austria and the Czech Republic due to reintroduction or natural recovery. So the presented results can act as benchmark for future monitoring protocols.

In summary, we recommend smaller nearest-neighbor distances and longer session length at the beginning of a study in unknown research areas to enhance the chance of high recapture rates and to create a solid basis for monitoring adaptations.

In the context of achieving a sufficient dataset for estimates (>20 recaptures), the importance of long-term monitoring becomes obvious, which enables optimization of trap sites for higher numbers of recaptures and ensures larger datasets of multi-sessions (Efford 2015) for more precise estimates. The use of demographically open SECR models (Gardner et al. 2010) avoid the problem of a too-short session length to ensure demographic closure but therefore does not achieve adequate data quality. Recent studies of elusive species have combined genetic data with SECR frameworks, which allows more precise population estimates by merging several sparse datasets (Sollmann et al. 2013).

Acknowledgments We are very grateful to Martin Gahbauer for providing his experience and knowledge for the camera-trapping project. We also thank Murray Efford for advice. This study was supported by the World Wide Fund for Nature Section Germany (WWF Germany) and was part of a project on the predator–prey relationships of Eurasian lynx, red deer, and roe deer carried out by the Bavarian Forest National Park and a long-term research project on the Eurasian lynx in the Šumava National Park. Financial support was also provided by EU Program Interreg IV (Objective 3 Czech Republic - the Independent State of Bavaria). Last but not least we are grateful to Karen A. Brune for linguistic supervision.

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