# **ORIGINAL ARTICLE**

# Optimizing the size of the area surveyed for monitoring a Eurasian lynx (*Lynx lynx*) population in the Swiss Alps by means of photographic capture–recapture

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## Abstract

We studied the influence of surveyed area size on density estimates by means of camera-trapping in a lowdensity felid population (1–2 individuals/100 km<sup>2</sup>). We applied non-spatial capture–recapture (CR) and spatial CR (SCR) models for Eurasian lynx during winter 2005/2006 in the northwestern Swiss Alps by sampling an area divided into 5 nested plots ranging from 65 to 760 km<sup>2</sup>. CR model density estimates (95% CI) for models M<sub>0</sub> and M<sub>h</sub> decreased from 2.61 (1.55–3.68) and 3.6 (1.62–5.57) independent lynx/100 km<sup>2</sup>, respectively, in the smallest to 1.20 (1.04–1.35) and 1.26 (0.89–1.63) independent lynx/100 km<sup>2</sup>, respectively, in the largest area surveyed. SCR model density estimates also decreased with increasing sampling area but not significantly. High individual range overlaps in relatively small areas (the edge effect) is the most plausible reason for this positive bias in the CR models. Our results confirm that SCR models are much more robust to changes in trap array size than CR models, thus avoiding overestimation of density in smaller areas. However, when a study is concerned with monitoring population changes, large spatial efforts (area surveyed  $\geq$ 760 km<sup>2</sup>) are required to obtain reliable and precise density estimates with these population densities and recapture rates.

Key words: area surveyed, density estimation, Lynx lynx, photographic capture–recapture, Swiss Alps

# **INTRODUCTION**

Good decisions in management and conservation rely on precise data about the size, density and structure of

*Correspondence*: Fridolin Zimmermann, KORA, Thunstrasse 31, CH-3074 Muri, Switzerland. Email: f.zimmermann@kora.ch the focal populations and their evolution over time (Fergus 1991; Sadlier *et al.* 2004). However, large carnivores, which often conflict with livestock breeders and hunters, tend to be difficult to monitor because they are generally nocturnal, secretive in nature, have large home ranges, often live in dense cover habitat and occur at low population densities. Home range size is a good measure of density for territorial species (Breitenmoser *et al.* 1993; Burch *et al.* 2005; Balme *et al.* 2009). However, radio-telemetry is rather time-consuming and expensive, and potentially risky, compared to non-invasive monitoring methods, and does not provide any measure of the precision of the estimation. In addition, there is uncertainty about the proportion of tagged individuals in the population, and, thus, density can generally only be estimated for the resident territorial animals.

Camera-traps have the advantage of being non-invasive and applicable over large areas, with relatively moderate effort. For species with individually-distinct fur patterns, data from camera-trapping can be analyzed using capture–recapture models, to estimate abundances and densities or population dynamics (Karanth *et al.* 2006). These models account for the fact that not necessarily all animals in the study area are observed. This methodology has been applied to a range of species, such as: common genets [*Genetta genetta* (Linnaeus, 1758)] (Sarmento *et al.* 2010); striped hyenas [*Hyaena hyaena* (Linnaeus, 1758)] (Harihar *et al.* 2010; Singh *et al.* 2010a), and, in particular, large cats with individual distinctive coat patterns (e.g. Karanth & Nichols 1998; Silver *et al.* 2004).

One important aspect of camera-trapping, when used in combination with non-spatial capture-recapture (CR) models, is the estimation of the area to which the abundance refers (i.e. area effectively sampled). In CR models, the 'area effectively sampled' is defined by adding a boundary strip to the trap polygon, to account for the additional area from which trapped individuals are taken. The buffer has traditionally been estimated as either the mean maximum distance moved (MMDM) (Dillon & Kelly 2008; Soisalo & Cavalcanti 2006) or half the mean maximum distance moved (1/2 MMDM) (Karanth 1995; Karanth & Nichols 1998, 2002) between photocaptures, for each individual caught at  $\geq 2$  camera-trapping sites in the area covered by the camera-traps. Study design must take into consideration both the spacing of traps, relative to individual movement, and the total size of the trap array (Foster & Harmsen 2011).

An important requirement of capture–recapture models is that no target-species individual within the sampled area has a zero probability of being captured, and there should be at least 1 sampling site per smallest home range (Karanth & Nichols 1998), resulting in an upper limit to possible trap spacing.

The resolution of the information on individual movement is determined by trap spacing. If trap spacing is too wide, most animals will only be captured at a single trap, and little or no information on movement will thus be gained. For example, Dillon and Kelly (2007) show that density estimates are significantly negatively correlated with distance between cameras. Furthermore, only an area covered by camera-traps that is large enough, relative to the movement of an individual, can capture the full extent of such movements. Various studies have reported that lower densities tend to be recorded for species when censused over larger areas (e.g. Cuellar et al. 2006; Jackson et al. 2006; Dillon & Kelly 2007; Foster 2008; Maffei & Noss 2008). Possible reasons for this positive bias, discussed by Foster and Harmsen (2011), are: individuals moving further than the maximum distance between traps, resulting in an underestimation of the true home range; high individual range overlaps in relatively small areas (i.e. 'edge effects' according to Gaston et al. 1999); and small survey areas that may fail to sample all available habitat types (e.g. Jackson et al. 2006). All these assumptions and considerations are related to the non-spatial models and guide the sampling design of capture-recapture studies.

Recently, a second method, using the location-specific individual capture histories, to construct a spatial capture-recapture (SCR) model was developed by Efford (2004) and Royle et al. (2009a,b). SCR explicitly describes a model of individual movement and distribution in space, relative to the trap array, and, therefore, the problem of estimating the effective area sampled is circumvented, as the trap array is embedded in a large area called the state space. So far, only a few studies have examined the sensitivity of SCR model estimates to study area size and shown that these models are much more robust to changes in trap array size and spacing (Margues et al. 2011; Sollmann et al. 2012). Here, we investigate the effect of the size of the area surveyed on density and movement estimates, in both CR and SCR models. The following questions are specifically addressed:

- 1. What is the effect of survey area size on the density and movement parameter estimates?
- 2. Which of the 2 approaches (CR or SCR) is less sensitive to the size of the study area?
- 3. What is the minimum survey area required for monitoring lynx with camera-traps in a fragmented landscape such as the Alps that will provide reliable results?

# **MATERIALS AND METHODS**

#### Study area

The study was conducted between the lake of Thun in central Switzerland and the lake of Geneva on the Swiss–French border, including the Simmental. The elevation ranges from 626–2749 m. The valley bottoms and slopes were increasingly deforested up to 1873, when a restrictive forest law was enacted (Breitenmoser & Breitenmoser-Würsten 2008) to provide pasture land for cattle and sheep. The human population density is 33 inhabitants/km<sup>2</sup>, in most parts of the study area, and people living in the lowlands use the area intensively for recreation (skiing and hiking). With 3.4 km/km<sup>2</sup>, there is a good network of forest roads and trails within the study area. Forests are highly fragmented and cover 27% of the study area. They extend along steep slopes up to the timberline at 1800–1950 m. The mean snow depth from Dec 2005–Apr 2006 was 0.5 m at 1200 m, and the temperature varied from -19.4 to 15.6 °C during this period.

# Timing of the camera-trapping session

The optima camera-trapping period for Eurasian lynx [Lynx lynx (Linnaeus, 1758)] is in the winter months, because there is an increased capture probability, due to lynx, including females accompanied by kittens, making larger movements, more frequently, before and during the mating season in Mar (Breitenmoser & Breitenmoser -Würsten 2008). Lynx use forest roads and trails more frequently in winter, and snowy ground conditions aid the optimization of camera-trap location sites, at the beginning of the survey, by revealing lynx tracks and their movement corridors. The creation of trails by field researchers after fresh snowfall also allows lynx to be directed in front of camera-trap sites. Therefore, cameratraps were operated from the night of 3 Dec 2005 to the morning of 6 Feb 2006, for a period of 65 nights. The short sampling period and biological seasonality justify considering the studied population as demographically and geographically closed: there are no births during this time (all births occur in May/Jun) (Breitenmoser-Würsten et al. 2001); the chances of a lynx dying over this short period of time is low; and immigration and emigration are at their lowest as the majority of juveniles only start to disperse by mid-Apr (Zimmermann et al. 2005).

# Sampling design and site selection

In 1998, Laass (1999) tested the application of camera-trapping in a 550 km<sup>2</sup> reference area (polygon D in Fig. 1) in the northwestern Swiss Alps (46.56°N, 7.44°E), parallel to radio-telemetry observation. In winter 2005/2006, the original reference area was extended towards the southwest, to encompass a total area of 760 km<sup>2</sup> (polygon E in Fig. 1). A 2.7 × 2.7 km grid, with



**Figure 1** The systematic camera-trapping study areas in the northwestern Swiss Alps (NWSA). Lynx densities were estimated for different areas surveyed, increasing in size (A–E: 65, 181, 320, 550 and 760 km<sup>2</sup>; black polylines), starting from the north to the southwest. Grid cells  $(2.7 \times 2.7 \text{ km})$  were placed over the area for study design, with more than two-thirds of the area above 1800 m altitude (dark gray areas) disregarded. An optimal site with paired camera-traps was chosen in every second grid cell (light gray cells). The outer polygon shows the area effectively sampled (polygon plus buffer) according to the method described by Karanth and Nichols (1998) for the total area (polygon E). The white dots show the camera-trap sites, and those with black dots the sites with lynx detections.

a random origin, was overlaid on the camera-trapping study area (Fig. 1). Grid cells with more than two-thirds of their area above 1800 m were discarded because lynx rarely use habitat above the timberline (Breitenmoser-Würsten et al. 2001) and accessibility for maintenance must be guaranteed. An optimal camera-trap site (i.e. principally on a forest road or hiking trails, or, on rare occasions, on a game pass or bridge known to be used by lynx) was chosen in every second grid cell. When it was not possible to find a suitable site, an ideal spot was chosen in an adjacent cell. A total of 54 trap sites were deployed, resulting in an overall trap site density of 1/15 km<sup>2</sup>. This camera-trap density ensured that the area sampled included no gaps that could contain an entire animal's home range, which is a prerequisite of CR studies. The sampling design, and the spatial analyses were performed using the Geographic Information System ArcView 3.3 (ESRI, Redlands, USA).

#### **Camera-traps and site maintenance**

We used 3 types of analogue camera-traps (Theodor Kocher Institute, University of Bern, Bern, Switzerland; Bandgenossenschaft–Bern; Camtrak, South, Watkinsville, GA, USA), which stamp each photograph with the time and the date of the event. At each site, 2 devices were placed opposite each other, to photograph both flanks of lynx and, therefore, guarantee identification. Because lynx are mostly crepuscular and nocturnal (Bernhart 1990) and to minimize activation by people, the units were set to operate from 1630–0900 hours. Camera delay (the minimum time between 2 photographs) was set to the minimum possible time, which corresponds to 15 s for the Theodor Kocher and Bandgenossenschaft–Bern camera-traps and 18 s for the Camtrakker.

The camera-traps were checked every 6 or 7 days, to change batteries and film, to remove fresh snow and to make a trail of at least 200 m on either side of the site.

#### Identification of the lynx

Lynx were identified from photographs, by comparing their distinct pelage patterns (Fig. 2). Reference photographs from earlier studies aided in the identification. The best body parts for identification are the hindlimbs, the forelimbs and the flanks. At least 2 people independently compared the relative position of several spots or rosettes on the animal's body.

# Estimation of abundances and densities using the capture-recapture model

The data for CR models are the capture histories of all observed lynx, each consisting of a string of '1' and '0', representing sampling occasions with and without capture (photograph) of the respective lynx (Otis *et al.* 1978). A sampling occasion was defined as 5 consecutive trap nights, resulting in a total of 13 sampling occasions. We analyzed these data using the module CAP-TURE in the program MARK 3.1 (White & Burnham 1999). Young lynx (juveniles) are visually distinct from adults and sub-adults in this season and still follow their mother, so a picture of any family group member counts as a capture of the respective female (if known) in the capture history. Independent dispersers (subadults) cannot be distinguished from resident animals (adults) using pictures, and, hence, the estimated abundance refers



**Figure 2** Camera-trap photographs of lynx showing 2 different coat patterns. Lynx B53 with large spots (a,b) and B100 (c,d) with rosettes.

to 'independent lynx'; that is, these are residents plus dispersers, or adults plus sub-adults.

We checked for population closure, using the closure test of Stanley and Burnham (1999) implemented in the program CloseTest 3.0. The module CAPTURE tests several models that differ in their assumed sources of variation in capture probability, including: constant capture probability  $(M_0)$ ; variation among individuals  $(M_h)$ ; variation across occasions (M<sub>t</sub>); and responses to previous captures  $(M_{\rm b})$ . It selects the 'best' model from a set of 8 closed-population models (M<sub>0</sub>, M<sub>h</sub>, M<sub>t</sub>, M<sub>b</sub>, M<sub>bh</sub>, M<sub>th</sub>, M<sub>th</sub> and M<sub>thh</sub>) (Otis et al. 1978). The overall model selection function scores potential models between 0.0 and 1.0, with a higher score indicating a better relative fit of the model to the specific capture history data generated by the survey. For each analysis, the program CAPTURE estimates capture probabilities (p) and the lynx abundance (N).

We followed the procedure described by Karanth and Nichols (1998) to estimate lynx density within the area surveyed. The area effectively sampled (A) was defined as the polygon connecting the outermost camera-traps of the selected camera location plus a buffer area whose width (W) is an estimate of the 'home range radius', averaged for lynx in the area surveyed. This width was estimated as 1/2 MMDM between photo-captures for each individual lynx captured at 2 or more camera-trap sites during the sampling period. Density was obtained by dividing the abundance by the area effectively sampled (for details, see Wilson & Anderson 1985; Karanth & Nichols 1998).

We estimated density for 5 different subsets of camera-traps covering different areas surveyed, each including only the data from the respective camera-traps in the subset. The size of the area surveyed was successively enlarged starting from the north to the southwest: A, 65 km<sup>2</sup>; B, 181 km<sup>2</sup>; C, 320 km<sup>2</sup>; D, 550 km<sup>2</sup>; and E, 760  $\text{km}^2$  (Fig. 1), where each area includes the previous areas (e.g. C contains A and B). The percentage of suitable habitat in each area effectively sampled (polygon plus buffer) was calculated using a habitat suitability model for lynx in Switzerland (Zimmermann 2004). We did not remove habitat deemed unsuitable from the area effectively sampled for density estimation but only performed this analysis to check if the amount of suitable habitat varied between the survey areas. This procedure excluded the highly unsuitable areas, such as settlements, intensively-used agriculture areas, lakes, large rivers and high mountain peaks above 2000 m, which are not used by resident lynx.

# Density estimation with spatial capturerecapture models

Spatial capture–recapture models are implemented in SPACECAP (Singh *et al.* 2010b), a package of the program R (R Development Core Team 2012). These models estimate animal density using individual and camera-trap site-specific capture histories in a Bayesian framework (Royle *et al.* 2009a,b). The same survey duration and number of sampling occasions were used as in the regular CR models. In SCR models, density is estimated as the number of individuals within the state space, a prescribed area that contains the trap array and that is large enough so that it contains all individuals that could have been exposed to the trapping.

Following Pesenti and Zimmermann (2013), estimates of the state space included the polygons (A–E), encompassing the area surveyed plus a buffer of 15 km, to ensure that no individual outside of the buffered regions had any probability of being photo-captured by the camera-traps during the survey. Each state space was described as a grid of  $1.5 \times 1.5$  km spaced points (2.25 km<sup>2</sup>), corresponding to areas of: A, 566 km<sup>2</sup>; B, 777 km<sup>2</sup>; C, 970 km<sup>2</sup>; D, 1200 km<sup>2</sup>; and E, 1541 km<sup>2</sup>.

Bayesian analysis of the model was conducted using data augmentation (Royle *et al.* 2007): the dataset was increased with 100 'all zeros' encounter histories. We ran a Markov chain Monte Carlo chain with 50 000 iterations, a burn in of 25 000 and a thinning rate of 3. Under the assumption of a bivariate normal model for animal movement, the movement parameter from the SCR model,  $\sigma$ , can be converted into an estimate of home range radius.

# RESULTS

# Photographic captures of lynx

Lynx were photographed 78 times at 34 of the 54 sites in the total area (63%; Fig. 1). At each camera-trap site where lynx were detected, lynx were photographed, on average, 2.3 times (1–7 times). With the exception of 1 blurred picture, all individual lynx were identified, resulting in 19 independent lynx, plus 5 juveniles. The

| capture pi            | obability per sar    | mple ( $\hat{p}$ ) and | d buffer width                | with sam   | ole size $(n)$ in the         | ne polygons  | A-E (Fig. 1)                  | (                                 |              | AT                                     |               |                |
|-----------------------|----------------------|------------------------|-------------------------------|------------|-------------------------------|--------------|-------------------------------|-----------------------------------|--------------|--|---------------|----------------|
|                       |                      |                        | Model $M_0$                   |            | Model $M_h$                   |              |                               |                                   |              |  |               |                |
| Polygon               | Positive/total sites | Number of<br>lynx      | $\hat{N} \pm S\hat{E}\hat{N}$ | ŷ          | $\hat{N} \pm S\hat{E}\hat{N}$ | ŷ            | Polygon<br>(km <sup>2</sup> ) | Buffer $\pm S\hat{E}\hat{W}$ (km) | ( <i>u</i> ) | Polygon +<br>buffer (km <sup>2</sup> ) | Increase (%)  | Habitat<br>(%) |
| A                     | 8/10                 | 8                      | 8 ± 0.92                      | 0.181      | $11 \pm 2.42$                 | 0.133        | 65                            | $4.86 \pm 1.1$                    | e            | 306                                    | 371           | 83             |
| В                     | 12/19                | 10                     | $10 \pm 0.79$                 | 0.208      | $12 \pm 2.03$                 | 0.173        | 181                           | $4.67\pm0.68$                     | 9            | 524                                    | 190           | 06             |
| C                     | 18/28                | 12                     | $12 \pm 0.83$                 | 0.211      | $15 \pm 2.42$                 | 0.169        | 320                           | $5.49 \pm 0.74$                   | L            | 840                                    | 163           | 91             |
| D                     | 24/37                | 14                     | $14 \pm 0.78$                 | 0.225      | $17 \pm 2.42$                 | 0.186        | 550                           | $4.98\pm0.67$                     | 6            | 1110                                   | 102           | 89             |
| Щ                     | 34/54                | 19                     | $19 \pm 0.80$                 | 0.239      | $20 \pm 2.79$                 | 0.227        | 760                           | $5.3 \pm 0.58$                    | 11           | 1587                                   | 109           | 89             |
| Increase <sup>9</sup> | 6, percentage of     | increase of th         | ie area survey                | ed when th | he buffer is add              | ed to the pc | lygon; habita                 | at %, percentage                  | of suitab    | le habitat in the p                    | olygon plus t | uffer.         |

Camera-trapping of lynx in the Swiss Alps

sex of 4 individuals (2 males and 2 females) was known from physical captures during the radio-telemetry work. Photographs allowed the sex of an additional 3 individuals (2 females and 1 male) to be identified. In the present study, 4 lynx were only detected on 1 occasion, 4 on 2 occasions, 3 on 3 occasions, 3 on 4 occasions, 4 on 5 occasions and 1 on 6 occasions. The number of different independent lynx reached a plateau at the ninth sampling occasion, stabilizing at 19 lynx, but the total captures increased steadily, to a total of 59 captures, as a result of condensing the 78 photographs to a 0/1 capture history format, on the last sampling occasion.

### Capture-recapture models

The statistical test for population closure of Stanley and Burnham (1999) supported our assumption that the sampled populations were closed (P > 0.05) for the study interval, in all surveyed areas, except for area C  $(\chi^2 = 21.58, df = 10, P = 0.017)$ . Although model M<sub>0</sub> was the apparent model of choice for all surveyed areas (model selection function score = 1.0), the estimator of abundance associated with this model is known to be sensitive to violations of the underlying model assumption of homogenous capture probabilities (e.g. Otis et al. 1978; Karanth & Nichols 1998). The next best model was M<sub>h</sub> (model selection function scores: 0.77–0.94), which, in contrast, is known to be robust to violations of the underlying model assumptions (Burnham & Overton 1978; Otis et al. 1978), and, therefore, is more biologically meaningful for solitary felids (Karanth & Nichols 1998).

The capture probability, per sampling occasion, ranged from 0.181–0.239 for M<sub>0</sub>. The corresponding abundance estimates ( $\hat{N}$ ) increased from 8, with an SE ( $\hat{SEN}$ ) of 0.92 in the smallest area surveyed, to 19 (± 0.80), in the largest area surveyed. The overall probability of capturing a lynx present in the area surveyed (number of identified individuals/ $\hat{N}$ ) was 100% for all surveyed areas.

To generate parameter estimates under the  $M_h$  model, we used the jackknife estimator implemented in CAP-TURE, which performed well in earlier capture studies of felids (Karanth 1995; Karanth & Nichols 1998). Using the  $M_h$  jackknife estimator, the average capture probability per sampling occasion ( $\hat{p}$ ) ranged from 0.133 to 0.227.  $\hat{N}$  increased from 11, with an  $S\hat{E}\hat{N}$  of 0.92, in the smallest area surveyed to 20 (2.79) in the largest area surveyed. Thus, the overall probability of

|            | Ν     |      | b    |      | $\lambda_0$ |        |                               | State space                    |                         |
|------------|-------|------|------|------|-------------|--------|-------------------------------|--------------------------------|-------------------------|
| Trap array | mean  | SD   | mean | SD   | mean        | SD     | 95% home range<br>radius (km) | $N (1.5 \times 1.5$ -km cells) | area (km <sup>2</sup> ) |
| A          | NA    | NA   | NA   | NA   | NA          | NA     | NA                            | 566                            | 1273.50                 |
| В          | 24.80 | 9.49 | 4.62 | 1.08 | 0.0839      | 0.0192 | 11.30                         |                                | 1748.25                 |
| C          | 27.55 | 7.89 | 5.21 | 0.88 | 0.0464      | 0.0129 | 12.75                         | 970                            | 2182.50                 |
| D          | 32.49 | 7.81 | 4.60 | 0.68 | 0.0624      | 0.0231 | 11.26                         | 1200                           | 2700.00                 |
| Ш          | 35.97 | 6.61 | 4.88 | 0.51 | 0.0632      | 0.0108 | 11.95                         | 1541                           | 3467.25                 |

capturing a lynx present in the area surveyed ranged from 72.7% to 95%.

The buffer width  $(\hat{W})$  and  $S\hat{E}\hat{W}$  remained almost stable, ranging from 4.67 km in polygon B ( $S\hat{E}\hat{W} = 0.68$  km) to  $5.49 \pm 0.74$  km in polygon C (Table 1). The area effectively sampled  $(\hat{A})$  ranged from 306 km<sup>2</sup> ( $S\hat{E}\hat{A} = 52.87$  km<sup>2</sup>: polygon A. Table 1) to  $1587.48 \pm 82.32 \text{ km}^2$  (polygon E. Table 1). The proportion of suitable habitat within the polygon plus buffer was approximately 90%, except for the smallest area, where it was 83% (Table 1). The density estimates  $(\hat{D})$  under models M<sub>0</sub> and M<sub>b</sub> ranged from 2.61 (95% CI 1.55-3.68) and 3.60 (95% CI 1.62-5.57) independent lvnx/100 km<sup>2</sup>, respectively, in polygon A (65 km<sup>2</sup>) to 1.20 (95%CI 1.04–1.35) and 1.26 (95% CI 0.89-1.63) independent lynx/100 km<sup>2</sup>, respectively, in polygon E (760 km<sup>2</sup>). Density estimates, and respective 95% CI, decreased rapidly from polygon A to C, but only decreased moderately in the larger polygons C to E (Fig. 3). Density estimates under model  $M_0$  in nested polygons A and B were significantly (i.e. mean of value a not within 95% CI of value b and vice versa) higher than those estimated in nested polygons C, D and E, but densities did not differ within each of these 2 groups. Density estimates under model M<sub>h</sub> did not differ significantly, except for the polygon pairs A/D, A/E and B/E. Density estimates (M<sub>0</sub> and M<sub>b</sub>) were significantly negatively correlated with polygon size (Spearman rank correlations:  $r_s = -1$ ; P < 0.05 for both models).

# **SPACECAP**

No results are shown for the smallest polygon A, as SPACECAP provided an unrealistically large value for the movement parameter  $\sigma$  (Table 2). The posterior mean of the baseline encounter rate,  $\lambda_0$  (posterior SD), ranged from 0.0464 (0.0129) in polygon C to 0.0839 (0.0192) in polygon B. The 95% home range radius estimates ranged from 11.26 km in polygon D to 12.75 km in polygon C (Table 2). Density was derived by dividing the estimated mean lynx population sizes (N) by the area of the state space (Table 2), resulting in mean posterior density estimates (95% posterior interval) ranging from 1.42 independent  $lynx/100 \text{ km}^2$  (0.57–2.40) in state space B (1748.25 km<sup>2</sup>) to 1.04 (0.69–1.38) in state space E (3467.25 km<sup>2</sup>; Fig. 3). Compared to the CR models, SCR density estimates were not significantly negatively correlated with polygon size (Spearman rank correlations:  $r_s = -1$ ; P = 0.083; Fig. 3). The decrease in their respective 95% posterior interval was, however,



Figure 3 Density estimates (independent lynx/100 km<sup>2</sup>) and 95% confidence interval or 95% posterior interval for the spatial model in relation to the size of the area surveyed (polygon around trap sites) for the non-spatial models  $M_0$  (triangles) and  $M_h$  (dots) and the spatial model (squares). Density estimate for the spatial model is missing for the smallest polygon (A), as the estimated movement parameter ( $\sigma$ ) was unrealistically large.

comparable to that observed for the CR models (Fig. 3). SCR density estimates in nested polygons (B–D) were included in the 95 posterior interval of density estimate for the full dataset (polygon E; Fig. 3). SCR model density estimates did not differ significantly from the regular CR model density estimates, irrespective of the polygon.

# DISCUSSION

Our evaluation of density estimates from lynx camera trapping data showed that when using CR models, the survey area size has a strong effect on density estimates. Closed population CR models do not only assume demographic but also geographic population closure. Although the former can be approximated with an adequate survey duration, the latter is only given when animal movement is physically restricted to the sampled area, for example by a fence or on an island. Otherwise, individuals will move in and out of the area surveyed during the study. The successive increase of the size of our area surveyed shows that the different 'populations' (polygons A to E) were not geographically closed, regardless of the size of the areas surveyed (65, 181, 320, 550 and 760 km<sup>2</sup>; Fig. 1). One individual in polygon A, 2 individuals in polygon B, another 2 in polygon C and 2 more in polygon D were also photographed outside of these respective areas in polygon E. To estimate density in a geographically-open population with CR models, the home range of the species should be negligible compared to the study area (White *et al.* 1982), which is generally not feasible for wide-ranging species such as large carnivores. Traditionally, a buffer width of 1/2 MMDM is added to the study area, representing the additional area used by the captured individuals outside of the trapping grid, but estimates of MMDM can be sensitive to the spatial study design. In contrast, SCR models explicitly include animal movement beyond the trapping grid into the model (e.g. Efford 2004; Royle & Young 2008).

In our study, the density estimates derived from CR models showed a significant downward trend with increasing size of the area surveyed (polygon). The decrease was strongest in the smallest polygons, confirming the tendency of small study areas to overestimate densities in traditional CR models. In small study areas, the buffer width may be biased by stochasticity due to a small sample size for calculating the 1/2 MMDM, the spacing of camera-trap sites and the size of the area surveyed. Small survey areas only generate small inter-trap distances and, thus, small MMDM, and, in turn, result in overestimates of density (e.g. Maffei & Noss 2008). However, in our study, the buffer width remained almost constant, with increasing area size. Other reasons for this positive bias in the non-spatial model, discussed by Foster and Harmsen (2011), are failure to sample all available habitat types in small survey areas (Jackson et al. 2006) and high individual range overlaps in relatively small areas (i.e. edge effects according to Gaston et al. 1999). Decreasing habitat quality, with increasing survey area, was not observed in our study, as suitable habitat covered 90% of the area effectively sampled for all polygons, except for the starting polygon A, with the highest density estimate, but only 83% of suitable habitat. Consequently, edge effects, where density estimates are likely to be disproportionately inflated by individuals using space beyond the boundary of the area surveyed in smaller areas, are the most plausible explanation. This is most obvious in the extreme case when the area surveyed is smaller than the territory of a single individual. This pattern becomes even more apparent when multiple individuals can overlap in a relatively small area, as would be the case at the border of adjacent lynx territories. Our findings are corroborated by the results of several regular CR camera-trapping studies on felids. In a study on ocelots [Leopardus par*dalis* (Linnaeus, 1758)], Maffei and Noss (2008) found that density estimates stabilized at the lower densities when the area surveyed reached the size of at least 3 to 4 home ranges. A similar relationship between density estimates and area surveyed has been observed in several non-spatial capture–recapture studies of felids (e.g. Silver *et al.* 2004; Soisalo & Cavalcanti 2006; Dillon & Kelly 2007).

In contrast to the CR model results, we did not observe a decline in density estimates from the SCR models with increasing area surveyed. This confirms that recent SCR models are much more robust than CR models to changes in trap array size (e.g. Sollmann et al. 2012). SCR models estimate movement as an explicit model component. As long as there is enough detection data across at least some range of distances, they are able to make predictions of detection across unobserved distances, even when they are larger (within reasonable limits) than the extent of the trap array (Sollmann *et al.* 2012). This also prevents density estimates being disproportionally inflated by individuals using space beyond the boundary of the area surveyed. In our study, the movement parameter  $\sigma$  remained almost stable with decreasing trap array size like the buffer width in the CR models. When converting estimates of  $\sigma$  to home range size, the respective areas would range between 398–511 km<sup>2</sup>. These values are much higher than the average home range size of 191 km<sup>2</sup> observed by means of radio-telemetry during a low lynx density at the end of the 1980s over the same duration and period of the year (Pesenti & Zimmermann 2013; suggesting that the SCR model overestimated the 2 month ranging parameter of lynx or that the model assumption of a circular home range (under the bivariate normal movement model) inflated the present home range estimates. Similar results were found by Noss et al. (2012) for ocelot and lowland tapir [Tapirus terrestris (Linnaeus, 1758)] in the Bolivian Chaco.

When monitoring populations, changes in density can only be detected if estimates are precise enough. Larger areas surveyed positively influenced the precision (95% CI and 95% posterior interval for SPACECAP) of the density estimates in the SCR and CR because surveying larger areas results in larger datasets (Fig. 3). For the CR model, following Karanth and Nichols (1998) in estimating the SE of density estimates, the impact of the SE of the buffer is larger in smaller camera-trap polygons. According to White *et al.* (1982), to obtain reliable abundance estimates with closed population CR models, the overall capture probability should be greater than or equal to 0.1, and the overall sample size should be >20 individuals. Harmsen *et al.* (2010) observe that the capture probabilities reported in many camera-trap studies of felids fall below this threshold, and Janecka et al. (2011) find that few studies of rare carnivores, including tigers [Panthera tigris (Linnaeus, 1758)], jaguars or ocelots, exceed the suggested benchmark of 20 individuals. In our study, the capture probability was >0.1 for all polygons sampled, but was only close to the benchmark of >20 individuals for the largest area (polygon E). Similarly, according to Efford et al. (2009), at least 20 recaptures are needed for a precise estimate using an SCR model, which can only be reached by sampling sufficient locations over a large enough area. Because lynx occur at low densities  $(0.8-2.1 \text{ independent } \text{lynx}/100 \text{ km}^2)$ (Breitenmoser-Würsten et al. 2001, 2007) we had to cover a very large area (i.e.  $760 \text{ km}^2$ ) to capture enough lynx to approach this sample size. Very few studies have sampled areas this large. A cursory review of the literature (N = 27) showed that most of the areas surveyed are smaller than 200 km<sup>2</sup> (N = 21), 2 are of similar size to ours and only 1 is larger. The adjacent block sampling design described in Nichols and Karanth (2002), where adjacent trapping grids are sequentially sampled and then combined, can help to achieve larger area coverage when camera-traps are limited. However, such a design extends the overall survey duration, which could lead to problems with population closure. Furthermore, it is less desirable from the perspective of modelling and estimation (e.g. time variation  $[M_t]$  will be difficult to deal with because each capture occasion covers multiple calendar days) (Nichols & Karanth 2002).

Our results showed that, for a low density species like lynx, large spatial efforts are required to obtain reliable and precise density estimates. For future capture-recapture studies of Eurasian lynx in mountainous terrain, with similar population densities (1-2 individuals/100 km<sup>2</sup>), we thus make the following recommendations. First, the sampling design should take into account available information on natural and artificial landscape features that lynx are likely to travel along in order to optimize detection probability, and should take into account accessibility of camera-traps so they can be checked regularly to avoid lost trap nights due to malfunctioning equipment. Second, to reach the benchmark of >20 individuals, and to thus obtain reliable and precise density estimates (White et al. 1982; Efford et al. 2009), the area should be at least as large as the largest polygon sampled in this study, namely 760 km<sup>2</sup>, which is considerably more than the 3 to 4 home ranges proposed by Maffei and Noss (2008). Because there is an upper limit to trap spacing, an adjacent block sampling design would enable us to maximize the size of the area surveyed when camera-traps are limited. Finally, lynx densities should be estimated using SCR models because they consider animal movements explicitly and are not biased by an informal estimation of the effective sampling area. Although we do not recommend sampling smaller areas because of sample size considerations, SCR models did provide reliable density estimates for areas as small as 181 km<sup>2</sup>, owing to their explicit treatment of animal movement. For many carnivores, where sampling areas that are large relative to individual home ranges is extremely challenging, SCR models are the preferable analytical approach. If studies are monitoring lynx populations, however, large sample sizes and, thus, large areas are essential to detect potential changes in density.

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