Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss Alps

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Use of photographic capture–recapture analyses to estimate abundance of species with distinctive natural marks has become an important tool for monitoring rare or cryptic species, or both. Two different methods are available to estimate density: nonspatial capture–recapture models where the trap polygon is buffered with the half or full mean maximum distance moved by animals captured at more than 1 trap (1/2 MMDM or MMDM, respectively); or spatial capture–recapture (SCR) models that explicitly incorporate movement into the model. We used data from radiotracked Eurasian lynx (*Lynx lynx*) in the northwestern Swiss Alps (NWSA) during a low (1.0 lynx/100 km^2) and a high (1.9–2.1 lynx/100 km^2) lynx population density to test if lynx space use was density dependent. Second, we compared lynx density estimates resulting from these 2 different methods using camera-trapping data collected during winters 2007–2008 and 2009–2010 in the NWSA. Our results indicated lynx space use was negatively correlated with density. Lynx density estimates in all habitats using MMDM (0.86 and 0.97 lynx/100 km^2 in winters 2007–2008 and 2009–2010, respectively) were significantly lower than SCR model estimates, whereas there was no significant difference between SCR model (1.47 and 1.38) and 1/2 MMDM (1.37 and 1.51) density estimates. In the NWSA, which currently harbors the most abundant lynx population in Switzerland, 1/2 MMDM and SCR models provided more realistic lynx density estimates compared to the MMDM, which lies in the lower range of densities. Overall, the SCR model is preferable because it considers animal movements explicitly and is not biased by an informal estimation of the effective sampling area.

Key words: camera-trapping, density, half mean maximum distance moved (1/2 MMDM), *Lynx lynx*, mean maximum distance moved (MMDM), spatial capture–recapture (SCR), Switzerland, telemetry

In human-dominated landscapes, large carnivores often conflict with livestock breeders and hunters (Karanth et al. 1999; Meriggi and Lovari 1996) and their conservation thus depends on sound management (Fergus 1991; Trevers and Karanth 2003). Wildlife conservation and management require precise data regarding size, density, and structure of the focal populations and their trends over time. Total counts of most organisms, especially nocturnal, forest-dwelling species occurring at low densities are difficult to establish (Cederlund et al. 1998). However, if each individual in a population can be identified by distinctive natural marks, we can estimate capture probabilities and abundance by means of photographic capture–recapture analyses.

Since its development in the early 1980s, the use of camera-trapping to study population size of large carnivores with distinctive natural marks has become an important tool for monitoring rare or cryptic species, or both, in a wide range of environments (Carbone et al. 2001; Karanth and Nichols 1998). This quantitative technique, which has relatively low labor costs, is noninvasive and causes minimal environmental disturbance (Henschel and Ray 2003; Silveira et al. 2003). However camera-trapping depends on capturing as many different individuals and as many photo-captures of each individual as possible (Karanth and Nichols 2002). Camera-trapping has been used to study a variety of felids, for example, tigers (*Panthera tigris*—Karanth et al. 2006), jaguars (*Panthera onca*—Maffei et al. 2004; Silver et al. 2004), pumas (*Puma concolor*—Kelly et al. 2008), ocelots (*Leopardus pardalis*—Dillon and Kelly 2007), bobcats (*Lynx rufus*—Kelly and Holub 2008), Geoffroy's cat (*Leopardus geoffroyi*—Cuellar et al. 2006), and snow leopards (*Uncia uncia*—Jackson et al. 2006).

The 1st estimation of Eurasian lynx (*Lynx lynx*) abundance by means of photographic capture–recapture was conducted in the northwestern Swiss Alps (NWSA) in 1998 (Laass 1999). It

was later extended to the central and eastern Swiss Alps (Ryser et al. 2009) and to the Swiss Jura Mountains (Zimmermann et al. 2007). Since 1998 lynx abundance and density have been estimated every 2nd year in the NWSA (Breitenmoser-Würsten et al. 2001; Laass 1999; Zimmermann et al. 2010).

Comparison of lynx abundance between study areas requires that abundance be converted to density by dividing it by the effective sampling area. The area delimited by trap sites is usually enlarged in order to account for additional area from which trapped individuals are taken. One method to define the effective sampling area uses 2 different measures, which are still a matter of debate within the scientific community (Sharma et al. 2010; Soisalo and Cavalcanti 2006). It consists of placing a buffer equivalent to either the mean maximum distance moved (MMDM—Dillon and Kelly 2008; Soisalo and Cavalcanti 2006) or half the mean maximum distance moved (1/2 MMDM—Karanth 1995; Karanth and Nichols 1998, 2002) between photo-captures for each individual caught at ≥2 camera-trapping sites. Unfortunately, this method is an ad hoc approach with little theoretical justification (Williams et al. 2002) and depends entirely on the buffer distance(s) used. The latter are influenced by the size of the trapping grid and trap spacing (Dillon and Kelly 2007) and the size of the study area (Maffei and Noss 2008). Because camera-trap data tend to underestimate the movement of the animals, several studies used radiotelemetry to calculate buffer width. Soisalo and Cavalcanti (2006) suggested that buffer-width estimates from telemetry can be extrapolated to other studies, but with a territorial species, we expect an individual's space use to be density-dependent. Recently, a 2nd 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, 2009b). SCR models circumvent the problem of estimating the effective area sampled because the trap array is embedded in a large area called the state-space.

We had 2 main objectives, the 1st of which was to test if lynx space use was density-dependent. This hypothesis was tested using data from radiotracked lynx collected in the same area as the camera-trapping study, during a period of low lynx densities in the 1980s (Breitenmoser and Haller 1993) and one of high lynx densities in the late 1990s (Breitenmoser-Würsten et al. 2001) in the NWSA. To fully understand any density-dependent association, we also explored the effects of 2 other variables on individual space use (i.e., period of the year and social status). As the 2nd objective, we compared density estimates resulting from 2 different methods (nonspatial [MMDM and 1/2 MMDM] and spatial [SCR model] methods) using camera-trapping data collected during winters 2007–2008 (Zimmermann et al. 2008) and 2009–2010 (Zimmermann et al. 2010) in the NWSA.

MATERIALS AND METHODS

Study area.—The study area was located in the NWSA (Fig. 1), a 2,800-km^2 patch isolated from the rest of the Swiss Alps.

Elevation ranged from 626 to 2,794 m above sea level. The valley bottoms and slopes were deforested during the Middle Ages and provided pastureland for cattle and sheep. The human population reached a density of 33 inhabitants/km^2 in most parts of the study area and people living in the lowlands used the area intensively for recreation (e.g., skiing and hiking). Forests were highly fragmented and covered 27% of the study area. They extended along steep slopes up to timberline at 1,800–1,950 m (for details see Zimmermann et al. [2005]).

Space use.—Three different measures were used to estimate space use of radiotracked lynx (e.g., Dillon and Kelly 2008): the maximal distance (MD) between the known locations of an individual (which corresponds to the MMDM in camera-trapping studies); the 95% fixed kernel density (FKD—Worton 1989); and a 100% minimum convex polygon (MCP—Hayne 1949). Because FKD and MCP are 2-dimensional measures, they were transformed into a 1-dimensional measure (such as MD) by using the diameter of a circle of the same area. All calculations were done in ArcGIS 9.3 (ESRI 2009) using the Hawths Analysis Tools extension (Beyer 2004).

We investigated the potential influence of 3 different covariates on lynx space use: density (D), period of the year (P), and social status (S). To analyze the effect of density on space use, we used data from radiotracked lynx collected during a period of low lynx density in the 1980s (2 males and 6 females—Breitenmoser and Haller 1993) and a high density period in the late 1990s (17 males and 22 females—Breitenmoser-Würsten et al. 2001). To test if the covariate period of the year (i.e., mating season) had an influence on lynx space use, we divided the year into 6 periods of 2 months each (period 1: December–January; period 2: February–March; period 3: April–May; period 4: June–July; period 5: August–September; and period 6: October–November). Primarily, the length and start of the periods were adjusted to match with our Eurasian lynx systematic camera-trapping monitoring schedule consisting of 2 sampling periods (December–January and February–March [e.g., Zimmermann et al. 2007, 2010]). However, some periods also were characterized by different breeding and social events. Period 2 mostly coincided with mating, period 3 with separation of cubs from their mother, period 4 with births and lactation when females with cubs have reduced mobility, and periods 6 and 1 with the time when females with cubs use a larger part of their home ranges because of higher mobility of their kittens (Zimmermann et al. 2005). Lynx were separated into 5 categories according to their social status: adult male, adult female, female with juvenile, subadult, and dispersing subadult (cf. Zimmermann et al. 2005) to determine if the social status had an influence on space use. Sexes of subadults were lumped because in the NWSA dispersal behavior (proportion of individuals that disperse and dispersal distances) did not differ between males and females (Zimmermann et al. 2005). Information about the spatiotemporal behavior of subadult lynx (time period when subadults dispersed and established a temporal or definitive home range) came from Zimmermann (2004).
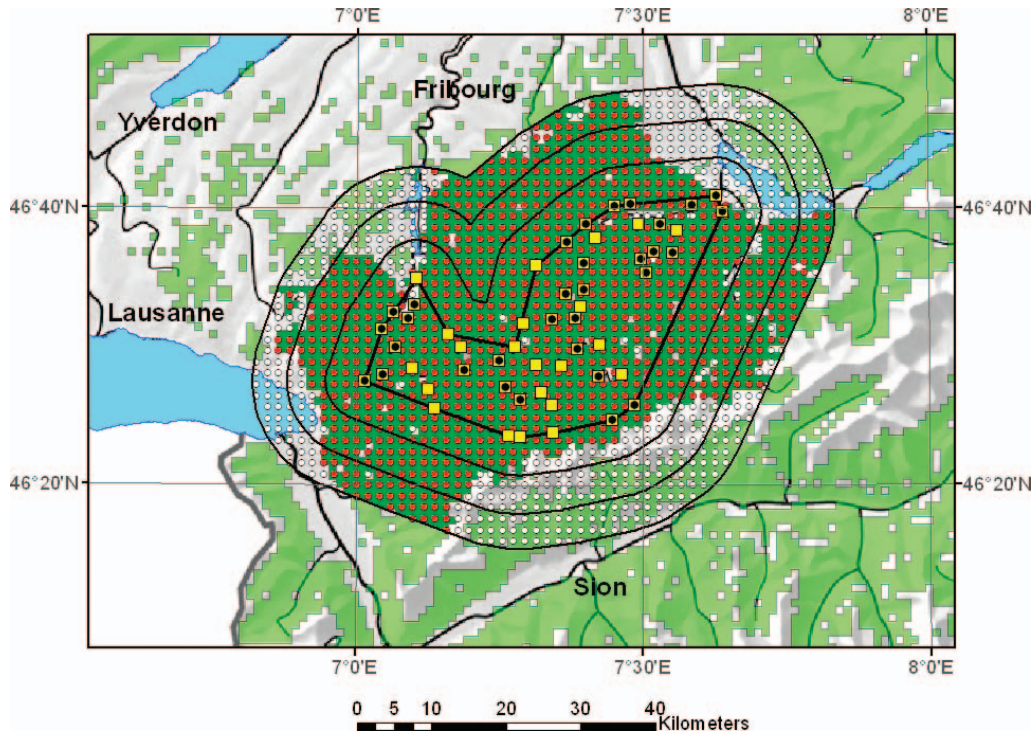
Fig. 1.—Study area in the northwestern Swiss Alps (NWSA). The yellow squares show the camera-trap sites, those with black dots indicate lynx detections; the thick black polygon delimits the most peripheral camera-trap sites. The thin lines from center moving outward correspond to the half mean maximum distance moved (1/2 MMDM), mean maximum distance moved (MMDM), and 15-km buffers added to the camera area, respectively. Suitable habitat (cells with habitat suitability >20) is light green and habitat fragments of orthogonally connected suitable habitat cells containing the camera-trap sites are dark green. Red and white dots within the 15-km buffer around the camera area show the hypothetical 1.5 × 1.5-km spaced activity centers within and outside suitable habitat fragments, respectively.

Because some individuals had several observations for each measure, we had to account for pseudoreplication (Hurlbert 1984). Consequently, we fitted 8 linear mixed-effects regression models with lynx individuals fitted as a random effect to investigate how MD, FKD, and MCP were affected by the covariates. To facilitate comparisons between models, no interactions between covariates were considered.

Models were compared and best fits were selected using the bias-corrected Akaike information criterion (AIC$_c$—Burnham and Anderson 1998). Differences in the AIC$_c$ values between the best fitting and remaining models were calculated as follows: $\Delta_i = (AIC_c) - (AIC_c)_{min}$. Akaike weights ($w_i$) also were calculated. Akaike weights sum to 1 for the set of models and are interpreted as the weight of evidence in favor of model i as being the best one of the models considered (Burnham and Anderson 1998). It is not always possible to select 1 outstanding model because several models could fit the data well. To avoid this problem we performed model averaging over the best models. The condition for model averaging was fixed at $\Delta AIC_c < 2$ (Burnham and Anderson 2002). The effect of density, social status, and period of the year were given relative to density in the 1980s, adult female, and period 1 (period of camera-trapping), respectively. The analyses were conducted using the nlme package (Pinheiro et al. 2010) and MuMIn package (Barton 2010) in the R statistical environment (R Development Core Team 2012).

Camera-trapping.—A 2.7 × 2.7-km grid with a random origin was overlaid on the camera-trapping study area. An optimal camera-trap site was chosen in every 2nd grid cell after cells with more than two-thirds of their area above 1,800 m were discarded. These cells were removed for biological and logistic reasons: lynx rarely use habitat above the timberline (Breitenmoser-Würsten et al. 2001) and accessibility for maintenance must be guaranteed. Camera-traps were set at optimal locations, principally on forest roads and hiking trails and rarely on game passes and bridges known to be used by lynx. Fifty-four and 53 camera-traps sites were deployed in a 790-km^2 area in the NWSA during winters 2007–2008 and 2009–2010, respectively. This camera-trap density ensured that the area sampled contained no holes that could contain an entire animal's home range, which is a prerequisite and assumption of capture–recapture studies. The traps were set for 60 nights from 1 December 2007 to 30 January 2008 and from 27 November 2009 to 26 January 2010, corresponding to 3,240 and 3,180 potential of trap-nights, respectively. We used 3 types of analogue camera-traps (Theodor Kocher Institute, University of Bern, Bern, Switzerland; Bandgenossenschaft-Bern, Bern, Switzerland; and Camtrak, South Inc., Watkinsville, Georgia) and 1 type of digital camera-trap (Cuddeback, Green Bay, Wisconsin). Lynx were identified from photographs by comparing their distinct pelage patterns using reference photographs from earlier studies to aid in the

identification. Individuals were sexed from photographs (observation of the genital area or female with cubs) using all available information from the camera-trapping sessions, when captured during the radiotelemetry project, or when found dead after the study. Following Zimmermann et al. (2007) we constructed individual capture histories for 12 occasions of 5 consecutive nights each. Population closure was checked using the closure test of Stanley and Burnham (1999) in the program CloseTest 3.0. The module CAPTURE within the program MARK (White and Burnham 1999) was used to estimate the abundance under the null model, M_0.

Buffer methods.—In the nonspatial capture–recapture methods, a buffer equal to the 1/2 MMDM (Karanth and Nichols 1998; Karanth et al. 2006) or MMDM (Dillon and Kelly 2008; Soisalo and Cavalcanti 2006) between photo-captures for each individual lynx caught at ≥2 camera-trap sites during the study was added to the polygon encompassing all camera-traps. Similar to Royle et al. (2009a, 2009b), we also calculated the density per unit of suitable habitat within the polygons plus buffers. A cutoff point of >20 for habitat suitability (habitat suitability ranges from 0 = unsuitable to 100 = highly suitable habitat) from a previously developed lynx habitat suitability model (Zimmermann 2004) was used to discriminate suitable habitat fragments of orthogonally connected suitable habitat cells. This procedure excluded the highly unsuitable areas such as settlements, intensively used agriculture areas, lakes, large rivers, and high mountains peaks above 2,000 m that are not used by resident lynx. We considered only suitable habitat that was available to resident lynx in our sampling area and thus restricted suitable habitat to the fragment containing the camera-trap sites (dark green area within the 15-km buffered region, the MMDM, and 1/2 MMDM buffers [Fig. 1]).

Spatial capture–recapture model.—The SCR model SPACECAP package (Singh et al. 2010) implemented in the R statistical environment (R Development Core Team 2012) directly estimates animal density using information on capture histories in combination with spatial locations of captures under a unified Bayesian modeling framework (Royle et al. 2009a, 2009b). Key assumptions of the SCR models are that individuals have independent activity centers with fixed locations, trap encounter probability is assumed to decrease with increasing distance from the individual's activity center (i.e., half normal), and each capture is an independent event (Foster and Harmsen 2011). Three input files are required: animal capture details, trap deployment details including dates when specific traps were active, and potential home-range centers. The trap array is embedded in a larger area called the state-space, which has to be chosen large enough so that no individual outside of the state-space has any probability of being photo-captured on the array. To define the state-space we buffered our trap array by 15 km. To determine if the chosen buffer width was large enough (whereon density estimates stabilize), we calculated the SCR densities for 10 different buffer widths ranging from 1 to 19 km with increments of 2 km. SCR density estimates decreased rapidly with increasing

buffer width and stabilized when the buffer width was ≥9 km. The state-space was described as a grid of 1,557 equally spaced potential home-range centers, each representing exactly 10% of the buffer distance (1.5×1.5 km = 2.25 km^2 [A. Royle, USGS Patuxent Wildlife Research Center, pers. comm.]). Of these, 1,016 (2,286 km^2) were within suitable lynx habitat fragments (red dots; Fig. 1) and the remaining 561 centers were within unsuitable habitat (white dots; Fig. 1). Similar to nonspatial models, we also estimated the lynx density per unit of suitable habitat. In this case, whether a potential activity center lies in suitable habitat (= 1) or not (= 0) is directly provided in the input matrix of the potential home-range centers. Bayesian analysis of the model was conducted using data augmentation (Royle et al. 2007): the data set was increased with 100 all-zero encounter histories. We ran 1 Markov chain Monte Carlo with 60,000 iterations, a burn-in of 10,000, and a thinning rate of 1. By assuming a bivariate normal model for detection, the estimated movement parameter (σ) can be converted into a 95% home-range radius estimate (Reppucci et al. 2011). The script in R is the following: $(\sigma)*(qchisq(0.95,2)^{0.5})$.

RESULTS

Radiotelemetry.—Model selection revealed strong support for the influence of the covariates population density and social status on lynx space use (Table 1). The model containing all covariates had the lowest AIC$_c$ when MCP or FKD home ranges were used as a measure of lynx space use. On the other hand, MD was best explained by a model including covariates population density and social status (Table 1).

Model-averaged parameter estimates showed that lynx space use in the late 1990s (MD: 13.4 km; MCP: 3.8 km; FKD: 3.5 km) decreased significantly (i.e., 0 not within the 95% confidence interval [95% CI]) by 8.2 km (95% CI = −11.8 to −4.7) with MD, 1.9 km (95% CI = −2.8 to −1.0) with MCP, and 0.8 km (95% CI = −1.2 to −0.5) with FKD compared to lynx space use in the 1980s (Table 2). Space use of dispersing subadults and adult males was significantly larger compared to space use of subadults, adult females, and females with juveniles independent of the methods used (Table 2). The covariate period of the year had no significant effect on lynx space use independent of the measure used (Table 2). Space use measured by means of MD, FKD, and MCP during the same period (December–January) and over the same duration (± SD) of 29.4 km (± 16.5 km) with MD, 15.6 km (± 4.7 km) with MCP, and 10.2 km (± 2.0 km) with FKD in the 1980s and of 12.9 km (± 7.2 km) with MD, 7.2 km (± 1.6 km) with MCP, and 6.6 km (± 0.7 km) with FKD in the late 1990s during peak lynx density.

Camera-trapping and estimation of the abundance.—For technical reasons, such as camera-trap failures, dead batteries, programming errors, snowfall, and sabotage, the number of trap-nights available was reduced to 3,020 and to 3,159 during winters 2007–2008 and 2009–2010, respectively. Sixty-four captures representing 22 independent lynx during winter 2007–

TABLE 1.—The AIC$_c$-based comparison of mixed-effects models explaining lynx spatial use calculated using 3 different measures: MD = maximum distance; MCP = minimum convex polygon; FKD = fixed kernel density. Sample size is equal to 334 for all measures. Models are sorted by decreasing Akaike weights. Models with ΔAIC$_c$ < 2 (in boldface type) were used for model averaging. D = density (low and high); S = social status of lynx; P = period of the year; AIC$_c$ = bias-corrected Akaike's information criterion for fitted models; Δ_i = (AIC$_c$) − (AIC$_c$)$_{min}$; Akaike w_i = Akaike weight.

Measures	Models	AIC$_c$	Δ_i	Akaike w_i
MD	**D + S**	**6,857.811**	**0**	**0.721**
	P + D + S	**6,859.732**	**1.920**	**0.276**
	S	6,870.186	12.375	0.001
	P + S	6,872.516	14.705	<0.001
	D	6,889.777	31.966	<0.001
	P + D	6,891.884	34.073	<0.001
	—	6,899.874	42.063	<0.001
	P	6,902.115	44.304	<0.001
MCP 100%	**P + D + S**	**5,962.858**	**0**	**0.904**
	D + S	5,968.526	5.667	0.055
	P + S	5,974.026	11.168	0.003
	S	5,979.553	16.695	<0.001
	P + D	6,000.266	37.408	<0.001
	D	6,005.568	42.710	<0.001
	P	6,009.733	46.875	<0.001
	—	6,015.099	52.241	<0.001
FKD 95%	**P + D + S**	**5,428.006**	**0**	**0.632**
	D + S	**5,429.209**	**1.203**	**0.346**
	P + D	5,435.638	7.631	0.013
	D	5,437.511	9.504	0.005
	P + S	5,441.987	13.981	<0.001
	S	5,443.675	15.669	<0.001
	P	5,447.549	19.543	<0.001
	—	5,449.831	21.825	<0.001

TABLE 2.—Parameter estimates for the 3 measures of lynx space use: MD = maximum distance; MCP = minimum convex polygon; and FKD = fixed kernel density. Model averaging was applied to the models with ΔAIC$_c$ < 2 to obtain unbiased parameter estimates with 95% CI (where AIC$_c$ is the bias-corrected Akaike information criterion). The model averaged parameters are given in kilometers.

Parameter	Model averaged parameter	Relative importance	Lower 95% CI	Upper 95% CI
MD				
(Intercept)	19.200	1.00	14.900	23.500
Density in the 1990s[a]	−8.260*	1.00	−11.800	−4.690
Subadult dispersing[b]	10.200*	1.00	6.060	14.400
Adult male[b]	6.620*	1.00	3.090	10.100
Subadult[b]	3.090	1.00	−0.954	7.140
Female + juvenile[b]	−1.020	1.00	−3.910	1.870
Period 2[c]	−0.432	0.28	−1.960	1.100
Period 3[c]	−0.577	0.28	−2.450	1.300
Period 4[c]	−0.663	0.28	−2.760	1.440
Period 5[c]	−0.396	0.28	−1.840	1.050
Period 6[c]	0.138	0.28	−0.779	1.060
MCP 100%				
(Intercept)	5.140	1.00	4.010	6.270
Density in the 1990s[a]	−1.950*	1.00	−2.850	−1.050
Subadult dispersing[b]	2.880*	1.00	1.800	3.960
Adult male[b]	1.810*	1.00	0.910	2.720
Subadult[b]	0.760	1.00	−0.282	1.800
Female + juvenile[b]	−0.115	1.00	−0.865	0.634
Period 2[c]	−0.446	0.94	−1.110	0.219
Period 3[c]	−0.437	0.94	−1.090	0.215
Period 4[c]	−0.599	0.94	−1.280	0.080
Period 5[c]	−0.437	0.94	−1.140	0.196
Period 6[c]	0.439	0.94	−0.232	1.110
FKD 95%				
(Intercept)	4.200	1.00	3.740	4.650
Density in the 1990s[a]	−0.831*	1.00	−1.190	−0.473
Subadult dispersing[b]	0.531*	1.00	0.064	0.998
Adult male[b]	0.451*	1.00	0.075	0.826
Subadult[b]	0.162	1.00	−0.285	0.608
Female + juvenile[b]	−0.095	1.00	−0.430	0.239
Period 2[c]	−0.039	0.65	−0.261	0.181
Period 3[c]	−0.044	0.65	−0.266	0.177
Period 4[c]	−0.156	0.65	−0.483	0.171
Period 5[c]	−0.001	0.65	−0.195	0.191
Period 6[c]	0.164	0.65	−0.175	0.504

[a] Density effect is given relative to density in the 1980s.
[b] Social status effects is given relative to adult female.
[c] Period effect is given relative to period 1.
* $P < 0.05$

2008 and 75 captures of 23 independent lynx during winter 2009–2010 occurred on the study area. In winters 2007–2008 and 2009–2010, the sex of 6 and 4 individuals, respectively, was known from physical captures during the radiotelemetry work. In winters 2007–2008 and 2009–2010, photographs allowed for the identification of sex of 7 and 8 additional individuals, respectively. Consequently, sex was known for 13 (5 females and 8 males) of 22 individuals and 12 (5 females and 7 males) of 23 during winters 2007–2008 and 2009–2010, respectively. Lynx were detected on 1–7 occasions in both winters, with a mean detection rate of 2.91 and 3.26 occasions per individual lynx during winters 2007–2008 and 2009–2010, respectively. The program CloseTest (Stanley and Burnham 1999; Stanley and Richards 2004) supported the population closure assumption (winter 2007–2008: χ^2 = 12.22, P = 0.42; winter 2009–2010: χ^2 = 12.78, P = 0.54). The model selection procedure in CAPTURE rated M$_0$ (with constant capture probability) as the most appropriate model. Its selection criterion was 1.0 independent of the period considered. Under model M$_0$ the abundance estimation was 22 independent lynx (SE = 1.01) in winter 2007–2008 and 23 lynx (SE = 0.76) in winter 2009–2010. Capture probability was 0.23 in winter 2007–2008 and 0.27 in winter 2009–2010. Thus,

all of the estimated lynx were photographed in both winters. SCR capture probabilities in winters 2007–2008 and 2009–2010 were 0.013 and 0.067, respectively, in all habitats and 0.013 and 0.073, respectively, in suitable habitat only.

Estimation and comparison of movement parameters and densities.—Movement parameters in all habitats in winters 2007–2008 and 2009–2010 were 5.17 and 4.72 km, respectively, with 1/2 MMDM, 10.34 and 9.44 km, respectively, with MMDM, and 11.15 and 11.00 km, respectively, with SCR model (95% home range radius). It is inherent to the 1/2 MMDM and MMDM models that estimates
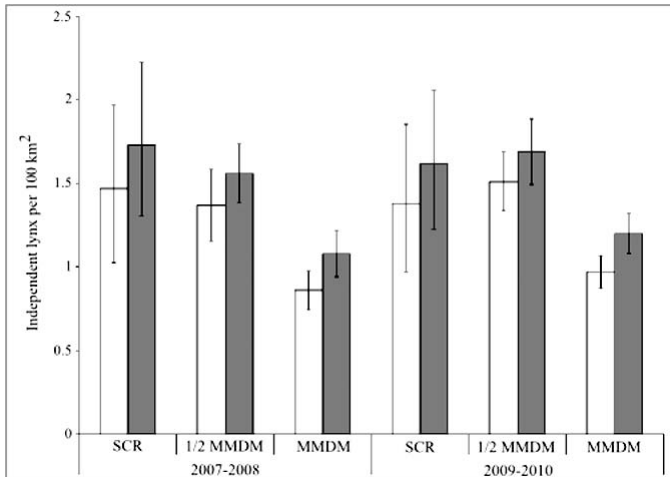
FIG. 2.—Lynx densities with 95% *CI* (95% posterior interval for SPACECAP) estimated in study area during winters 2007–2008 and 2009–2010 using 2 different methods: the spatial capture–recapture model (SCR) and the nonspatial model using the average (MMDM) and the half average (1/2 MMDM) of the maximum distance moved. Densities were calculated for all habitats (in white) and for suitable lynx habitat only (in gray).

do not differ between all habitats and suitable habitat only. However, in the SCR model the movement parameter (95% home-range radius) is estimated anew and was 11.10 and 10.71 km for suitable habitat during winters 2007–2008 and 2009–2010, respectively.

Density estimates in all habitats (*SE* for the nonspatial models and posterior *SD* for SPACECAP) in winters 2007–2008 and 2009–2010 were 1.37 (± 0.11) and 1.51 (± 0.09) independent lynx/100 km^2 with 1/2 MMDM, respectively, 0.86 (± 0.06) and 0.97 (± 0.05) with MMDM, respectively, and 1.47 (± 0.25) and 1.38 (± 0.23) with SCR model, respectively (Fig. 2). Lynx density estimates in all habitats using MMDM were always significantly (i.e., mean of value *a* not within 95% *CI* [95% posterior interval for SPACECAP] of value *b* and vice versa) lower than the SCR model, whereas there was no significant difference between SCR model and 1/2 MMDM density estimates (Fig. 2). The same pattern was found when density was estimated for suitable habitat only (Fig. 2). Density estimates in suitable and all habitats only differed significantly for MMDM (Fig. 2).

DISCUSSION

Radiotelemetry.—Our results indicated that season had no effect on lynx space use compared to the covariates density and social status. Lynx space use was negatively correlated to density. Similarly, Benson et al. (2006) observed an increase in population density and a decrease in annual mean home-range and core-area sizes for male and female bobcats during a 9-year study. The effect of social status on space use was as great as the effect of density. Space use of females with juveniles is mainly triggered by the limited mobility of the juveniles during the first 4 months after birth (Kaczensky 1991) and later by kill

opportunities to provide constant access to food for the kittens (Molinari and Molinari-Jobin 2001). Adult males regularly patrol their territory borders to find potential mates during the mating season, to deposit scent marks, and to defend their territory against potential intruders (Breitenmoser and Breitenmoser-Würsten 2008). These differences in movement patterns could affect the capture probability of the different lynx categories. Usually, male lynx are more frequently photographed than are females with juveniles during a camera-trapping survey (F. Zimmermann, KORA, pers. comm.). However, the social status of lynx cannot be integrated into photographic capture–recapture analyses because it is only possible to distinguish juvenile lynx from lynx older than 1 year (i.e., independent lynx including adults and subadults) and generally only possible to sex part of the animals pictured during a camera-trapping session from the photographs.

Radiotelemetry in camera-trapping studies.—In our study, comparison of radiotelemetry with camera-trapping data was only partly possible because radiotelemetry data were collected prior to the systematic camera-trapping sessions. The lowest MD estimates from radiotelemetry ($\bar{X} = 12.9$ km) were observed in the late 1990s within the same area as our camera-trapping sampling area. Even though MD was measured during a peak lynx density and thus should correspond to one of the lowest values, it was still slightly higher than MMDM (10.3 km in winter 2007–2008 and 9.4 km in winter 2009–2010) from camera-trapping data in both winters. For the nonspatial models it can be expected that space-use estimates from radiotelemetry would always be higher than those measured using camera-trapping data because the latter depend on the spacing of camera-trap sites and the size of the area surveyed and its relative position to the animal's home range, and therefore can only capture a subset of the individual movement patterns collected by means of radiotelemetry. On the other hand, SCR 95% home-range diameter estimates (22.3 km in winter 2007–2008 and 22.0 km in winter 2009–2010) were in between MD estimates in the 1980s (29.4 km) and those in the late 1990s (12.9 km). Because SCR models estimate movement in a different way than nonspatial models, they are much less constrained by trap spacing, and survey area size.

Because camera-trapping renders an incomplete representation of the movement of the animals, several papers (Balme et al. 2009; Dillon and Kelly 2008; Soisalo and Cavalcanti 2006) suggest using radiotelemetry data to calculate buffer width. Soisalo and Cavalcanti (2006) further suggest the buffer width estimated from radiotelemetry could be used in subsequent camera-trapping sessions within the same area. According to our findings buffer width should be estimated anew for each camera-trapping session using contemporary telemetry data because space use of territorial animals varies with density (e.g., Benson et al. 2006) and possibly other factors.

The MD and MCP (Dillon and Kelly 2008; Soisalo and Cavalcanti 2006), FKD (Dillon and Kelly 2008), and the mean

maximum distance moved by individuals outside the area delineated by the outer camera-traps (MMDMOSA; Balme et al. 2009) are among the different measures derived from radiotelemetry. In our study, MD always produced the highest distance values and thus would result in the lowest density estimates, whereas FKD distances were always lowest and thus would result in the highest density estimates; MCP values were in between. Thus, the measures (MD, MCP, and FKD) used to calculate the buffer width and hence the effective sampling area have a profound influence on the density estimates. Similarly, Dillon and Kelly (2008) found that MD resulted in greater distances compared to FKD and MCP for ocelots. However, in contrast to our study, FKD and MCP did not differ substantially. Soisalo and Cavalcanti (2006) found no differences between distances measured by means of half MD and half 95% MCP (5.2 km versus 5.1 km, respectively) for jaguars. Such incongruent findings may result from variation in the degree of landscape fragmentation and the presence–absence of specific landscape features (e.g., deep valley system and riverbeds). In a mountainous landscape such as NWSA, the Swiss Jura Mountains, and Hedmark in Norway, lynx establish their home ranges along predominant ridge lines (Breitenmoser-Würsten et al. 2001, 2007; Linnell et al. 2007) resulting in oval-shaped home ranges with high length to width ratio. Similar results were found by Jackson and Ahlborn (1989) for snow leopard in Nepal. In a flat terrain, such as the study area of Soisalo and Cavalcanti (2006) in the Pantanal biome, home ranges tend to have a circular shape and MCP and MD measures provide very similar distance values. In the same biome but interrupted by several major water courses, male jaguars had elliptical-shaped home ranges because they predominately were following these linear features (Sollmann et al. 2011). Thus, when areas with predominant landscape features are surveyed by means of camera-traps, SCR movement parameter estimates or buffer widths of nonspatial models that are not constant in all cardinal directions would be more appropriate to estimate densities.

Camera-trapping.—The MMDM in winters 2007–2008 (10.3 km) and 2009–2010 (9.4 km) were about half the 95% home-range diameter of the SCR model (22.3 km in winter 2007–2008 and 22.0 km in winter 2009–2010). Estimation of buffer widths (1/2 MMDM and MMDM) is constrained by the size of the sampling area and the spacing of the camera-traps. Even though our study area encompassed about 4 or 5 male lynx home ranges and was among the largest ever reported in camera-trapping studies, the nonspatial models underestimated the movement parameters. SCR estimation of movement parameters could be constrained by the spacing of the activity centers. We believe the chosen width of 1.5 km was narrow enough compared to lynx space use measured by means of radiotelemetry to minimize the underestimation of movement parameters. We nevertheless encourage simulations using different spacing of activity centers to investigate its influence on SCR model density estimates.

Lynx density estimates in all habitats using MMDM were significantly lower than those of the SCR model, whereas there was no significant difference between the SCR model and 1/2 MMDM density estimates. In contrast to previous camera-trapping studies (Dillon and Kelly 2008; Obbard et al. 2010; Soisalo and Cavalcanti 2006), our results suggest that the MMDM method tends to underestimate lynx density. Indeed in the NWSA, which currently harbors the most abundant lynx population in Switzerland (Zimmermann et al. 2011), the MMDM measure (0.86 and 0.97 lynx/100 km^2 in winters 2007–2008 and 2009–2010, respectively) would fall in the lower end of the density range (1.0–2.1 independent lynx/100 km^2) estimated by means of radiotelemetry in this mountain range (Breitenmoser-Würsten et al. 2001). On the other hand, lynx density estimates by means of the 1/2 MMDM (1.37 and 1.51 lynx/100 km^2 in winters 2007–2008 and 2009–2010, respectively) and SCR model (1.47 and 1.38) did not differ significantly and provide more realistic lynx density estimates.

Similar results were found in several camera-trapping studies that either showed that 1/2 MMDM was a good proxy for home-range radius (Maffei and Noss 2008; Núñez-Pérez 2011) or that 1/2 MMDM did not result in gross overestimation of population density when compared to the reference density estimated by means of radiotelemetry data (Balme et al. 2009). Conversely, similar studies on jaguar (Soisalo and Cavalcanti 2006) and ocelot (Dillon and Kelly 2008; Trolle and Kéry 2005) came to the opposite conclusion, namely, that full MMDM was more realistic.

These inconsistencies raise doubts about the usefulness of buffering approaches based on distance measures derived from the camera-trapping grid. Spatial models have the advantages of considering animal movements explicitly. In SCR models there is no need to delimit the borders of the area surveyed because the trapping grid is included in a larger area allowing for animal movements beyond the trapping grid (e.g., Efford 2004; Royle and Young 2008). If this area is not chosen large enough, it will influence density estimates. Therefore, testing that the trapping grid has been buffered sufficiently should be part of applying an SCR model.

In contrast to nonspatial models, where suitable habitat is simply subtracted from the effective sampling area, the spatial model enables the inclusion of this information directly into the calculation of density by taking into account whether a potential activity center lies within suitable habitat. Although the Bayesian framework of the SCR model provides valid inference for small sample size, the consideration of animal movements explicitly increased the variance of the resulting density estimates compared to the nonspatial models. In our study, the 95% posterior interval (95% *CI* interval for the nonspatial models) was up to 4 times larger in the spatial than the nonspatial model MMDM, although our sample size was adequate in comparison with other published studies. Higher variances in density estimates from SCR models also were reported from other camera-trapping studies (e.g., Reppucci et al. 2011; Sharma and Jhala 2011). As with the buffer estimation in the nonspatial estimates, SCR models assume home ranges to be circular. When individuals establish their home ranges along predom-

inant landscape features resulting in high home-range length to width ratios this assumption is no longer supported. Further developments of SCR models should reevaluate the assumption of home-range shape by providing the possibility of including the effects of habitat and specific landscape features (e.g., mountain ridges or large rivers) on individuals' movements directly into the model.

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