Variation in diet, prey selectivity and home-range size of Eurasian lynx Lynx lynx in Switzerland

Authors: Molinari-Jobin, Anja, Zimmermann, Fridolin, Ryser, Andreas, Breitenmoser-Würsten, Christine, Capt, Simon, et al.

Source: Wildlife Biology, 13(4) : 393-405

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/0909-6396(2007)13[393:VIDPSA]2.0.CO;2

Variation in diet, prey selectivity and home-range size of Eurasian lynx *Lynx lynx* in Switzerland

Anja Molinari-Jobin, Fridolin Zimmermann, Andreas Ryser, Paolo Molinari, Heinrich Haller, Christine Breitenmoser-Würsten, Simon Capt, Roman Eyholzer & Urs Breitenmoser

Molinari-Jobin, A., Zimmermann, F., Ryser, A., Molinari, P., Haller, H., Breitenmoser-Würsten, C., Capt, S., Eyholzer, R. & Breitenmoser, U. 2007: Variation in diet, prey selectivity and home-range size of Eurasian lynx *Lynx lynx* in Switzerland. - Wildl. Biol. 13: 393-405.

To analyse the factors responsible for the interplay of Eurasian lynx *Lynx lynx* predation and home-range size, we reviewed patterns of lynx predation in Switzerland by comparing the prey spectrum of lynx in five studies performed in the following study areas: the northwestern Alps, where lynx were studied both in the 1980s and 1990s, the central Alps, the Jura Mountains, and northeastern Switzerland. We then compared home-range size of female lynx with two indirect measures of prey abundance, roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* harvested per km^2 and habitat suitability for roe deer and chamois as derived from a GIS model. Lynx diets were similar among sites. Roe deer and chamois made up 90% of prey items in all five studies. Comparing the proportion of roe deer and chamois in the diet with availability, Manly's preference indices indicated selective predation in all studies. Roe deer were preferred over chamois in all areas except in the Jura Mountains where relatively few chamois were present. Predation was least selective in northeastern Switzerland, where the initial phase of recolonisation by lynx was studied. Variation in prey availability is often identified as an important factor explaining intraspecific variation in home-range size. Due to differences in roe deer and chamois abundance from one study area to another, we expected female lynx home ranges to decrease with increasing prey abundance. The predictors for Minimum Convex Polygon (MCP) and Kernel home-range estimators differed. MCP home-range sizes were best explained by the interactions of study with the number of locations per lynx, roe deer harvested per km^2, and good roe deer habitat, whereas Kernel home-range sizes were best explained by the interactions of study with good roe deer habitat, good chamois habitat, and the interaction of good roe deer and chamois habitat plus an additive effect of the study. Contrary to our expectations, there was no simple correlation of prime roe deer and chamois habitat nor between the number of roe deer and chamois harvested per km^2 and the size of female lynx home ranges. The comparison of the five studies suggested that this expectation may only be valid if lynx populations are close to carrying capacity (e.g. the Jura Mountains and the northwestern Alps in the 1990s). For predictions of home-range size both habitat (spatial factor) and the status and dynamic of the predator/prey populations (temporal factor) need to be taken into account.

Key words: home range, Lynx lynx, predation, Switzerland

Anja Molinari-Jobin, Fridolin Zimmermann, Andreas Ryser, Christine Breitenmoser-Würsten, Simon Capt & Urs Breitenmoser, KORA, Thunstrasse 31, CH-3074 Muri b. Bern, Switzerland - e-mail addresses: a.molinari@kora.ch; (Anja Molinari-Jobin); f.zimmermann@kora.ch (Fridolin Zimmermann); a.ryser@kora.ch (Andreas Ryser); ch.breitenmoser@kora.ch (Christine Breitenmoser-Würsten); s.capt@unine.ch (Simon Capt); urs.breitenmoser@ivv.unibe.ch (Urs Breitenmoser)
Paolo Molinari, Progetto Lince Italia, Via Roma 35, I-33018 Tarvisio, Italy - e-mail: p.molinari@kora.ch
Heinrich Haller, Schweizerischer Nationalpark, CH-7530 Zernez, Switzerland - e-mail: heinrich.haller@nationalpark.ch
Roman Eyholzer, Wildark, Tillierstrasse 6a, CH-3005 Bern, Switzerland - e-mail: Roman.Eyholzer@wls.ch

Corresponding author: Anja Molinari-Jobin

Received 12 August 2004, accepted 28 June 2006

Associate Editor: John D.C. Linnell

Large felids are usually specialist predators (Sunquist & Sunquist 1989). Even though their prey spectrum is often very wide, large cats usually have 1-3 preferred prey species, switching between their main and their 1-2 alternative prey species. Hence, the relative preference for a given prey species by a predator is an important aspect of their impact on prey populations. The Eurasian lynx *Lynx lynx* fits this pattern very well. Their prey spectrum ranges from small rodents to adult female red deer *Cervus elaphus*, but they specialise on hunting roe deer *Capreolus capreolus* if they are available (Jędrzejewski et al. 1993).

Since the reintroduction of lynx to the Swiss Alps and the Jura Mountains in the early 1970s (Haller & Breitenmoser 1986, Breitenmoser & Baettig 1992), five studies on lynx land tenure system and predation pattern have been carried out, allowing us to review similarities and differences regarding lynx abundance and prey preferences. These studies were performed in situations with different lynx populations. The first research project was started in the northwestern Alps, at the centre of the lynx population distribution (Haller & Breitenmoser 1986). The second area of interest was located in the central Alps where the late colonisation phase was studied (Haller 1992). During 1988-1998, a long-term study was conducted in the Jura Mountains, and during 1997-2000, lynx were again studied in the northwestern Alps where the density of the species had increased (Breitenmoser-Würsten et al. 2001) compared to the study performed in the 1980s. One aim of these studies was to provide baseline data on lynx predation, as local hunters complained about decreasing game abundance due to the impact of lynx. In the northwestern and central Alps, predation on livestock (mainly sheep) was additionally an important topic, though livestock never constituted an important part of lynx diet. The latest study in northeastern Switzerland was the result of the translocation of nine lynx into an area not previously colonised (Ryser et al. 2004). In total, 97 lynx were captured and radio-collared within five different studies during 1983-2004.

In this paper, we describe lynx prey selection and examine 1) the interplay of the lynx's most important prey species, roe deer, and the main alternative prey, chamois *Rupicapra rupicapra*, and 2) the effect of their abundance on lynx density. We use female home-range size as a measure for lynx density, implying a correlation between female home-range size and lynx density. Our expectations were: 1) that female home-range size would decrease with increasing prey abundance, and 2) that we would find the smallest home ranges, and thus the highest lynx abundance, in the areas where roe deer abundance was highest. We used two indirect indices of prey abundance, roe deer and chamois harvested per km^2 and habitat suitability for roe deer and chamois as derived from a GIS model. Thus, we analysed the effect of prey abundance (indexed from hunting statistics of roe deer and chamois), study area/period (referred to throughout as 'study'), and roe deer and chamois habitat potential within individual

home ranges on home-range size. This understanding is vital in management and conservation in order to scale the size of management units (Linnell et al. 2001, Herfindal et al. 2005) and to extrapolate predation magnitude and impact from a reference area to a larger conservation or management unit.

Study areas

Of our study areas, four were situated in the Swiss Alps entirely, while one study area was in the Jura Mountains (Fig. 1). The Alps and the Jura Mountains differ in their physiographic characteristics. The former have a reduced and more fragmented forest cover, steeper slopes and higher elevations. All study areas were subdivided into smaller units, called reference areas. Most of the lynx kills found were within these areas. The reference areas also correspond to ungulate management units, and data on ungulate statistics originate from these areas only.

In the following paragraphs we briefly describe each study area. For more detailed information we refer to the original publications (Breitenmoser & Haller 1987, Haller 1992, Breitenmoser et al. 2007, Breitenmoser-Würsten et al. 2001, Ryser et al. 2004).

Northwestern Alps 1

This study area comprised the Bernese Oberland, the canton of Obwalden and parts of the cantons of Lucerne, Nidwalden, Fribourg and Vaud. The reference area (NWA1) was confined to the Niedersimmental with a size of 378 km^2. The highest peak reached an altitude of 2,362 m a.s.l. Forest covered 26% of the area. Chamois were considered to be more abundant than roe deer, red deer presence was reported sporadically and ibex *Capra ibex* were confined to a few colonies. Other potential prey species with an adult body weight of > 1 kg were red fox *Vulpes vulpes*, badger *Meles meles*, pine marten *Martes martes*, stone marten *M. foina*, brown hare *Lepus europaeus*, mountain hare *L. timidus*, marmot *Marmota marmota*, black grouse *Tetrao tetrix* and capercaillie *T. urogallus*. From late spring to autumn, domestic sheep *Ovis ammon* grazed unguarded on remote mountain meadows.

Central Alps

This study area comprised the eastern and central parts of the canton of Valais in southwestern Switzerland. The reference area (CA) had a size of 330 km^2 and included the Turtmanntal, a wildlife sanctuary of 37 km^2. The highest peak reached an altitude of 4,634 m a.s.l. Forest covered 30% of the area. The same potential prey species as in the NWA study areas are present. However, the CA study area is special regarding its ungulate community, as both chamois and red deer are more abundant than roe deer.

Jura Mountains

This study area included the Jura parts of the cantons of Vaud and Bern, as well as the canton of Neuchâtel, and neighbouring France. The reference area (JM) consisted of the Jura part of the canton of Vaud with a size of 703 km^2. The high-

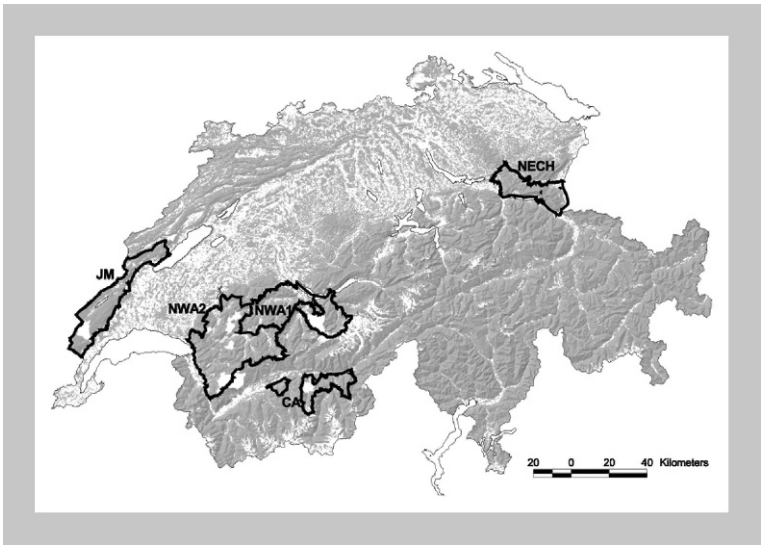

Figure 1. Location of reference areas within Switzerland (JM = Jura Mountains, NWA1 and NWA2 = northwestern Alps 1 and 2, CA = central Alps, NECH = northeastern Switzerland). Grey shows the definition of the study area, i.e. all the area excluding glaciers, rivers, lakes, traffic lines, settlements, industrial areas, intensive agricultural areas and wildlife sanctuaries.

est peak reached an altitude of 1,718 m a.s.l. Forest covered 58% of the area. Prey availability differed from that in the Alpine study areas in that ibex, mountain hare and black grouse do not occur in the Jura Mountains. Instead, the wild cat *Felis sylvestris* is present. Sheep occurred in low numbers only, even though all lynx in JM had access to some sheep.

Northwestern Alps 2

This study area comprised the Bernese Oberland and the Alpine part of the cantons of Fribourg and Vaud, and thus overlapped partly with NWA1. The reference area (NWA2) comprised the Nieder- and Obersimmental and the Saanenland, and the Alpine parts of Vaud and Fribourg with a size of 2,215 km^2. The highest peak reached an altitude of 2,362 m a.s.l. Forest covered 27% of the area. The prey community was as described under NWA1.

Northeastern Switzerland

This study area included the cantons of Thurgau, Appenzell and parts of the cantons of Zurich and St. Gallen. The reference area (NECH) was confined to the area north of the Walensee entirely within the canton of St. Gallen, with a size of 446 km^2. The highest peak reached an altitude of 2,384 m a.s.l. Forest covered 34% of the area. All the prey species that occur in the other Alpine study areas occur in this area as well.

Methods

We captured lynx using foot snares or a remotely controlled blowpipe close to fresh kills, or in large double-door live traps according to Breitenmoser & Haller (1993) and Ryser et al. (2005). Radio-marked lynx were subsequently relocated from the ground with a precision of 1 km^2, 1 ha or direct observation. For the purpose of this study, we considered only kills found by means of radio-telemetry. To find kills, we monitored the movements of individual lynx daily. Lynx usually fed for several days on a kill, hiding during the day and returning to the carcass each evening. If lynx stayed for more than half an hour in one place at dusk, we located it precisely by approaching it to a distance of 50-200 m. The next day, we searched this area for prey remains. Both in NWA1 and JM we used dogs to aid in the search for kills. Some kills were also found during the daily radio-tracking, as lynx sometimes rested very close to the kill. Whenever snow conditions permitted, we also followed lynx tracks to find kills. The JM study lasted for 10 years and because roe deer and chamois density increased during the study period (Molinari-Jobin et al. 2002), we divided it into three study periods (Table 1) according to the status of the lynx population (Breitenmoser-Würsten et al. 2007).

Prey preference within the study areas was studied by calculating Manly's preference index α for constant prey populations (Chesson 1978). The val-

Table 1. Lynx prey spectrum expressed as number of kills found in five study areas in Switzerland. The JM study was divided into three periods according to Breitenmoser-Würsten et al. (2007).

	NWA1	CA	JM P1	JM P2	JM P3	NWA2	NECH	
Years of study	1983-1988	1986-1989	1988-1991	1992-1994	1995-1997	1997-2000	2001-2004	Total
Nr of resident females	4	3	3	2	4	15	3	34
Roe deer *Capreolus capreolus*	48	20	127	46	234	101	79	655
Chamois *Rupicapra rupicapra*	30	48	43	16	62	61	34	294
Red fox *Vulpes vulpes*			16	3	18	15	1	53
Brown hare *Lepus europaeus*	3	1	3	5	5	6	2	25
White hare *L. timidus*	2	1				10		13
Sheep *Ovis ammon*	2	7						9
Marmot *Marmota marmota*	1		1			4	2	8
Stone marten *Martes foina*						2		2
House cat *Felis domesticus*			1			1		2
Red deer *Cervus elaphus*		1						1
Goat *Capra aegagrus*		1				1		2
Pine marten *Martes martes*			1					1
Wild cat *Felis sylvestris*			1					1
Capercaillie *Tetrao urogallus*			1					1
Black grouse *Tetrao tetrix*		1						1
Squirrel *Sciurus vulgaris*	1							1
Total	87	80	194	70	319	201	118	1069

ues of this index range within 0-1, with higher values implying higher selectivity. Chesson's selection index for prey in the i^{th} category is formulated as:

$$\alpha_i = (r_i/n_i)/\sum(r_j/n_j)$$

where α_i = preference index for prey type i, r_i, r_j = proportion of prey type i or j in the diet, and n_i, n_j = proportion of prey type i or j in the environment. We used both hunting statistics and habitat (see below) to define the proportion of roe deer and chamois in the environment. Kills made by a male lynx when he stayed in the vicinity of the city of Zurich, where no chamois are available, were excluded from the analysis.

Data on home ranges were either obtained from the original publications for NWA1 (Haller & Breitenmoser 1986, Breitenmoser & Haller 1993), CA (Haller 1992), JM (Breitenmoser-Würsten et al. 2007), NWA2 (Breitenmoser-Würsten et al. 2001), and NECH (Ryser et al. 2004) or calculated using 95% minimum convex polygons and 95% Kernel area as described in Breitenmoser-Würsten et al. 2007. For all range analyses, we used the Animal Movement Analysis Extension for Arc View 3.1 (Esri 1996, Hooge & Eichenlaub 1997).

The numbers of roe deer, chamois, red deer and wild boar *Sus scrofa* shot within the smallest unit available were recorded for the respective study years. In NWA1, NWA2 and CA this unit was the municipality, and in NECH it was the hunting grounds (Reviere). The size of the municipalities averages 31 km^2 (range: 1.3-165 km^2) and the size of the hunting grounds averages 14 km^2 (range: 0.6-34 km^2). In JM, the data were only available for the whole of the reference area. From the data sets obtained, we calculated a roe deer and chamois density index based on killed animals per km^2 of the reference area. We used the environmental variables from GEOSTAT (Swiss Federal Statistical Office) to define the functional size of the reference areas by excluding glaciers, rivers, lakes, traffic lines, settlements, industrial areas and wildlife sanctuaries. We removed wildlife sanctuaries from our analysis as no hunting is permitted despite the fact that game densities are usually higher in these areas than in the surrounding hunted areas. Each lynx home range was overlaid with the roe deer and chamois density map. Average roe deer and chamois density within the lynx home range was calculated, weighted by the proportion of home range within each municipality or hunting ground to obtain an index of roe deer and chamois within the lynx' minimum convex polygon and Kernel home range. Roe deer and chamois habitat suitability was modelled according to Eyholzer et al. (2003). This habitat model determines the suitability for roe deer and chamois within 1 ha from factors such as altitude, present vegetation and human disturbance (e.g. settlements, roads and outdoor activities) and assigns a value within the given unit (i.e. lynx home range) to each hectare. The values considered were habitat suitabilities of 0, 0.05, 0.2, 0.5, 0.8 and 1; e.g. a value of 0.8 indicates that of this hectare, 80% are suitable habitat. We used the following habitat parameters in the linear regression model: 1) good habitat (suitability of 0.8 and 1) over bad habitat (suitability of 0 and 0.05), 2) good habitat over the size of the home range, and 3) average habitat (suitability of 0.2 and 0.5) over the size of the home range.

To explain the variation in home-range size, we fitted several linear regression models with the log(minimum convex polygon home-range size) as dependent, and the roe deer and chamois density index, study, percentage of forest within a home range, an index of forest edge per forest area and an index of roe deer and chamois habitat suitability as explanatory variables. In addition, we used biological meaningful two-way interactions in the global model. We only used home ranges of resident females in the analyses, as the size of male home ranges is mainly expected to be influenced by the distribution of female ranges (Sandell 1989). Females that were followed for < 1 year and females with < 50 locations were omitted from the analysis. In JM, some females were followed for > 1 period. We, however, considered only one period per female.

Model selection was based on the small-sample-size corrected Akaike Information Criterion (AIC_c; (Burnham & Anderson 1998). The AIC_c is calculated as 22 log (likelihood) plus twice the number of free parameters of the model, with a correction factor taking sample size into account. The model with the lowest value of AIC_c is the most parsimonious one, i.e. the one providing the best balance between bias (due to underfitting) and lost precision (due to overfitting). When two models differ in their AIC_c values by < 2 units, the models can be considered comparable. A difference of > 2 units indicates a considerable difference in the ability of the models to fit the data, and a difference of ≥ 7 units suggests

a bad fit of the model with the higher AIC_c value (Burnham & Anderson 1998). In a second step, we fitted linear regression models with the log(Kernel home-range size) as dependent, and study, roe deer and chamois index and the evaluation of roe deer and chamois habitat suitability as explanatory variables. All the statistical analyses were performed using Splus (Venables & Ripley 1994).

Results

The number of different species in the lynx' diet ranged within 4-9, depending on the study site and/or period (see Table 1). Nevertheless, lynx diets were generally similar among sites. Roe deer and chamois made up > 80% of prey items in all study areas. Only one red deer was killed, and neither ibex nor wild boar were found in our sample. Red foxes, brown hares and mountain hares were the most important non-ungulate prey species. A complete list of all prey items found per study area is given in Table 1. The study areas NWA1, NWA2 and CA were the only areas where killed livestock were found by means of radio-telemetry, although livestock were available to lynx also in the other study areas.

We found great variation both in the relative habitat suitability for roe deer and chamois and in the number of ungulates shot per km^2 between study areas (Table 2). The highest numbers of roe deer were harvested in NECH, followed by JM. In contrast, the highest number of chamois was reported from CA, followed by NWA1 while in JM few chamois were shot. Both in NECH and CA, red deer made up 10% of the hunting bag. In NWA2 twice as many chamois were shot than roe deer, whereas in JM 10 times more roe deer were shot than chamois. In Figure 2, we show the trend of roe deer and chamois harvested in JM and NWA. In these two areas, lynx have been followed by means of radio-telemetry for a total of 10 years each. While lynx density remained very stable in JM, the density was much lower during the NWA1 than during the NWA2 study (Breitenmoser-Würsten et al. 2001, Breitenmoser-Würsten et al. 2007).

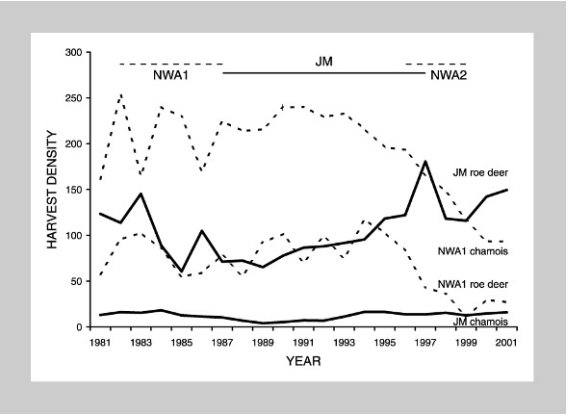

Figure 2. Comparison of the number of roe deer and chamois harvested/100 km^2 in JM (——) and NWA (--------). The data of NWA refer to 15 municipalities in the centre of the NWA2 reference area. The dashed and solid bars on top of the figure show the duration of the studies in NWA and JM, respectively.

Comparing the proportion of roe deer and chamois in lynx diet with availability between study areas using hunting statistics, Manly's preference indices indicated selective predation in all study areas (Fig. 3). Roe deer were preferred over chamois in all areas except in JM during all three periods. Predation was least selective in NECH, where the initial phase of recolonisation of lynx was studied. The preference indices were slightly different if lynx kills were compared with habitat. In JM lynx still

Table 2. Average number (with range given in parentheses) of ungulates harvested per km^2, and study area and relative habitat suitability (HS) for roe deer and chamois for each of the five studies. The JM study was divided into three study periods according to Breitenmoser-Würsten et al. (2007). Data on red deer harvested were not available for all periods.

	Study						
	NWA1 (1983-1988)	CA (1985-1988)	JM P1 (1988-1991)	JM P2 (1992-1994)	JM P3 (1995-1997)	NWA2 (1997-2000)	NECH (2001-2004)
Roe deer	0.96 (0.71-1.30)	0.11 (0.03-0.27)	0.83 (0.72-0.96)	1.01 (0.97-1.05)	1.55 (1.31-1.99)	0.32 (0.17-0.43)	2.98 (2.55-3.28)
Chamois	1.84 (1.46-2.08)	1.10 (0.99-1.19)	0.06 (0.04-0.08)	0.13 (0.08-0.18)	0.16 (0.15-0.18)	0.76 (0.59-0.85)	1.53 (1.19-1.75)
Red deer	0	0.13 (0.10-0.20)	?	?	0.02 (0.01-0.03)	0.01 (0-0.01)	0.49 (0.47-0.52)
Total	2.80	1.18	0.82	1.04	2.10	1.06	5.01
HS roe deer	27%	13%	60%	60%	60%	25%	43%
HS chamois	49%	45%	23%	23%	23%	49%	37%

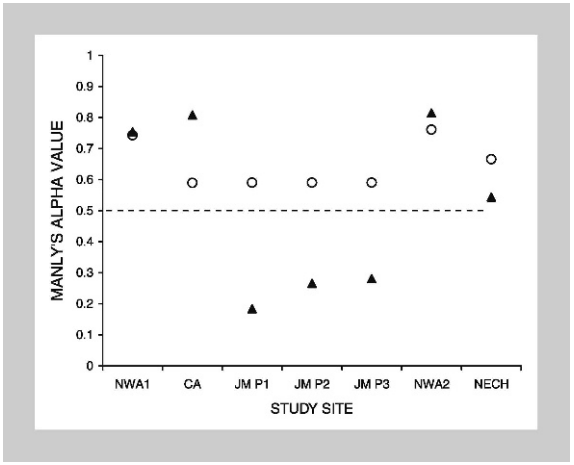

Figure 3. Dietary preference of lynx for roe deer versus chamois for each of the five study area. Manly's α values of 0.5 indicate that use reflected availability, values of > 0.5 indicate preference for roe deer and values of < 0.5 indicate preference for chamois. Triangles represent lynx kills compared to the hunting bag of roe deer and chamois, while circles represent lynx kills compared with habitat potential as modelled by Eyholzer et al. (2003).

showed the least preference for roe deer but were followed by CA instead of NECH.

In total, we used 34 home ranges of female lynx in our analyses. The MCP and Kernel home-range size of resident females in Switzerland averaged 115 ± 64 km^2 and 80 ± 33 km^2, respectively. MCP home-range sizes differed from study to study. These differences were less pronounced in the Kernel home-range estimator (Kruskal-Wallis rank sum test: MCP: $\chi^2 = 15.7528$, df = 4, P = 0.003; Kernel: $\chi^2 = 8.8613$, df = 4, P = 0.06). The smallest home ranges were found in CA, the largest in NWA1.

The predictors for the two home-range estimators differed in that Kernel home-range size was best explained by a model including the study and the interactions of good chamois habitat with study, good roe deer habitat with study as well as the interaction of good chamois habitat with good roe deer habitat ($r^2 = 0.70$, F = 2.857, df = 15, 18, P = 0.018; Table 3). The same model with the MCP home-range size as the dependent variable was not significant ($r^2 = 0.62$, F = 1.998, df = 15, 18, P = 0.082). MCP home-range sizes were best explained by a model including study, and the interactions of the number of locations with study, the number of roe deer harvested per km^2 with study, and good roe deer habitat with study. As for the best model there were too many parameters involved for the calculation of the regression compared to the sample size, we used the second best MCP model for further analyses, i.e. the model with the interactions of locations with study, roe deer harvested with study and good roe deer habitat with study ($r^2 = 0.79$, F = 4.389, df = 15, 18, P = 0.002; see Table 3). Study

Table 3. AIC_c values for models based on MCP and Kernel home-range analyses with the following variables: area = study area; cgood = good chamois habitat; rgood = good roe deer habitat; cindex = good/bad chamois habitat; rindex = good/bad roe deer habitat, raverage = average roe deer habitat; caverage = average chamois habitat, cbad = bad chamois habitat, rbad = bad roe deer habitat, duration = duration of study in months, edge = index forest edge to forest, locations = number of locations, rharvested = roe deer harvested/km^2, charvested = chamois harvested per km^2. We only show the 10 best ranking models.

	Model	AIC_c	R^2 adjusted
MCP	area+area:locations+area:rharvested+area:rgood	-142.0677	0.79
	area:locations+rharvested:area+rgood:area	-139.3747	0.76
	area:locations+rharvested:area+rgood:area+locations	-136.4065	0.76
	area:locations+rharvested:area+rgood:area+rharvested	-136.4065	0.76
	area:locations+rharvested:area+rgood:area+rgood	-136.4065	0.76
	rharvested:area+rgood:area	-132.6624	0.70
	area+area:locations+rharvested:area	-132.0825	0.71
	area:locations+rharvested:area+charvested:area	-131.5081	0.70
	area:locations+rharvested:area	-130.7962	0.68
	area:locations+rharvested:area+cgood:area	-130.5967	0.69
Kernel	area+area:cgood+area:rgood+cgood:rgood	-148.0137	0.66
	area+cgood+area:cgood+area:rgood+cgood:rgood	-144.8172	0.65
	area+rgood+area:cgood+area:rgood+cgood:rgood	-144.8172	0.65
	area:cgood+area:rgood+cgood:rgood	-144.7312	0.61
	area:locations+rharvested:area+cgood:area	-144.5933	0.59
	area+area:locations+cgood:area	-143.9856	0.58
	cgood+area:cgood+area:rgood+cgood:rgood	-141.7629	0.60
	rgood+area:cgood+area:rgood+cgood:rgood	-141.7629	0.60
	area+cgood+rgood+area:cgood+area:rgood+cgood:rgood	-141.3649	0.64
	area+area:cgood+area:rgood	-140.6531	0.56

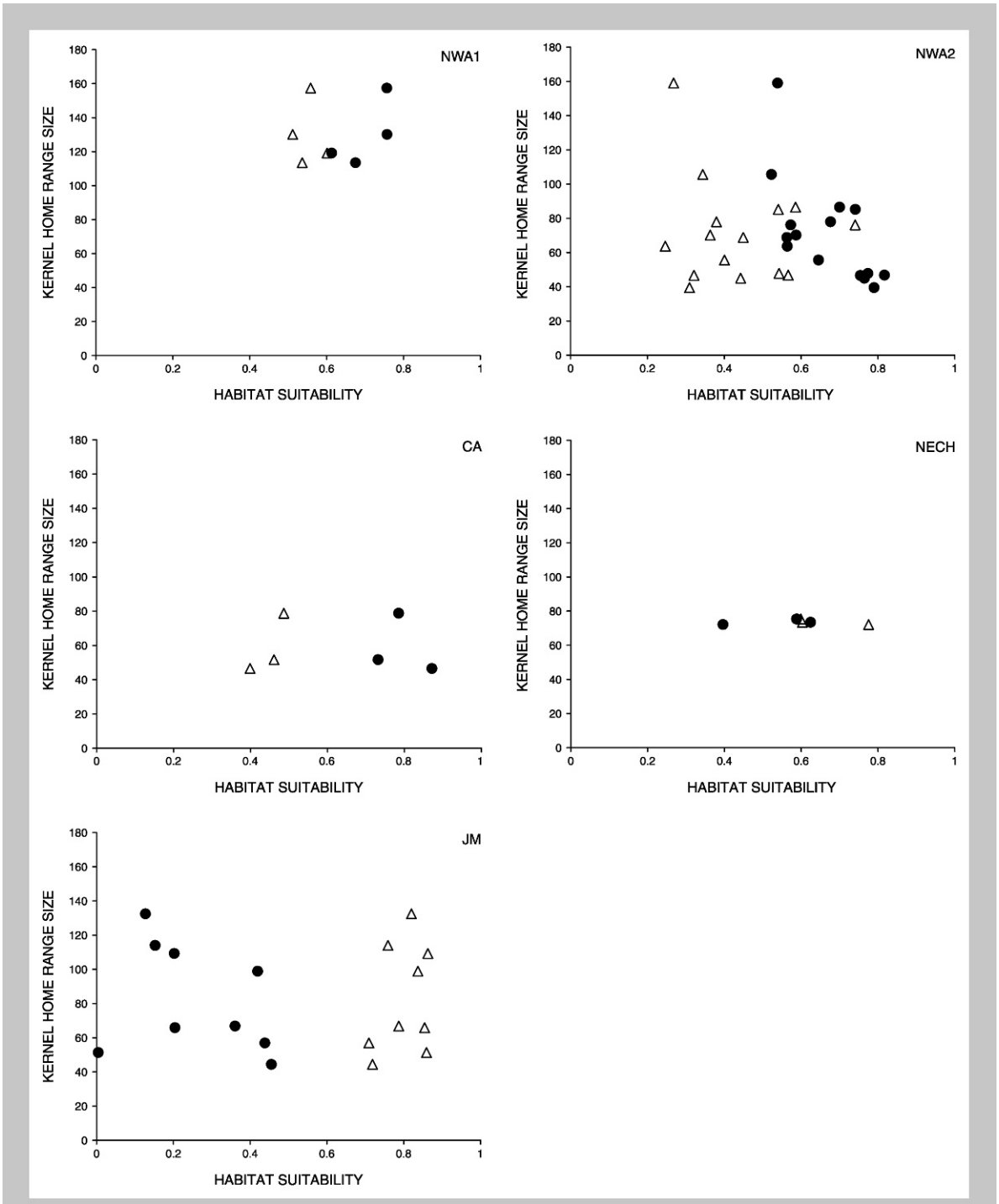

Figure 4. Relationships between Kernel home-range size and good roe deer (△) and chamois (●) habitat for each of the five study areas. The higher the value of habitat suitability, the better the habitat for the respective species.

was an important factor for both home-range predictors.

The MCP method was better suited to explain variation in home-range size than the Kernel method. The best MCP model explained 76% of the variation vs 66% in the Kernel analyses. In the best Kernel model, the interactions of JM with good chamois habitat (ß = -4.9720, t = -2.5687, df =

Table 4. Parameter estimates for the final model of the Kernel analyses.

Variable	Beta	SE	t-value	df	P
(Intercept)	2.8926	1.548	1.8686	15,18	0.078
[JM]	1.0094	1.4733	0.6851	15,18	0.502
[NWA1]	0.2145	0.9485	0.2261	15,18	0.824
[NWA2]	0.5007	0.3256	1.5378	15,18	0.142
[NECH]	0.2361	1.1441	0.2063	15,18	0.839
[CA]:[good chamois habitat]	-1.1356	2.2496	-0.5048	15,18	0.620
[JM]:[good chamois habitat]	-4.972	1.9356	-2.5687	15,18	0.019
[NWA1]:[good chamois habitat]	-2.0337	2.0153	-1.0091	15,18	0.326
[NWA2]:[good chamois habitat]	-3.7364	1.0684	-3.4972	15,18	0.002
[NECH]:[good chamois habitat]	-3.9444	4.4677	-0.8829	15,18	0.389
[CA]:[good roe deer habitat]	-0.8383	3.6774	-0.228	15,18	0.822
[JM]:[good roe deer habitat]	-1.2168	1.2155	-1.0011	15,18	0.330
[NWA1]:[good roe deer habitat]	-2.4147	3.2249	-0.7488	15,18	0.464
[NWA2]:[good roe deer habitat]	-3.6324	1.5064	-2.4113	15,18	0.027
[NECH]:[good roe deer habitat]	-2.8848	5.2427	-0.5503	15,18	0.589
[good roe deer habitat]:[good chamois habitat]	5.9268	2.3446	2.5278	15,18	0.021

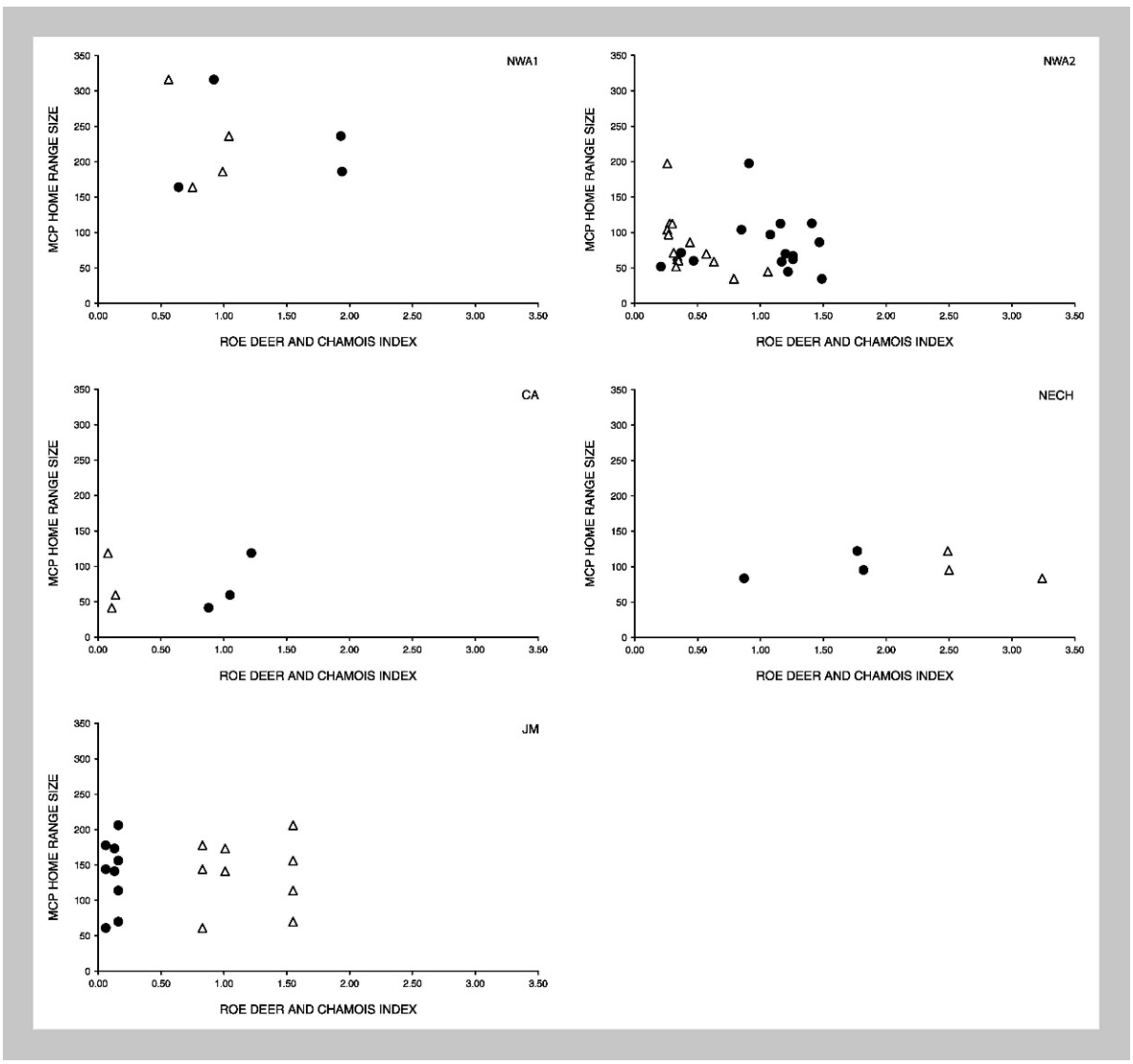

Figure 5. Relationships between MCP home-range size and relative number of roe deer (△) and chamois (●) harvested for each of the five study areas.

Table 5. Parameter estimates for the final model of the MCP analyses.

Variable	Beta	SE	t-value	df	P
(Intercept)	2.0540	0.1479	13.8910	15,18	0.0000
[CA]:[locations]	-0.0022	0.0054	-0.4161	15,18	0.6823
[JM]:[locations]	-0.0006	0.0005	-1.2234	15,18	0.2369
[NWA1]:[locations]	-0.0012	0.0013	-0.9733	15,18	0.3433
[NWA2]:[locations]	0.0005	0.0004	1.2122	15,18	0.2411
[NECH]:[locations]	-0.0004	0.0009	-0.4801	15,18	0.6369
[CA]:[roe deer harvested]	-7.6234	5.7377	-1.3287	15,18	0.2006
[JM]:[roe deer harvested]	-0.0910	0.1257	-0.7236	15,18	0.4786
[NWA1]:[roe deer harvested]	0.1476	0.5591	0.2640	15,18	0.7947
[NWA2]:[roe deer harvested]	-0.5185	0.1768	-2.9324	15,18	0.0089
[NECH]:[roe deer harvested]	0.3673	0.8829	0.4160	15,18	0.6823
[CA]:[good roe deer habitat]	1.3663	1.8997	0.7192	15,18	0.4812
[JM]:[good roe deer habitat]	0.8346	0.3733	2.2355	15,18	0.0383
[NWA1]:[good roe deer habitat]	0.4976	0.4567	1.0898	15,18	0.2902
[NWA2]:[good roe deer habitat]	-0.0463	0.1953	-0.2369	15,18	0.8154
[NECH]:[good roe deer habitat]	-0.1667	0.9776	-0.1705	15,18	0.8665

15, 18, P = 0.019), NWA2 with good chamois habitat (ß = -3.7364, t = -3.4972, df = 15, 18, P = 0.003), NWA2 with good roe deer habitat (ß = -3.6324, t = -2.4113, df = 15, 18, P = 0.026), and good chamois with good roe deer habitat (ß = 5.9268, t = 2.5278, df = 15, 18, P = 0.021) were significant (Fig. 4, Table 4). In the MCP model, the interactions of the NWA2 with the number of roe deer harvested (ß = -0.5185, t = -2.9324, df = 15, 18, P = 0.009), and JM with good roe deer habitat (ß = 0.8346, t = 2.235, df = 15, 18, P = 0.04) were significant (Fig. 5, Table 5).

Discussion

Observing the prey selection of carnivores living in forests is difficult, so information on this subject accumulates slowly. We described lynx prey selection from five different studies conducted over 22 years in Switzerland and examined the interplay of the lynx's most important prey species within these areas, the roe deer, and alternative prey species. The patterns of prey selection were generally consistent with those found in other studies where roe deer was the primary prey species. However, if roe deer are scarce, lynx readily substitute them with other available ungulate prey such as chamois (Haller 1992) or red deer (Okarma et al. 1997). In Switzerland, roe deer were the most important prey for lynx, and in all studies the main alternative to roe deer were chamois (see Table 1). Thus, together the two species made up 90% of the diet. Within this common pattern, the amount of roe deer vs chamois in the diet showed great variation. In CA, where roe deer were relatively scarce, they made up only 25% of the diet, whereas in JM-P3, 73% of prey items were roe deer. All other prey species are marginal. Exceptionally, red foxes and hares can have a high importance for lynx during special phases in life such as during dispersal (Zimmermann 1998) or for females with kittens (Okarma et al. 1997). But lynx predation probably has a negligible effect on red fox and hare population dynamics. Even though red deer are an important prey of lynx in the eastern Alps of Italy (Molinari et al. 2001), they have so far been insignificant in the diet of lynx in Switzerland. However, red deer only occurred in significant numbers in CA and NECH (see Table 2), where obviously enough roe deer or chamois were available for lynx not to need to prey extensively on red deer. Although the JM and NECH study areas host the largest capercaillie populations in Switzerland (Schmid et al. 1998), only one individual was found killed by lynx, contrary to findings from Scandinavia (Sunde et al. 2000), where tetraonids occur more frequently in lynx diet.

Lynx showed clear preferences for one prey species. Generally, they preyed on roe deer more than could be expected from its proportion in the hunting bag or from habitat potential (see Fig. 3). Even in CA, where chamois outnumbered roe deer by a factor of 10, lynx preferred roe deer over chamois. The only exception was JM, where the relatively scarce chamois (see Fig. 2) were preferred during all periods when compared to their proportion in the hunting bag (see Fig. 3). The preference for chamois vs roe deer in JM could be due to habitat characteristics. In this mountain chain lacking an alpine zone, chamois mainly live in the forests, as pastures

are occupied by cattle. Therefore, larger herds are confined to a few areas; otherwise chamois are scattered throughout the forests, where they proved to be very vulnerable to predation while feeding (Molinari-Jobin et al. 2004). Predation of roe deer vs chamois was least selective in NECH, where lynx were newly reintroduced. In the NECH area, the prey may still have been naïve, thus 'allowing' lynx to kill upon encounter.

We compared roe deer and chamois harvested per km^2 vs roe deer and chamois habitat, two indirect indices of prey density, as predictors for lynx home-range size and found differences in the predictors for MCP and Kernel home-range estimators. We found that MCP home-range sizes were best explained by the interactions of study with the number of locations, roe deer harvested per km^2 and good roe deer habitat, whereas Kernel home-range sizes were best explained by the interactions of study with good roe deer habitat, good chamois habitat and the interaction of good roe deer and chamois habitat plus an additive effect of study.

Consequently, unlike in Norway (Herfindal et al. 2005), hunting statistics were only partly able to predict MCP lynx home-range size in Switzerland, whereas they failed to explain Kernel lynx home-range size altogether. Switzerland has two different hunting systems. NWA1, NWA2, CA and JM have a licence hunting system, while NECH has closed hunting grounds. Generally, more animals are harvested per km^2 in the closed hunting grounds than in the licence hunting system. But still, the two hunting systems have in common that the ungulate management aims at providing good hunting opportunities and at the same time minimising browsing damage on forests. Quotas therefore consider perceived changes in the population size, however, with a certain time lag, which may increase but at least seem not to prevent fluctuations of the ungulate populations. While hunting statistics are not good predictors for the present ungulate population density, they can, however, indicate the population trend and allow for relative comparisons between the present studies. Good habitat was a better predictor for lynx home-range size than the number of roe deer and chamois harvested per km^2, as the interaction of good habitat and study appeared in the best models for both MCP and Kernel analysis.

Contrary to our expectation, there was no simple correlation of habitat quality nor of the number of roe deer and chamois harvested per km^2 and the size of female home ranges (expectation 1). With similar values for both good roe deer and good chamois habitat we expected similar Kernel home-range sizes in the NWA1 and NWA2 study areas. This was not the case, as the largest home ranges were observed in NWA1, and home ranges in NWA2 were among the smallest. The prediction of decreasing female home-range size with increasing prey abundance was also falsified with the example of NWA. In the 1980s, three times as many roe deer and twice as many chamois were shot than at the end of the 1990s (see Table 2), but home-range sizes were almost three times larger during the 1980s, contrary to our expectation. In the 1980s, female home-range size was estimated at 165 km^2 (range: 130-195), while in the 1990s the home-range size was estimated at 100 km^2 (range: 45-210; Breitenmoser-Würsten et al. 2001). Besides, lynx had colonised new habitat in the meantime (Breitenmoser-Würsten et al. 2001). Roe deer were not the key predictor of lynx home-range size either (expectation 2). The smallest lynx home ranges were found in the CA study area, where roe deer abundance was lowest.

In JM and NWA, a similar number of roe deer were shot per 100 km^2 (see Fig. 2). Lynx home-range size in NWA differed from that in JM, however, during both studies (see Fig. 5): in the 1980s female home ranges were larger, and in the 1990s female home ranges were smaller than in the JM. A possible explanation for this phenomenon might be that lynx in the NWA1 study had not yet reached carrying capacity, whereas lynx in the JM and NWA2 studies were close to carrying capacity. Both for the Kernel and for the MCP method the interactions of good habitat or roe deer shot with JM and NWA2 were significant (see Tables 4 and 5). We indeed observed smaller lynx home ranges in the NWA2 study than in the JM study, as expected from the number of roe deer and chamois harvested per km^2, and the comparison of the good roe deer and chamois habitat. Even if both roe deer and chamois decrease, as was observed in the Alps at the end of the 1990s (see Fig. 2), the total prey available was still similar to what it was in JM. Thus, the correlation between prey abundance and home-range size may only be important when lynx populations are close to carrying capacity.

Herfindal et al. (2005) have shown that simple indices like productivity and seasonality are able to explain coarse-scale variation in lynx home-range sizes at a European scale and they found a sig-

nificant negative relationship between harvest density and home-range size for lynx in Norway. However, we observed a significant fine-scaled variation in home-range sizes within Switzerland that cannot be explained by indices of prey abundance. Clearly, other factors, such as lynx social organisation, human land use and topography, influence the distribution and abundance of lynx in Switzerland. At local, regional and national scales, the factors that may contribute to the prediction of home-range size are both constant and variable, spatial and temporal. Constant and spatial factors like habitat and hunting statistics can only partly explain lynx abundance. Variable and temporal factors are as important. For extrapolations from a reference study we need to take both habitat (spatial factor) and the status and dynamic of the predator/prey populations (temporal factor) into account. Especially the second parameter cannot be evaluated without specific local knowledge and monitoring. Thus, the inherent dangers in extrapolating information on the interaction of home-range size and habitat or prey animals shot from one area to another, or even within one area, to the future justifies similar types of studies in other regions and/or times.

Acknowledgements - many people and institutions have contributed to this study. We would like to sincerely thank them all for their contribution, especially the people from the KORA team and the game wardens. We also thank the cantons of Bern, Fribourg, St. Gallen, Valais and Vaud who have kindly provided their hunting statistics. Statistical advice was provided by Anne Loison and Jean-Michel Gaillard. The study was funded by the Swiss Agency for Environment (SAEFL), by the Swiss League for Protection of Nature (Pro Natura), WWF Switzerland, the cantons of Aargau, Basel-Land, Bern, Fribourg, Geneva, Jura, Obwalden, Solothurn, St. Gallen, Ticino, Thurgau, Valais, Vaud, and the Society for the Protection of Animals of the Canton of Vaud, the Agassiz Foundation, the Stotzer-Kästli Foundation and the Dr. Berthold Suhner Foundation, and in the initial phase by the Swiss Foundation for the Scientific Research (project no. 3.119-0.85), the 'Silberner Bruch' and the Schweizerischer Schafzuchtverband.

References

Breitenmoser, U. & Baettig, M. 1992: Wiederansiedlung und Ausbreitung des Luchses (Lynx lynx) im Schweizer Jura. - Revue suisse de Zoolgie 99: 163-176. (In German).

Breitenmoser, U., Breitenmoser-Würsten, C., Capt, S., Molinari-Jobin, A., Molinari, P. & Zimmermann, F. 2007: Conservation of the lynx Lynx lynx in the Swiss Jura Mountains. - Wildlife Biology 13: 340-355.

Breitenmoser, U. & Haller, H. 1987: Zur Nahrungsökologie des Luchses Lynx lynx in den schweizerischen Nordalpen. - Zeitschrift für Säugetierkunde 52: 168-191. (In German).

Breitenmoser, U. & Haller, H. 1993: Patterns of predation by reintroduced European lynx in the Swiss Alps. - Journal of Wildlife Management 57: 135-144.

Breitenmoser-Würsten, C., Zimmermann, F., Ryser, A., Capt, S., Laass, J., Siegenthaler, A. & Breitenmoser, U. 2001: Untersuchungen zur Luchspopulation in den Nordwestalpen der Schweiz 1997-2000. - KORA Bericht 9: 1-88. (In German with an English summary).

Breitenmoser-Würsten, C., Zimmermann, F., Stahl, P., Vandel, J-M., Molinari-Jobin, A., Molinari, P., Capt, S. & Breitenmoser, U. 2007: Spatial and social stability of an Eurasian lynx Lynx lynx population - an assessment of 10 years of observation in the Jura Mountains. - Wildlife Biology 13: 365-380.

Burnham, K.P. & Anderson, D.R. 1998: Model selection and interference: a practical information-theoretic approach. - Springer-Verlag, New York, 496 pp.

Chesson, J. 1978: Measuring preference in selective predation. - Ecology 59: 211-215.

Esri 1996: Using Arc View GIS. - Environmental System Research Institut, Redlands, CA.

Eyholzer, R., Baumann, M. & Manser, R. 2003: Zwischenevaluation des Wald-Wild-Management-Instruments (WWMI) im Pilotprogramm effor2 "Wald und Wild". - Schweizerische Zeitschrift für Forstwesen 154: 305-313. (In German).

Haller, H. 1992: Zur Ökologie des Luchses Lynx lynx im Verlauf seiner Wiederansiedlung in den Walliser Alpen. - Mammalia depicta 15: 1-62. (In German).

Haller, H. & Breitenmoser, U. 1986: Zur Raumorganisation der in den Schweizer Alpen wiederangesiedelten Population des Luchses Lynx lynx. (In German with an English summary: Spatial organization of the reintroduced population of the lynx (Lynx lynx) in the Swiss Alps). - Zeitschrift für Säugetierkunde 51: 289-311.

Herfindal, I., Linnell, J.D.C., Odden, J., Birkeland Nilsen, E. & Andersen, R. 2005: Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). - Journal of Zoology 265: 63-71.

Hooge, P.N. & Eichenlaub, B. 1997: Animal Movement Analysis Extension ver. 1.1. to Arc View (3.1). - U.S. Geoglogical Survey, Alaska biological science centre, Anchorage, AK.

Jędrzejewski, W., Schmidt, K., Milkowski, L., Jędrzejewska, B. & Okarma, H. 1993: Foraging by lynx and its role in ungulate mortality: the local (Białowieża Forest) and the Palaearctic viewpoints. - Acta Theriologica 38: 385-403.

Linnell, J.D.C., Andersen, R., Kvam, T., Andren, H., Liberg, O., Odden, J. & Moa, P.F. 2001: Home range size

and choice of management strategy for lynx in Scandinavia. - Environmental Management 27: 869-879.
Molinari, P., Rotelli, L., Catello, M. & Bassano, B. 2001: Present status and distribution of the Eurasian lynx (Lynx lynx) in the Italian Alps. - Hystrix 12: 3-9.
Molinari-Jobin, A., Molinari, P., Breitenmoser-Würsten, C. & Breitenmoser, U. 2002: Significance of lynx Lynx lynx predation for roe deer Capreolus capreolus and chamois Rupicapra rupicapra mortality in the Swiss Jura Mountains. - Wildlife Biology 8: 109-115.
Molinari-Jobin, A., Molinari, P., Loison, A., Gaillard, J-M. & Breitenmoser, U. 2004: Life cycle period and activity of prey influence their susceptibility to predators. - Ecography 27: 323-329.
Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R. & Jędrzejewska, B. 1997: Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. - Acta Theriologica 42: 203-224.
Ryser, A., Scholl, M., Zwahlen, M., Oetliker, M., Ryser-Degiorgis, M-P. & Breitenmoser, U. 2005: A remote-controlled teleinjection system for the low-stress capture of large mammals. - Wildlife Society Bulletin 33: 721-730.
Ryser, A., von Wattenwyl, K., Ryser-Degiorgis, M.P., Willisch, C., Zimmermann, F. & Breitenmoser, U. 2004: Luchsumsiedlung Nordostschweiz 2001-2003. - KORA Bericht 22: 1-60. (In German with an English summary).
Sandell, M. 1989: The mating tactics and spacing patterns of solitary carnivores. - In: Gittleman, J.L. (Ed.); Carnivore Behavior, Ecology, and Evolution. Cornell University Press, Ithaca, New York, pp. 164-182.
Schmid, H., Luder, R., Naef-Daenzer, B., Graf, R. & Zbinden, N. 1998: Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996. - Schweizerische Vogelwarte, Sempach, 574 pp. (In German).
Sunde, P., Kvam, T., Bolstad, J.P. & Bronndal, M. 2000: Foraging of lynxes in a managed boreal-alpine environment. - Ecography 23: 291-298.
Sunquist, M.E. & Sunquist, F.C. 1989: Ecological Constraints on Predation by Large Felids. - In: Gittleman, J.L. (Ed.); Carnivore Behavior, Ecology, and Evolution. Cornell University Press, Ithaca, New York, pp. 283-301.
Venables, W. & Ripley, N. 1994: Modern applied statistics with S-PLUS. - Springer, 462 pp.
Zimmermann, F. 1998: Dispersion et survie des Lynx (Lynx lynx) subadultes d'une population réintroduite dans la chaîne du Jura. - KORA Bericht 4: 1-50. (In French).