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Demography of lynx *Lynx lynx* in the Jura Mountains

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We radio-collared a total of 29 lynx in the Swiss Jura Mountains and collected data on demography during 1988-1998. We were able to observe 10 2-14 year-old females for 32 female years. Lynx kittens were born between 12 May and 13 June (26 May \pm 9 days). One female gave birth to a litter on 26 August after she had lost her first litter born in May. The average litter size was 2.00 ± 0.75 kittens (range: 1-3). The sex ratio of 1.67 females:1 male did not differ significantly from the expected ratio of 1:1. On average, 81% of adult females reproduced each year. The overall reproduction rate was 1.67 kittens/female year. Of 49 kittens, 43-49% survived until independence at the age of about 10 months. The survival rate of subadults and adults was 53 and 76%, respectively. Litter size and survival of kittens and subadults varied considerably between three observation periods, i.e. P1-P3 (P1: 1988-1991, P2: 1992-1994, P3: 1995-1997), characterised by substantial changes in the social structure of the population. During P2 only one resident male was present in the main study area, and during this period, the average litter size was lowest with 1.50 kittens only. The survival of kittens was with 37-44% lowest as well, mainly because of the high proportion of litters where all kittens were lost. However, the survival of subadults was highest during P2, when observed animals survived to adulthood. During 1974-2002, 124 mortalities were documented for the whole of the Jura Mountains. Human related mortalities were responsible for 70% of known losses. An estimation based on the radio-collared lynx suggested that poaching may have been responsible for as much as 32% of total mortality. In contrast to other study areas, traffic accidents were very important in the Jura Mountains. They might represent as much as 29% of mortality. During our 10-year study period, no significant spatial expansion of the population was recorded in Switzerland. We suppose that the high human-related mortalities limited the population, which also would explain the lack of a numerical response to an increase in prey abundance observed during the same period in the study area in Switzerland.

Key words: demography, litter size, Lynx lynx, mortality, survival

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The conservation of carnivore populations depends on accurate assessment of abundance and distribution. Any management decision requires a sound understanding of the factors affecting population density and how populations change. For most carnivore species, prey abundance is the major factor influencing population viability under natural conditions, and their population density is positively correlated with the availability of food (Fuller & Sievert 2001).

The lynx *Lynx lynx* was reintroduced to the Jura Mountains in the 1970s. After an initial expansion, the spreading slowed down in Switzerland in the late 1980s (Capt 2007). Today, not all suitable habitat has been recolonised by resident, reproducing lynx (Zimmermann & Breitenmoser 2007), although observations have been documented for almost the entire range (Capt 2007). In 1988, we started an intensive study of lynx in the Swiss part of the Jura Mountains. During the following 10 years, we studied social and spatial organisation (Breitenmoser et al. 1993, Breitenmoser-Würsten et al. 2007), dispersal (Zimmermann 1998), predation (Molinari-Jobin et al. 2007) and habitat use (Zimmermann & Breitenmoser 2002). Roe deer *Capreolus capreolus*, the main prey of lynx, was abundant when lynx were reintroduced, and Molinari-Jobin et al. (2007) showed an increase in the population of the main prey during the study period in Switzerland. However, lynx showed no adequate numerical response (Breitenmoser-Würsten et al. 2007), suggesting that other factors were limiting the population.

The aim of this paper is to 1) present basic demographic data of the lynx in the Swiss Jura Mountains, 2) understand the importance of the different mortality factors, and 3) establish the reasons for the slow expansion and the lack of a numerical response to an increasing prey population.

Study area

The study area, in which demographic data were collected, encompassed the Jura Mountains in the cantons of Neuchâtel and Vaud and extended along the first chain of the Jura Mountains into France southwards to Gex. It corresponds to the area in

which lynx caught in Switzerland were radio-tracked (Breitenmoser-Würsten et al. 2007). About half of the Jura Mountains are covered by forest (Breitenmoser et al. 2007), deciduous trees along the slopes and coniferous forest on the ridges. The Jura Mountains are a secondary limestone mountain chain rich in rock lairs and block heaps which offer shelter to animals. The elevation of the study area ranges within 484–1,718 m a.s.l. (Crêt de la Neige). The main prey of lynx in the Jura Mountains is roe deer and chamois *Rupicapra rupicapra* (Molinari-Jobin et al. 2007). A detailed description of the Jura Mountains is presented in Breitenmoser et al. (2007).

Material and methods

Demographic parameters were collected during the study period, i.e. during 1988–1998, when 29 lynx were radio-collared in the Swiss Jura Mountains. Animals were classified as juveniles while they were with their mother (from birth up to 10 months of age), as subadults during dispersal until they established a permanent home range (Zimmermann 1998), and as adults thereafter. To identify the exact age of adults, we removed an incisor for age determination using the *cementum-annuli* method (Jensen & Nielsen 1968). For animals that died during the study period, the age determination was repeated on a canine for more reliable results (Kvam 1984).

Natality

Lynx were closely followed during the mating season from mid-February to mid-April to document rendez-vous between males and females. Females were then closely monitored from early May onwards to detect the moment when they became sedentary to give birth. Females remained around den sites for 6–9 weeks before they again started to roam over larger areas (Kaczensky 1991). During the first four years of the study, we tried to observe the kittens as early as possible after they started coming out of the den. From 1992 onwards, we approached the den site at least one month earlier, when the

kittens were about four (3-5) weeks old to count them, assess their health condition, weigh and measure them and to identify their sex. To make the sex identification at this early age safe, we measured the distance between the anus and the genital aperture. For females this distance was on average 14 mm (9-16 mm) and for males it was 23 mm (17-23 mm; Mann Whitney U = 17.5, $P < 0.001$). The lynx kittens were marked with a small ear tag.

Survival of kittens

To assess the survival of kittens, we tried to count them during three periods after the litter size had been identified at the den: in summer (July-September) through direct observation, in winter (November-January) and spring, just before they left their mother (February-March) by snow tracking or direct observation. If a female was observed alone, at least two more observations were made to make sure that she really was alone. The same was applied to tracks in the snow as females more often travel alone with increasing age. The minimum number of kittens born and their survival up to the dispersal at the age of about 10 months was assessed for the whole 10-year study period and additionally for the three intervals: Period 1 (P1; 1988-1991), Period 2 (P2; 1992-1994), and Period 3 (P3; 1995-1997), as defined by Breitenmoser-Würsten et al. (2007).

Survival rates for subadult and adult lynx

Survival rates of adults and subadults were estimated using censored telemetry data. Animals with transmitters that failed were not included in the analysis to avoid bias towards survival (White & Garrott 1990). The survival rate for adults and subadults was calculated as $\hat{S} = 1 - (\text{deaths/number of lynx years})$ and for juveniles as $\hat{S} = 1 - (\text{dead juveniles/kittens born})$. Censored animals do appear neither in the numerator nor in the denominator.

Mortalities

To assess the importance of the different mortality reasons, mortality records were analysed for the whole of the Jura Mountains for the period from 1974 to 2002. Mortalities were classified as natural (diseases and accidents), human-caused (poaching, traffic accidents, human related accidents and legal removal), and 'other causes' (cause of death unknown and orphaned kittens). For orphans it was not always possible to assess whether their mother was really dead and whether her death was human-caused or natural.

We must assume that lynx dying from different causes were not discovered with the same probability. To assess the importance of the different mortality factors we analysed the number of radio-collared dead lynx that were found also without radio-telemetry to estimate the probability of discovering a dead lynx.

Results

Mating and birth date

Male and female lynx living in the same area usually met several times during the mating season, and often for more than one day at a time. The rendez-vous started as early as mid-February and went on until mid-April. The mean date of 69 documented meetings was 18 March.

Kittens were born between 12 May and 13 June (mean: 26 May \pm 9 days; $N = 33$) after a gestation period (last observed rendez-vous until female became stationary) of 67-72 days. Den sites were mostly in rocky areas and well-sheltered against weather and predation (Boutros 2001). Kittens were moved several times during the early stage of their lives.

We observed one replacement litter of the female F_{ELSA} in 1993. She gave birth to her first litter on 17 May. On 11 June she left the denning place and moved far to the southwestern edge of her home range (see Breitenmoser-Würsten et al. 2007). We were not able to find any traces of the kittens, nor to find out why they disappeared. On 15/16 June, F_{ELSA} met with M_{TARO}, who all of a sudden had arrived for this rendez-vous from the southernmost tip of his home range. On 26 August, i.e. 72 days later, F_{ELSA} gave birth to a female kitten, which survived to independence in spring 1994.

Natality

During the 10-year study period, we observed 10 females (2-14 years old) over 32 female years (Table 1). For four of the females, the age of first reproduction was known: three females reproduced the first time at the age of two years and one female at the age of three years. For 26 litters, we found an average of 2.00 ± 0.75 kittens. The litters consisted of one cub ($N = 7$), two cubs ($N = 12$) and three cubs ($N = 7$), respectively. Females usually had a litter every year, but we observed six females of very different age which never settled down to give birth in one year (i.e. litter size zero in summer in Table 1). Including these cases, the average litter

Table 1. Reproduction data for female lynx in the Swiss Jura Mountains. Under radio-telemetry (RT) a + indicates that the female was monitored by radio telemetry, (+) that the female was monitored by radio telemetry for part of the year, - that no data were available. In number of kittens with female in summer \geq indicates a minimum estimate based on an observation later in the year.

Lynx mother	Year	RT	Number of kittens with female in		Number of kittens independent in spring
			Summer	Winter	
F _{KIRA}	1987		≥ 2	2	1-2 ^a
	1988	+	2	1	1
	1989	+	2	1	1
	1990	+	2	2	1-2 ^a
	1991	+	0	0	0
F _{MARA}	1989	+	2	1	1
	1990	+	3	0	0
	1991	+	0	0	0
F _{LORA}	1989		-	0	0
	1990	+	0	0	0
	1991	+	1	1	1
	1992	+	2	2	0
F _{AIDA}	1988		≥ 1	1	-
	1989		≥ 1	1	-
	1990	+	≥ 1	1	1
	1991	+	2	2	1
	1992	+	0	0	0
	1993	+	2	2	1-2 ^a
	1994	+	2	2	0
	1995	+	2	2	2
	1996	+	3	2	2
F _{AMBA}	1992	+	1	1	0
	1993	+	1	1	1
	1995	(+)	3	3	1-2 ^a
	1996	+	3	0	0
	1997	+	2	-	-
F _{ELSA}	1993	+	≥ 1	0	0
	1993	+	1	1	1
	1994	+	1	1	1
	1995	+	3	3	2
	1996	+	3	3	0
F _{NINA}	1996	+	1	1	1
	1997	+	3	-	-
F _{NADA}	1993	+	1	0	0
F _{WINA}	1993	+	2	2	1
	1994	+	0	0	0
F _{ROYA}	1993	+	2	2	1
	1994	+	0	0	0

^a One kitten survived to independence for sure, the fate of the second one was not known. It could have dispersed earlier.

size over the 10 years of study was 1.63 ± 1.04 . The litter size increased with the age of the females ($r^2 = 0.204$, $P = 0.020$). Average litter size was smaller for first litters (1.40 ± 0.55 kittens; $N = 5$) than for subsequent litters (2.14 ± 0.73 , $N = 21$; Mann-Whitney: $U = 24$, $P = 0.046$). The overall reproduction rate (including years and females with no reproduction) was 1.67 kittens/female year. The observed reproduction rate, however, varied greatly between females, i.e. from 1.00 to 2.25 kittens/female year (2-7 litters/female; see Table 1).

Litter size varied considerably between the periods P1-P3; P1: 2.00 ± 0.58 , P2: 1.50 ± 0.52 and P3: 2.56 ± 0.72 (Kruskal Wallis: $H = 9.43$, $P = 0.009$), but mean age of the females ($H = 4.74$, $P = 0.094$) did not. There was, however, no significant relationship between litter size and individual years ($r^2 = 0.072$, $P = 0.184$) or between age of the mothers and year ($r^2 = 0.007$, $P = 0.682$). The difference in litter size must therefore be inherent in the respective periods.

During P2 and P3, we marked the kittens at the den when they were 3-5 weeks old. We have no data

on losses before this age. We were only able to detect total losses at this early age, like for F_{ELSA} in 1993 or F_{AMBA} in 1996, because the females all of a sudden started to move over large distances again and never again returned to the den site. But there was no way to observe partial losses before the tagging. During P1, the first observation of the females with the kittens after birth was made when the kittens were already 9-12 weeks old. In 1990, the kittens of F_{KIRA} were discovered by accident only when they were just one week old. The average litter size of 2.0 ± 0.58 for P1 might therefore be underestimated, and yet it was higher than during P2.

For the 17 litters in which we were able to tag the lynx kittens the sex ratio of 20 females to 12 males (1.67 female/male) did not differ from the expected 1:1 ratio ($\chi^2 = 2.00$; $P = 0.16$). During P2, the sex ratio was balanced (six females and seven males), but during P3 there were significantly more females than males (2.8 females/male, $N = 19$; $\chi^2 = 4.26$, $P = 0.04$).

Survival of kittens in their first year

We were able to assess survival from den to dispersal (independence from their mothers) at the age of 10 months for a total of 49 kittens (Table 2). In fall, at the age of about five months, 78% (53-88%) of the kittens observed at the den were still alive, but in the following spring only 43-49% were still alive. Just before dispersal in spring, we were not always able to assess whether a juvenile lynx had died or was an early disperser. Young lynx usually separate from their mother during late March to mid-April, but occasionally, separation took place as early as January (Zimmermann 1998). In each of the three periods analysed, there was at least one litter for which the fate of one kitten was not known (see Table 1), which resulted in the estimate of survival being expressed as ranges rather than as fixed values. Survival was lowest during P2, mainly because of a high proportion of total losses. In five of the 11 litters observed, no kittens survived to independence. In P1, the losses occurred almost exclusively

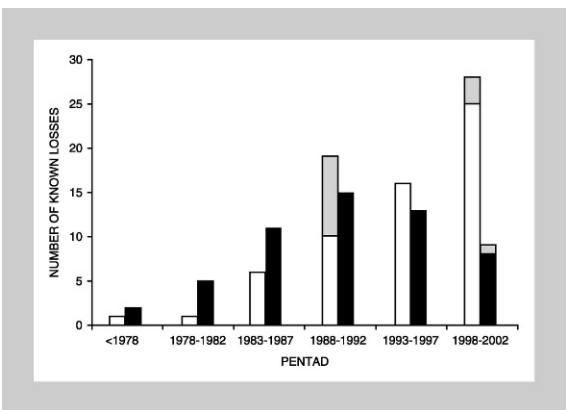


Figure 1. Development of known mortalities (in pentads) in the French (□) and Swiss (■) parts of the Jura Mountains since the releases of lynx in the early 1970s. Legal removals of animals that were undertaken to decrease predation on livestock are shown in grey.

during the summer, whereas during P2 and P3 they mostly occurred during the winter.

Mortalities

The first known loss in the Jura population after the reintroduction occurred in 1974, shortly after the first releases. The number of dead lynx was initially high in Switzerland and peaked in the late 1980s with 15 known losses (Fig. 1). After this, numbers decreased to eight losses during the last pentad. The number of known mortalities in France reached higher values in the 1990s, and during the last pentad, 28 losses were recorded from the French Jura Mountains. In the late 1980s and early 1990s, a considerable number of sheep-raiding lynx had been legally removed in France (Stahl et al. 2001).

Human activities were responsible for 54-77% of known losses (Table 3). There was a considerable difference in the frequency of the causes of mortality between the sample of the radio-tagged lynx and lynx accidentally found dead. Of the radio-collared individuals and their offspring in Switzerland, five were illegally killed. For seven additional animals, we had strong indications that some illegal acts had

Table 2. Survival of lynx kittens in the Jura Mountains during the periods 1998-1991 (P1), 1992-1994 (P2) and 1995-1997 (P3).

Period	Number of females			Number of kittens born	Losses of total litters	Kittens alive in spring before dispersal		
	Surveyed	With litter	Without litter			In fall	Number	%
P1	11	8	3	15	1	8	7-8	46.7-53.3
P2	14	11	3	16	5	14	6-7	37.5-43.8
P3	7	7	0	18	2	14	8-9	44.4-50.0
Total	32	26	6	49	8	36	21-24	42.9-49.0

Table 3. Causes of known losses in the lynx population in the Jura Mountains in different samples during 1974-2002. Animals mentioned as probably illegally killed are cases where the carcass of a radio-tagged lynx could not be retrieved, but where there were strong indications that an illegal act had occurred. CI gives the 95% confidence interval. Some of the animals radio-collared in Switzerland died in France. They show up in both samples.

Cause of mortality	Animals from the telemetry study in Switzerland			Animals accidentally found or intentionally removed in					
	N	%	CI	Switzerland			France		
Human-related losses									
Illegally killed	5	20.8	7.1-42.7	5	14.3	4.8-30.3	8	11.3	5.0-21.3
Probably illegally killed	7	29.2	12.6-51.1						
Traffic (train, road)	5	20.8	7.1-42.2	10	28.5	14.5-46.4	30	42.3	30.3-55.1
Other human-related accidents	2	8.3	1.0-27.0	3	8.6	1.8-23.2	3	4.2	0.9-11.9
Legal killed/removed				1	2.9	0.1-33.0	12	16.9	9.6-27.7
Natural losses									
Diseases	4	16.4	4.7-37.4	1	2.9	0.1-33.0	2	2.8	0.3-9.9
Accident, natural	1	4.2	0.1-21.1				1	1.4	0.03-6.7
Other causes									
Orphans				4	11.4	3.2-34.0	4	5.6	1.6-13.8
Unknown				11	31.4	17.0-49.4	11	15.5	5.8-26.0
Total	24	100.0		35	100.0		71	100.0	

occurred, but we were unable to retrieve the carcasses. Added up, illegal killings were responsible for up to 55% of known losses. The second most important mortality factors were traffic accidents and diseases. Other accidents, human-caused or natural, were of minor importance.

For losses that were discovered by chance, the most important mortality factor was traffic accidents in both France and Switzerland, being responsible for 29 and 42% of known losses, respectively, and the second most important factor was the legal removal of lynx attacking domestic sheep in France and illegal killings in Switzerland.

In the lynx population, 41.1% of known losses were adults, 14.5% subadults, 39.5% juveniles,

and 4.9% were lynx of unknown age (Table 4). The last category mainly consisted of adults and subadults, which could not always be differentiated. There were more females than males in all age categories, but the sex ratio did not differ from 1:1 in any of the three categories (all $\chi^2 < 3.84$, all $P > 0.05$).

Male and female lynx of different ages were not equally affected by the same causes of mortality. Adult females were more often killed in traffic accidents and illegal acts, whereas losses of males were mainly due to legal removals ($\chi^2 = 8.97$; $df = 2$, $P = 0.011$). In subadults, females were also more affected by traffic accidents than males, who more often died from diseases and natural accidents ($\chi^2 = 3.75$;

Table 4. Causes of known losses in the lynx population in the Jura Mountains during 1974-2002 for the age groups adults, subadults and juveniles. ? indicates that the sex of the lynx was unknown.

Cause of loss	Adults				Subadults				Juveniles				?	Total	
	♀	♂	?	Σ	♀	♂	?	Σ	♀	♂	?	Σ	?	N	%
Human related losses															
Traffic (train/road)	9	5		14	6	2		8	7	11	4	22		44	35.5
Illegal killing	6	3	2	11						2		2	3	16	12.9
Probable illegal killing	4	1		5	1	1		2						7	5.6
Other human-related accidents	2	1		3					4			4		7	5.6
Legal killing/removal	1	8		9					3	1		4		13	10.5
Natural losses															
Disease	1	1		2	1	3		4		1		1		7	5.6
Accident, natural	1			1		1		1						2	1.6
Other causes															
Orphans									6	1	1	8		8	6.6
Unknown	1	1	4	6	1		2	3	5	1	2	8	3	20	16.1
Total	25	20	6	51	9	7	2	18	25	17	7	49	6	124	100.0

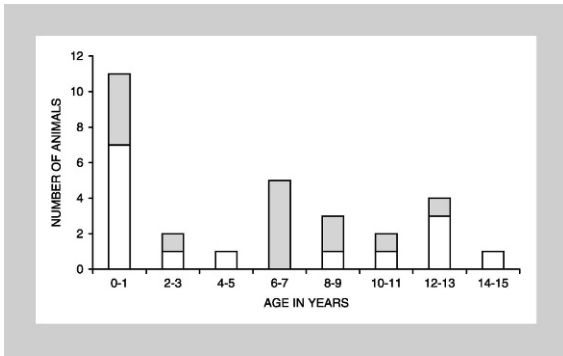


Figure 2. Age distribution of 29 lynx at the time of death in the Jura Mountains. Animals that were illegally killed are shown in grey.

df = 1, $P = 0.05$). In juveniles, males were mainly killed in traffic accidents and illegal acts, whereas females died from other accidents directly related to human activities, were shot as stock raiders or picked up as orphans ($\chi^2 = 7.83$, df = 2, $P = 0.020$). The orphans were, at least in some cases, related to illegal killings of adult females. Poaching affected young animals the hardest, but also middle-aged animals were affected (Fig. 2). More than half of the animals shot illegally were females, and four of these had at least eight kittens between them who either died or had to be removed from the population as a consequence of their mothers' deaths. Of the 29 lynx with known age at death, 14 were illegally killed (see Fig. 2). All other causes of mortality were more prominent in young and very old age classes.

The seasonal distribution of known mortalities was different for the three age categories (Fig. 3). The highest number of losses in subadults occurred during April-June, i.e. during their first months of

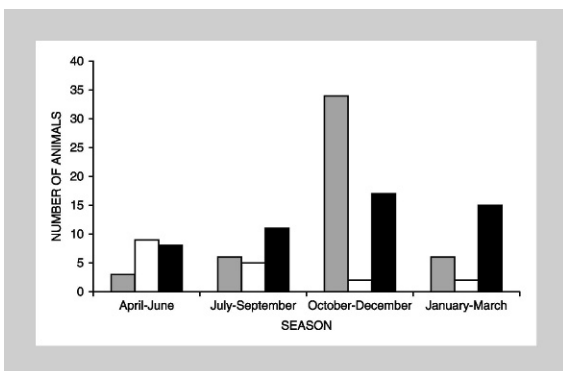


Figure 3. Seasonal distribution of known lynx mortalities in the Jura Mountains during 1974-2002 for the age categories juveniles (■), subadults (□) and adults (■).

independence; four died in traffic accidents, three from diseases and accidents, one was poached and in one case the reason was not clear. In juveniles, the seasonality of the mortalities was most prominent, with a clear peak from October to December, encompassing 69% of known losses. The most important mortality cause for juveniles during this period was traffic accidents (cars, trains). In late fall, females with kittens are more mobile again (Kaczensky 1991) which makes them more susceptible to traffic accidents. In addition, orphaned juveniles have a high risk of ending up as road kills, and five orphaned juveniles showed up near settlements and were caught. Juvenile mortality and illegal killings of adults (including mothers) were seasonally correlated. Out of 11 known illegal killings, nine occurred during the months of September-December, the principal hunting season.

Probability of discovering mortalities

We used mortalities of radio-collared animals in the Swiss study ($N = 23$) in an attempt to estimate discovery probabilities in relation to causes of death and age classes. Of the dead lynx, 30% were discovered without the support of telemetry. Of the animals that died from causes directly related to human activities, 39% were found independently. Illegal killings, however, had a discovery probability of only 18%. One case was announced immediately after the shooting, probably because the animal was radio-collared. On the other hand, 60% of traffic accidents were discovered independently of the study. The two accidents directly related to other human activities were both reported. Yet none of the natural losses, be it through diseases or accidents, were discovered by chance. These natural causes of death were also rare in the overall sample of known mortalities (seven and two out of 124, respectively; see Table 4). Considering the different discovery rates, the small sample size and the large confidence intervals, illegal killings would have been the most important mortality factor during the study period of 1988-1997 (32%), followed by traffic accidents (29%) and natural losses (22%). In the last pentad (1998-2002), traffic accidents significantly increased, especially in France, and was estimated to account for 44% of mortalities, whereas illegal killings were estimated to account for 12% only. For the different age classes, the discovery probability of animals estimated from the radio-tagged individuals was 27% for adults, 14% for subadults and 17% for juveniles, respectively.

Survival of subadult and adult lynx

A subsample of 16 subadult lynx allowed us to estimate the survival rate in this age class. We lost contact with three of the 16 animals during dispersal. Of the remaining 13, six survived until they were able to establish their own home ranges in new areas. Only one of four (25%) subadult males survived, compared to five out of nine females (56%), of which three were followed until their first reproduction. The lower survival of males was, however, not statistically significant ($\chi^2 = 1.04$, $P = 0.308$). The overall survival rate for subadults was 53.3%, and for the survey periods P1-P3 it was 20, 100 and 62.5%, respectively.

We were able to monitor 18 adults for a total of 53 lynx years. We lost contact with six animals due to technical failures. Of the remaining 12, 10 died after a few months up to seven years of survey (Breitenmoser-Würsten et al. 2007). The overall survival rate for adults was 76%, and for P1-P3 it was 75, 77 and 75%, respectively.

Discussion

Natality

Demographic parameters have been assessed in only very few free ranging Eurasian lynx populations. Most references give a litter size of 1-4 kittens, rarely 1-5 kittens, with two and three being most common (e.g. Matjuschkin 1978, Heptner & Sludskij 1980, Hemmer 1993). In the Swiss Alps, the mean number of kittens per litter was 2.09 ($N = 28$) and 88% of females had kittens (Breitenmoser-Würsten et al. 2001). Litters of > 3 kittens have been a rare event in the two lynx populations in Switzerland. In the Alps, two litters of four kittens have been documented. In the Jura Mountains, we know of only one litter of four kittens discovered by forestry workers in the study area in June 1987. Kvam (1991) analysed lynx carcasses in Norway and discovered an average of 2.5 (range: 2-3) embryos in the uterine tracts of eight obviously pregnant females. In Białowieża, Poland, Schmidt (1998) found three litters with one, two and three kittens, respectively. In the same study area, Jędrzejewski et al. (1996) noted three females with three, three and four kittens during the first 100 days after birth. In Sweden and Norway, Andrén et al. (1998) observed 49 females for 60 reproductive seasons. They found an average litter size of 1.97 ($N = 29$ litters) and 67% of sexually mature females repro-

duced. In the Sarek area in northern Sweden, Andrén et al. (2002) observed 1.43 kittens per adult female in June, and 28% of females did not reproduce. In Bergslagen in southern Sweden they found 2.05 kittens/adult female and 24% of females without kittens, and in Hedmark, Norway, 1.1 kitten/adult female and 37% of females without kittens (Andrén et al 2002).

Kaczensky (1991) reported reproduction data from 11 European zoos. The average litter size was 2.08 ($N = 141$), and there was one litter with five kittens. Stehlik (1984, 2000) found an average of 2.14 kittens per litter in 36 litters from the Ostrava Zoo for the period 1967-1996. Additionally, he reviewed litters from 14 European zoos from the years 1905-1978. For this period he found an average litter size of 2.28 ($N = 58$). Overall, there was no significant difference between average litter size in zoos and average litter size in the wild (Student $t = 0.102$, $P = 0.919$). Litters in zoos are detected earlier than in the field. The missing difference in litter size could have two explanations. Losses in the wild during the first few weeks of life were not as significant as they were in captivity, where 66% of losses occurred during the first two weeks of life (Kaczensky 1991). Stillbirth and disease were the two most important mortality factors of young lynx in captivity, but unfortunately we have no data on this from the wild. The second possible explanation is that litter size is larger in the wild than it is in captivity. Females in captivity are supposed to be in better physical condition than their counterparts in the wild, because they have access to superabundant food, which should lead to higher litter size. On the other hand, captivity in itself might induce more stress, which again might lead to more stillbirths or lower litter sizes. Assuming the same mortality rate during the first weeks of life as found by Kaczensky (1991) in captivity, the mean litter size in the Jura Mountains would have been 2.38 kittens instead of the 2.00 observed. But to answer these questions, we need to collect data from the wild.

Evidence for replacement litters, as we observed it for the lynx F_{ELSA} in 1993, was scarce. Kaczensky (1991) reported two cases of replacement litters in 141 litters from 11 zoos. Both times, the kittens were born in August after the first litter was lost in May. In one case the first litter was born on 17 May, and the second exactly 100 days later on 25 August. F_{ELSA} gave birth to her first litter on 17 May and to her replacement litter on 26 August, a striking similarity. V. Herrenschmidt (pers. comm.) ob-

served newborn lynx in the Vosges Mountains in France in August, which also might have been a replacement litter. Rutting and mating seasons and birth time of lynx are strictly punctual. A birth in August is a very exceptional and rare event, and it has only been observed to occur following the loss of a first litter in May. One historic case of a pregnant female in late October has been documented from the subsequently extinct lynx population of the Alps (David-Martin 1894 in Schauenberg 1969).

P2 (1992-1994) was characterised by a small average litter size and a high proportion of total losses of litters. In the study area, only the male M_{TARO} was present (Breitenmoser-Würsten et al. 2007). During the mating season of 1993, he met with six different females instead of two, as in P1 and P3, so he spent less time with each of these six females. Lynx are induced ovulators, and one could speculate that the frequency of mating may influence average litter size. In the same period, we also observed the highest number of total losses of litters. The lost litters belonged to both first-time breeders and experienced mothers. The male M_{TARO} covered a huge range during P2 and had an extraordinary (genetic) impact on the population in the study area and its surroundings. The observed demographic disturbance during P2 may have been a consequence of the unbalanced socio-spatial structure (Breitenmoser-Würsten et al. 2007), but we cannot exclude a negative genetic impact of M_{TARO} (paternity analyses of the litters are in preparation). The unbalanced sex ratio in kittens of 1.7 females/male was not statistically significant, but the bias towards females during P3 indicates that it still might be biologically relevant. In two zoo studies, sex ratios of 1.1 females/male (Kaczensky 1991) and 1.2 females/male (Stehlík 1984, 2000) were reported. In the northwestern Swiss Alps, we observed a sex ratio of 1.1 females/male (Breitenmoser-Würsten et al. 2001). If, as discussed above, there was a high mortality at a very early age, males kittens would seemingly have been more affected than female kittens. In 1992, a hunting dog killed a young male lynx, which turned out to be crippled. This abnormality gave rise to concerns regarding congenital problems in the lynx population in the Jura Mountains (Breitenmoser et al. 1994, Ryser-Degiorgis et al. 2004). The population in the Jura Mountains was founded with few, probably even related animals (Koubek & Červený 1996, Breitenmoser et al. 1998). Correlates of an inbreeding depression are

very difficult to detect (Frankham et al. 2002) without very careful long-term monitoring of demographic parameters and health problems. Inbreeding depression has a strong stochastic element as it depends on the frequency of deleterious alleles, and small populations experience genetic drift. The stochastic nature suggests that different species and populations vary in the components of fitness that are affected by inbreeding. For instance, inbred populations of red wolves *Canis rufus* and Mexican wolves *C. lupus baileyi* in captivity did not lead to reduced survival in juveniles (Kalinowski et al. 1999), only in adults (Wilcken 2001). This implies that the whole set of demographic parameters must be considered.

Population dynamics

The survival rates of lynx in the Jura Mountains were comparable to those in the Alps for juveniles and adults and higher for subadults (juveniles: Alps 45-54%, Jura Mountains 43-49%; subadults: Alps 44%, Jura Mountains 53%; and adults: Alps 72%, Jura Mountains 76%; Alps: Breitenmoser-Würsten et al. 2001, Jura Mountains: this study). In Poland, the survival rates were 52% for juveniles, and 63% for subadults and adults pooled (Jędrzejewski et al. 1996). In the Scandinavian study, the mean yearly survival estimates varied greatly between study areas. The juvenile survival estimate was 39% in Bergslagen, 42% in Sarek and 73% in Hedmark, respectively (Andrén et al. 2002). The survival rates for subadults were considerably larger in all three Scandinavian areas than in the two Swiss studies: 70, 77 and 71%, respectively, and so were adult survival rates: 87, 91 and 84%, respectively.

Mortality rates in lynx in Norway were high during the first year of life, then low throughout adulthood (subadult and adult animals), and high again after the age of 16 (Kvam 1990). In contrast to this, the mortality rate remained high during the subadult age in the Jura Mountains, and only decreased thereafter, but less prominently than in Norway, and at the age of 12 it started to increase again. Throughout adulthood, human-related mortalities were very important in our study (see Fig. 2).

The different trends in the number of dead lynx in Switzerland and France reflect the development of the population and the spread of the lynx through the Jura Mountains, as documented by monitoring data (Vandel 2001, Capt 2007). In the early years after the releases in Switzerland, most of the observations were collected along the first and second

mountain chains, mainly in the Swiss part of the Jura Mountains. However, since the mid-1980s, the core area of the population has been in France, in the western part of the Jura Mountains.

Poaching seems to be the most important mortality factor for lynx populations in many areas, whether the species is protected as in Switzerland, the Czech Republic and Poland (Breitenmoser et al. 2007, Červený et al. 2000) or hunted on quotas as in the Scandinavian countries (Andrén et al. 1998). In Poland, poaching was responsible for 71% of known mortalities (Jędrzejewski et al. 1996), in Scandinavia for 14-43% (Andrén et al. 1998), and in the Šumava Mountains (Czech Republic), four out of nine radio-collared animals were poached (44%; Červený et al. 2002). For the 10-years study period in the Jura Mountains, 14% of known losses were illegal killings, and our estimate based on radio-collared lynx suggested that poaching might account for as much as 32% of mortality. This is still within the range reported from other European investigations. Contrary to the other studies, however, traffic accidents were of considerable importance in the Jura Mountains, representing 39% of known and 29% of estimated mortality during 1988-1997 (see Table 3). During our 10 years of study, no important expansion of the population was recorded in Switzerland. The spatial and social structure of the part of the population observed by telemetry was stable in the long term, but showed short-term disturbances (Breitenmoser-Würsten et al. 2007). Altogether, human-caused mortality in the Jura population was very high for a legally protected population, and we assume that the high total mortality has been limiting the population. Given the favourable ecological situation in the Jura Mountains (Breitenmoser et al. 2007), including increasing prey abundance (Jobin-Molinari et al. 2007), and a natality comparable to that reported from other studies of the species, the lack of numerical response of the lynx and the halt of the expansion in the first half of the 1990s (Capt 2007) can only be explained by the high human-related mortality and the resulting demographic disturbance.

Since the end of our intensive study in 1998, the lynx population has spread both in France (Vandel 2001, ONCFS-Réseau Lynx 2001, 2002) and Switzerland (Capt 2007). Illegal killing seems to have decreased. An increase in the number of traffic accidents in France, with a high proportion of juveniles among the victims, indicates increased dynamics in

the population. This was confirmed by monitoring data, which showed a further spread of the population since the late 1990s (ONFS-Réseau Lynx 2001, 2002, Capt 2007). If it is possible to keep the limiting factors low using appropriate management measures, reduction of conflict with livestock through preventive measures and increase of acceptance in the hunting society through public involvement, then the population has a chance to reoccupy all suitable habitat and maybe produce enough surplus animals to build up connections to neighbouring populations in the Alps, the Vosges Mountains (France) or the Black Forest (Germany) as deemed possible by Zimmermann & Breitenmoser (2007).

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