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Spatial and social stability of a Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains

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A total of 18 Eurasian lynx *Lynx lynx* were radio-tagged between March 1988 and June 1998 in the Swiss Jura Mountains, and during 1995-1997 eight animals were radio-tagged on the French side of the mountain chain. Adult males occupied larger long-term home ranges than adult females (283 km^2 vs 185 km^2). Neighbouring males shared 7.3% of their home ranges and females 0.2%. The mean distance between males and females living in the same area for fixes taken the same day was 10.94 ± 8.61 km, underlining the solitary character of the species. Consecutive individual annual home ranges overlapped 71.7 ± 7.3% for females and 77.5 ± 7.9% for males, indicating high spatial stability over time. In the Swiss study area, two adult animals were followed for seven and nine years, respectively, and another two lynx were observed in the study area for nine years. Range size did not vary across three distinct periods, P1-P3, but the sex ratio did. Generally, males covered the ranges of 1-2 females, but during the second period, P2, the range of a single male overlapped with those of six females. Dead females were all immediately replaced, but dead males were not. Two poached males were only replaced after three and five years, respectively. Population density, ranging within 0.7-0.8 adult resident lynx/100 km^2, did not vary significantly over time in Switzerland. Including kittens and subadults, the density was 1.1-1.6 lynx/100 km^2. Our study in the Jura Mountains indicated that there is long-term stability in the social and spatial structure of the lynx population, but this stability was temporarily disturbed by the lack of adult resident males.

Key words: home range, long-term observation, Lynx lynx, social dynamics, spatial structure

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Large carnivores are long-lived animals with slow turn-over rates (Gittleman 1986), and scientific studies, generally running for only a few years, allow researchers to study a small time window in the development of populations only. To understand the functioning of populations and to be able to develop effective conservation strategies, it is imperative to know more about the dynamics of such populations during a wider time window. The interpretation of the status and conclusions regarding the conservation will depend on the time frame studied (Pelton & van Manen 1996). We reviewed the Journal of Wildlife Management from 1980 through 1995 for the survey periods of wildlife studies. Of 1,398 publications, 80% dealt with ≤ 5 years, and only 8% covered ≥ 10 years. Furthermore, long-term studies on large and medium-sized cats are relatively sparse. Prominent among others are projects on lions *Panthera leo* in the Serengeti and the Ngorongoro Crater in Tanzania since the early 1960s (Schaller 1972, Packer et al. 1991), on tigers *Panthera tigris* in Royal Chitwan Nation Park, Nepal, from 1977 until 1987 (Smith 1993), on cougars *Puma concolor* in the San Andreas Mountains of New Mexico from 1985 until 1995 (Logan & Sweanor 2001), on Iberian lynx *Lynx pardinus* in the Coto Doñana in southwestern Spain since 1983 (Palomares et al. 2000, 2001, Ferreras et al. 1997), and on Canada lynx *Lynx canadensis*, studied in the Northwest Territories from 1989 until 1993 (Poole 1995) and the Yukon Territory from 1986 until 1994 (Slough & Mowat 1996).

Eurasian lynx *Lynx lynx* are medium-sized cats, growing as old as 15-17 years in the wild (Breitenmoser-Würsten et al. 2007). The species' spatial organisation has been studied in Norway (Andersen et al. 1998, Sunde et al. 2000), Sweden (Andrén et al. 1997), Norway and Sweden (Linnell et al. 2001), Poland (Jędrzejewski et al. 1996, Schmidt et al. 1997) and in the Swiss Alps (Haller 1992, Breitenmoser & Haller 1993, Haller & Breitenmoser 1986, Breitenmoser-Würsten et al. 2001). All of these studies had survey periods of 3-4 years, with very few individuals surveyed for > 2 years, and came to quite different conclusions in regard to territoriality and social and spatial stability. The differences could be related to the methods used or the environmental conditions in the study areas, but they could also have arisen due to the narrow time windows into a changing world. Three studies on lynx in the Swiss Alps, performed in an identical environment using the same field techniques, revealed very different levels of population status (Haller 1992, Breitenmoser & Haller 1993, Breitenmoser-Würsten et al. 2001).

We had the unique chance to work for 10 years from 1988 until 1998 in the Swiss Jura Mountains, which allowed us to study the long-term aspects of the land tenure system and the social structure of the lynx population. Another study was conducted in the adjacent part of the French Jura Mountains during 1995-1997; in this study additional data on the spacing behaviour of lynx were collected. All animals followed in these two studies belonged to the same lynx population. In this paper, we present the combined data sets and address the following aspects concerning the dynamics of the lynx population: 1) home-range size and overlap, 2) spatial and social organisation and its dynamics, and 3) development of the population density.

Material and methods

Study area

The Swiss study area encompassed the part of the Jura Mountains in the cantons of Neuchâtel and Vaud and extended along the first chain of the Jura Mountains into France south to Fort de Vaucluse. The intensive study area where adult animals were regularly located covered 1,300 km^2. A detailed description of the Jura Mountains is presented in Breitenmoser et al. (2007). The French study area was located in the southeastern part of the Département

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du Jura and covered 1,100 km^2; for more details see Vandel (2001). The two study areas bordered onto each other along the Mijoux valley, behind the first chain of the Jura Mountains west of Geneva. 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 Swiss study area ranged in elevation within 484-1,718 m a.s.l. (Crêt de la Neige), the study area in France within 246-1,226 m a.s.l. The main prey of lynx in the Jura Mountains is roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* (Molinari-Jobin et al. 2007, Breitenmoser et al. 2007).

Study population

Lynx went extinct in the Jura Mountains during the 18th century. The last evidence of lynx was an animal killed near Lignerolle (Canton of Vaud) in 1830 (Schauenberg 1969). Lynx were brought back to the mountain chain through a reintroduction project in Switzerland in the 1970s (Breitenmoser & Baettig 1992). Authorised releases of four individuals originating from Slovakia took place in 1974 and 1975 in the Swiss Jura Mountains. Additional animals were released in clandestine events resulting in a maximum founder population of 8-10 lynx (Breitenmoser et al. 1998). The increasing population spread into France, mainly during the 1980s. Today, the French part constitutes the core area of the Jura population (Vandel & Stahl 2005). During our study period, all suitable habitat had not yet been occupied, in particular areas north and northwest of the study area had not been permanently occupied (Capt 2007). The lynx population in the Jura Mountains is still isolated from the populations in the Alps and Vosges Mountains (Zimmermann & Breitenmoser 2007).

Capture and tracking

Lynx were trapped with foot snares installed around lynx kills during 1988-1997 in Switzerland and during 1995-1997 in France. The survey period ended in June 1998. Additionally large double-door box-traps were placed on frequently used paths in Switzerland during the winter months. One lynx in France was caught with a foot snare set on a trail regularly used by lynx. All traps were equipped with an alarm system, allowing for remote control. Animals caught in Switzerland were immobilised with a Ketamin/Xylazin mixture until 1992. From 1993 onwards, we used 0.1-0.15 mg/kg methetomidin (Domitor®) and 0.8-1 mg/kg ketamin (Ketasol®) for anaesthesia, and 0.5-0.75 mg/kg atipamezol (Antisedan®) for reversal. Lynx caught in France were immobilised with Zoletil. Animals were classified as 1) juveniles when they were still with their mother (up to 10 months of age; Zimmermann et al. 2005), 2) subadults during their dispersal until they established a permanent home range (Zimmermann 1998) and 3) adults thereafter. Residents were adult animals occupying their own territory (a home range stable over several years excluding other animals of the same sex), and floaters were non-resident adult lynx. We tried to capture young lynx while they were still with their mothers, i.e. during February-April, so that we would be able to follow them during their dispersal (Zimmermann et al. 2005). In this paper, we include only lynx who later settled down as resident adults. Lynx were fitted with radio-collars weighing 220 g (Wagener, Cologne, Germany). From adult animals in Switzerland an incisor was removed 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).

Animals were located by 'homing-in' (White & Garrott 1990) with a precision of 1 ha or by drawing the bearings on a topographical map without approaching the lynx, yielding locations with an accuracy of 1 km^2.

Spatial and statistical analyses

For spatial analyses, we only accepted one location per 24 hour period for each lynx to avoid autocorrelation. We defined as total range the convex polygon of all locations according to the minimum-area method of Mohr (1947). To eliminate outliers, i.e. locations apparently outside the normal use, we applied the method described in Breitenmoser et al. (1993), where a stem-and-leaf analysis (Tukey 1977) was performed on $\sqrt{\text{DCent} * \text{DLocs}}$, where DCent was the distance to the arithmetic centre, and DLocs the mean distance to all other locations. An observation was identified as an outlier if its outside value was larger than H75 + 1.5*HS, where H75 is the upper hinge and HS the hinge spread. We then defined as home range the convex polygon of all locations excluding the outliers.

To describe range use, we chose the 95%-kernel area (Worton 1989, Seaman & Powell 1996). For the smoothing factor H, we applied the user-defined option, because the Ad Hoc or Least Squares Cross Validation (LSCV), did not produce satisfying re-

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sults, as the distribution of locations and the shape of the home ranges did vary considerably between animals. Additionally, we calculated annual home ranges for adult animals present for at least 10 months in any given 12-month period.

For all range analyses, we used the Animal Movement Analysis Extension for Arc View 3.1 (Esri 1996, Hooge & Eichenlaub 1997). The increment analysis was performed within Arc View using a script (U. Müller, pers. comm).

Percent overlap of total ranges and home ranges between animals A and B was calculated as:

$$\sqrt{\text{OverlapAB/rangeA} * \text{OverlapAB/rangeB}}.$$

We calculated the different range-use models for the entire survey period of each animal and called this long-term home ranges. Additionally, we divided the 10 years of observation into four periods, according to significant changes in the spatial be-

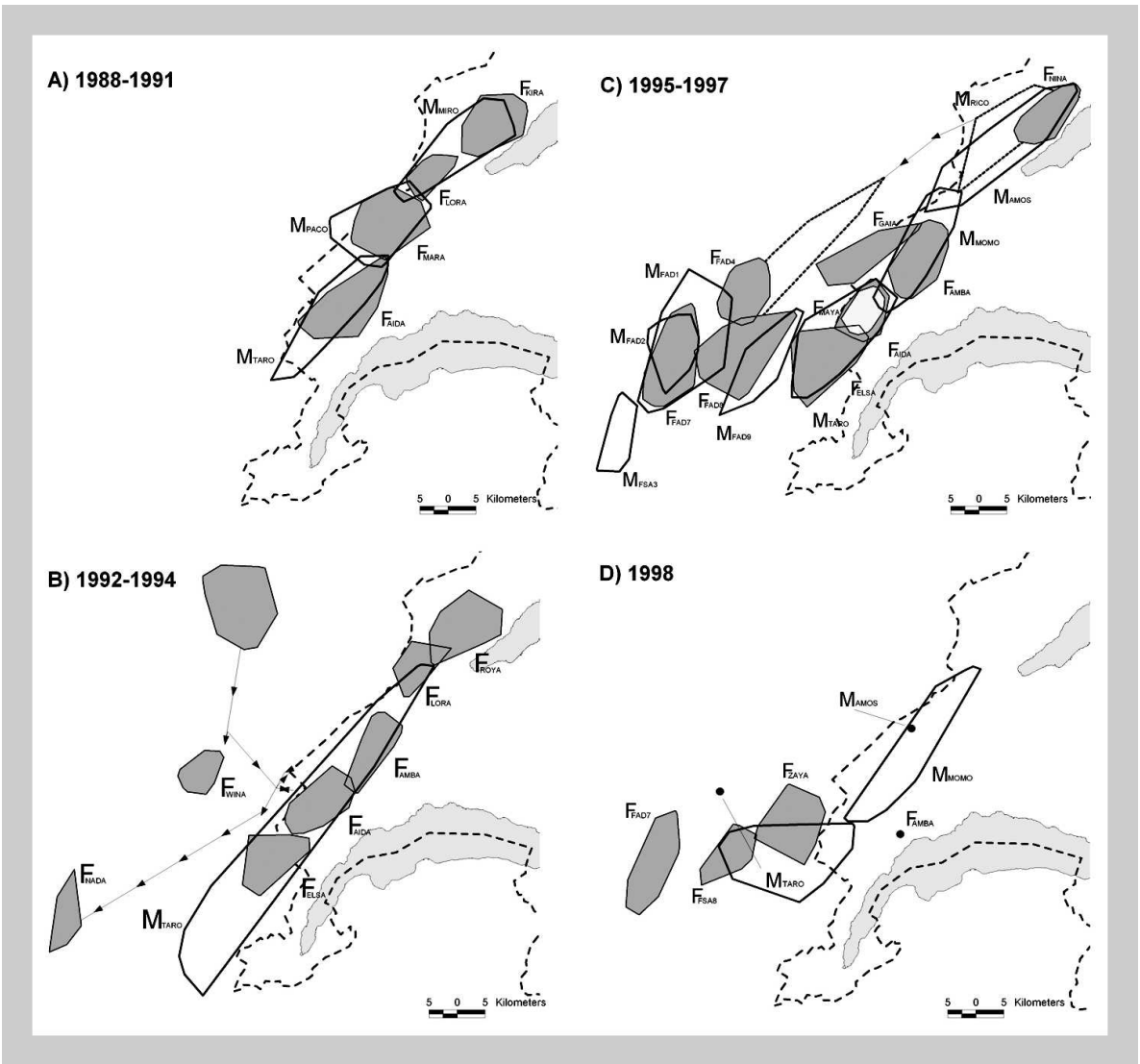


Figure 1. Distribution of home ranges (i.e. total range excluding outliers) of adult resident lynx in the Jura Mountains for the four observation periods P1-P4 (A-D). Ranges of males are delineated by solid lines, and those of females are dark grey. The pale grey area in C) indicates the home range of F_{MAYA} who remained in the home range of her mother F_{AIDA}. Dashed lines indicate the border between France and Switzerland, light grey shows major lakes, and lines with arrows indicate migration routes and directions of adult animals. Black dots show the locations where $F_{AMBA,}$ M_{AMOS} and M_{TARO} were found dead in 2001, 2002 and 2005, respectively.

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haviour of the observed animals as well as the loss and appearance of new animals (Fig. 1). Period 1 (P1) included the years 1988-1991, Period 2 (P2) the years 1992-1994, Period 3 (P3) the years 1995-1997, and Period 4 (P4) the year 1998 until the end of June when the survey was terminated. As the last period is considerably shorter than the previous periods, data from this period were only used to show changes in spatial behaviour of animals that were also followed in previous periods. For comparison between sexes or time periods, we only included animals that were followed for > 1 year.

For the density estimation of adult animals in Switzerland, we used the radio-collared lynx and collected all available information of individuals not radio-tagged. If signs of presence of a lynx could not be assigned to one of the radio-collared animals, efforts were intensified to trap this individual. If an animal died or disappeared, trapping efforts were intensified as well to collar the successor as quickly as possible. All observed total ranges together defined the reference area for the density estimation. For gaps with no information, we measured the surface and defined the number of animals fitting in there based on the mean home-range size and overlap of the respective sex (Mace & Waller 1997). For the total density, we added the mean number of kittens and the number of subadults per female in the study area during the winter for the respective numbers of adult females present. These

Table 1. Data on the 26 lynx radio-tracked in the Jura Mountains during March 1988 - June 1998. Lynx captured in France are marked with * and animals that were still under control at the end of the survey period in June 1998 are marked with **. Animals marked with [1] were captured as subadults, followed during their dispersal and as resident adult lynx. F_{AMBA} was poached in the study area in November 2001; M_{AMOS} died in August 2002 in the study area due to an accident ; M_{TARO} died in 2005 at the edge of his 1998 range, and F_{MAYA} was last observed in the study area in January 2003.

Lynx	Year born	Capture date	Weight (kg)	Date of loss	Reason for loss
Adult females					
F_{AIDA}	1985	02.12.1990	18.5	22.04.1997	disease
F_{AMBA} 1	~1988	01.03.1992	16.5	07.08.1993	breakdown of collar
2		26.01.1996	18.5	14.08.1997	breakdown of collar
F_{ELSA}	1985	26.03.1993	18.0	21.09.1996	probably poached
F_{FAD4}*		29.03.1995	18.0	27.11.1996	collar breakdown
F_{FAD5}*		29.08.1995	16.5	15.10.1996	collar breakdown
F_{FAD7}*		07.04.1996	16.5	**	
F_{GAIA}	1983	20.12.1995		15.02.1996	accident
F_{KIRA}	1984	30.03.1988	17.0	18.12.1991	probably poached
F_{LORA}	1986	08.02.1990	19.5	18.01.1993	poached
F_{MARA}	1976	08.07.1989	17.2	01.11.1991	traffic accident
F_{NINA}	~1993	05.03.1996	15.0	17.10.1997	collar breakdown
Adult males					
M_{AMOS}	1993	30.01.1995	19.5	23.02.1997	end of collar
M_{FAD1}*		05.03.1995	22.5	22.10.1997	end of collar
M_{FAD2}*	1991	05.04.1995	19.0	08.10.1995	disease
M_{FAD9}*		28.04.1996	19.0	21.09.1996	unknown
M_{MIRO}	1983	21.03.1988	23.5	25.09.1991	poached
M_{MOMO}	1992	11.02.1995	21.5	**	
M_{PACO}	1982	10.04.1988	22.0	23.10.1989	probably poached
M_{RICO}	~1993	19.03.1996	18.2	22.05.1997	end of survey
M_{TARO} 1	~1984	20.02.1989	20.5	10.02.1990	breakdown of collar
2		21.02.1993	22.5	**	
Subadult females					
F_{FAD8}* [1]	1995	22.10.1996	13.8	**	
F_{MAYA}[1]	1995	17.02.1996	11.0	16.12.1997	breakdown of collar
F_{NADA}[1] 1	1990	16.03.1991	10.0	31.12.1993	left the study area
2		01.12.1994		21.02.1995	poached in November 1995
F_{ROYA}[1]	1991	13.03.1992	12.5	15.02.1995	injured by chamois
F_{WINA}[1]	1991	03.03.1992	12.5	25.11.1994	probably poached
F_{ZAYA}[1]	1996	04.03.1997	11.0	**	
Subadult male					
M_{FSA3}* [1]	1994	07.03.1995	13.0	31.03.1998	animal removed

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Table 2. Survey period for 26 adult lynx in the Jura Mountains during 1988-1998. The numbers beneath the years indicate quarterly periods (1-4). Lynx marked with * were caught while they were still with their mothers and then followed by telemetry during their dispersal (d; Zimmermann 1998) and as adults occupying their own home ranges (X). † indicates death of the animal and ? indicates that fate of animal is unknown. c indicates collar breakdown or battery failure, lc a lost collar, o that the animal was observed after the collar stopped working, m that the animal moved far off the study area, e that the survey of the animal ended, r that the animal was recaptured, rm that the animal was removed because of excessive damage to livestock (Stahl et al. 2001).

	1988				1989				1990				1991				1992				1993				1994				1995				1996				1997				1998	
Lynx	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2
M_{MIRO}	X	X	X	X	r	X	X	X	X	X	X	r	X	X	†																											
F_{KIRA}		X	X	X	r	X	X	X	X	X	X	r	r	X	r	?																										
M_{PACO}		X	X	X	X	X	X	†																																		
M_{TARO}					X	X	X	X	c				o				o				r	X	X	X	X	X	X	r	X	X	X	X	X	X	X	X	r	X	X	X	X	X
F_{MARA}						X	X	X	X	X	r	X	X	X	r	†																										
F_{LORA}									X	X	r	X	X	X	X	X	X	X	r	X	†																					
F_{AIDA}												X	X	X	X	X	r	X	X	X	X	X	X	X	r	X	X	X	X	X	X	X	X	X	X	X	r	†				
F_{NADA}*													d	d	d	d	X	X	X	X	X	X	r	X	m			X	c			†										
F_{AMBA}																	X	X	X	X	X	X	c				o					o	r	X	X	X	X	X	c			
F_{WINA}*																	d	d	d	X	X	X	X	X	r	X	X	?														
F_{ROYA}*																	d	d	d	X	r	X	X	X	X	X	X	X	†														
F_{ELSA}																					X	X	X	X	X	X	X	X	X	r	X	X	X	X	†							
M_{AMOS}																													X	X	X	X	X	X	X	X	c					
M_{MOMO}																													X	X	X	X	X	X	X	X	X	r	X	X	X	X
M_{FSA3}																													X	X	X	X	X	X	X	X	X	X	X	X	rm	
M_{FAD1}																														X	X	X	X	X	X	X	X	X	X	c		
F_{FAD4}																														X	X	X	X	X	X	c						
M_{FAD2}																															X	†										
F_{GAIA}																																X	†									
F_{FAD5}																																X	X	X	c							
F_{NINA}																																	X	X	X	X	X	X	X	c		
F_{MAYA}*																																	d	d	X	X	X	X	X	c		
M_{RICO}																																	f	f	f	f	f	e				
M_{FAD9}																																		X	?							
F_{FAD7}																																		X	X	X	X	X	X	X	X	X
F_{FAD8}																																				d	X	X	X	X	X	X
F_{ZAYA}*																																					d	d	d	d	X	X

two figures were taken from Breitenmoser-Würsten et al. (2007) and are based on the survival rates in these two age categories.

Results

Observed lynx and survey period

A total of 27 lynx were caught 47 times from March 1988 until the end of 1997; 18 lynx were equipped with radio-collars in Switzerland and so were eight in France (Table 1). Of the animals captured, nine were adult males, 10 were adult females, one was a subadult male and six were subadult females. Adult males were significantly heavier than females (20.8 kg, SE = 0.6, vs 17.2 kg, SE = 0.4; t-test: $P < 0.001$).

Adult animals were observed for a mean of 2.2 years (N = 25, range: 0.4-6.4 years; Table 2). Only three animals had a survey period of < 1 year. For the remaining 22 lynx the mean survey period was 2.5 years (1.1-6.4 years). The survey period for males and females was not different (Mann-Whitney: U = 81, P = 0.610). For the animals M_{TARO} and F_{AMBA}, the observation by telemetry was interrupted because of a breakdown of their radio-collars. Both animals were observed within their home ranges several times while their radio-collars stopped functioning. They were recaptured within their ranges after two and a half and three years, respectively (see Table 2). A total of 10,605 radio locations were included in the range analyses for adult animals.

We aimed to locate each adult lynx at least twice a week. However, we were not able to fulfil this aim for all animals (Table 3). An exceptionally low rhythm was applied to animals that had moved off the study areas (F_{WINA}, F_{NADA} and M_{RICO} for Switzerland and M_{FAD9} for France) and animals that were still surveyed after the intensive study period had ended (e.g. F_{FAD8} in France; see Table 1).

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Table 3. Home-range size of 26 adult lynx in the Jura Mountains during the periods P1-P4. Location rhythm is expressed as survey period/number of locations. Total range is expressed as 100% minimum convex polygon and home range as restricted convex polygon excluding excursions. Dbdl gives the distance between daily locations and N = sample size for Dbdl. F_{KIRA} was present during limited time spans until the appearance of F_{LORA} in February 1990, after which F_{KIRA} shifted her home range (Breitenmoser et al. 1993). After the death of her mother F_{LORA} in January 1993, F_{ROYA} took over her home range. F_{AIDA} was present in her first home range until 31.12.1996 and in her second home range in 1997.

Lynx	Survey period (days)	Number of locations	Total range (km^2)	Number of outliers	Home range (km^2)	Kernel 95% (km^2)	Dbdl (km)	N
P1: 1988-1991								
F_{AIDA}	395	136	186	0	186	97	0.978	70
F_{KIRA} 1	680	376	196	33	130	69	1.118	283
2	679	500	263	62	144	83	0.586	413
F_{LORA}	692	442	98	48	61	44	0.912	330
F_{MARA}	847	437	337	35	178	114	0.781	318
M_{MIRO}	1274	677	304	12	243	199	2.983	489
M_{PACO}	562	236	465	15	241	194	3.430	151
M_{TARO}	356	143	327	12	237	168	3.258	100
P2: 1992-1994								
F_{AIDA}	1096	314	195	27	141	109	1.037	108
F_{AMBA}	525	190	189	4	112	82	1.595	69
F_{ELSA}	644	162	250	6	136	73	0.476	46
F_{LORA}	384	257	123	11	86	57	1.124	194
F_{NADA} 1	1035	235	528	27	237	132	0.866	86
2	83	60	75	7	33	-	1.520	54
F_{ROYA} 1	232	127	227	21	173	76	1.867	67
2	758	250	247	28	115	68	1.415	113
F_{WINA}	774	148	213	23	68	68	0.135	39
M_{TARO}	679	193	912	10	888	346	0.638	96
P3: 1995-1997								
F_{AIDA} 1	731	414	193	36	109	93	0.814	273
2	112	82	422	-	-	-	2.052	67
F_{AMBA}	567	381	223	18	156	66	1.136	286
F_{ELSA}	630	275	288	19	206	132	0.800	143
F_{FAD4}	610	428	280	47	131	120	0.877	324
F_{FAD5}	414	289	181	7	161	157	1.005	231
F_{FAD7}	634	422	210	13	199	148	1.020	353
F_{FAD8}	436	102	370	11	259	169	1.281	65
F_{GAIA}	58	26	137	-	-	-	0.670	18
F_{MAYA}	579	308	107	29	70	51	1.477	198
F_{NINA}	592	233	240	26	114	99	0.853	121
M_{AMOS}	756	336	418	3	344	263	2.568	181
M_{FAD1}	963	734	507	24	413	328	2.342	632
M_{FAD2}	187	153	153	13	139	-	0.500	127
M_{FSA3}	395	226	145	7	113	110	3.047	168
M_{FAD9}	147	29	171	-	-	-	1.000	21
M_{MOMO}	1055	670	308	38	242	140	3.086	486
M_{TARO}	1095	502	759	32	328	254	2.232	289
P4: 1998								
F_{FAD7}	181	126	150	0	150	-	1.136	86
F_{FAD8}	181	21	89	-	-	-	-	
F_{ZAYA}	181	72	223	6	166	-	1.078	51
M_{MOMO}	181	73	400	7	276	-	2.997	45
M_{TARO}	181	67	604	3	360	-	2.885	41

Home-range size

Long-term total ranges were not different for adult males and females (median 465 km^2 and 280 km^2; Mann Whitney: U = 27, P = 0.072), but males had significantly larger home ranges than females (median 283 km^2 and 185 km^2; Mann-Whitney: U = 16, P = 0.010; Table 4). With 1,744 km^2, M_{TARO} had an outstandingly large long-term total range, and, with 672 km^2, also a very large long-term home range. At the other end of the scale was

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Table 4. Long-term ranges of adult lynx in the Jura Mountains. Location rhythm is expressed as survey period/number of locations. Total range is expressed as 100% minimum convex polygon. Home range is expressed as restricted convex polygon (outliers excluded). [a] only animals that were followed for at least one year were included in the medians and for b1-b7 the ranges were computed only during their respective resident phases (dispersal excluded): [1] 01.06.1996 - 31.12.1997; [2] 01.01.1992 - 31.10.1994; [3] 01.012.1994 - 21.02.1995; [4] 01.06.1992 - 15.02.1995; [5] 13.10.1992 - 24.11.1994; [6] 1998; [7] 01.12.1996 - 31.12.1997.

Lynx	Survey period (days)	Number of locations	Total range (km^2)	Number of outliers	Home range (km^2)	Kernel 95% (km^2)
Adult females						
F_{AIDA}	2334	946	488	119	194	185
F_{AMBA}	1092	571	245	23	164	98
F_{ELSA}	1276	437	396	34	186	119
F_{FAD4}	610	428	280	47	131	120
F_{FAD5}	414	289	181	7	161	157
F_{FAD7}	815	548	210	13	199	170
F_{FAD8}	617	123	370	11	259	224
F_{KIRA}	1359	876	332	82	190	67
F_{LORA}	1076	699	139	72	81	62
F_{MARA}	847	437	337	35	185	114
F_{MAYA}[b1]	579	308	107	29	70	70
F_{NADA}[b2] 1	1035	235	528	27	237	132
[b3] 2	83	60	75	7	33	-
F_{NINA}	592	233	240	26	114	99
F_{ROYA}[b4]	990	377	377	14	280	125
F_{WINA}[b5]	774	148	213	23	68	68
F_{ZAYA}[b6]	181	72	223	6	166	97
Median	N = 15		280		185	119
Adult males						
M_{AMOS}	756	336	418	3	344	263
M_{FAD1}	963	734	507	24	413	328
M_{FAD2}	187	153	153	13	139	-
M_{FSA3}[b7]	485	232	145	7	113	110
M_{FAD9}	147	29	171	-	-	-
M_{MIRO}	1274	677	304	12	243	199
M_{MOMO}	1236	743	466	21	283	226
M_{PACO}	562	236	465	14	241	194
M_{TARO}	2312	905	1744	142	672	318
Median	N = 7		418		283	226

M_{FSA3}, with a total range of only 145 km^2 and a home range of 113 km^2. This young male had specialised in killing sheep and was therefore removed from his territory in 1998 (Stahl et al. 2001). The small home-range size of this animal caused the lack of significance in total range size between the sexes. All other males that were surveyed for at least one year by telemetry had higher and fairly similar values (see Table 4). If M_{FSA3} was excluded, the total ranges of males were larger than those of females (Mann Whitney: U = 14, P = 0.016).

We performed a multiple regression analysis with the dependent variable home-range size and the independent variables sex, body weight, number of locations and survey time. These four factors explained 75% of the variance in the size of lynx home ranges (N = 15; P = 0.005). The values of the male

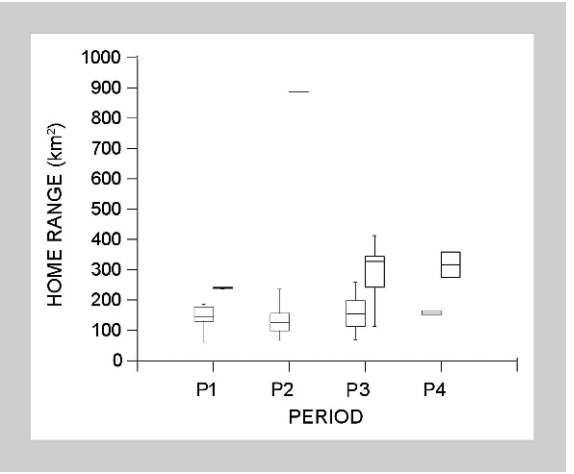


Figure 2. Home-range size of adult females (grey lines) and adult males (black solid lines) for the observation periods P1-P4. The data are presented as box plots, with the centre line showing the median.

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M_{TARO} were excluded, as he was identified as an outlier (leverage 0.591-0.674; studentised residual 3.361-6.872). In the stepwise backward elimination, sex was the remaining variable explaining 66% of the variance ($P < 0.001$). The next important variable was body weight ($r^2 = 0.39$, $P = 0.012$). Number of locations and survey time were not significant.

Looking at the total range during the three periods P1-P3 (see Table 3), males roamed during all periods over larger total ranges than females (Mann-Whitney: $U = 22$, $P = 0.045$). The same was true for home ranges (Mann-Whitney: $U = 19$, $P = 0.017$; see Fig. 1 and Table 3). For both sexes, the range sizes did not vary across the three periods (Fig. 2 for home ranges; females: Kruskal Wallis: $H = 0.085$ for total ranges and $H = 1.192$ for home ranges, both $P > 0.05$; males: $H = 2.560$ and $H = 3.271$, respectively, both $P > 0.05$). The exceptional large range of male M_{TARO} in Period 2 (see Fig. 1) did not influence this result for males.

The restricted polygon contained a larger proportion of the total number of locations for males (mean: 96.0%) than for females (mean: 91.1%; Mann-Whitney: $U = 14.5$, $P = 0.006$). The home range was 58.8% of the total range for females and 73.6% for males, respectively (Mann-Whitney: $U = 22.5$, $P = 0.032$). In females, these two proportions were positively correlated ($r^2 = 0.68$, $N = 13$, $P = 0.001$), but in males they were not ($r^2 = 0.033$, $N = 8$, $P = 0.669$). This demonstrates the different range use of the two sexes. Females have an outer circle that they use infrequently, whereas males regularly patrol the boundaries of their home ranges, and additionally some make short excursions into neighbouring territories, which are excluded in the restricted polygon. This can lead to a low value for the proportion home range over total range and still a high value for the ratio of the locations as these excursions can have a great impact on the total range, but not on the number of locations.

Overlap

The mean overlap of total ranges and home ranges of males and females living in the same areas was 49.6 and 51.5%, respectively. For females, the mean overlap with the resident male was 81% of their home range, whereas for the male home ranges, the mean overlap with the home range of a resident female was only 36%. Neighbouring females shared 16.7% of their total ranges and 0.2% of their home ranges, neighbouring males 16.2% of their total ranges and 7.3% of their home ranges, respectively. Additional to the females within their home ranges, males had access to 1-4 neighbouring females (see Fig. 1). The overlap with the total ranges of the neighbouring females was 21.3% and 5.4% with their home ranges.

There were two exceptions from these patterns. One concerned the males M_{FAD1} and M_{FAD2}. They were living in the same area from April to early October 1995. Nevertheless, 24.7% of the locations of M_{FAD1} were within the home range of M_{FAD2}. After the death of M_{FAD2}, M_{FAD1} used this area more often, and 55.9% of his locations were in the former range of M_{FAD2} ($\chi^2 = 20.724$, $P < 0.001$). The distance between the two animals when located on the same day was 11.80 km (SD = 6.09 km, N = 137, range: 0.90-31.77). Even though they had overlapping ranges, they clearly avoided each other. The second exceptions were the two females F_{AIDA} and her daughter F_{MAYA} described below.

Sociality

As a measure of sociality, or solitude, we used the distance between two individuals located the same day. Males and females living in the same area only met occasionally and were usually separated in space or time. They were 10.94 km (SD = 8.61 km, N = 2,793, 14 male-female pairs) from each other when located on the same day. We observed 75 meetings of male and female lynx; 52 (70%) of them during the mating season from mid-February to mid-April. On an additional 105 occasions, males and females were < 1 km apart. Neighbouring males were closer than 1 and 2 km only three and 11 out of 1,143 times, respectively. The mean distance between them was 25.23 ± 13.55 km. A similar pattern was observed with neighbouring females. On only seven and 14 out of 1,791 occasions were females found < 1 km and < 2 km apart, respectively. With 16.51 ± 7.04 km, the mean distance was smaller than the distance between neighbouring males, reflecting the higher density of resident females.

Home-range use

The mean 95%-kernel area, calculated for animals that were followed for at least one year, was 119 km^2 for females and 226 km^2 for males (Mann-Whitney: $U = 11$, $P = 0.003$; see Table 4). The 95%-kernel area covered 41% of total range for females and 63% for males, which was not significantly different (Mann-Whitney: $U = 35$, $P = 0.217$). There was one exception in males, M_{TARO}, whose 95%-kernel area

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covered only 18% of his total range. His total range was very large, but he used a core area comparable to those of the other males. In females, for F_{FAD5} and F_{FAD7}, the 95%-kernel area constituted as much as 87 and 81% of their total ranges, respectively. For the other females, this value ranged within 20-65%. Without the three obvious exceptions, the difference in the share of the 95%-kernel area of the total range between the sexes would be significant (Mann-Whitney: $U = 8$, $P = 0.006$). For both sexes, there was no difference in the size of the 95%-kernel area across the periods P1-P3 (females: Kruskal Wallis: $H = 2.809$, $P = 0.245$; males: Kruskal Wallis: $H = 2.560$, $P = 0.278$).

Distance between daily locations

Overall, male lynx moved significantly further than females (2.51 km, SE = 0.11, vs 0.96 km, SE = 0.04; Mann-Whitney: $U = 4.26 \times 10^6$, $P < 0.001$). This was also true for P1, P3 and P4 (all $P < 0.001$). An exception was M_{TARO}. Although he occupied the largest range during P2, he did not move further than the females ($P = 0.988$). There was a significant negative correlation between the distance between daily locations and the size of the total range and the home range of males, as animals with larger ranges moved less from day to day (total ranges: $r^2 = 0.638$, $N = 11$, $P = 0.003$; home ranges: $r^2 = 0.874$, $N = 11$, $P < 0.001$). This was not the case for females (total ranges: $r^2 = 0.047$, $N = 26$, $P = 0.29$; home ranges: $r^2 = 0.001$, $N = 26$, $P = 0.85$). This could have been influenced by a difference in the location rhythm (mean number of days between locations) of the two sexes, assuming that males were harder to find because they roamed over larger areas, and the longer displacements could have been missed. Once they were found, they could have been located frequently. But the location rhythm was not significantly different for males and females (Mann Whitney: $U = 164.5$, $P = 0.751$), and did not differ across the four periods (Kruskal Wallis: $H = 6.465$, $P = 0.091$).

Stability of the spatial organisation

The increment analysis is a method to find out how long and how often animals need to be located to seize their entire home ranges. In both sexes, 95% of long-term home ranges were reached after a mean of 1.7 years (Mann-Whitney: $U = 47$, $P = 0.876$; Fig. 3) and 337 locations (Mann-Whitey: $U = 40$, $P = 0.697$). After one year of survey, females and males had roamed over a mean of 75% of their

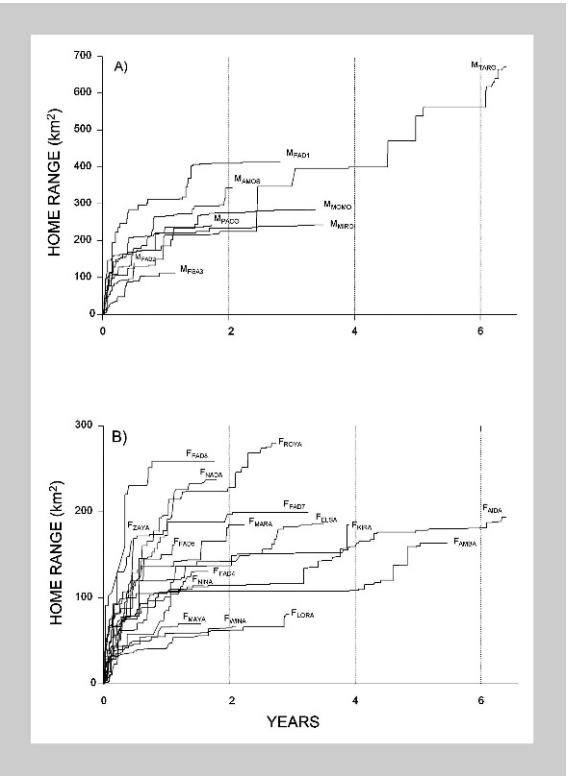


Figure 3. Cumulative area of home range (i.e. total range excluding outliers) of adult male (A) and female (B) lynx in the Jura Mountains. For each additional location in chronological order, the convex polygon is plotted against time.

home ranges (Mann-Whitney: $U = 40$, $P = 0.697$). Exceptional low values were noted for F_{KIRA} (46%) and M_{TARO} (32%), indicating a shift of the home ranges (Breitenmoser et al. 1993; see Fig. 1).

Mean annual home ranges were smaller for females (126 km^2, range: 53-259 km^2) than for males (270 km^2, range: 184-347 km^2; Mann-Whitney: $U = 2$, $P = 0.001$). It covered a similar proportion of the long-term home range in both sexes (74% for females and 81% for males; Mann-Whitney: $U = 34$, $P = 0.391$). They did not vary across years for both sexes (females: Kruskal Wallis: $H = 1.257$, $P = 0.939$; males: $H = 5.977$, $P = 0.308$). The mean overlap of consecutive annual home ranges was similar for females and males ($71.7 \pm 7.3\%$, $N = 13$, vs $77.5 \pm 7.9\%$, $N = 6$; Mann-Whitney: $U = 21$, $P = 0.114$), indicating a high stability of the spatial structure in the study area. The lowest values were observed for F_{KIRA} with 55%, F_{ROYA} with 58% and M_{TARO} with 58%, respectively. All three animals had shifted their home ranges during the survey period.

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Stability of the social organisation

During P1, four resident females and three males were monitored in the Swiss study area. At the end of this period, four animals were dead, leaving the two adult females F_{AIDA} and F_{LORA}, and the adult male M_{TARO} (Breitenmoser et al. 1993). The two poached males were not replaced until three and five years later (Table 5).

During the whole P2, M_{TARO} was the only resident male in the Swiss study area (see Fig. 1). During the mating season in 1993, he met with six different females, four of which were radio-collared (Breitenmoser-Würsten et al. 2007). The two females who had vanished at the end of P1 were replaced within a maximum of half a year (see Table 5). In the southwest, the adjacent female F_{ELSA} was trapped and radio-collared (see Fig. 1). The two subadult females F_{NADA} and F_{WINA} dispersed into France, where they established their own home ranges and reproduced for the first time in 1993. At the end of October 1993, F_{NADA} left the home range that she had established in early 1992 and moved southwest (see Fig. 1), where she settled down at the edge of the Jura Mountains in 1994 (Zimmermann & Breitenmoser 2007). At the end of P2 and early in P3, F_{WINA} and F_{ROYA} died (see Table 1).

Towards the end of P2, M_{TARO} started to change his spatial behaviour. He did not use the northeastern part any more. In early 1995, the two males M_{AMOS} and M_{MOMO} were trapped and radio-collared in this area (see Table 5). M_{AMOS} was born in 1993 as a son of M_{TARO} and F_{AMBA} (KORA, unpubl. data). The overlap of the total ranges of M_{AMOS} with the former range of M_{MIRO} as well as of the home ranges was 80%. The situation in P3 was similar to the situation in P1: three neighbouring males and the corresponding neighbouring females were living in the Swiss part of the study area (see Fig. 1C). In P3, additional animals were radio-collared in the study area in France (Vandel 2001; see Table 1). These lynx were neighbouring the already monitored animals in the southwest of the Swiss study area (see Fig. 1C). In 1996, the young adult male M_{RICO} was trapped in the northeast at lake Neuchâtel. He was roaming over large areas. His origin was unknown and his social status remained unclear; probably M_{RICO} was a floater, i.e. one of the rare non-resident adult males.

During P3, the long-term resident adult female F_{AIDA} was replaced by her daughter F_{MAYA}. F_{MAYA} was born in 1995. She did not leave the maternal home range, as subadult lynx usually do, during their first year of independence (Zimmermann 1998), but stayed within the home range of her mother (see Fig. 1C).

The largest home range during P3 was occupied by M_{FAD1} (413 km^2), who also had the largest 95%-kernel area (328 km^2; see Table 3). M_{TARO} had the largest total range (759 km^2). His home range and

Table 5. Replacement of lynx that died or moved away from their home ranges. Lynx 1 is the disappearing, dying or shifting animal and Lynx 2 the newly appearing or intruding animal.

Lynx 1	Lynx 2	Relationship	Date of death or disappearance, shift of home range	Date of appearance of new lynx
P1				
F_{KIRA}	F_{LORA}	unknown	January 1990	F_{LORA} was captured in February 1990
F_{KIRA}	F_{ROYA}	unknown	F_{KIRA} disappeared in December 1991	F_{ROYA} took over the home range in June 1992
M_{PACO}	M_{TARO}	unknown	Probably poached in October 1989	After three weeks
M_{MIRO}	M_{TARO}	unknown	M_{MIRO} was poached in September 1991	M_{TARO} was observed in the former home range of M_{MIRO} during the next mating season
P2				
F_{MARA}	F_{AMBA}	unknown	November 1991	F_{AMBA} was captured in March 1992
F_{LORA}	F_{ROYA}	mother-daughter	January 1993	Immediately after the death of the mother
F_{AIDA}	F_{AMBA}	unknown	F_{AIDA} shifted her activities to the southwest in 1993	F_{AMBA} was captured in March 1992
P3				
M_{TARO}	M_{AMOS}	father-son	Late 1994	January 1995
M_{TARO}	M_{MOMO}	unknown	Late 1994	February 1995
F_{WINA}	F_{FAD4}	unknown	November 1994	March 1995
F_{ROYA}	F_{NINA}	unknown	Death of F_{ROYA} in February 1995	Capture of F_{NINA} in March 1996
F_{AIDA}	F_{MAYA}	mother-daughter	January 1997	F_{MAYA} never left the maternal home range since her birth
F_{ELSA}	F_{AIDA}	unknown	September 1996	January 1997

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95%-kernel area have a bias, as he was less often located in the southwestern than in the northern part of his home range. As a consequence, the locations in the south were identified as outliers. He occupied the same area in the south during P3 and P2. The centre of activity (mean of X and Y coordinates of all fixes) only shifted 2.0 km.

During P4, the two males M_{TARO} and M_{MOMO} both shifted their range activities compared to P3 (see Fig. 1). M_{TARO} moved his centre of activity 10.0 km to the west. After that, he spent most of his time in France, east of the Mijoux valley; only eight of 67 locations were still in Switzerland. M_{MOMO} reacted on this and shifted his centre of activity 4.3 km to the southwest. M_{TARO} had lost his two long-term mates F_{AIDA} and F_{ELSA}. His range had overlapped with their home ranges for at least 7-8 years. The only female left in his old home range was his own daughter, F_{MAYA}. They had met during the mating season of 1997, but F_{MAYA} did not reproduce. The shift of his home range in 1998 gave M_{TARO} access to at least two new females (F_{ZAYA} and F_{FAD8}; see Fig. 1D). In 2005, his radio-collar was found at the edge of his range of 1998, so probably he had stayed in this area for seven years. The locations where F_{AMBA} and M_{AMOS} were found dead in 2001 and 2002 suggest that these two animals also had shifted their home ranges along the first chain of the Jura Mountains southwards (see Fig. 1D).

Population density

For P1-P3, the density of adult resident lynx was fairly constant in the Swiss study area, varying between 0.7 and 0.8 lynx/100 km^2 (Table 6). The reference area varied between 1,007 km^2 and 1,297 km^2. During P2 and P3, the Swiss study area reached further to the southwest than during P1 (see Fig. 1). Additional to the adults, we calculated 0.50-1.29 kittens per female and year, and 0.1-0.55 subadults per female and year during the winter. The total number of lynx in the Swiss study area was therefore 1.1-1.6 lynx/100 km^2.

Discussion

Spatial structure

The observed social and spatial structure of the lynx population in the Jura Mountains confirms findings obtained in other telemetry studies on Eurasian lynx. The home-range sizes in the Jura Mountains for males (283 km^2) and females (185 km^2) were in between those reported from Poland and Norway, but they are comparable to those found in the Swiss Alps in the 1980s (Breitenmoser & Haller 1993). However, lynx home ranges observed in the northwestern Alps of Switzerland during the late 1990s (Breitenmoser-Würsten et al. 2001) were significantly smaller; males occupied on average only 169 km^2, and females 100 km^2, respectively. Range sizes computed might also depend on the period of time an individual was followed. The increment analyses revealed that we had reached the asymptotic value for most animals. Neither observation period nor number of locations influenced home-range size any further. In a study in Poland by Schmidt et al. (1997), where most animals were observed for 12-15 months, this was not the case, and, especially for adult males, long-term home ranges in reality may have been larger than the figures published (248 km^2 for males and 133 km^2 for females).

Home-range sizes of females in solitary felids depend on resources to rear the young, whereas males' range structure depends on the distribution of females (Eisenberg 1986). In central Norway, where ungulate density was 4-6 times lower than in the Jura Mountains, male lynx roamed over 1,906 km^2 and females over 561 km^2, respectively (Sunde et al. 2000, Molinari-Jobin et al. 2002). In Switzerland, the roe deer population seemed to have increased

Table 6. Density estimation of resident lynx in the Swiss study area for the three periods P1-P3. The reference area was defined through the boundaries of all total ranges of the radio-collared animals. Marked lynx are radio-collared resident animals, unmarked lynx are resident animals that were observed or that were assumed to be in the area based on the social and spatial behaviour of the radio-collared animals. Densities are given in number of lynx/100 km^2. The number of kittens/female and the number of subadults are from Breitenmoser-Würsten et al. (2007).

Period	Years	Reference area (km^2)	Marked lynx ♀	Marked lynx ♂	Unmarked lynx ♀	Unmarked lynx ♂	Total	Density of adults	Kittens/ female	Subadults/ female	Total density
P1	1988-1991	1007	4	3	1.3	0	8.3	0.8	0.73	0.10	1.3
P2	1992-1994	1227	5	1	1	1	8	0.7	0.50	0.38	1.1
P3	1995-1997	1297	4	3.5	2	0	9.5	0.7	1.29	0.55	1.6

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during the 10 years of observation (Molinari-Jobin et al. 2007). However, the lynx population did not increase in space or numbers during the study period (Vandel & Stahl 2005, Capt 2007), as one would have expected from other carnivore studies (e.g. Stander et al. 1997). Very likely, the mortality rate in lynx reached a level that, due to illegal killings, did not allow the population to grow further (Breitenmoser-Würsten et al. 2007). Additionally, the increase in the roe deer population was probably not significant enough to cause an important numeric response in lynx (Molinari-Jobin et al. 2007).

The overlap between neighbouring animals of the same sex was small and $< 10\%$, underlining the exclusiveness of the home ranges (Sandell 1989). Only when new animals appeared, was the overlap temporarily larger until the situation was settled again. In the northwestern Swiss Alps, where a larger number of neighbouring animals were observed, the overlap was $< 10\%$ as well (Breitenmoser-Würsten et al. 2001). In contrast to these findings, Schmidt et al. (1997) found an overlap of 30% between males and 8-29% for females. The population observed in Poland experienced large turnover during the study period. This could, further to the relatively short survey periods of individual lynx, result in an overestimation of the overlap between animals of the same sex. We observed on several occasions that a newly arriving female initially had a big overlap with the resident female, which steadily decreased until the animals had divided up the area between them. In Iberian lynx, high overlap with newly appearing animals of the same sex have also been observed. In contrast to the Eurasian lynx, it was not uncommon that overlapping individuals were involved in fights which usually determined the end of the high overlap (Ferreras et al. 1997).

Males with large home ranges moved less from day to day than males with smaller ranges. A similar observation was made in the Swiss Alps. The male with the largest home range (M1 in Breitenmoser & Haller 1993) covered on average a straight line distance of only 1.133 km from day to day, whereas another male (M2), who occupied a home range of 275 km^2, moved 1.821 km. The males observed in the Swiss Alps during 1997-2000 had a mean home-range size of 169 km^2, and moved 3.527 km from day to day. Males with larger home ranges seem to use their range in a different way than males with smaller ranges, who control and mark their range boundaries on a regular basis (Dötterer 1992), probably as a consequence of the closeness of neighbouring males. During P2, M_{TARO} was clearly no longer able to be constantly present along the borders of his territory, but as no obviously rivals were around, he did not need to be so. He may have switched to a different strategy, and instead of controlling the boundary he may have surveyed the females.

Social and spatial stability

Successors of vanished resident lynx occupied almost the same home ranges. However, the sex ratio was not stable. Dead females were in all cases quickly replaced, but dead males were not (see Table 5). The two resident males that died in the Swiss study area in 1989 and 1991 were not replaced until 1994/1995. During P1, we observed a low survival of male kittens and subadults (Breitenmoser-Würsten et al. 2007). This had consequences for the replacement of dead males. The two males appearing in 1995 were both young, one born in 1993, the other not much older. During 1989-1991, nine animals were removed in France as livestock raiders (four adult males, two juvenile males, one female and two of unknown sex; Stahl et al. 2001). The temporarily high mortality of (resident) males in the two study areas probably led to a lack of dispersers and a disturbed social structure in Switzerland. This allowed M_{TARO} to meet with six females during the mating season of 1993. The lynx population in the Jura Mountains has been reintroduced with a small founder population (Breitenmoser & Baettig 1992). Dramatic changes in the sex ratio of a population can increase inbreeding considerably, and jeopardise genetic stability. Additionally, disturbance of the social structure may have a large impact on the breeding success of solitary carnivores like the lynx (Breitenmoser-Würsten et al. 2007).

In New Mexico, USA, researchers removed 71% of adult females and 60% of adult males of a cougar population, and investigated the reaction of the remaining animals (Logan & Sweanor 2001). The removal of neighbours of the same sex did not cause females to expand their home ranges. The prominent male in the treatment area, however, immediately expanded his range, obviously looking for new mates. These results correspond well with our observations of the reaction of M_{TARO} after the loss of his two neighbours M_{PACO} and M_{MIRO}. Males try to maximise breeding opportunities and will adjust their home ranges in a direct response to the availability of mates and the presence of rivals. Fe-

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males, on the other hand, need to secure the resources for successful breeding and will adjust their home ranges to prey availability. As demonstrated by the very low overlap between neighbouring females, they hardly have encounters with conspecifics.

Conclusions

The observation period of 10 years in the Jura Mountains has shown that there is a potential for long-term stability in the social and spatial structure of a lynx population. In the Swiss study area, four lynx remained in rather stable home ranges for 7-9 years, and successive individuals of the same sex occupied congruent home ranges. After a disturbance (loss of adult resident males), the pre-disturbance social and spatial setup was re-established, however, only after $>$ 3 years. Anthropogenic losses brought the population out of balance, and the recruitment remained low for a few years. Natural mortalities cannot be influenced, and legal removal of problem animals is an important management tool to uphold local people's acceptance of the predator, but laws should be strictly implemented to prevent poaching. The lack of males can lead to a situation where, as in the Swiss study area, one male fathered many litters and all the cubs born in this area were half-sibs. The pronounced topographic and anthropogenic structure of the Jura landscape seems to promote spatial and, hence, social stability of the population, but it also seems to limit the flexibility of the land tenure system.

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