

Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland

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(Accepted 16 March 2005)

Abstract

Dispersal influences the dynamics and persistence of populations, the distribution and abundance of species, and gives the communities and ecosystems their characteristic texture in space and time. The Eurasian lynx *Lynx lynx* is a medium-sized solitary carnivore that has been re-introduced in central Europe and currently occurs in rather small populations, where dispersal is believed to play a prominent role for the recolonization of unsettled areas and persistence of subpopulations. Between 1988 and 2001 the spatio-temporal behaviour of sub-adult Eurasian lynx was studied in two re-introduced populations in Switzerland, based on 31 juveniles of which 24 were radio-tagged to find out which factors influence dispersal. Age at independence ranged from 8.1 to 10.7 months and did not differ between populations or sex. Independence began from January to the beginning of May with a peak in April. After independence, sub-adults stayed a few days in the maternal home range. Age at dispersal differed between the areas of origin and was possibly affected by sex and the presence of new progeny. Dispersers of both sexes established transient home ranges; however, only one male in the saturated population established a transient home range. Although only females took over the maternal home range, there was no significant sex bias in the proportion of individuals that dispersed in both populations. Successful dispersers settled in a territory at distances that differed between populations with effects of sex, but not condition. The mean dispersal distance in the high-density population was 25.9 km compared to 63.1 km in the low-density population. Dispersal distances in the high-density population – shorter than those reported in other Eurasian lynx studies but comparable to those observed in an Iberian lynx population – are limited by habitat restrictions hindering connections with a neighbouring population.

Key words: dispersal, *Lynx lynx*, spatio-temporal behaviour, Swiss Alps, Jura

INTRODUCTION

Dispersal influences the dynamic and persistence of populations, the distribution and abundance of species, and the community structure. It has been considered as a glue cementing sub-populations and making connections between isolated populations (Waser, Sorbeck & Paetkau, 2001; Wiens, 2001). Howard's (1960) definition of dispersal as the movements of an animal from its point of origin to another area where it might reproduce was used for the purpose of this article. In mammals and birds, dispersing individuals are usually young individuals (Greenwood, 1980). In addition, dispersal in mammals is often male-biased whereas in birds it is female-biased (Greenwood, 1980). Many studies have discussed possible reasons for the observed age and sex bias in dispersal.

Lidicker & Stenseth (1992) distinguish between ultimate (evolutionary) and proximate (triggering) factors.

Three major hypotheses have been proposed to explain the ultimate cause of dispersal and sex-biased dispersal: avoidance of close inbreeding (Wolff, 1993, 1994), competition for mates (Dobson, 1982), and competition for resources (Greenwood, 1980, 1983). Perrin & Goudet (2001) emphasized that potential causes are too often considered as alternative rather than interacting factors. Plasticity in the presence and direction of sex-biased dispersal within taxa revealed by new studies argue against a single factor accounting for the interspecific patterns in dispersal (Lambin, Aars & Pieltney, 2001).

The proximate factors that are most likely to affect dispersal include increased social pressures associated with increased density (Snyder, 1961), reduced food availability (Messier, 1985; Harrison, 1992), intraspecific aggression (Christian, 1970), and individual physical condition (Holekamp & Smale, 1996; Nunes *et al.*, 1998).

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Most studies on natal dispersal come from birds (e.g. Greenwood & Harvey, 1982; Adriaensen, Verwimp & Dhondt, 1998; Keller, 1998; Kenward, Walls & Hodder, 2001) and small mammals (e.g. Anderson, 1989; Ims, 1990; Lambin, 1994; Kaporowski, 1996; Favre *et al.*, 1997). In carnivores there have mainly been studies on social living species (e.g. fox *Vulpes sp.*: Zimen, 1984; Harris & Trewhella, 1988; Allen & Sergeant, 1993; Koopman, Cypher & Scrivner, 2000; lion *Panthera leo*: Hanby & Bygott, 1987; badger *Meles meles*: Woodroffe, Macdonald & da Silva, 1993; jackal *Canis mesomelas* and *C. adustus*: Loveridge & Macdonald, 2001). Few studies have focused on solitary felids and most of them dealt with large cats (e.g. tiger *Panthera tigris*: Smith, 1993; puma *Puma concolor*: Beier, 1995; Sweanor, Logan & Hornocker, 2000; Maehr, Land, Shindle *et al.*, 2002). Only four studies are known within the genus *Lynx* (Poole, 1997; Schmidt, 1998; Sunde *et al.*, 2000; Ferreras *et al.*, 2004). A representative set of species should be considered to have a complete picture of the mechanisms and function of dispersal.

The dispersal characteristics of the Eurasian lynx (*Lynx lynx*), a solitary medium-sized felid with a moderate polygynous mating system, was studied in two populations, one in the Jura Mountains and one in the north-western Swiss Alps. Up to now there has only been a moderate presence of the species outside the north-western Swiss Alps, in the central and south-western Alps and no or hardly any lynx found in the eastern and southern Alps of Switzerland, although suitable habitats are available (Molinari-Jobin, Zimmermann *et al.*, 2001). This uneven distribution is a consequence of the eradication of the lynx in western Europe in the 19th century and the subsequent re-introduction of the species in the Swiss Alps and in the Jura Mountains in the early 1970s (Breitenmoser, Breitenmoser-Würsten & Capt, 1998). The Alps and the Jura Mountains differ in their physiographic characteristics. The former have a reduced and more fragmented forest cover, steeper slopes, higher elevations, and their ridgelines have no predominant orientation compared to the latter. These differences must have consequences for the dispersal of a mainly forest-living species.

Comparing the spatio-temporal behaviour of sub-adult lynx in the two mountain ranges may consequently help to understand the mechanism of dispersal. Our objectives were to describe the dispersal pattern of sub-adult lynx, the characteristics of transient and definitive home ranges, and to analyse how differences between areas of origin, sex, body condition and presence of a new progeny affect the time and distance of dispersal. Understanding the factors influencing lynx dispersal is important for the conservation and management of the species in a human-dominated landscape.

STUDY AREAS

The dispersal patterns of sub-adult lynx were examined in two study sites in the Swiss Alps and the Jura Mountains. The north-western Swiss Alps (NWSA), is a 2800 km²

patch limited in the north-east by the valley of the Aare River with the lakes of Brienz and Thun, in the north-west by the Swiss Plateau, in the west by the Rhone valley with the Lake of Geneva, and in the south by the Bernese Alps rising to 4000 m (Fig. 1). The valley bottoms have been deforested and are densely populated. The human population reaches a density of 28/km² (alpine areas included) in most parts of the study area and people living in the lowlands use the Alps intensively for recreation (skiing, hiking). Forests cover 30% of the study area but are highly fragmented. They extend along steep slopes up to the timberline at 1800–2200 m. Lower ridges and gentle slopes were deforested a long time ago and provide summer pastures for cattle and sheep. From late spring to autumn, domestic sheep graze unguarded on remote mountain meadows. The main prey of lynx in the study area are roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* (Breitenmoser & Haller, 1987) which were locally depressed during a peak of the lynx density at the end of the 1990s. On rare occasions lynx prey upon sheep. In 1999, the year with the highest loss, 157 sheep were killed, which is 0.4% of the 39 000 sheep pastured over summer in the study area (Angst, Olsson & Breitenmoser, 2000). The overall lynx density in the NWSA based on the distribution of radio-collared animals and information on additional, untagged individuals from photo-trapping and from reports by game wardens was rather high and estimated at 1.4–1.5 resident lynx/100 km² during the study period (Breitenmoser-Würsten, Zimmermann, Ryser *et al.*, 2001; Molinari-Jobin, Zimmermann *et al.*, 2001).

The Jura Mountains (JM), a secondary limestone mountain chain forming the north-western border of Switzerland with France (Fig. 1), are more homogeneous than the Alps, forming basically a block of contiguous suitable habitat of 6670 km² (Zimmermann & Breitenmoser, in press). The altitude ranges from *c.* 500 m to 1718 m (Crêt de la Neige). Deciduous forests along slopes and coniferous forests on the ridges cover 53% of the study area. Agricultural areas are typically pastures. The human population reaches a density of 120/km² in most parts of the JM but is more clustered than in the Alps. People living on the Swiss Plateau use the highlands intensively for recreation. As in the Swiss Alps, roe deer and chamois are the main prey of lynx (Jobin, Molinari & Breitenmoser, 2000; Molinari-Jobin, Molinari *et al.*, 2002). Prey base was not a limiting factor during the study time (Stahl *et al.*, 2001; Molinari-Jobin, Molinari *et al.*, 2002). The overall lynx density in the main study area remained fairly constant over the whole study period and was estimated at 0.7–0.8 resident lynx/100 km² (Breitenmoser, Kaczensky *et al.*, 1993; Molinari-Jobin, Molinari *et al.*, 2002).

MATERIALS AND METHODS

Field study

Sub-adult lynx were captured with foot snares at fresh kills from January to April 1988–2001, just before they separated from their mother and had the adequate size

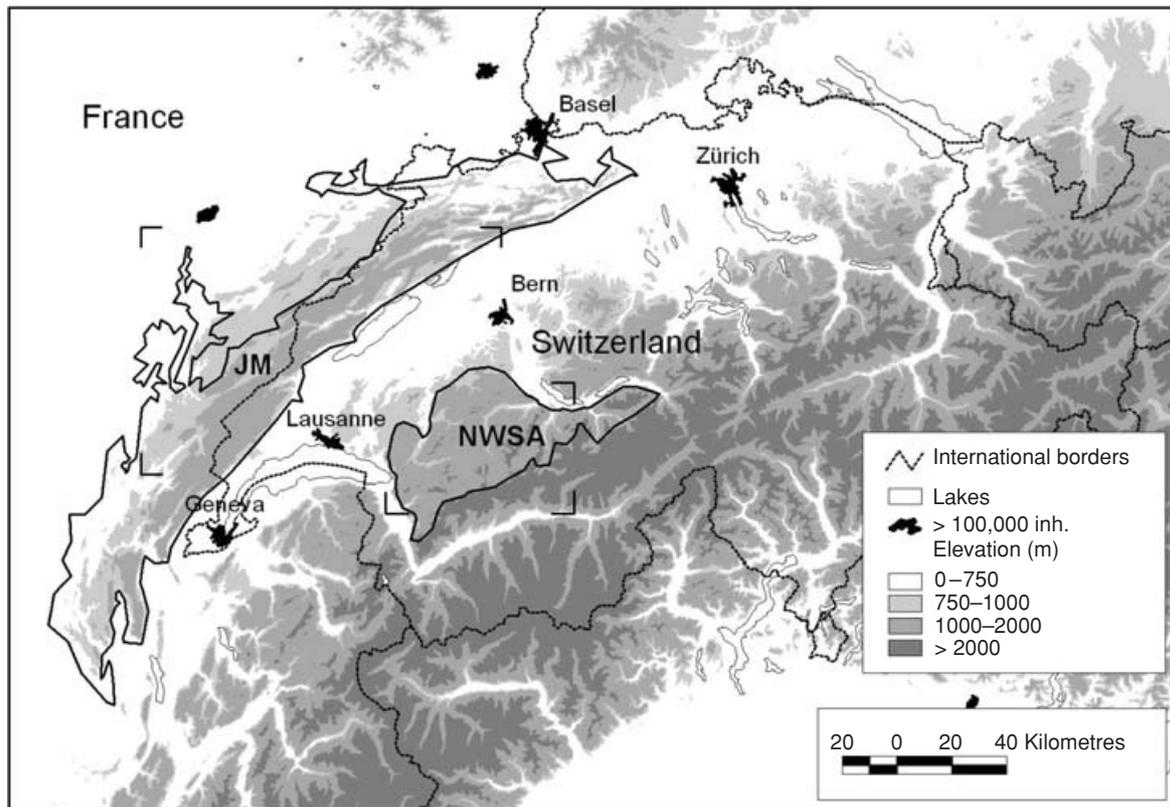


Fig. 1. Study areas in the Jura Mountains (JM) and the north-western Swiss Alps (NWSA) are delimited by thick black lines. Inserted corners correspond to the maximal range of lynx *Lynx lynx* dispersal trajectories and home-range establishments shown in Figs 5 & 6.

to be radio-collared. This was at this time the most efficient way to catch this category of individuals. The foot snares were surveyed by means of an alarm system so that the lynx was narcotized within 15–30 min. Three out of 31 lynx considered in this paper were caught in large double-door box traps. The foot snares were also preferred because lynx caught in box traps often showed some abrasions at the head or paws. Lynx were immobilized with 0.1–0.15 mg/kg medetomidin (Domitor®, Farnos, Finland) and 0.8–1 mg/kg ketaminum (Ketasol®, Graeb, Switzerland) and fitted with radio-collars (200 g; K. Wagener, Germany). Atipamezol (0.5–0.75 mg/kg; Antisedan®, Farnos, Finland) was used as an antagonist. Each radio-collar has a self-breaking part allowing the radio-collar to drop off. The dropping of the radio-collar has been documented for several individuals using pictures taken by camera traps. None of the lynx recaptured or observed had any abrasion caused by the collar.

Dispersal characteristics were obtained for 15 and 16 lynx in the NWSA and the JM, respectively (Table 1). Dispersal data came mainly from radio-telemetry; additional information was available from cubs tagged at the den and later live-trapped or ‘captured’ in a camera trap. Radio-marked lynx were relocated from the ground to a precision of 1 km² to 1 ha. Dispersing lynx were located almost every day when they moved through new terrain, and at least every week once home ranges were established for > 1 month. Each sub-adult was monitored until it occupied a definitive home range (see below), or was lost

because it died or because the radio-collar failed. After independence sub-adults were considered ‘dispersers’ when they had established a home range overlapping not > 5% of their natal (= maternal) home range based on 90% minimum convex polygon (MCP) or were last located outside their natal area (Sweaner *et al.*, 2000; Zimmermann, 2004). All other independent progeny (establishing home ranges with > 5% overlap with their natal range) were considered philopatric (Ph in Table 2).

Dispersers were classified in 2 categories: (1) dispersers (Di in Table 2), individuals that most likely completed their natal dispersal and exhibited 6 months of site fidelity suggestive of home range (HR) establishment and/or reached sexual maturity; (2) failed dispersers (fD in Table 2), dispersers that exhibited < 6 months site fidelity and/or died before they established a HR. The start of dispersal was defined as when a sub-adult made its first movement outside its natal home range without returning. Data were not available for all dispersing lynx for each of the questions, so sample sizes could differ for different analyses.

Dispersal and body condition

Captured lynx were weighed and body measurements taken, e.g. head-body length. Body condition was calculated as the residual value obtained in a reduced major axis regression of log mass on log head-body length (Sokal & Rohlf, 1995). Reduced major axis regression are

Table 1. Characteristics and fate of juvenile lynx *Lynx lynx* followed in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). Information: den, individuals ear-tagged as kittens; rt, radio-telemetry; ct, camera-trap; cr, carcass retrieved. No. of days = number of days in maternal home range after separation. Fate: alive, survived the whole year after separation from the mother; reproduced, strong evidence from genetic analyses or observations in the field that the individual has reproduced; (reproduced), lynx reached sexual maturity according to Kvam (1991) but there was no proof of reproduction

Lynx	Kitten of female	Date of first observation	Information	Date of last observation	Separation from mother	No. of days	No. of locations	Fate
NWSA								
M18 ^a	F37	22.01.97	rt, ct	16.05.99	06.03.97	77	94	Alive, (reproduced)
M20 ^a	F30	25.03.97	rt, ct	02.12.98	25.03.97	–	15	Alive
M24 ^a	F47	24.02.98	rt, ct	27.01.04	15.04.98	164	433	Alive, reproduced
M25	F33	28.06.97	den, rt	14.09.00	03.04.98	13	229	Alive, (reproduced)
M29	F34	25.06.98	den, rt, ct	07.05.03	22.04.99	42	124	Alive, (reproduced)
M30 ^a	?	05.03.99	rt	21.09.99	?	–	59	Died, disease
M31 ^a	F52	08.12.98	ct, rt	10.08.00	26.04.99	64	210	Alive
M35	F35	31.10.98	ct, rt, ct	12.02.04	?	–	139	Alive, (reproduced)
F31 ^a	F32	06.01.97	rt, ct	26.09.98	08.03.97	221	78	Alive, (reproduced)
F40	?	13.03.97	rt	20.03.98	?	–	42	Unknown
F48	F38	05.07.97	den, rt	18.05.98	10.04.98	–	23	Unknown
F49	F34	23.06.97	den, rt	27.08.99	01.05.98	106	156	Alive, (reproduced)
F50	F37	13.03.98	rt	19.05.98	13.03.98	–	24	Unknown
FB22	F34	25.06.98	den, ct, cr	18.10.01	?	–	–	Alive, (reproduced)
FB44	F34	11.12.01	ct	01.08.03	?	–	–	Alive, (reproduced)
JM								
M11	F21	19.06.93	den, rt, cr	08.02.02	?	–	337	Alive, reproduced
M13	F18	18.09.93	den, rt	27.06.95	?	–	45	Alive, (reproduced)
M14 ^a	F21	31.12.95	rt	26.02.98	28.01.96	1	200	Alive, (reproduced)
M15	F18	23.06.95	den, rt	21.09.96	15.04.96	40	96	Died, illegal killing
M16	F11	08.03.90	rt	19.06.90	03.04.90	30	72	Died, disease
F12 ^a	F11	20.04.88	rt	20.12.88	30.03.88	30	99	Died, illegal killing
F13	F11	23.03.89	rt	17.08.89	27.03.89	30	56	Died, disease
F17	F14	25.03.90	rt	23.05.90	10.04.90	12	23	Died, car accident
F19 ^a	F18	04.03.91	rt	05.05.91	15.04.91	–	–	Unknown
F20	F11	16.03.91	rt	xx.11.95	24.03.91	65	393	Alive, reproduced
F22 ^a	F18	04.03.92	rt	25.11.94	14.03.92	76	332	Alive, reproduced
F23 ^a	F15	14.03.92	rt	15.02.95	12.04.92	–	423	Alive, reproduced
F25 ^a	F30	20.12.95	rt	02.07.96	15.02.96	–	27	Unknown
F26	F18	23.06.95	den, rt, ct	08.01.03	15.04.96	–	354	Alive, reproduced
F27	F24	30.06.95	den, rt	27.04.96	10.04.96	–	6	Unknown
F36	F29	04.03.97	rt	24.06.98	26.03.97	14	152	Alive, (reproduced)

^a Exact birth date unknown and hence estimated as the mean birth date of all known births.

recommended when both y and x variables are subject of errors. Regressions were fitted separately for males and females producing correlation indices of 0.55 for females and 0.71 for males. Index of body condition was used as a predictor of dispersal at a given age, dispersal distance, as well as dispersal duration. Only weights of lynx between 7 and 11 months old were considered to reduce possible effects owing to age.

Temporal behaviour

If not exactly known, the date of independence, dispersal, death, or entry into a home range was calculated by the mid point between the closest known dates before and after the event. The time sub-adults separated from their mother was measured in days starting from the beginning of the year. The age at independence was calculated in months. The birth date, when not known, was estimated by using the mean birth date of all known litters in the JM and in

the NWSA (Breitenmoser-Würsten, Zimmermann, Ryser *et al.*, 2001). Three seasons characterized by different breeding and social events were considered. The first third of the year (January–April) mostly coincided with mating, pregnancy and separation of cubs from their mother, the second third (May–August) with births and lactation when females with cubs have a reduced mobility, and the last third (September–December) with the time when females with cubs use a larger part of their home ranges owing to a higher mobility of their kittens (Fig. 2; Kaczensky, 1991; Breitenmoser, Kaczensky *et al.*, 1993). The observed number of lynx starting dispersal during each season was compared with the expected number of dispersers. As the number of radio-tracked sub-adults differed between seasons (some individuals died, others were newly captured) the number of potential dispersers was not identical for each season. Therefore, the number of expected dispersers was calculated relative to the number of days all sub-adults were under radio-telemetric control for each season. The age at start of dispersal as well as

Table 2. Dispersal distance and age at dispersal for 13 sub-adults lynx *Lynx lynx* in the north-western Swiss Alps (NWSA) and 14 in the Jura Mountains (JM). DT, dispersal type: Ph, remained philopatric; Di, most likely completed dispersal; fD, failed dispersal. TELE, individuals followed by means of radio-telemetry; PROG, presence of a new progeny; COND, body condition measured as the residual value obtained in a reduced major axis regression of log mass on log head–body length

	DT	TELE	PROG	COND	Distance (km)	Age at dispersal (days)
NWSA						
M18	Di	no	yes	−0.010	50.7	360
M20	Di	no	no	−0.027	15.2	–
M24	Di	yes	no	0.067	4.5	486
M25	Di	yes	yes	0.002	33.1	316
M29	Di	yes	yes	−0.027	56.0	379
M30	fD	yes	?	−0.018	5.1	–
M31	Di	yes	yes	0.007	36.7	397
M35	Di	no	?	–	20.1	–
F31	Di	yes	yes	−0.136	22.1	506
F40	Di	yes	?	−0.021	33.3	–
F49	Di	yes	yes	−0.026	7.4	451
FB22	Di	no	yes	–	10.7	–
FB44	Di	no	?	–	20.6	–
JM						
M11	Di	no	?	–	31.4	–
M13	Di	no	yes	–	97.3	–
M14	Di	yes	yes	0.057	81.1	248
M15	fD	yes	yes	−0.020	27.0	363
M16	fD	yes	yes	−0.031	19.1	333
F12	Di	yes	yes	0.066	80.7	339
F13	fD	yes	yes	0.015	18.4	315
F17	fD	yes	yes	0.045	31.9	332
F20	Di	yes	no	−0.057	54.9	361
F22	Di	yes	no	0.177	27.6	369
F23	Ph	yes	yes	0.040	11.0	–
F25	fD	yes	no	−0.018	24.9	–
F26	Ph	yes	yes	−0.025	2.1	–
F36	Di	yes	yes	−0.061	68.8	318

the duration of dispersal (time between start of dispersal and settlement), were also computed. The effects of area of origin (*A*), sex (*S*), condition (*C*), presence of a new progeny (*P*), and their second-order interactions on time of start at dispersal were analysed.

Dispersal distances

Dispersal distance was defined as the distance from the arithmetic centre of a progeny’s natal home range (natal centre) to the arithmetic centre of its independent home range (independent centre). When complete dispersal information was not available, dispersal distance was calculated based on one of the following combinations: natal centre to mortality site or last location; or capture site to independent centre, mortality site, or last location. Dispersal distances came from 20 radio-collared individuals and 7 re-sighted individuals (TELE in Table 2). A Mann–Whitney *U*-test was performed to test whether dispersal distances differed between re-sighted and radio-collared individuals. Because of the small sample size

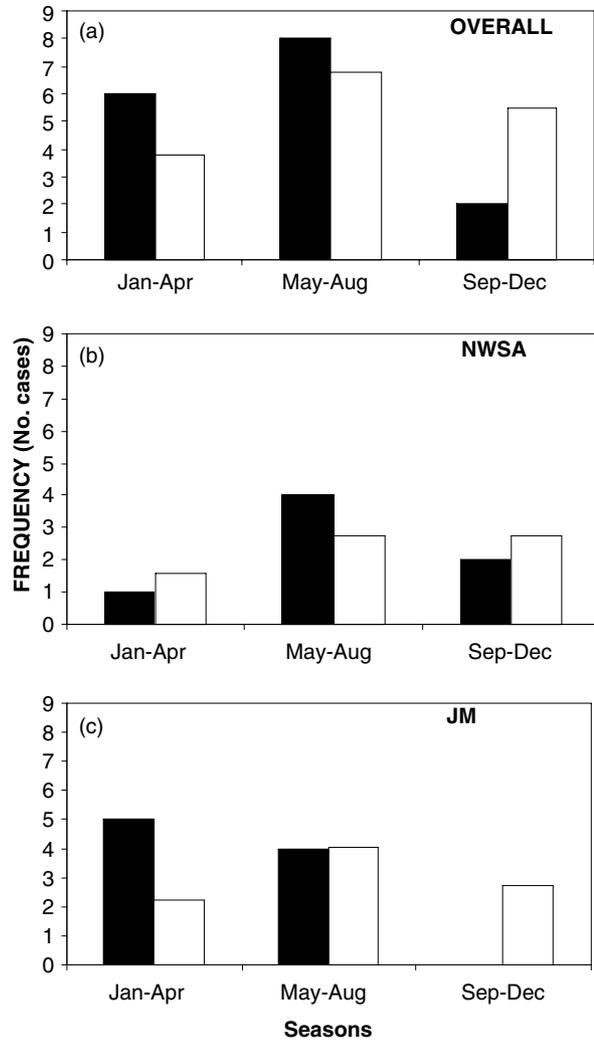


Fig. 2. Seasonal pattern of observed (black bars) and expected (open bars) dispersal events for *Lynx lynx* in: (a) overall sample; (b) NWSA; (c) JM. Number of expected dispersers was calculated relative to the number of days all sub-adults were under radio-telemetric control for each season. The observed frequency significantly differs from the expected frequency for the dataset from the JM ($\chi^2 = 6.28$, d.f. = 2, $P < 0.05$) but not for the remaining datasets (all $P > 0.1$).

comparisons could only be done within the group NWSA (males and females) and within males from both areas. There was no significant difference between both categories of individuals within each group (Mann–Whitney *U*; NWSA: $U = 19$, $n_{yes} = 8$, $n_{no} = 5$, $P = 0.88$; males: $U = 17$, $n_{yes} = 8$, $n_{no} = 5$, $P = 0.66$). The non-collared animals have therefore been pooled in the coming analyses. Analyses were conducted with: (1) all sub-adults (dispersal of Ph, fD and Di in Table 2) including those that remained philopatric (recovery distance, according to Trehwella, Harris & MacAllister, 1988); (2) only individuals that dispersed (fD, Di in Table 2; distance to the end of dispersal); (3) only those that completed dispersal (Di in Table 2; effective dispersal; see Zimmermann,

2004). The effects of area of origin (A), sex (S), body condition (C), and their second order interaction on dispersal distances (recovery distance, distance to the end of dispersal, and effective dispersal) were analysed.

Transient home ranges (THR), definitive home ranges (DHR)

A temporary home range (THR) was retrospectively identified as the area an animal used after leaving its natal range but later abandoned (Beier, 1995). The area a lynx used for ≥ 6 consecutive months without subsequent change in location was regarded as definitive home range (DHR). Home range sizes (THR and DHR) were computed by means of the 100% minimum convex polygon (MCP) method (Hayne, 1949). The calculations were done in ArcView (ESRI, 1996*a,b,c*) using the animal movement extension (Hooge & Eichenlaub, 2000).

Statistical analysis

To analyse how age at dispersal and dispersal distances were affected by area of origin, sex, condition, and presence of a new progeny, we constructed several linear regression models. Only biological meaningful models were considered. Models were compared and the best fitting ones selected using the bias corrected Akaike information criterion (AIC_c):

$$AIC_c = n \log_e(RSS/n) + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where RSS is the residual sum of square, n the sample size, and K the number of parameters in the model including the intercept and the error (Burnham & Anderson, 1998).

Differences in the AIC_c values between the best fitting and remaining models were calculated ($\Delta_i = (AIC_c) - (AIC_c)_{\min}$). Akaike weights (W_i) were calculated as:

$$W_i = \frac{\exp(-0.5\Delta_i)}{\sum_{j=1}^J \exp(-0.5\Delta_j)}$$

where J is the number of models. Akaike weights sum up to 1 for the set of models investigated and are interpreted as the weight of evidence in favour of model i as being the best one of the models considered (for details and assumptions see Burnham & Anderson, 1998). In addition, coefficients of determination R^2_{adj} were calculated for each model, indicating the proportion of variance explained by the models.

To analyse the effects on the 3 types of dispersal distances models comprised all possible combinations of the variables area of origin (A), sex (S), condition (C) and their two-way interaction. Those for the effects on age at dispersal comprised in addition the variable presence of a new progeny (P).

The response variables were normalized as much as possible using the log transformation. Calculations were done in S-PLUS (MathSoft, Inc., Seattle, Washington, U.S.A.) using generalized linear models with the Gaussian family (GLM; McCullagh & Nelder, 1983; see Nicholls, 1989).

RESULTS

Temporal behaviour

The fate of 31 juvenile lynx was studied in the NWSA and the JM (Table 1). For 24 animals (nine males and 15 females; Table 1), which had been radio-tracked before and after becoming independent from their mothers, age at independence was comparable between the study areas. It ranged from 9.3 to 10.6 months (mean = 10.3 months) in the NWSA ($n=10$) and from 8.1 to 10.7 months (mean = 10.0 months) in the JM ($n=14$), respectively. Our sample size was small, but males seemed to become independent from their mothers at about the same age (NWSA: mean = 10.3 months; JM: mean = 9.6 months) as females (NWSA: mean = 10.2 months; JM: mean = 10.1 months) in both areas. Independence started from the beginning of March to the beginning of May in the NWSA and from January to the beginning of April in the JM with a peak during April in both areas (Table 1). Sub-adult lynx did not separate earlier in the year from their mother in the JM than in the NWSA. The mean was equal to 85 and 93 days since the beginning of the year for the JM and the NWSA, respectively. In the JM, four out of seven radio-tracked adult females undertook excursions out of their home range just before the family break-up. This behaviour was only observed in one out of 10 females in the NWSA. In one case separation of lynx kittens from their mother occurred outside of the maternal home range (Molinari & Molinari-Jobin, 2001). In two cases (F36 and M14) the mothers abandoned their kittens in the vicinity of a kill and in another case two sub-adult males (M25 and M29) left their mother when they made the first kill on their own. Anecdotal observations suggest that some young males actively left their mother, but in most cases, the mother seemed to have left the juveniles. Sub-adults usually stayed for a few days close to the place where the separation occurred and finally moved on. Females were never observed interacting aggressively with their kittens. Independence took place in the core area as well as in the periphery of the maternal home range. All sub-adults except one male (M14) spent some time in their maternal home range. Only three out of 24 were relocated together with their mother during this time.

After independence, sub-adults in the NWSA stayed from 13 to 221 days (mean = 98 days) in the maternal home range, in the JM from 1 to 76 days (mean = 32 days). In the JM, two females (F23 and F26) never left the maternal home range apart from an excursion in autumn. Both took over their mother's home range after she had died. One female (F25) in the JM, however, dispersed after

Table 3. AIC_c -based comparison of linear regression models explaining variability in age at dispersal for *Lynx lynx*. Models are sorted by decreasing Akaike weights. *A*, area of origin; *S*, sex; *P*, presence of new progeny; *C*, condition; *A*S*, *A*P* and *S*C*, interactions. AIC_c , bias-corrected Akaike's information criterion for fitted models; Δ_i , $(AIC_c) - (AIC_c)_{\min}$; Akaike W_i , Akaike weights; R^2_{adj} , adjusted coefficient of determination

Model	AIC_c	Δ_i	Akaike W_i	R^2_{adj}
<i>A * P + A * S</i>	-93.41	0	0.618	0.71
<i>A * S + P</i>	-91.33	2.07	0.219	0.67
<i>A * S</i>	-88.29	5.11	0.048	0.53
<i>A * S + A + P</i>	-86.97	6.44	0.025	0.64
<i>A * S + P + S</i>	-86.97	6.44	0.025	0.64
<i>A * P</i>	-86.81	6.60	0.023	0.49
<i>A * S + C</i>	-84.71	8.70	0.008	0.50
<i>A + A * S</i>	-84.66	8.75	0.008	0.50
<i>A + S</i>	-83.55	9.86	0.004	0.46
<i>A * P + P</i>	-83.17	10.24	0.004	0.45
<i>A + A * P</i>	-83.17	10.24	0.004	0.45
<i>A + P</i>	-82.99	10.42	0.003	0.44
<i>A</i>	-82.88	10.53	0.003	0.34
<i>A + P + S * C</i>	-81.91	11.50	0.002	0.50
<i>A + A * S + P + S</i>	-81.63	11.77	0.002	0.61
<i>A * S + C + S</i>	-80.34	13.07	< 0.001	0.46
<i>A + A * S + C</i>	-80.34	13.07	< 0.001	0.46
<i>A + A * S + S</i>	-80.30	13.11	< 0.001	0.46
<i>A + C</i>	-79.48	13.93	< 0.001	0.31

her mother had been killed and left a vacant home range. In the NWSA all individuals of both sexes dispersed whereas in the JM a slightly greater proportion (5/5) of males than females (7/9) dispersed, but the difference was statistically not significant (two-tailed Fisher's exact test, $P = 0.51$). In the NWSA, sub-adults left the maternal home range between April and mid-October, in the JM between the end of January and the end of May with a peak in April and May (Fig. 2). Dispersal events were evenly distributed over the year, even after considering the seasonal differences in tracking days overall and in the NWSA, but not in the JM ($\chi^2 = 6.28$, d.f. = 2, $P < 0.05$; Fig. 2).

The best approximate model explaining age at dispersal included the interaction of area of origin with presence of new progeny, and sex respectively, but neither condition nor its two-way interaction with the other terms (Table 3). Lynx from the JM dispersed at younger ages (mean = 330.9 days; range: 248–369 days) than those in the NWSA (mean = 413.6 days; range: 316–506 days; Mann-Whitney U -test: $U = 10$, $n_{JM} = 9$, $n_{NWSA} = 7$, $P < 0.05$). Differences between areas of origin were more pronounced in females than in males (Fig. 3), and sub-adults whose mothers did not have new cubs tended to stay longer in their maternal home ranges than those confronted with new progeny. These results must be viewed with care, however, as there was a predominance of females in the JM and males in the NWSA and there were only two females in the JM and one in the NWSA without a new litter (Table 2).

Sub-adults in the JM took more time to complete dispersal than their conspecifics in the NWSA (JM: $n = 5$, range: 20–190 days, mean = 112 days; NWSA: $n = 6$,

range: 1–251 days, mean = 72 days), but the difference was statistically not significant (Mann-Whitney U -test: $U = 10$, $n_{JM} = 5$, $n_{NWSA} = 6$, $P = 0.36$).

Dispersal distances

Dispersal distances (recovery distance, distance to the end of dispersal, effective dispersal) were best explained by a model including only the interaction of area of origin with sex but neither condition nor its two-way interaction with the other terms (Table 4). The second best models included area of origin only. All other models showed much lower weights (Akaike W_i) leading to the conclusion that area of origin mainly affected dispersal distances, with sex as an additional factor. The differences in dispersal distance between areas of origin were more pronounced for males than for females (Fig. 4). However, caution is required as the sample size is small and the sex ratios differed between the areas of origin. Moreover, low adjusted coefficient of determination (R^2_{adj}) indicates that additional factors affected dispersal distances. Dispersing lynx from the JM were recovered farther (recovery distance: mean = 41.2 km, $n = 14$) from their point of origin than those from the NWSA (mean = 24.3 km, $n = 13$; Fig. 4a) but the difference was statistically not significant (Mann-Whitney U -test: $U = 64$, $n_{JM} = 14$, $n_{NWSA} = 13$, $P = 0.19$). Distances to the end of dispersal were also longer in the JM (mean = 46.9 km, $n = 12$) than in the NWSA (mean = 24.3, $n = 13$; Fig. 4b; Mann-Whitney U -test: $U = 42$, $n_{JM} = 12$, $n_{NWSA} = 13$, $P = 0.05$). Furthermore, lynx from the JM settled at farther distances (effective dispersal: mean = 63.1, $n = 7$) than those from the NWSA (mean = 25.9, $n = 12$; Fig. 4c; Mann-Whitney U -test: $U = 11$, $n_{JM} = 7$, $n_{NWSA} = 12$, $P < 0.01$).

Home range (THR, DHR)

NWSA

Of all dispersing lynx with a known fate, one male (M30) died 5 km from his maternal home range (Table 2) after a journey of 62 km. One male showed a circular dispersal (M24; Fig. 5); he established a definitive home ranges (DHR) besides his mother's home range. Ten sub-adults (e.g. M24, F31, F49; Fig. 5) established a DHR directly after their dispersal within the NWSA. Their areas ranged from 26 to 150 km² (Table 5). Female F49 made several excursions out of her DHR (Fig. 5). M25 was the only individual who used a transient home range (THR). He occupied a 122 km² large THR overlapping 42% with the home range of a resident male. After 200 days, he moved on and established a DHR (Fig. 5). All sub-adults established their DHR within the NWSA in the vicinity of home ranges of adult resident lynx of the same sex, which were radio-tracked as well (e.g. M24, M25, F31, F49; Fig. 5) or in areas where signs of presence of conspecifics were reported within the same period (Breitenmoser-Würsten,

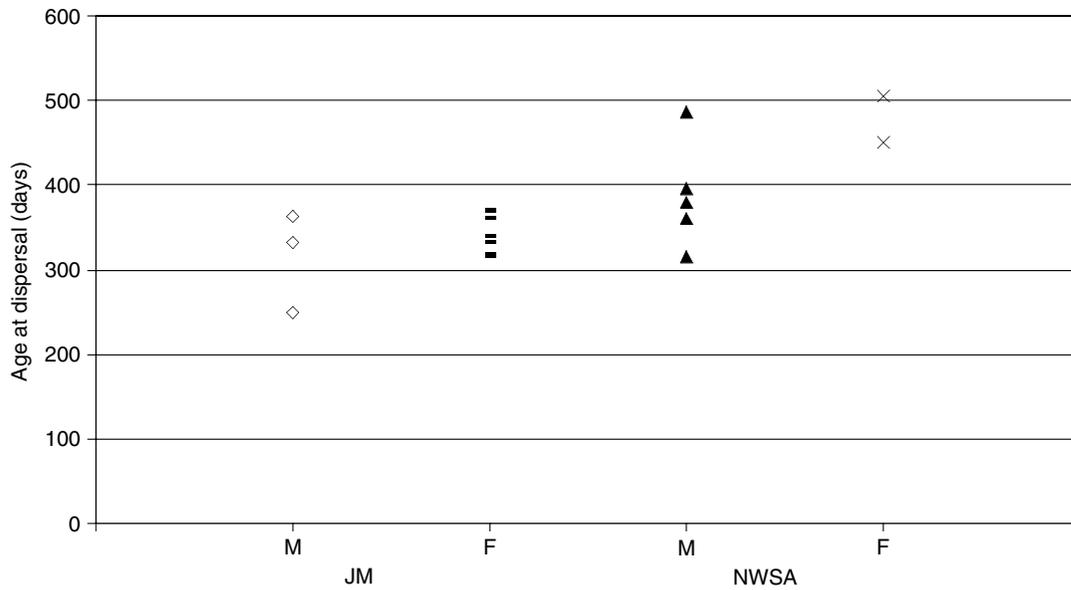


Fig. 3. Age at dispersal of males (M) and female (F) *Lynx lynx* in the Jura Mountains (JM) and the north-western Swiss Alps (NWSA).

Table 4. AIC_c -based comparison of linear regression models explaining variability in dispersal distances for *Lynx lynx*. Models are sorted by decreasing Akaike weights. A , area of origin; S , sex; $A * S$, interaction between area of origin and sex. AIC_c , bias-corrected Akaike's information criterion for fitted models; Δ_i , $(AIC_c)_i - (AIC_c)_{min}$; Akaike W_i , Akaike weights; R^2_{adj} , adjusted coefficient of determination

Distance	Models	AIC_c	Δ_i	Akaike W_i	R^2_{adj}
Recovery distance	$A * S$	-45.84	0	0.49	0.076
	A	-44.44	1.40	0.25	0.027
	S	-43.06	2.78	0.12	-0.024
	$A + S$	-42.80	3.04	0.11	0.028
	$A + A * S + S$	-40.03	5.81	0.03	-0.004
Distance to the end of dispersal	$A * S$	-52.69	0	0.46	0.206
	A	-52.42	0.27	0.40	0.198
	$A + S$	-49.80	2.89	0.11	0.169
	$A + A * S + S$	-46.68	6.02	0.02	0.131
	S	-45.86	6.83	0.01	-0.043
Effective dispersal	$A * S$	-41.83	0	0.56	0.373
	A	-40.67	1.16	0.31	0.334
	$A + S$	-38.43	3.40	0.10	0.329
	$A + A * S + S$	-34.82	7.02	0.02	0.290
	S	-32.01	9.82	< 0.01	-0.051

Zimmermann, Ryser *et al.*, 2001). None of the sub-adults established a DHR in an area without conspecifics.

JM

As in the NWSA, sub-adults normally crossed the territories of resident lynx. Only one male (M16) from the six sub-adults that crossed known territories of resident lynx avoided the resident home ranges by following their borders (Fig. 6). He died after having spent 24 days in the Swiss Plateau, an area with intensive agriculture and a high human presence. Three females and one male established

Table 5. Size (km², based on 100% minimum convex polygon) and duration of sub-adult *Lynx lynx* home ranges in the north-western Swiss Alps (NWSA) and the Jura Mountains (JM). THR, transient home range; DHR, definitive home range; ?, unknown

Lynx	Home range type	Size (km ²)	No. of locations	Days
NWSA				
M24	DHR	93	136	366
M25	THR	122	60	200
	DHR	149	71	360
M29	DHR	129	96	322
M31	DHR	150	118	327
F31	DHR	26	13	166
F33	DHR	69	53	364
F40	DHR	38	14	198
F42	DHR	57	41	364
F49	DHR	67	86	378
F54	DHR	55	86	315
F57	DHR	93	144	326
JM				
M14	THR	22	50	72
	DHR	133	76	185
M15	?	78	53	119
F12	DHR	223	80	216
F13	THR	120	33	114
F20	THR	230	56	109
	DHR	642	138	361
F22	THR	108	87	113
	DHR	109	76	363
F23	DHR	226	155	280
F26	DHR	68	192	365
F36	DHR	431	113	372

a THR (e.g. F22, M14; Fig. 6). The orientation of the THR was parallel to the mountain ridge and their area ranged from 22 to 230 km² (Table 5). Two individuals (M14, F13) established their THR at the edge of the suitable habitat of the JM. The overlap of their THR with the home range of

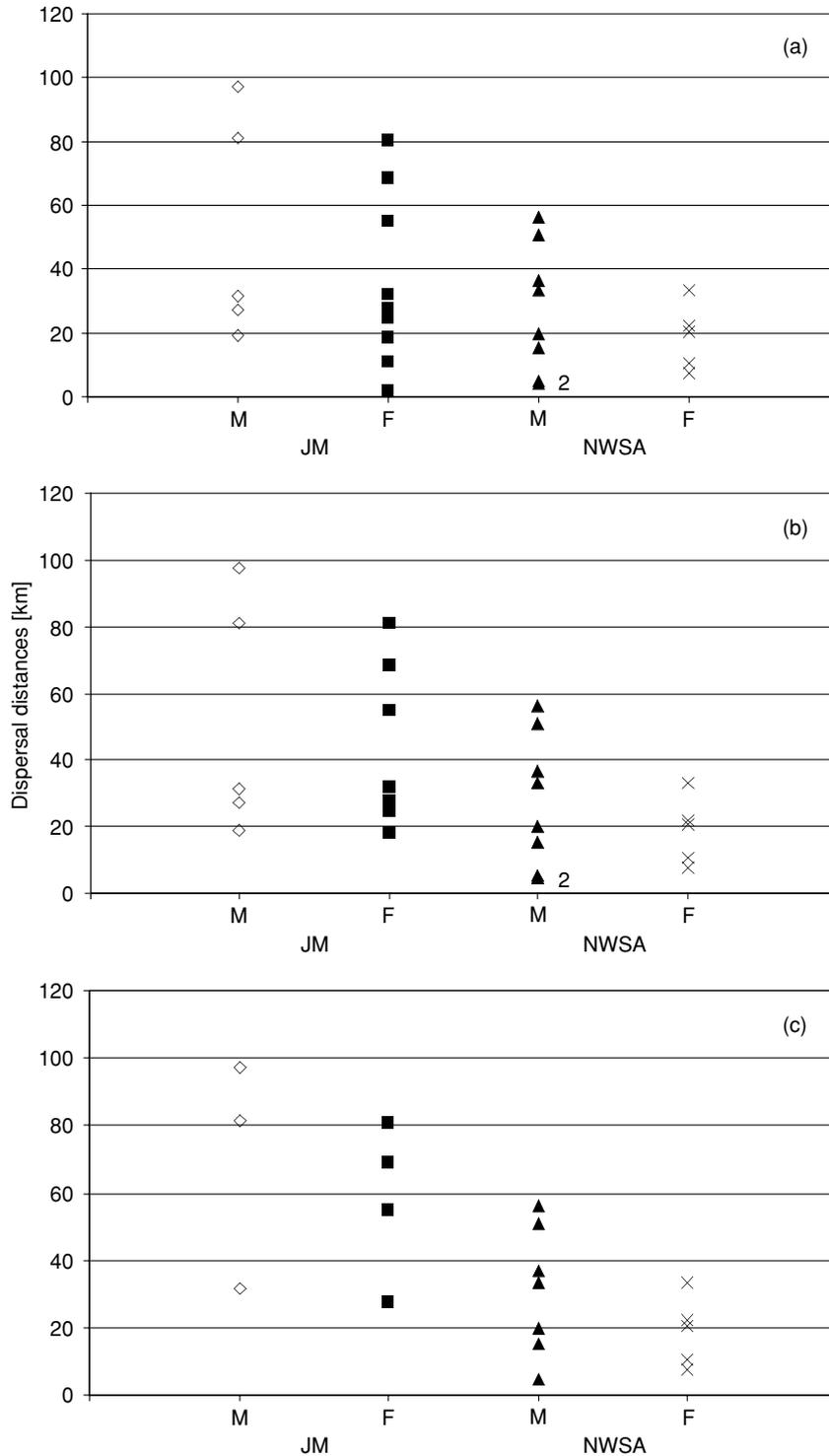


Fig. 4. Recovery distances (a), distances to the end of dispersal (b), and effective dispersal distances (c) for males (M) and female (F) *Lynx lynx* in the Jura Mountains (JM) and the north-western Swiss Alps (NWSA). When points are overlapping, their number is indicated.

neighbouring resident lynx of the same sex was 21% and 9%, respectively. Sub-adults occupied their THR from 72 to 113 days. Both females left their THR between mid-August and the end of September, whereas M14 already left his THR by mid-June. Six females established a DHR (e.g. F22; Fig. 6). Their areas ranged from 68 to 642 km² (Table 5). All individuals established their DHR within

well-suited habitat, with the exception of female F20. Her large DHR (642 km²) was probably a result of the high forest fragmentation in this area. Two females (F23 and F26) took over their mother's home range after she had died. Both made an excursion outside their home ranges in October (e.g. F26; Fig. 6). The maximum distance from the centroid of their home ranges was 34 and 30 km,

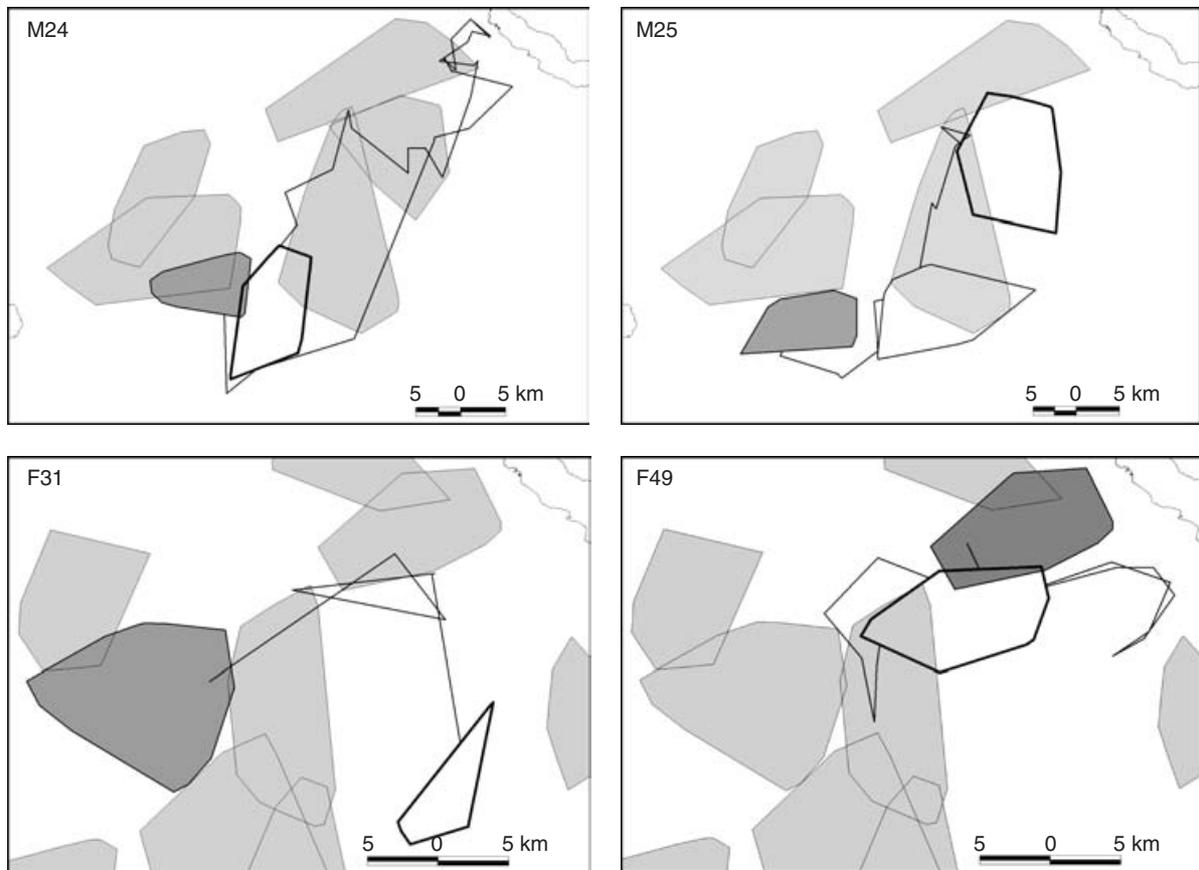


Fig. 5. Dispersal trajectories and home-range establishment of two males (M24, M25) and two female (F31, F49) *Lynx lynx* from the north-western Swiss Alps (NWSA). Thin and fat outlined polygons, transient home range (THR) and definitive home range (DHR), respectively. Black lines, movement during dispersal; light grey, home ranges of the residents of the same sex.

respectively. All sub-adults (e.g. M14, F22, F26; Fig. 6) established their DHR in the vicinity of home ranges of adult resident lynx of the same sex followed by means of radio-telemetry during the same time or in respectively close to areas where signs of presence of conspecifics have been reported within the same period (Vandel, 2001; Capt, in press).

DISCUSSION

Possible causes affecting onset of independence

Most behavioural studies on dissolution of lynx family groups come from observations in captivity (e.g. Jonsson, 1984; Sokolov, Naidenko & Serbenyuk, 1994; Naidenko, 2001), there are only a few anecdotal observations from the wild (e.g. Molinari & Molinari-Jobin, 2001). Even in our study where direct observations were rare and the results principally relied on radio-telemetry data, different aspects of the spatio-temporal behaviour suggest that disintegration of family groups in free-ranging lynx is not caused by female parent aggression as stated by Stroganov (1962) and later by Jonsson (1984): (1) aggressive interactions between female parents and juvenile lynx

were never observed in the wild (Schmidt, 1998; Molinari & Molinari-Jobin, 2001; this study), it is unlikely that they have been missed as aggressive encounters between adults of the same sex have been reported (Wölfel & Wölfel, 1996; Sunde *et al.*, 2000; A. Burri, pers. comm.), (2) one female dispersed even in the absence of her mother, (3) separation occurred at the periphery as well as in the core area of the maternal home range, (4) all sub-adults except one stayed a few weeks in the maternal home range and even close to the spot of separation before they started dispersal, and none was chased away by its mother during this time, and (5) a few sub-adults were occasionally during one day relocated with their mother after separation. A few anecdotal observations suggest that contacts get looser close to the separation time. Females sometimes make parallel kills to ensure constant access to food for her kittens (Molinari & Molinari-Jobin, 2001). While the kittens are still feeding at the old kill, the female is already at the new one, spending more time away from her kittens. Family break-up may be initiated by the female abandoning the kittens at a kill. On some occasions, sub-adults separated from their mother when they made their own first kill as shown by two juvenile males (M29 and M25) in the NWSA. The cause in either separation may be shortage of food in the sense that females may not be able to kill enough prey to feed their almost adult offspring, and

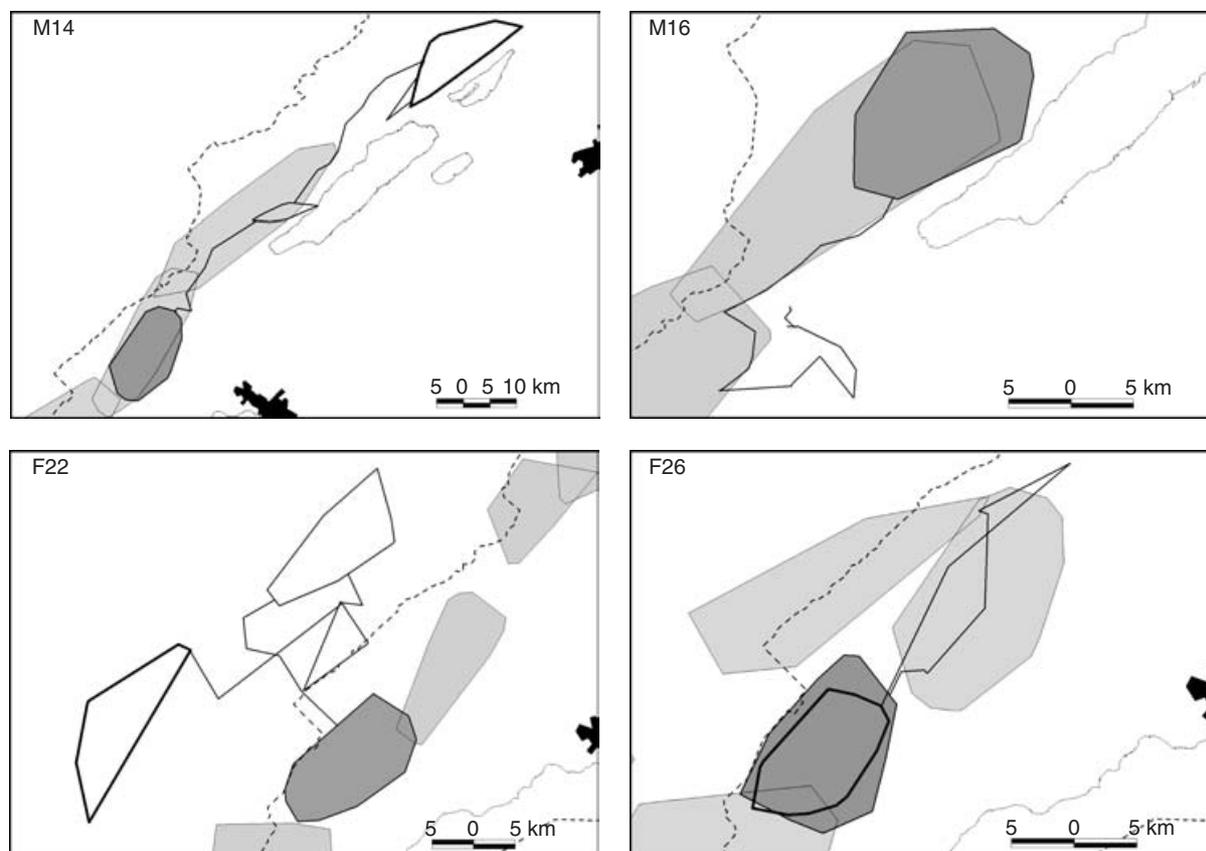


Fig. 6. Dispersal trajectories and home range establishment of two males (M14, M16) and two female (F22, F26) *Lynx lynx* from the Jura Mountains (JM). Thin and fat outlined polygons, transient home range (THR) and definitive home range (DHR), respectively. Black lines, movement during dispersal; light grey, home ranges of the residents of the same sex.

not because resources are limited. The start of the mating season in February–March may also induce the process, as most family break-ups occurred in March and April (Schmidt, 1998; Sunde *et al.*, 2000; this study). In cougars (*Puma concolor*) Beier (1995) did not observe aggression of females towards her kittens either: the mother often left her kittens from 0–3 km at the edge of her home range while she moved to the opposite edge of her home range.

Possible causes affecting timing of dispersal

In both areas, sub-adults stayed a few months in the maternal home range after separation. Making their first hunting experiences in a familiar environment is certainly an advantage as prey-catching techniques may be expected to take time to acquire. Interaction with their mother is also reduced at this time, as most females give birth to a new litter in June and therefore only use a reduced part of their home range until September (Kaczensky, 1991). Such an initial phase of independence was also observed in a former study in the Alps (Haller & Breitenmoser, 1986) but not in the autochthonous population in Bialowieza, Poland, where all sub-adults left the maternal home range just after separation (Schmidt, 1998).

We concluded that the distribution of age at dispersal is best explained by the factor of area of origin in combination with sex and the presence of progeny. We furthermore did not observe any influence of body condition on dispersal in lynx. The presence of a new litter may trigger dispersal in lynx as the late dispersal of three sub-adults not confronted with new progeny seems to indicate. In tigers, variation of age at dispersal seems most closely related to variation in the reproductive interval of the mothers (Smith, 1993). In the NWSA, where a high lynx density was found (Breitenmoser-Würsten, Zimmermann, Ryser *et al.*, 2001), compared to the JM, sub-adults were older when dispersing and dispersal onsets were distributed over a longer time period than in the JM (Fig. 2). In the Iberian lynx *Lynx pardinus*, in contrast, seasonality was more marked in the area where lynx densities were low, and sub-adults dispersed at older ages than in the high lynx density area (Ferrerias *et al.*, 2004). In contrast to the Iberian lynx, there was no indication that intraspecific competition for resources was an ultimate cause of dispersal in Eurasian lynx. Delayed dispersal at high density is an important factor in the evolution of cooperative breeding in birds and mammals (Brown, 1987), but it has also been reported from non-social species (see Lambin *et al.*, 2001). Among carnivores it has been observed in black bear *Ursus americanus* (Lindzey & Meslow,

1977a,b) and in Canadian lynx *Lynx canadensis* where yearlings of both sexes still remained in the home ranges of their mothers 1 year after the snowshoe hare peak (Breitenmoser, Slough & Breitenmoser-Würsten, 1993). If a resident is forced to share its once exclusive home range with conspecifics as a consequence of increased density, it may be more advantageous to share it with its own offspring.

Duration of dispersal and home range establishment

The duration of dispersal was short, with a mean of 72 days in the NWSA and 112 days in the JM, suggesting that sub-adults in both areas were quickly integrated into the population, probably as a consequence of a relative high turn-over. Illegal killing in the JM together with legal removal of stock riding individuals in the NWSA was the most important cause of mortality for adult resident lynx during the study period (Breitenmoser-Würsten, Zimmermann, Ryser *et al.*, 2001) leading to vacant territories.

Both sexes established a THR in the JM, whereas only one male established a THR in the NWSA. In puma, only males established a THR, while females were more quickly integrated in the resident population (Beier, 1995). Such a difference was not seen in the JM, and is consistent with our findings that in lynx, both sexes actually disperse. In the JM, most individuals left their THR from mid-August to the end of September coinciding with the time resident females with kittens start to occupy a larger part of their home range (Kaczensky, 1991). All sub-adults established their DHR in the vicinity of known adult lynx home ranges or close to areas with known lynx occurrences. Individuals in solitary territorial species define their home-range borders in relation to the spatial distribution of conspecifics. This propensity combined with a low ability of sub-adults to cross unfamiliar land and barriers (Zimmermann, 2004) hamper the expansion of lynx populations. Lynx is a conservative disperser when compared to wolf and bear. Male wolves and bears are known to move long distances even through landscapes with no conspecifics, searching for access to partners (Swenson, Sandegren & Söderberg, 1998; Merrill & Mech, 2000; Stratman *et al.*, 2001).

Factors influencing dispersal distances

Our analyses revealed that the area of origin is an important factor shaping the dispersal distances in our study sites. Dispersal distances of males were generally larger, but even more prominent were the longer dispersal distances in the JM compared to the NWSA (Fig. 4). As site specific differences were more pronounced in males, we can assume that sex may be relevant in conjunction with area of origin. Dispersal in solitary felids is usually biased towards males with most of the females remaining philopatric, and dispersal distances are generally larger for males than for females (Logan, Irwin & Skinner,

1986; Anderson, Bowden & Kattner, 1992; Lindzey *et al.*, 1992; Ross & Jalkotzy, 1992; Smith, 1993; Beier, 1995; Sweanor *et al.*, 2000; Maehr, Land, Shindle *et al.*, 2002). In Poland, dispersal distances in Eurasian lynx ranged from 5 to 129 km (Schmidt, 1998). The maximum distance was reached by a male. Although sample size was limited, it seemed that males dispersed for long distances, whereas females remained philopatric. In our study, there was no significant sex bias in the proportion of individuals that dispersed although only females took over maternal home ranges. Furthermore sex by itself did not affect the recovery distance, the distance of settlement from the natal home range (effective dispersal) nor the distance travelled until dispersal ended (distance to the end of dispersal). The insignificantly larger dispersal distances of the males do not support inbreeding avoidance as an ultimate cause of dispersal in Eurasian lynx. Ferreras *et al.* (2004) came to similar conclusions for the Iberian lynx. It has been hypothesized that sex-biased dispersal is linked to the mating system (Greenwood, 1980). Polygyny, the predominant mating system among mammals, favours the evolution of male-biased dispersal because of intrasexual competition among males for mates (Greenwood, 1980; Dobson, 1982). Lynx are rather monogamous, but males tend to mate with several females given the opportunity. The male-biased dispersal observed was not very pronounced; environmental factors such as habitat fragmentation or prey density may influence dispersal more than the mating system, and as a consequence, the area of origin was found to be the predominant factor.

Dispersal distances in the NWSA were shorter than those reported from other studies on Eurasian lynx (Schmidt, 1998; Sunde *et al.*, 2000; J. Linnell, pers. comm.) as well as from other solitary felids of related size such as Canadian lynx (Poole, 1997) and bobcat (Knick & Bailey, 1986; Knick, 1990). In the NWSA, dispersal distances were close to those reported by Ferreras *et al.* (2004) in a critically endangered Iberian lynx population in the Coto del Rey area of the Doñana National Park. Differences in dispersal distances between the NWSA and the JM are probably related to the size and arrangement of suitable habitat in each area as well as linear barriers (e.g. fenced highways). Severe habitat restrictions (suitable habitat as well as linear barriers) led to circular dispersal in males in the NWSA (Zimmermann, 2004). A similar dispersal pattern has also been reported in two endangered cats: the Florida panther *Puma concolor coryi* (Maehr, Land & Roof, 1991; Maehr, Land, Shindle *et al.*, 2002) and the Iberian lynx (Ferreras *et al.*, 2004). However, intrinsic demographic differences and the prospect that dispersal rates and distances may be negatively correlated with density may also be relevant. Evidence is mounting for negative density-dependent dispersal, so that a smaller fraction of individuals disperses at higher densities (Wolff, 1997; Lambin, Aars & Pieltney, 2001), and dispersers may be expected to move relatively short distances (McCarty, 1997). Wolff (1997) suggest that dispersal should be inversely density-dependent in territorial species because territoriality at high density can impede immigration and make it difficult for juveniles to leave their natal area.

This pattern has been reported, for example, for red foxes (Trehella *et al.*, 1988), roe deer (Linnell, Wahlström & Gaillard, 1998; Wahlström & Liberg, 1995), Townsend's voles *Microtus townsendii* (Lambin, 1994), and Canadian lynx (after the snowshoe hare crash both female and male yearlings were tolerated in the parental home ranges; Breitenmoser, Slough & Breitenmoser-Würsten, 1993), and this seems to be also true for Eurasian lynx (Zimmermann, 2004). The small proportion of variance explained by the models indicates that additional factors not included in the models may be relevant, such as vacancy of territories, habitat fragmentation, and the pattern of settled and unsettled areas. Furthermore it is not known how dispersal would look in areas continuously occupied by lynx. There are virtually no data on dispersal from a situation comparable to the Alps. The sparse information available is either from the central European lowland (Schmidt, 1998) or from Norway with its very low lynx density (Sunde *et al.*, 2000; J. Linnell, pers. comm.). At the present stage of knowledge, we cannot assess the respective importance of population status (e.g. abundance and distribution), habitat distribution and fragmentation, and landscape features (topography) for shaping the dispersal of lynx. There are, however, good reasons to suppose that dispersal in the Alps may look different once the entire range is settled by lynx.

Acknowledgements

We thank C. Angst, A. Burri, S. Capt, P. Molinari, A. Molinari-Jobin, A. Ryser, and many more unnamed colleagues for gathering field data during the past 20 years. Special thanks go to P. Molinari for his help during the capture of sub-adult lynx in the north-western Alps. P. Enggist gave valuable advice for the GLM analyses and the model selection procedure. We also appreciated J. Hauser's assistance in the analyses and P. Jackson's help with the language. This work would not have been possible without the help of the game wardens, especially G. Beaud, A. Chappalley, L. Jaggi, P. Jordan, W. Kunz, E. Peissard, M. Pharisa, J. C. Roch, P. Schwendimann, R. Zumbrennen and P. Zysset. M. von Arx provided welcome comments on the manuscript. The study in the Jura Mountains was supported by the Swiss Agency for Environment, Forest and Landscape (SAEFL), the canton of Vaud, the Swiss League for Protection of Nature (Pro Natura), WWF Switzerland, the Agassiz Foundation and, in the early phase, by the Swiss Foundation for Scientific Research (project no. 3.119-0.85).

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