

Spatial and temporal variation in natal dispersal by Eurasian lynx in Scandinavia

G. Samelius¹, H. Andrén¹, O. Liberg¹, J. D. C. Linnell², J. Odden², P. Ahlqvist¹, P. Segerström³ & K. Sköld¹

¹ Department of Ecology, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden

² Norwegian Institute for Nature Research, Trondheim, Norway

³ Vaikijaur 617, Jokkmokk, Sweden

Keywords

natal dispersal; male biased dispersal; Eurasian lynx; *Lynx lynx*.

Correspondence

Gustaf Samelius, Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden.

Tel: +46-581-697334; Fax: +46-581-697310

Email: gustaf.samelius@slu.se

Editor: Andrew Kitchener

Received 1 February 2011; revised 19 July 2011; accepted 21 July 2011

doi:10.1111/j.1469-7998.2011.00857.x

Abstract

Dispersal patterns are male biased in most mammals whereas the patterns are less clear within the genus *Lynx* (four species), with findings ranging from male biased dispersal to males and females dispersing equally far and with equal frequency. In this study, we examined various aspects of natal dispersal by Eurasian lynx in Scandinavia by comparing dispersal patterns of 120 radio-marked lynx in two study areas in Sweden (Sarek and Bergslagen) and two study areas in Norway (Hedmark and Akershus). We found that male lynx dispersed farther than female lynx with mean dispersal distances of 148 and 47 km for male and female lynx that were followed to the age of 18 months or older (range = 32–428 and 3–215 km for each sex, respectively). In fact, female lynx often established home ranges that overlapped or partly overlapped that of their mothers. Similarly, the dispersal rate was greater among male lynx than among female lynx, with 100% of the males dispersing compared with 65% of the females dispersing. This study showed that dispersal patterns by lynx in Scandinavia were male biased, with (1) male lynx dispersing farther and more frequently than female lynx and (2) female lynx often settling near their natal areas. These patterns, in turn, will have large impact on gene flow and the ability by lynx to colonize new and formerly occupied areas.

Introduction

Dispersal is a key process affecting the genetic and demographic structure of populations (Begon, Harper & Townsend, 1996; Clobert *et al.*, 2001). Specifically, it is the process that links populations together and it is crucial for colonization of new and formerly occupied areas and enhancing gene flow within and between populations (Clobert *et al.*, 2001). Young animals are often more prone to disperse than adult animals (Greenwood, 1980), and dispersal is generally categorized as either natal or breeding dispersal, where natal dispersal is emigration from the natal area to the site of first reproduction and breeding dispersal is emigration from one breeding area to another (Howard, 1960; Clobert *et al.*, 2001). Natal dispersal rate and dispersal distances are generally male biased in mammals and female biased in birds (Greenwood, 1980; Dobson, 1982; Clarke, Sæther & Røskaft, 1997). Natal dispersal patterns are generally male biased for large solitary felids (Smith, 1993; Beier, 1995; Sweanor, Logan & Hornocker, 2000; Maehr *et al.*, 2002), whereas the patterns are less clear among the four species of *Lynx*, with no clear patterns within species and findings ranging from male biased dispersal (Mowat & Slough, 1998; Schmidt, 1998; Janečka *et al.*, 2007)

to male and female lynx dispersing equally far and with equal frequency (O'Donoghue *et al.*, 1997; Poole, 1997; Ferreras *et al.*, 2004; Zimmermann, Breitenmoser-Würsten, & Breitenmoser, 2005; Campbell & Strobeck, 2006).

There are three main hypotheses proposed to explain ultimate causes of natal dispersal: resource competition (Greenwood, 1980), mate competition (Dobson, 1982) and inbreeding avoidance (Pusey, 1987; Wolff, 1993). However, these hypotheses are not mutually exclusive and there is growing evidence that ultimate dispersal strategies may be shaped by multiple selective pressures (Gandon & Michalakis, 2001). Moreover, dispersal distances are predicted to vary depending on the main selective force. Specifically, relatively short dispersal distances (e.g. moving immediately outside the natal area) may be enough to reduce mate and resource competition whereas longer dispersal distances may be necessary to avoid close inbreeding in situations when opposite-sex relatives form kin-related clusters (Ronce *et al.*, 2001).

Eurasian lynx (*Lynx lynx*, lynx hereafter) are solitary animals with male home ranges being larger than female ranges (Herfindal *et al.*, 2005) and a spatial organization where male home ranges generally overlap (at least partially) those of a few females (Schmidt, Jędrzejewski & Okarma,

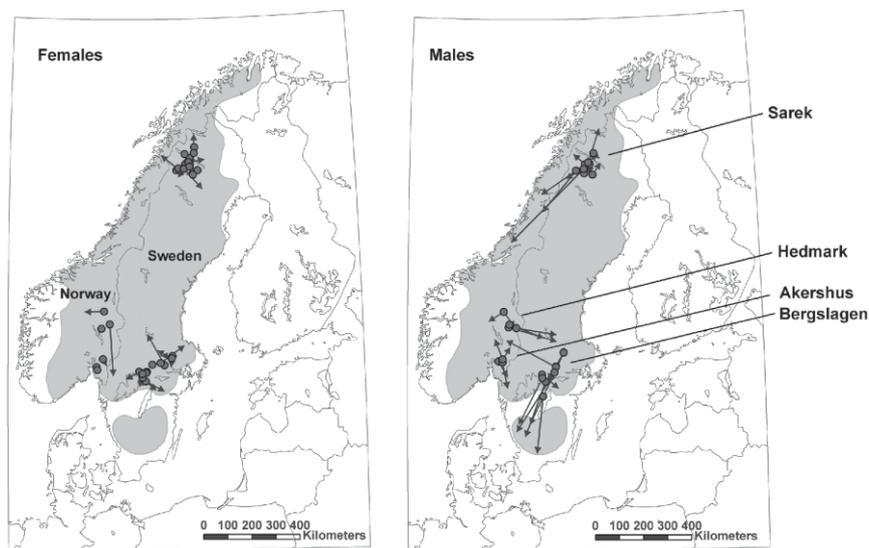


Figure 1 Dispersal patterns by female (left) and male (right) lynx that were followed to the age of 18 months or older in the Sarek, Hedmark, Akershus and Bergslagen study areas in 1994 to 2008. Arrows indicate straight-line distances that lynx dispersed and circles indicate natal areas. The distribution of lynx in Sweden and Norway is indicated in grey (modified from von Arx *et al.*, 2004 and based on national surveys of reproductive units). The southernmost part of the distribution in Sweden was colonized during this study, with only scattered distribution of reproductive units even at the end of this study (cf. von Arx *et al.*, 2004; Andrén *et al.*, 2010).

1997; Breitenmoser-Würsten *et al.*, 2007b). Lynx mate in March and the young are born in late May or early June (Breitenmoser-Würsten *et al.*, 2007a). The young remain with their mother to the age of about 8–11 months (Breitenmoser *et al.*, 1993; Schmidt, 1998; Zimmermann *et al.*, 2005). The majority of female lynx appear to breed at the age of 2 years (Breitenmoser-Würsten *et al.*, 2007a), although the proportion of females that breed at this age is lower at the northern edge of their distribution in Scandinavia (Andrén, unpublished data).

The objective of this study was to examine various aspects of natal dispersal by lynx in Scandinavia. Specifically, we compared age at separation from mothers, age at the start of dispersal, dispersal rate, dispersal distances and direction of dispersal by lynx in northern Sweden (Sarek), southern Norway (Hedmark and Akershus) and south-central Sweden (Bergslagen). Lynx were rare in areas south of Bergslagen at the start of this study (von Arx *et al.*, 2004; Andrén *et al.*, 2010) so we were especially interested in whether lynx dispersed into southern Sweden.

Methods

Study area

This study is based on long-term research by the joint Swedish and Norwegian Lynx Projects *Scandlynx* (<http://scandlynx.nina.no>) and was conducted in the Sarek, Hedmark, Akershus and Bergslagen areas in 1994 to 2008 (Fig. 1). The Sarek study area (67°00 N, 17°40 E) is located on the eastern edge of

the Scandinavian mountain range and range from boreal forest (dominated by Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*) in the eastern part of the study area to mountain birch forest (*Betula* spp.), mountain meadows and high alpine areas in the western part of the study area. The Hedmark study area (61°15 N, 11°30 E) is located at the south-eastern edge of the Scandinavian mountain range and is dominated by boreal forest with limited farmland along valley bottoms. The Akershus study area (59°45 N, 11°15 E) consists of low hills and is characterized by boreal forest intermixed with a high proportion of agricultural lands and high density of humans. The Bergslagen study area (59°30 N, 15°30 E) is located at the southern edge of the boreal forest of Scandinavia and is relatively flat compared with the other study areas. Areas south of Bergslagen are characterized by greater proportions of agricultural lands and greater densities of humans (especially the areas around the large lakes immediately south of Bergslagen and the areas at the very south of Sweden). Semi-domestic reindeer (*Rangifer tarandus*) are the main prey of lynx in the Sarek study area whereas roe deer (*Capreolus capreolus*) are the main prey of lynx in the Hedmark, Akershus and Bergslagen study areas (Pedersen *et al.*, 1999; Odden, Linnell & Andersen, 2006; Nilsen *et al.*, 2009). Hares and birds are important secondary prey items in all study areas and, on the Norwegian side, free-ranging sheep are also available as prey in summer (Odden *et al.*, 2006). Population densities of roe deer were low in Hedmark, intermediate in Bergslagen, and high in Akershus and areas south of Bergslagen (Linnell *et al.*, 2007; Nilsen *et al.*, 2009). The lynx population in Scandinavia is the result of natural recoveries during the late 20th century from small remnants (Linnell

et al., 2009, 2010). Lynx are subject to recreational harvest, lethal control and illegal killing in both countries (Andr n *et al.*, 2006; Linnell *et al.*, 2009, 2010).

Lynx capture and telemetry

We captured and radiomarked 120 juvenile lynx that were followed to the age of 10 months or older in the Sarek, Hedmark, Akershus and Bergslagen study areas from 1994 to 2008. The mothers to 101 of these 120 animals were radiomarked, which allowed us to relate dispersal patterns to that of their mother's known range for the majority of individuals in this study. Lynx were captured by hand at their natal lairs when less than 2 months old or in walk-through box traps, foot snares placed at kill sites, treed using trained dogs, or darted from a helicopter or the ground when 3 to 10 months old (Arnemo *et al.*, 1999, 2006). Animals were immobilized with a mixture of ketamine (5 mg/kg) and medetomidine (0.2 mg/kg) and equipped with a radio collar (Telonics Mod 80, Mod 315, Mod 335, Mod 400, Mesa, AZ, USA; or Televilt TXH-3, Lindesberg, Sweden) or implanted transmitter (Telonics Imp 400 L) following protocols by Arnemo, Evans & Fahlman (2011). Capture and handling protocols were approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee and followed their ethical requirements for research on wild animals as well as the relevant national wildlife management agencies.

Animals were located from the ground or from the air at least once to twice per month although the schedule for locating animals varied throughout the study (e.g. some animals were located intensively during periods of 1–2 months whereas some animals were missed during inclement weather that prevented us from flying). Animals from the study areas in Hedmark, Akershus and Bergslagen were monitored throughout the southern half of Sweden and part of Norway, whereas animals from the Sarek area were monitored up to about 250 km from their natal areas because of logistical restrictions of working in this remote area. We did not know the exact date of birth for kittens so we assumed 1 June to be the date of birth for all kittens. We used month as our sampling unit for age because the temporal precision in our data was about ± 2 weeks.

Dispersal analyses

We followed Howard's (1960) definition of *natal dispersal* (called dispersal hereafter) as emigration by an animal from its natal area to another area where it might reproduce. Similarly, we defined *dispersal rate* to be the proportion of animals that dispersed and we considered animals that established home ranges outside their maternal home ranges (see independent home ranges below) or were outside their maternal home ranges when last encountered to have dispersed (cf. Sweanor *et al.*, 2000; Zimmermann *et al.*, 2005). Furthermore, we defined dispersal to start the first time an animal was encountered outside its maternal home range without returning (called *age at the start of dispersal* hereafter) following Sweanor *et al.* (2000) and Zimmermann *et al.* (2005). *Age at separation from mothers* was estimated as the midpoint between the last time

animals were located together with their mothers (i.e. located at the same coordinates) and the following relocation (cf. Zimmermann *et al.*, 2005). We derived maternal home ranges by calculating minimum convex polygons (100% MCP) by using the MCP function in Hawth's Analysis Tools (<http://www.spatial ecology.com>) for ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), and we derived spatial relationships between animal locations and that of their maternal home range by using the spatial join function in ArcGIS 9.2. We calculated maternal home ranges on telemetry positions from all years following the first year of reproduction except for two females who moved and for whom we calculated a separate home range from each time period ($n \geq 26$ positions per home range). We excluded 10 animals from our analyses on age at the start of dispersal and dispersal rate because we were uncertain whether they dispersed or not as we lost contact with them while they were still in their natal area (e.g. transmitter failure and poaching) and they were less than 18 months old, which was the age after which we detected only limited dispersal movements (Fig. 2). Similarly, we excluded another 14 animals from our analyses on timing of dispersal because we were missing data from more than two consecutive months prior to their first encounter outside their natal areas without returning.

We defined *dispersal distance* to be the distance from the arithmetic center of the natal area to the arithmetic center of the independent home range (Zimmermann *et al.*, 2005). Moreover, we considered (1) the maternal home range to be the natal area for animals with radiomarked mothers and (2) the home range during the first 10 months of life to be the natal area for animals whose mothers were not radiomarked (cf. Zimmermann *et al.*, 2005). Similarly, we considered (1) the area used after the age of 2 years to be the independent home range for animals that were followed to the age of 2 years or older and (2) the last encounter to be the center of the independent home range for animals that were between 18 months and 2 years old when last encountered. We limited our analyses on dispersal distances to animals that were followed to the age of 18 months or older because this was the age after which we observed only limited dispersal movements (Fig. 2) and we used the arithmetic center of the area used during the last year of encounter in our calculations of dispersal distance for animals that were followed ≥ 1 year after they turned 2 years old. We included 11 animals that were re-encountered after we had lost contact with them during the dispersal stage in our calculation of dispersal distance following Zimmermann *et al.* (2005) and Long *et al.* (2008). Five of these animals were from the Sarek area, three were from the Hedmark area, two were from the Akershus area and one animal was from the Bergslagen area. We derived home ranges and spatial relationships between natal areas and independent home ranges by following the methods described previously.

Statistical analyses

We examined how age at separation from mothers, age at the start of dispersal, and dispersal distances varied among study areas and sex of lynx by a mixed linear model (Proc Mixed,

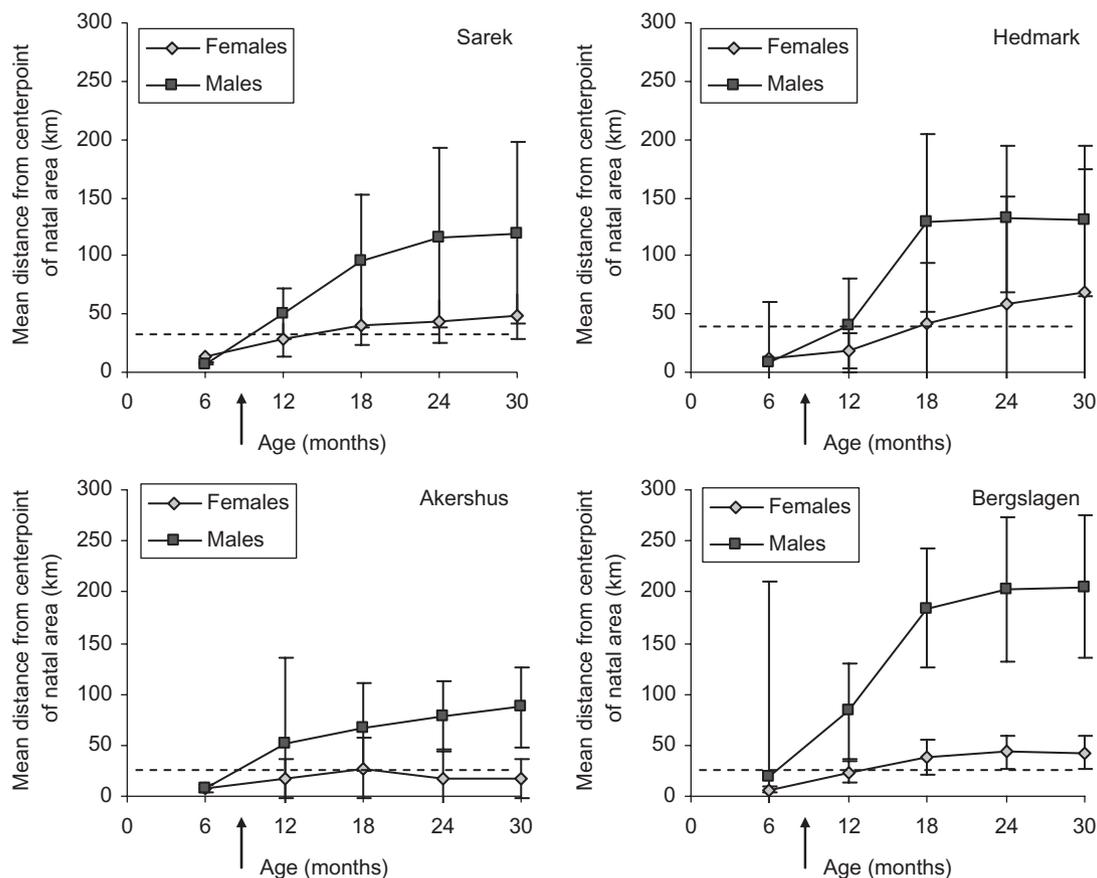


Figure 2 Temporal variation in mean dispersal distance ($\pm 95\%$ CI) by lynx that were followed to the age of 18 months or older in Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008. We included the last known position for animals that were lost before the age of 30 months in the calculation of these means (22 animals were lost between the ages of 18 and 24 months and another 16 animals were lost between the ages of 24 and 30 months). Arrows indicate the mating season by lynx and dashed horizontal lines the diameter of an average-sized home range by breeding females adjusted for each study area. We assumed 1 June to be the date of birth of kittens.

SAS Institute Inc., Cary, NC, USA) where we used maternal identity as random factor to control for repeated observations of related individuals. We performed analyses separately for age at separation from mothers, age at the start of dispersal and dispersal distances ($n = 57, 59$ and 78 animals for each analysis, respectively). We derived five *a priori* candidate models for each of these analyses (Table 1) where models ranged from none of the variables study area and sex to both of these variables – including the interaction between study area and sex. We used variation around the grand mean as a *null model* of no effect of either of the variables examined. We used Akaike's information criterion (AIC) with small-sample adjustment (AIC_C) to rank quality of models (Burnham & Anderson, 2002). Furthermore, we selected the model with the lowest AIC_C value as the best model and considered models within 2 AIC_C units to be of similar quality (Burnham & Anderson, 2002).

We examined whether dispersal rate of lynx varied among study areas and sex of lynx by using a Fisher's exact and χ^2 test, respectively (Proc Freq, SAS Institute Inc.), where we

performed the analyses on sex and study area separately ($n = 91$ animals, where 49 animals were classed by establishment of independent home ranges and 42 animals were classed by last encounter outside maternal home range). Dispersal rate was not significantly different between study areas (Fisher's exact test, $P = 0.85$) so we pooled data from all study areas before performing final analyses on sex effects. Finally, we examined whether dispersal directions were uniformly distributed for animals that were followed to the age of 18 months or older by using Rayleigh's test (Zar, 1999, $n = 78$ animals).

Results

The model including study area, sex, and the interaction between study area and sex described variation in age at separation from mothers, age at the start of dispersal and dispersal distances better than other models and accounted for 95 to >99% of the model weight (Table 1). Specifically, variation in age at separation from mothers and age at the start of dispersal were driven largely by lynx in Bergslagen separating from

Table 1 Model selection for variables affecting separation from mothers, timing of dispersal and dispersal distance by lynx in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008

Model	K	Δ_i	w_i
Separation from mothers ($n = 57$ lynx)			
Study area + sex + study area \times sex	5	0	0.95
Study area + sex	4	7.4	0.02
Study area	3	7.5	0.02
Sex	3	16.0	<0.01
No effect	2	16.7	<0.01
Timing of dispersal ($n = 59$ lynx)			
Study area + sex + study area \times sex	5	0	>0.99
Study area + sex	4	19.5	<0.01
Study area	3	21.1	<0.01
Sex	3	38.5	<0.01
No effect	2	39.4	<0.01
Dispersal distance ^a ($n = 78$ lynx)			
Study area + sex + study area \times sex	5	0	>0.99
Study area + sex	4	34.2	<0.01
Sex	3	64.4	<0.01
Study area	3	74.9	<0.01
No effect	2	101	<0.01

^aDispersal distances for lynx that were followed to the age of 18 months or older.

Included in the table are differences in AIC_c values between each model and the best fitting model (Δ_i), number of model parameters (K) – including the intercept and σ^2 , and model weights (w_i). We used variation around the grand mean as our null model (called ‘no effect’ in the table).

their mothers and starting to disperse when they were about 1 month younger than lynx in the other study areas (Table 2, Figs 3 and 4). However, variation in these parameters was also driven by a tendency for female lynx in Sweden to separate from their mothers and start to disperse when they were younger than male lynx, whereas the opposite was true in Norway (Table 2, Figs 3 and 4). Variation in dispersal distances was driven largely by male lynx dispersing farther than female lynx, but also by lynx in Akershus dispersing shorter distances than lynx in the other study areas and by male lynx in Bergslagen dispersing farther than male lynx in the other study areas (Table 3, Figs 2 and 5).

Dispersal rate was greater among male lynx than among female lynx [$\chi^2_{(1)} = 16.83$, $P < 0.001$], with 100% of the males dispersing compared with 65% of the females dispersing ($n = 39$ males and 52 females). In fact, 18 of 52 females established home ranges that overlapped or partly overlapped that of their mothers (i.e. did not disperse according to our definition) and another six females established home ranges that were within 10 km of home ranges of their mothers (home range edge to edge distances). All males, in contrast, established home ranges that were >20 km outside home ranges of their mothers. Dispersal direction by male lynx in Bergslagen was biased toward the south-southwest (Rayleigh’s test, $z = 5.66$, $P < 0.002$, dispersal direction = 203°), whereas dispersal directions were uniformly distributed for lynx in other study areas

Table 2 Mean age at separation from mothers and start of dispersal for lynx in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008

Sex and area	Mean age in months \pm 95% CI (sample size in parenthesis)	
	Separation from mothers	Start of dispersal
Females		
Sarek	9.2 \pm 0.9 (10) Range: 6–11	10.7 \pm 1.2 (11) Range: 6–12
Hedmark	9.9 \pm 0.5 (8) Range: 9–11	13.8 \pm 3.5 (4) Range: 11–16
Akershus	10 \pm na (1) Range: na	18 \pm na (1) Range: na
Bergslagen	8.3 \pm 0.9 (11) Range: 6–11	10.0 \pm 2.4 (10) Range: 7–16
Males		
Sarek	10.1 \pm 0.5 (14) Range: 9–11	11.4 \pm 0.6 (16) Range: 10–13
Hedmark	9.6 \pm 0.7 (7) Range: 9–11	11.7 \pm 1.9 (7) Range: 10–15
Akershus	9.5 \pm 6.4 (2) range: 9–10	11.0 \pm 4.3 (3) Range: 10–13
Bergslagen	8.5 \pm 1.6 (4) Range: 7–9	9.6 \pm 1.0 (7) Range: 7–10

na, not applicable.

and female lynx in Bergslagen (Rayleigh’s test, $z = 0.06$ –2.38, $P > 0.05$).

Discussion

This study showed that male lynx dispersed farther and more frequently than female lynx, and that female lynx often established home ranges that overlapped or partly overlapped that of their mothers. Dispersal by lynx in our study was thus clearly male biased, which is consistent with that of male-biased dispersal in some studies of Eurasian lynx and other *Lynx* species (Mowat & Slough, 1998; Schmidt, 1998; Janečka *et al.*, 2007) but differs from that of males and females dispersing equally far and equally frequent in other studies of these species (O’Donoghue *et al.*, 1997; Poole, 1997; Ferreras *et al.*, 2004; Zimmermann *et al.*, 2005; Campbell & Strobeck, 2006). Dispersal by Eurasian lynx and other *Lynx* species thus appears to be a dynamic process where ultimate strategies may vary with existing conditions in a manner similar to that of innate and environmental dispersal as discussed by Howard (1960). Dispersal patterns observed in our study, in turn, suggest that dispersal by lynx in Scandinavia have been shaped largely by inbreeding avoidance rather than by mate or resource competition given that male lynx dispersed considerably farther than just outside their natal ranges, which would be expected if reduction of mate or resource competition was the ultimate cause of dispersal (cf. Ronce *et al.*, 2001).

Lynx in our study dispersed two to four times farther than Eurasian lynx in previous studies (Schmidt, 1998; Sunde *et al.*, 2000; Zimmermann *et al.*, 2005), whereas they dispersed two

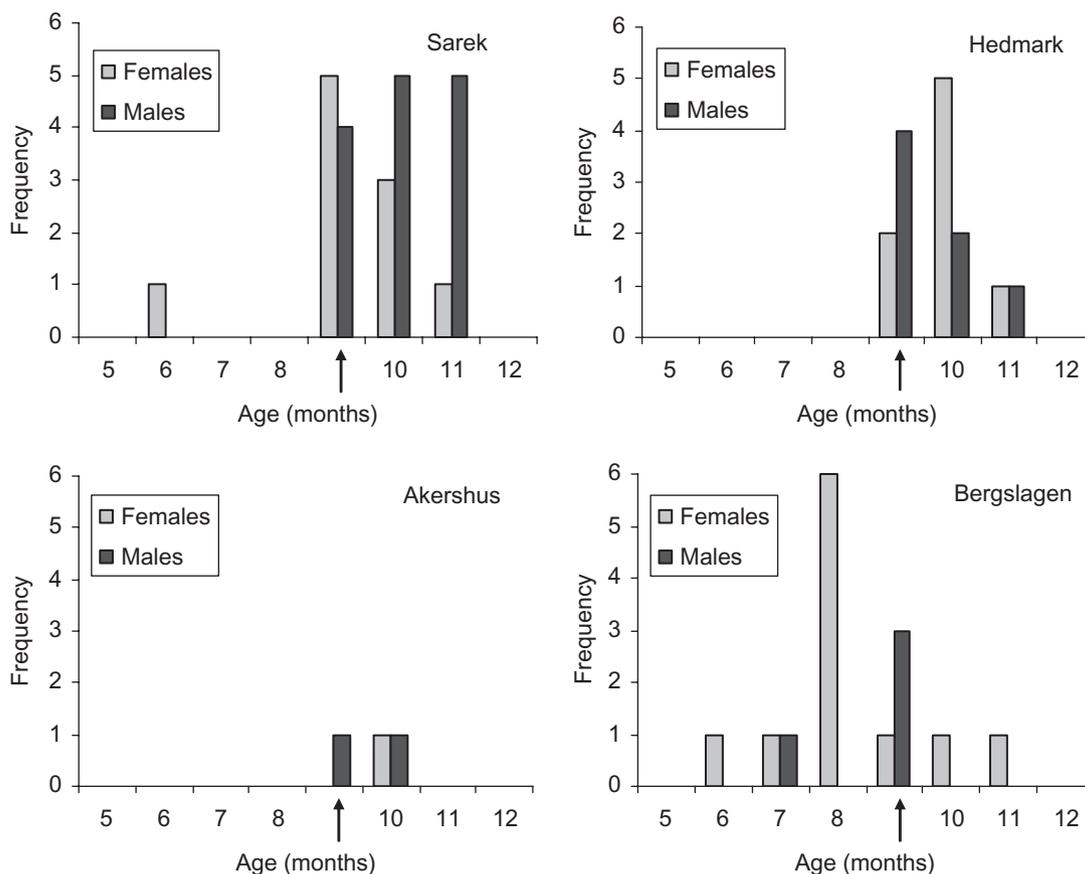


Figure 3 Age of separation from mothers by lynx in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008. Arrows indicate the mating season by lynx. We assumed 1 June to be the date of birth of kittens.

to four times shorter than Canada lynx (*Lynx canadensis*) in northern Canada (Slough & Mowat, 1996; O'Donoghue *et al.*, 1997; Poole, 1997). Similarly, dispersal distances by male lynx in our study were about four times greater than dispersal distances by Eurasian lynx in Switzerland when controlling for the number of sex-specific home ranges crossed during dispersal (cf. Zimmermann, Breitenmoser-Würsten & Breitenmoser, 2007). Dispersal distances by female lynx in our study, in contrast, were similar to those by Eurasian lynx in Switzerland when controlling for the number of sex-specific home ranges crossed during dispersal (cf. Zimmermann *et al.*, 2007). Differences in dispersal distances among study sites and species may largely be related to differences in the ecology and environments of these systems. For example, the ecology of Canada lynx is closely related to fluctuations in snowshoe hare (*Lepus canadensis*) abundance, with extreme dispersal distances (800–1100 km) observed during periods of declining or low snowshoe hare abundance (Slough & Mowat, 1996; O'Donoghue *et al.*, 1997; Poole, 1997). Dispersal distance by Eurasian lynx in previous studies, in contrast, appeared to be driven largely by availability of suitable habitats, barriers (roads and agricultural areas) and vacant territories nearby (Schmidt, 1998; Sunde *et al.*, 2000; Zimmermann *et al.*, 2005).

Dispersal distances by lynx in our study were driven largely by differences in dispersal distances between sexes (see above) but also by variation in dispersal distances among study areas where lynx in Akershus dispersed about half the distance of lynx in the other study areas. Short dispersal distances by lynx in Akershus may have resulted from high harvest rates that led to vacant territories in the vicinity of the natal area or by high population densities of prey similar to that suggested by Sunde *et al.* (2000). Moreover, variation in dispersal distances in our study was also a consequence of long-distance dispersal by male lynx in Bergslagen into southern Sweden. These long-distance movements were consistent with dispersal distances often being greater in expanding populations than they are in more stable populations (Hartman, 1995; Swenson, Sandgren & Söderberg, 1998; Andersen *et al.*, 2004) and may be related to animals searching for mates and suitable habitat in peripheral areas (Hartman, 1995; Støen *et al.*, 2006).

The fact that female lynx in our study dispersed shorter and less frequently than male lynx and that the majority of female lynx settled near their natal areas suggest that expansion into new areas (e.g. colonization of southern Sweden) is limited by female dispersal. Specifically, these patterns suggest that new areas will be characterized by a shortage of females during the

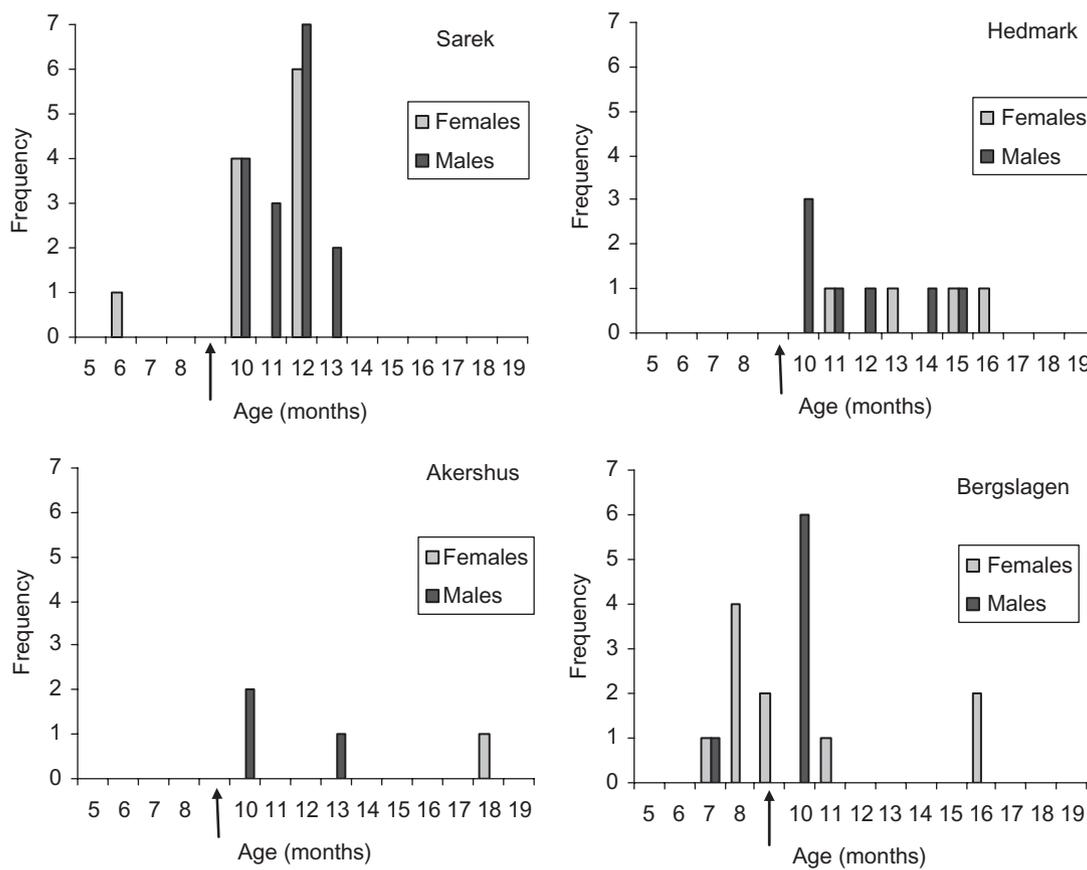


Figure 4 Age at the start of dispersal by lynx in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008. Arrows indicate the mating season by lynx. We assumed 1 June to be the date of birth of kittens.

Table 3 Mean dispersal distances for lynx that were followed to the age of 18 months or older in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008

Sex and area	Mean dispersal distance in km ± 95% CI (sample size in parenthesis)
Females	
Sarek	47 ± 19 (21) Range: 5–169
Hedmark	69 ± 107 (5) Range: 12–215
Akershus	15 ± 23 (4) Range: 3–33
Bergslagen	47 ± 19 (19) Range: 4–146
Males	
Sarek	130 ± 82 (11) Range: 32–428
Hedmark	136 ± 72 (5) Range: 74–206
Akershus	83 ± 34 (4) Range: 59–110
Bergslagen	205 ± 69 (9) Range: 70–330

establishment phase and that settlement of females in new areas will occur as a slow-moving front. However, our results also showed that some females are capable of long-distance dispersal which, in turn, will result in a more patchy distribution of females when colonizing new areas. In fact, rare long-distance dispersal by females in combination with the majority of females settling near their mothers can result in matrilineal assemblages (Støen *et al.*, 2005; Zedrosser *et al.*, 2007) that can have strong impact on the genetic and social structure of populations for many generations (Ibrahim, Nichols & Hewitt, 1996). In fact, the genetic structure of the Swedish lynx population is characterized by at least three subpopulations (Hellborg *et al.*, 2002; Rueness *et al.*, 2003 – but see Pamilo 2004 for a different interpretation of the genetic composition of the Swedish population) that may, in part, be explained by founder effects and matrilineal assemblages similar to that in brown bears (*Ursus arctos*) in Scandinavia (Støen *et al.*, 2005; Zedrosser *et al.*, 2007). Similarly, the males that dispersed into southern Sweden settled in one region rather than evenly throughout southern Sweden (Fig. 1), which suggests that landscape features and habitat suitability may affect the genetic structure of the Scandinavian lynx population in a manner similar to that of Eurasian lynx and

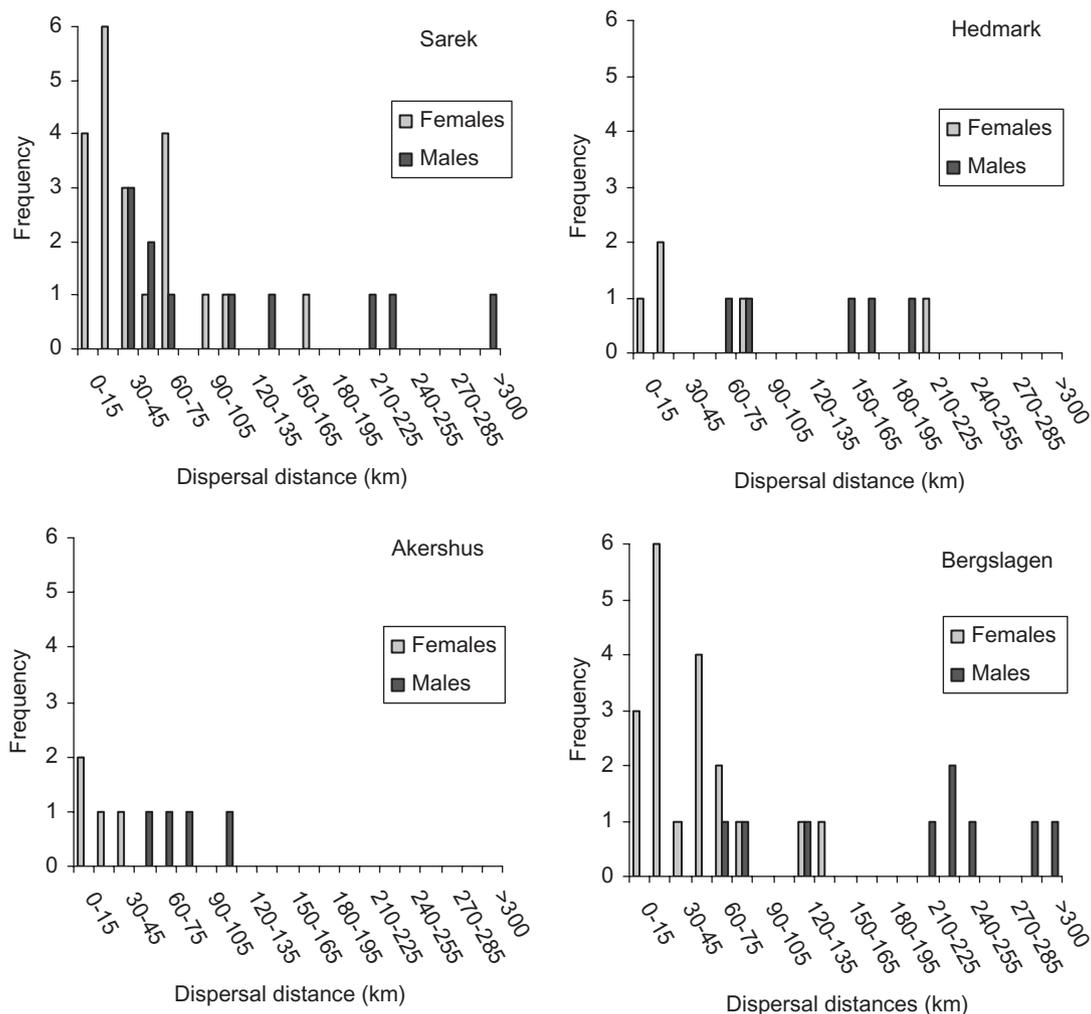


Figure 5 Dispersal distances by lynx that were followed to the age of 18 months or older in the Sarek, Hedmark, Akershus and Bergslagen study areas in Norway and Sweden in 1994–2008.

Iberian lynx (*Lynx pardinus*) in central and southern Europe (Ferrerias *et al.*, 2004; Zimmermann *et al.*, 2005).

Dispersal by male lynx in Bergslagen was biased toward the south and into areas where population densities of lynx (especially that of female lynx) were lower than in other directions (von Arx *et al.*, 2004; Andrén *et al.*, 2010). This pattern was consistent with immigration by many species of territorial mammals and birds appearing to be limited by crowding (Wolff, 1997; Lambin, Aars & Pieltney, 2001) and suggests that poor ability to establish in areas of high population densities occurs at the cost of reduced probability of finding a mate.

We detected only limited dispersal movements after the age of 18 months (Fig. 2), which was similar to that of Eurasian lynx in Switzerland (Zimmermann *et al.*, 2005) and suggest that the majority of lynx in our study settled already at the age of about 18 months. However, limited dispersal movements after the age of 18 months in our study may also have resulted

in part from loss of contact with animals before they reached their independent home ranges (e.g. collar failure or loss of contact with long-distance dispersers), although the risk of loss of contact with long-distance dispersers in Hedmark, Akershus and Bergslagen was low given that we monitored dispersal by animals throughout the lower half of the Scandinavian Peninsula.

Lynx in Bergslagen separated from their mothers and started to disperse when they were about 1 month younger than the lynx in other study areas and the majority of Eurasian lynx in previous studies (Schmidt, 1998; Sunde *et al.*, 2000; Zimmermann *et al.*, 2005), although they fell within the range of age at separation found in Schmidt (1998) and the range at age at start of dispersal by Breitenmoser *et al.* (1993). Part of the difference in the timing of separation from mothers and the start of dispersal between Bergslagen and other study areas in our study may be explained by 1–2 weeks earlier birth dates by lynx in Bergslagen (Andrén *et al.*, 2010).

Furthermore, lynx in our study remained in their natal areas for an average of 2 months from the time that they separated from their mothers until they started to disperse. Animals remaining in their natal areas for extended periods after separating from their mothers were similar to that recorded for Eurasian lynx in a Swiss study (Zimmermann *et al.*, 2005) but differed markedly from that recorded for Eurasian lynx in a Polish study where lynx started to disperse immediately after separation from their mothers (Schmidt, 1998). However, lynx in both our study (Andrén and Linnell, unpublished data) and that by Zimmermann *et al.* (2005) made exploratory movements outside their natal areas after they had separated from their mothers but prior to departing their natal areas permanently. Such excursions appear to be common in other carnivore species and may be important in assessing habitat quality and territory vacancy outside natal areas (Messier, 1985; Vangen *et al.*, 2001). Two females in our study separated from their mothers already at the age of 6 months. These females were followed to the age of 13 and 41 months and illustrate that lynx can survive on their own even when separating from their mothers at such young age. Zimmermann *et al.* (2005) reported a similar situation where a male lynx separated from its mother at the age of 8 months and survived on its own for at least 2 years after the separation.

In summary, this study showed that dispersal patterns by lynx in Scandinavia were male biased, with (1) male lynx dispersing farther and more frequently than female lynx and (2) female lynx often settling near their natal areas. However, there was considerable variation in dispersal distances within each sex, with both male and female lynx dispersing great distances. The frequency of these long-distance movements will have a large impact on gene flow and the ability by lynx to colonize new and formerly occupied areas. In the context of large carnivores in Scandinavia, lynx appear to be intermediate between brown bears and wolverines (*Gulo gulo*) on one hand and wolves (*Canis lupus*) on the other hand in terms of dispersal distance (Vangen *et al.*, 2001; Linnell *et al.*, 2005; Kojola *et al.*, 2006; Wabakken *et al.*, 2007; Zedrosser *et al.*, 2007), which will have to be taken into account when making decisions on conservation and management of large carnivores in Scandinavia.

Acknowledgements

We thank numerous people for their help to capture and radio-track animals for this study (especially S.O. Svensson who has spent numerous hours in airplanes all over southern Scandinavia searching for dispersing animals) and M. Aronsson, R. Kerbes, J. Persson, F. Zimmermann and an anonymous reviewer for comments that helped to improve the paper. This study was funded by the Swedish Environmental Protection Agency, the Norwegian Directorate for Nature Management, the Research Council of Norway, the Swedish Association for Hunting and Wildlife Management, the county environmental authorities from Hedmark, Oppland, Akershus and Østfold counties (Norway), the Regional Management Board from Region 4 (Norway), the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning

(Formas), the World Wildlife Fund (Sweden), and the Swedish University of Agricultural Sciences.

References

- Andersen, R., Herfindal, I., Linnell, J.D.C., Odden, J., Liberg, O. & Sæther, B.E. (2004). When range expansion rate is faster in marginal habitats. *Oikos* **107**, 210–214.
- Andrén, H., Linnell, J.D.C., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R. & Segerström, P. (2006). Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biol. Conserv.* **131**, 23–32.
- Andrén, H., Svensson, L., Liberg, O., Hensel, H., Hobbs, N.T. & Chapron, G. (2010). The Swedish lynx population 2009–2010 and predictions for 2011–2012. Report by the Wildlife Damage Center (in Swedish). Available at Wildlife Damage Center, Grimsö Wildlife Research Station, SE-730 91 Riddarhyttan, Sweden. ISBN 978-91-86331-21-4.
- Arnemo, J.M., Ahlqvist, P., Andersen, R., Berntsen, F.E., Ericsson, G., Odden, J., Brunberg, S., Segerström, P. & Swenson, J.E. (2006). Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. *Wildl. Biol.* **12**, 109–113.
- Arnemo, J.M., Evans, E. & Fahlman, Å. (2011). Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Unpublished report available at <http://www1.nina.no/RovviltPub/pdf/Biomedical%20Protocols%20Carnivores%202011.pdf>.
- Arnemo, J.M., Linnell, J.D.C., Wedul, S.J., Ranheim, B., Odden, J. & Andersen, R. (1999). Use of intraperitoneal radio-transmitters in lynx kittens (*Lynx lynx*): anaesthesia, surgery, and behaviour. *Wildl. Biol.* **5**, 245–250.
- von Arx, M., Breitenmoser-Würsten, C., Zimmermann, F. & Breitenmoser, U. (2004). Status and conservation of the Eurasian lynx (*Lynx lynx*) in 2001. KORA Bericht no. 19. Available at KORA, Thunstrasse 31, CH-3074, Muri, Switzerland.
- Begon, M., Harper, J.L. & Townsend, C.R. (1996). *Ecology: individuals, populations and communities*. 3rd edn. Boston: Blackwell Scientific Publications.
- Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *J. Wildl. Manage.* **59**, 228–237.
- Breitenmoser, U., Kavczenky, P., Dötterer, M., Breitenmoser-Würsten, C., Capt, S., Bernhart, F. & Liberek, M. (1993). Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. *J. Zool.* **231**, 449–464.
- Breitenmoser-Würsten, C., Vandel, J. M., Zimmermann, F. & Breitenmoser, U. (2007a). Demography of lynx *Lynx lynx* in the Jura Mountains. *Wildl. Biol.* **13**, 381–392.
- Breitenmoser-Würsten, C., Zimmermann, F., Stahl, P., Vandel, J.M., Molinari-Jobin, A., Molinari, P., Capt, S. & Breitenmoser, U. (2007b). Spatial and social stability of a

- Eurasian lynx *Lynx lynx* population: an assessment of 10 years of observation in the Jura Mountains. *Wildl. Biol.* **13**, 365–380.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edn. New York: Springer.
- Campbell, V. & Strobeck, C. (2006). Fine-scale genetic structure and dispersal in Canada lynx (*Lynx canadensis*) within Alberta, Canada. *Can. J. Zool.* **84**, 1112–1119.
- Clarke, A.L., Sæther, B.E. & Røskaft, E. (1997). Sex bias in avian dispersal: a reappraisal. *Oikos* **79**, 429–438.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001). *Dispersal*. Oxford: Oxford University Press.
- Dobson, F.S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**, 1183–1192.
- Ferreras, P., Delibes, M., Palomares, F., Fedriani, J.M., Calzada, J. & Revilla, E. (2004). Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behav. Ecol.* **15**, 31–40.
- Gandon, S. & Michalakis, Y. (2001). Multiple causes of the evolution of dispersal. In *Dispersal*: 155–167. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). New York: Oxford University Press.
- Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162.
- Hartman, G. (1995). Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. *Wildl. Biol.* **1**, 97–103.
- Hellborg, L., Walker, C.W., Rueness, E.K., Stacy, J.E., Kojola, I., Valdmann, H., Vilà, C., Zimmermann, B., Jakobsen, K.S. & Ellegren, H. (2002). Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrial DNA analysis. *Conserv. Genetics*. **3**, 97–111.
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. (2005). Prey density, environmental productivity, and home range size in the Eurasian lynx (*Lynx lynx*). *J. Zool., London* **265**, 63–71.
- Howard, W.H. (1960). Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* **63**, 152–161.
- Ibrahim, K.M., Nichols, R.A. & Hewitt, G.M. (1996). Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity* **77**, 282–291.
- Janečka, J.E., Blankenship, T.L., Hirth, D.H., Kilpatrick, C.W., Tewes, M.E. & Grassman, L.I. (2007). Evidence for male-biased dispersal in bobcats *Lynx rufus* using relatedness analysis. *Wildl. Biol.* **13**, 38–47.
- Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C. & Ronkainen, S. (2006). Dispersal in an expanding wolf population in Finland. *J. Mammal.* **87**, 281–286.
- Lambin, X., Aars, J. & Pieltney, S. (2001). Dispersal, intraspecific competition, kin competition and kin facilitation: a review of empirical evidence. In *Dispersal*: 110–122. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). New York: Oxford University Press.
- Linnell, J.D.C., Breitenmoser, U., Breitenmoser-Würsten, C., Odden, J. & von Arx, M. (2009). Recovery of Eurasian lynx in Europe: what part has reintroduction played? *Reintroduction of top-order predators*: 72–91. Hayward, M.W. & Somers, M.J. (Eds). Oxford: Wiley-Blackwell.
- Linnell, J.D.C., Brøseth, H., Odden, J. & Nilsen, E.B. (2010). Sustainably harvesting a large carnivore? Development of Eurasian lynx populations in Norway during 160 years of shifting policy. *Environ. Manage.* **45**, 1142–1154.
- Linnell, J.D.C., Brøseth, H., Solberg, E.J. & Brainerd, S. (2005). The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. *Wildl. Biol.* **11**, 383–391.
- Linnell, J.D.C., Odden, J., Andrén, H., Liberg, O., Andersen, R., Moa, P., Kvam, T., Brøseth, H., Segerström, P., Ahlqvist, P., Schmidt, K., Jedrejewski, W., Jedrejewski, W. & Okarma, H. (2007). Distance rules for minimum counts of Eurasian lynx *Lynx lynx* family groups under different ecological conditions. *Wildl. Biol.* **13**, 447–455.
- Long, E., Diefenbach, D.R., Rosenberry, C.S. & Wallingford, B.D. (2008). Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. *Behav. Ecol.* **19**, 1235–1242.
- Maehr, D.S., Land, E.D., Shindle, D.B., Bass, O.L. & Hootor, T.S. (2002). Florida panther dispersal and conservation. *Biol. Conserv.* **106**, 187–197.
- Messier, F. (1985). Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* **63**, 239–245.
- Mowat, G. & Slough, B. (1998). Some observations on the natural history and behaviour of the Canada lynx, *Lynx canadensis*. *Can. Field-Nat.* **112**, 32–36.
- Nilsen, E.B., Linnell, J.D.C., Odden, J. & Andersen, R. (2009). Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *J. Anim. Ecol.* **78**, 741–751.
- O'Donoghue, M., Boutin, S., Krebs, C.J. & Hofer, E.J. (1997). Numerical response of coyotes and lynx to the showshoe hare cycle. *Oikos* **80**, 150–162.
- Odden, J., Linnell, J.D.C. & Andersen, R. (2006). Diet of Eurasian lynx, *Lynx lynx*, in the boreal forest of southeastern Norway: the relative importance of livestock and hares at low roe deer density. *Eur. J. Wildl. Res.* **52**, 237–244.
- Pamilo, P. (2004). How cryptic is the Scandinavian lynx? *Mol. Ecol.* **13**, 3257–3259.
- Pedersen, V., Linnell, J.D.C., Andersen, R., Andrén, H., Segerström, P. & Lindén, M. (1999). Winter lynx predation on semi-domestic reindeer in northern Sweden. *Wildl. Biol.* **5**, 203–211.
- Poole, K.G. (1997). Dispersal patterns of lynx in the Northwest Territories. *J. Wildl. Manage.* **61**, 497–505.

- Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**, 295–299.
- Ronce, O., Olivieri, I., Clobert, J. & Danchin, E. (2001). Perspectives on the study of dispersal evolution. In *Dispersal*: 341–357. Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (Eds). New York: Oxford University Press.
- Rueness, E.K., Jorde, P.E., Hellborg, L., Stenseth, N.C., Ellegren, H. & Jakobsen, K.S. (2003). Cryptic population structure in a large, mobile mammalian predator: the Scandinavian lynx. *Mol. Ecol.* **12**, 2623–2633.
- Schmidt, K. (1998). Maternal behaviour and juvenile dispersal in the Eurasian lynx. *Acta Theriol.* **43**, 391–408.
- Schmidt, K., Jędrzejewski, W. & Okarma, H. (1997). Spatial organization and social relations in the Eurasian lynx population in Białowieża primeval forest, Poland. *Acta Theriol.* **42**, 289–312.
- Slough, B.G. & Mowat, G. (1996). Lynx population dynamics in an untrapped refugium. *J. Wildl. Manage.* **60**, 946–961.
- Smith, J.L.D. (1993). The role of dispersal in structuring the Chitwan tiger population. *Behaviour* **124**, 165–195.
- Støen, O.G., Bellemain, E., Sæbø, S. & Swenson, J.E. (2005). Kin-related spatial structure in brown bears *Ursus arctos*. *Behav. Ecol. Sociobiol.* **59**, 191–197.
- Støen, O.G., Zedrosser, A., Sæbø, S. & Swenson, J.E. (2006). Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia* **148**, 356–364.
- Sunde, P., Kvam, T., Moa, P., Negård, A. & Overskaug, K. (2000). Space use by Eurasian lynxes *Lynx lynx* in central Norway. *Acta Theriol.* **45**, 507–524.
- Sweanor, L.L., Logan, K.A. & Hornocker, M.G. (2000). Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conserv. Biol.* **14**, 798–808.
- Swenson, J.E., Sandgren, F. & Söderberg, A. (1998). Geographic expansion of an increasing brown bear population: evidence for presaturated dispersal. *J. Anim. Ecol.* **67**, 819–826.
- Vangen, K.M., Persson, J., Landa, A., Andersen, R. & Seggerström, P. (2001). Characteristics of dispersal in wolverines. *Can. J. Zool.* **79**, 1641–1649.
- Wabakken, P., Sand, H., Kojola, I., Zimmermann, B., Arnemo, J.M., Pedersen, C. & Liberg, O. (2007). Multi-stage, long-range natal dispersal by a Global Positioning System-collared Scandinavian wolf. *J. Wildl. Manage.* **71**, 1631–1634.
- Wolff, J.O. (1993). What is the role of adults in mammalian juvenile dispersal? *Oikos* **68**, 173–176.
- Wolff, J.O. (1997). Population regulation in mammals: an evolutionary perspective. *J. Anim. Ecol.* **66**, 1–13.
- Zar, J.H. (1999). *Biostatistical analysis*. 2nd edn. New Jersey: Prentice-Hall, Inc.
- Zedrosser, A., Støen, O.G., Sæbø, S. & Swenson, J. (2007). Should I stay or should I go? Natal dispersal in the brown bear. *Anim. Behav.* **74**, 369–376.
- Zimmermann, F., Breitenmoser-Würsten, C. & Breitenmoser, U. (2005). Natal dispersal of Eurasian lynx (*Lynx lynx*) in Switzerland. *J. Zool.* **267**, 381–395.
- Zimmermann, F., Breitenmoser-Würsten, C. & Breitenmoser, U. (2007). Importance of dispersal for the expansion of a Eurasian lynx *Lynx lynx* population in a fragmented landscape. *Oryx* **41**, 358–368.