

Characteristics of dispersal in wolverines

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Abstract: We studied patterns of dispersal and sizes of home ranges of juvenile wolverines (*Gulo gulo*). Mean dispersal age was 13 months for both male ($n = 11$) and female ($n = 9$) wolverines. Females displayed more variation in dispersal age (7–26 months) than males (7–18 months). Of the animals used in the dispersal analyses, all males and 69% of females dispersed. All sedentary females ($n = 4$) occupied their mother's territory when she died or shifted territory, and no females dispersed from a territory vacated by their mother. Competition for resources seemed to determine the female dispersal pattern, while competition for mates seemed to explain the male dispersal pattern. Dispersal distances averaged 51 km for males and 60 km for females. However, this is likely to be an underestimation. Eight cases of exploratory movements were observed, and on average, these immediately preceded dispersal movements. The size of juvenile home ranges of males (85 km²) and females (81 km²) corresponded to the home-range area of denning females during the summer period. Wolverines have the capacity to recolonize gaps in the present distribution of the species in Scandinavia. Other factors, therefore, most likely explain the large proportion of vacant wolverine habitats.

Résumé : Nous avons étudié la dispersion et la taille des domaines vitaux des juvéniles chez le Carcajou (*Gulo gulo*). L'âge moyen au moment de la dispersion a été évalué à 13 mois, aussi bien chez les mâles ($n = 11$) que chez les femelles ($n = 9$). L'âge au moment de la dispersion s'est avéré plus variable chez les femelles (7–26 mois) que chez les mâles (7–18 mois). Parmi les animaux comptés dans les analyses, tous les mâles et 69 % des femelles ont quitté leur lieu d'origine. Toutes les femelles sédentaires ($n = 4$) ont adopté le territoire de leur mère au moment où elle est morte ou au moment où elle est partie, et aucune femelle n'a quitté le territoire laissé vacant par sa mère. La compétition pour les ressources semble le facteur déterminant de la dispersion chez les femelles, alors que la dispersion chez les mâles est liée à la compétition pour des partenaires sexuels. La distance de dispersion moyenne a été estimée à 51 km pour les mâles et à 60 km pour les femelles. Cependant, ces mesures sont probablement des sous-estimations. Huit cas de déplacements exploratoires ont été observés, juste avant le moment moyen des déplacements de dispersion. La taille du domaine des juvéniles mâles (85 km²) et des juvéniles femelles (81 km²) correspond à la surface du domaine d'une femelle au terrier durant l'été. Les Carcajous sont capables de recoloniser les lacunes dans leur répartition actuelle en Scandinavie. Il faut donc penser à d'autres facteurs pour expliquer l'abondance des habitats vacants de Carcajou.

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Introduction

Following a long period of decreasing densities and distribution, the Scandinavian wolverine (*Gulo gulo* L.) population increased as a result of the enactment of protection in 1968 in Sweden and in 1973 and 1982 in southern and northern Norway, respectively. However, the population is still considered vulnerable (Landa et al. 1999) and the Swedish part of the population has decreased significantly, while it has been stable or has slightly increased in Norway during the last 5 years (Landa et al. 2001). Legal and illegal hunting is the most important cause of mortality of adult wolverines

in Troms and Sarek, respectively (unpublished data). Furthermore, the Norwegian government has increased harvest quotas during recent years with the goal of decreasing the population size, owing to conflicts with sheep and reindeer husbandry (Miljøverndepartementet 2001). The distribution of Scandinavian wolverines is still discontinuous and knowledge of dispersal movements is therefore essential to determine the ability of individuals to travel between subpopulations and to ensure that the species can recolonize parts of its former range (Landa et al. 1999). The issuing of too high harvesting quotas and illegal hunting of these subpopulations might have severe consequences because small populations could face problems caused by demographic and environmental stochasticity or genetic deterioration (Lande 1988; Caughley 1994). Moreover, dispersal is important for the longevity and composition of animal populations (Gese and Mech 1991). Dispersal movements have been described for many species of mammals (Greenwood 1980), but information on the dispersal of wolverines is limited (Weaver et al. 1996).

In most species, individuals disperse (see the definition in Howard 1960) from their natal area before, or at least by, the age of sexual maturity (Krebs and Davies 1997), but dispersal patterns vary greatly across taxa and also among individuals of the same species (Waser 1996). Dispersal is not a

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single event but a dynamic process that sometimes extends over a long period, and exploratory movements outside the natal territory often come as a prelude to dispersal (Van Ballenberghe 1983; Lidicker and Stenseth 1992; Waser 1996). The act of dispersal can be classified as voluntary or not. Voluntary dispersers leave even though their home environment is not physically or socially restricted. Involuntary dispersers leave because resources are inadequate for survival, or they are forced to leave by conspecifics or members of another species (Lidicker and Stenseth 1992).

Various hypotheses, including inbreeding avoidance, mate competition, and resource competition, have recently been put forward to explain the ultimate causes of dispersal and sex-biased dispersal in mammals (Greenwood 1980; Dobson 1982; Dobson and Jones 1985; Waser 1985; Pusey 1987; Sandell 1989; Wolff 1993).

Dispersal can be a way of achieving outcrossing (Dobson 1982; Pusey 1987; Waser 1996). In polygynous species, females probably suffer higher costs from inbreeding depression than males, owing to their greater investment in offspring and more limited breeding potential (Pusey 1987). Female dispersal should therefore be predominant if inbreeding avoidance determines dispersal. However, inbreeding depression as a selective force for the evolution of dispersal as an inbreeding-avoidance mechanism is disputable, and other social mechanisms, such as the ability to discriminate between kin and non-kin, can be more important in avoiding inbreeding (Pusey and Wolf 1996).

Males have the potential to increase individual reproductive output by mating with several partners. Therefore, according to the mate-competition hypothesis, males should disperse when they reach sexual maturity because they are often unlikely to mate in their natal area (Dobson 1982). Sex bias in dispersal rate could therefore be a consequence of the type of mating system. Polygamy should favour philopatry of the limiting sex and dispersal of the other (Greenwood 1980). In most mammals, females are the limiting sex and will benefit more than males from familiarity with food resources and denning sites (Pusey 1987). Males benefit by moving to areas where there are larger numbers of potential mates (Greenwood 1980; Pusey 1987).

Competition for resources (e.g., food and denning sites) with resident conspecifics is an extrinsic factor that can lead to involuntary dispersal (Lidicker and Stenseth 1992). The competitively subordinate age and sex group of a population, or the sex group competing most for resources, should be the one to disperse (Dobson 1982; Sandell 1989). Intersexual competition for a limiting resource and male dominance over females can therefore explain female-biased dispersal (Gauthreaux 1978).

The concept of home range is important for any study of dispersal. For the idea of dispersal to make sense, we must assume that organisms are not randomly distributed but have a spatial domain with which they are familiar (Lidicker and Stenseth 1992). Home-range sizes of wolverines are relatively well studied, although not in juveniles. The basic social system of wolverines has been described as intrasexual territoriality, which means that only home ranges of opposite sexes overlap (Powell 1979; Magoun 1985; Copeland 1996). Males hold large territories that encompass those of several females. In such a spatial strategy the spacing of females is

determined by the abundance and dispersion of food, whereas the distribution of males is probably determined by the distribution of females, at least in the breeding season (Macdonald 1983; Magoun 1985; Sandell 1989).

The results of earlier wolverine studies (see review in Banci 1994) and observations from other predator species (Waser 1996) imply that males are generally more likely to disperse than females. Magoun (1985) proposed that female wolverines typically establish residency next to, or within, the natal home range. These observations are in concordance with theoretical predictions that polygamous species should exhibit male-biased dispersal if females are the limiting sex (Greenwood 1980). Magoun (1985) hypothesized that young will disperse as early as January and as late as May (age 10–14 months), just before they reach sexual maturity, and Banci (1994) suggested that the dispersal distances of females would be shorter than those of males.

This paper is the first long-term study of wolverine dispersal to be published. Our purpose was to test predictions regarding age at natal dispersal, to determine the dispersal rate, and to learn whether or not a sex bias exists in these processes; we also look into the ultimate causes of dispersal in wolverines and explore the distances moved by dispersers and those making exploratory movements. Furthermore, we describe the home-range areas used by juveniles before they separate from their mother. Based on earlier studies and theoretical predictions, we expect (i) that male dispersal will be predominant and (ii) that the mean dispersal age will be prior to, or at, sexual maturity. (iii) We also expect that males will disperse farther than females. Finally, we suggest possible causes of dispersal in wolverines.

Material and methods

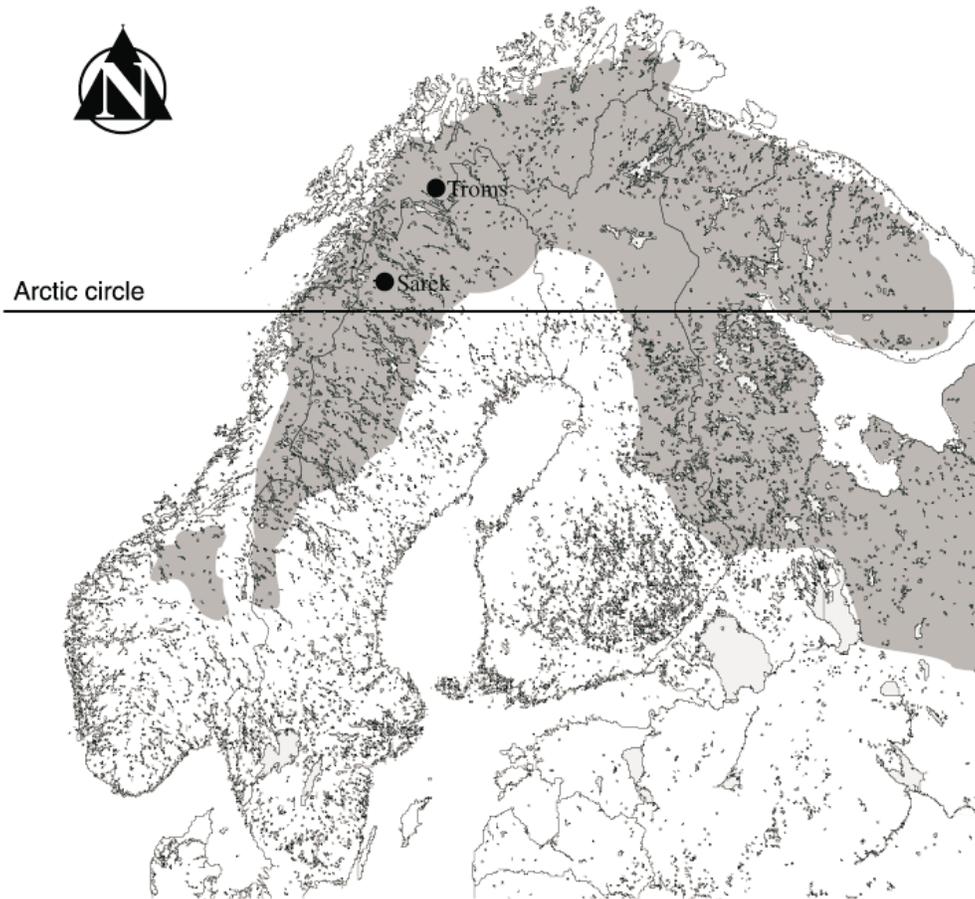
Study areas

The study was carried out in the southeastern part of the county of Troms in northern Norway (Dividalen; 68°50'N, 19°35'E) and in and around Sarek National Park in the county of Norrbotten, Sweden (Kvikkjokk; 67°00'N, 17°40'E) (Fig. 1). The climate in both areas is continental, with cold winters (−10 to −13°C in January) and moderately warm summers (13–14°C in July). Annual precipitation is low in southeastern Troms and the eastern part of the Swedish area (500–1000 mm) but higher (around 2500 mm) in the western part of the Swedish area (Påhlson 1984; Bjärvall et al. 1990; Ryvarden 1997). The ground is usually covered with snow from October to May. In Troms the area contains plateau-topped mountains and peaks up to 1700 m asl. The valleys are dominated by downy birch (*Betula pubescens*) and Scots pine (*Pinus sylvestris*). The Sarek area is characterized by downy birch, Scots pine, and Norway spruce (*Picea abies*) and consists of deep valleys, glaciers, and high plateaus with peaks up to 2000 m asl (Grundsten 1997). Downy birch forms the tree line in both areas and reaches a maximum elevation of 600–700 m asl (Grundsten 1997; Ryvarden 1997). During 1995–1997, the minimum population size of wolverines (1 year old and older) in Troms and Norrbotten was estimated to be 64 ± 17 (mean \pm SD) and 271 ± 57 , respectively (Landa et al. 2001).

Capture and instrumentation

In total, 61 juveniles were captured and equipped with transmitters at maternal dens or rendezvous sites (see the definition in Magoun and Copeland 1998) from late April to June (age 2–3 months) during 1993–1998. Juveniles were located either by locating the transmitter-equipped mother or by snow-tracking nonmarked

Fig. 1. Present distribution of wolverines (*Gulo gulo*) in northern Europe. The solid circles indicate the wolverine study locations in the north, at Troms and Sarek (redrawn from Landa et al. 1999).



females. They were captured by hand and then immobilized with Xylazin and Ketamin (Sarek) or Medetomidin and Ketamin (Troms) (Arnemo et al. 1998). During the first years (1993–1996) juveniles were initially equipped with a transmitter attached to the fur (Telonics® Mod 055, Mesa, Arizona, U.S.A., 31–34 g; $n = 19$) and then later in the summer relocated and equipped with a collar-mounted radio transmitter (Telonics® Mod 315, 150–200 g). After 1996, juveniles were equipped with an intraperitoneally implanted transmitter (Telonics® Imp/210/L, Imp/300/L, or Imp/400/L, 30–90 g; $n = 42$) from the outset. Animals handled in the study were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1993).

Radio-tracking and home-range analyses

The wolverines were radio-tracked from the ground or from the air approximately once every second week, and a standard triangulation technique (Mech 1983) and Global Positioning System (GPS) were used to determine their position. The computer program RANGES V (R.E. Kenward and K.H. Hodder, Institute of Terrestrial Ecology, Wareham, U.K.) was used to analyse home-range data. We used the minimum convex polygon (MCP; Mohr 1947) and kernel method for home-range analyses. The MCP is probably the most commonly used method of calculating home-range size and is advantageous because the results of different studies can be compared. However, the kernel method (Worton 1989) not only gives the circumference of the animal's range, but calculates the home range on the basis of the intensity of use within the range (Worton 1987; Harris et al. 1990). A smoothing factor of 0.75 was chosen.

The outer convex polygon method (100% MCP) is unaffected by

autocorrelation, so here all the available fixes were used. Because the other methods are affected by autocorrelation (Worton 1987; Harris et al. 1990), only independent fixes were used for them, since a positive autocorrelation will result in underestimation of the size of a home range (Swihart and Slade 1985). Twenty-four hours was determined to be an adequate interval to define independence between locations based on the maximum daily movements of wolverines (Haglund 1966; Magoun 1985). A vast majority of the locations used in the analyses of juveniles were obtained in June–September, when the use of rendezvous sites had stopped, therefore the use of rendezvous sites should not affect independence of locations. The home-range size was only calculated for the summer period (May–September) for juveniles. This period was chosen because the juveniles left the den in May and the first individuals initiated dispersal in October, at 7 months of age. In late autumn the juveniles' activity radii increased and exploratory movements and dispersal became common (see Results). Home-range sizes were calculated on the basis of relatively small sample sizes because of the limited period chosen. However, all datasets with fewer than 10 fixes were excluded from the analyses. Not all juveniles were captured at the same time, but this should have little effect on the calculated home-range sizes, considering that very few fixes were obtained in May.

Wolverines are born in late February or early March (Rausch and Pearson 1972; Myrberget and Sørungård 1979) and reach sexual maturity at 15–24 months of age (Rausch and Pearson 1972; Banci and Harestad 1988). The term juvenile is applied to all animals up to the age of 1 year (date of birth is set to 1 March). The term subadult implies an animal between 1 and 2 years, and adults are animals older than 2 years.

Dispersal

Fixed criteria are needed to segregate dispersal movements from other kinds of movements (White and Garrott 1990). The only way to positively identify dispersing individuals is to record when the movements of a specific individual no longer encompass its previously determined home range (McShea and Madison 1992).

To investigate when the wolverines dispersed from their natal area, the distance between all the independent tracking points for the individuals and the activity centre (kernel fix) of their respective mothers' home ranges (95% kernel, May–February) was calculated. These distances were calculated as monthly mean values for all male and female juveniles and subadults. In those cases where more than one individual per litter was marked, all individuals were used in the analyses if enough data were obtained. The fact that some individuals were from the same litter did not seem to influence monthly mean values, since in most cases the juveniles were radio-tracked separately after July. Previous studies have implied that there is significant variation in resident females' activity radii throughout the year. For resident females there is a late-autumn increase in activity radii (Landa et al. 1998a). Therefore, the natal area was defined as the denning females' home ranges during the whole year. But because the onset of a new denning period may influence the activity centre, March and April were omitted when the activity centre for denning females was calculated. Individuals were considered to have dispersed when they were located more than 2 home-range radii (which varied between 9 and 24 km) outside their mother's activity centre and did not return. Individuals that returned within the limit of 2 home-range radii of their mother's activity centre were considered to have made exploratory movements. Individuals that moved outside their natal area and were lost were considered to be dispersing individuals. Two home-range radii was chosen as a threshold for dispersal because individuals were then assumed to be outside their mother's home range irrespective of the location of the activity centre (assuming a circular home range).

Data analyses

Data were analysed using the computer programs SPSS/Win v. 7.0 (SPSS Inc., Chicago, Illinois, U.S.A.), Microsoft® Excel 97, and GPOWER version 2.0 (Faul and Erdfelder 1992). Power analyses were used to find the probability of a false null hypothesis being rejected (White and Garrott 1990; Thomas and Juanes 1996), and we determined the effect size detectable with a power of 0.8 with our sample sizes ("reverse power analysis"). All home-range statistics were performed on 95% kernel areas.

Results of statistical tests were considered significant at $P < 0.05$, and the asymptotic significance value was used in all Mann–Whitney U tests (Mundry and Fischer 1998). All tests are two-tailed unless otherwise mentioned.

Results

In total, 61 juveniles were captured and equipped with transmitters during 1993–1998. Thirteen percent ($n = 8$) lost their transmitter after less than 1 month, 5% ($n = 3$) were lost from unknown causes the first 3 months (possibly illegal hunting or transmitter failure), 20% ($n = 12$) died during the summer period, and 7% ($n = 4$) of the juveniles had no available datasets at the time of the analyses. These cases were not included in the analyses. In total, 56% ($n = 34$) of the juveniles were used in the home-range analyses or the dispersal analyses.

Age, rate, and distance of dispersal

Of the 34 juveniles, 10 were excluded from the dispersal analyses because they were lost or died within their natal area prior to making any dispersal movement.

The age at dispersal varied between 7 and 18 months among dispersing males and between 7 and 26 months among dispersing females (Figs. 2 and 3). The mean dispersal age, independent of sex, was 13 ± 3 months (mean \pm SD) in Sarek and 12 ± 7 months in Troms. However, since this difference was not significant (Mann–Whitney U test, $Z = -1.751$, $n = 6$ for Troms and $n = 14$ for Sarek, $P = 0.08$), the data were pooled when testing for differences between the sexes.

The average age of dispersal was 13 ± 3 months for males and 13 ± 6 months for females, and there was no significant sex difference (Mann–Whitney U test, $Z = -0.691$, $n = 11$ males and $n = 9$ females, $P = 0.49$; Figs. 2 and 3). Median values were 11 and 10 months for males and females, respectively. However, owing to a relatively large standard deviation in the age of dispersal, this test showed a small power at $\alpha = 0.05$, given the observed effect size. With our sample size, the difference in the age of dispersal between males and females would have to be approximately 8 months to obtain a power of 0.80 with our test. This corresponds to a "detectable" effect size of 1.33.

Of the animals used in the dispersal analyses ($n = 24$), 83% dispersed and there was a male bias in the dispersal rate. All of the males ($n = 11$) dispersed and 69% of the 13 females dispersed. However, this was not significantly different (Fisher's exact test, $P = 0.10$). Of the four females in our study that did not disperse, two occupied their mother's territory when she died and two took over the vacant territory when the mother shifted territory (Table 1). No females dispersed from a territory vacated by their mother.

The average dispersal distance from the mothers' activity centres was 51 ± 30 km (mean \pm SD) (range = 11–101 km; $n = 11$) for males and 60 ± 48 km (range = 15–178 km; $n = 9$) for females (Figs. 2 and 3). There was no significant difference in dispersal distance between the sexes (Mann–Whitney U test, $Z = -0.266$, $n = 11$ males and $n = 9$ females, $P = 0.79$).

Exploratory movements

Exploratory movements were observed in eight cases, and 25% of the individuals that later dispersed ($n = 20$) showed predispersal movement patterns. On average, exploratory movements (11 ± 5 months) immediately preceded dispersal. One male was already located outside his mother's home range in August at 5 months of age. One female subadult left the natal area in the second winter, at 22 months of age. She made several exploratory movements before dispersing in May at 26 months of age.

Home-range analyses

Some home-range sizes were calculated on the basis of small sample sizes, but there was no correlation between the number of fixes and the home-range size of juveniles (Spearman's rank correlation, $r_s = 0.158$, $n = 29$, $P = 0.21$, one-tailed). Home-range size was calculated for the juveniles' first summer period, prior to any known dispersal movement (May–September) (Table 2). Because no difference was found

Fig. 2. Dispersal distances (mean \pm SE) of male wolverines expressed as the number of home-range radii from their mother's activity centre. The horizontal dotted line indicates dispersal, defined as 2 home-range radii.

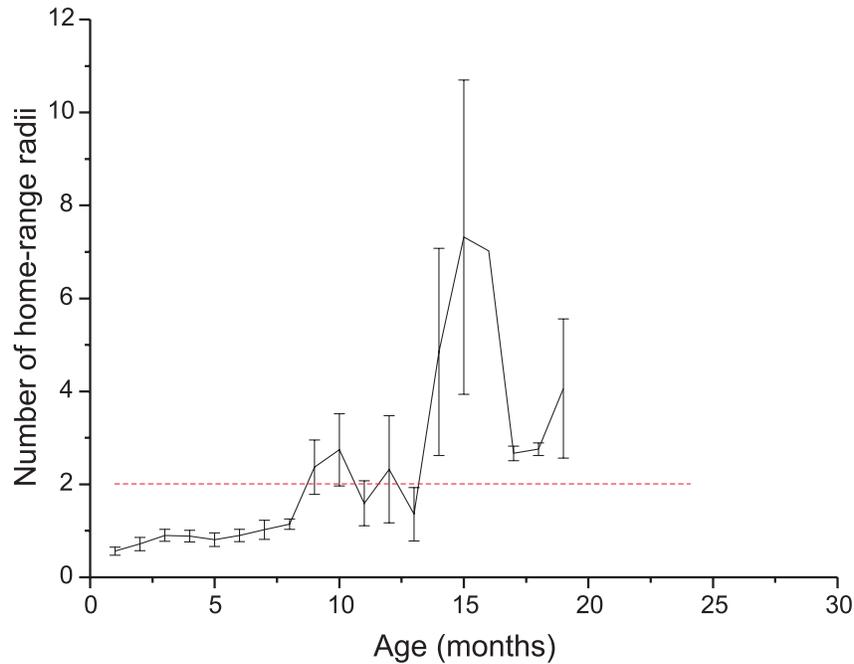
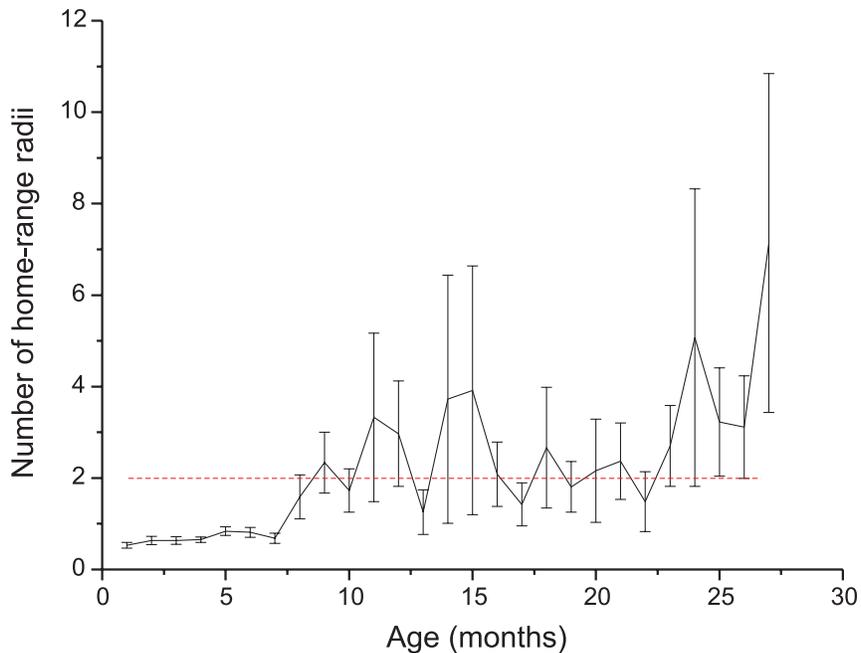


Fig. 3. Dispersal distances (mean \pm SE) of female wolverines expressed as the number of home-range radii from their mother's activity centre. The horizontal dotted line indicates dispersal, defined as 2 home-range radii.



between juveniles in Troms and Sarek independently of sex (Mann–Whitney *U* test, $Z = -0.917$, $n = 15$ for Troms and $n = 14$ for Sarek, $P = 0.36$), the two datasets were pooled.

In this period, the home ranges of male juveniles varied between 30 and 186 km² (mean \pm SD = 85 \pm 47 km², 95% kernel, $n = 14$; Table 2) and those of female juveniles between 34 and 158 km² (81 \pm 37 km², 95% kernel, $n = 15$; Table 2).

During the study in Troms and Sarek, the summer home ranges of denning females were estimated to be 91 and

77 km², respectively (Landa and Andersen 1999; unpublished data).

Discussion

Age, rate, and possible causes of dispersal

The wolverines in our study area dispersed, on average, at 13 months of age, before reaching sexual maturity; this is similar to our predictions and comparable to what was tentatively shown by Magoun (1985). In agreement with our

Table 1. Numbers of young female wolverines (*Gulo gulo*) occupying vacant areas in connection with abandonment by, or killing of, established females.

Female ID No. ^a	Region	Age (months)		Reason for abandonment of areas for established females
		When occupying new areas (dispersing individuals)	When mother died/left the area (sedentary individuals)	
03/96	Troms	26		Hunting
11/96	Troms	9		Hunting
14/96	Troms		14	Hunting
19/97	Troms		14	Territory shifting
46/96	Sarek		14	Other mortality causes
62/97	Sarek		12	Territory shifting

^aIndicates year of radio-collaring.

Table 2. Home ranges (km²) of juvenile wolverines during the summer (May–September).

ID No. ^a	Region	No. of fixes ^b	Summer		
			100% MCP	95% MCP	95% kernel
Males					
10/96	Troms	23/22	66	45	48
18/97	Troms	31/25	79	75	88
28/98	Troms	16/16	62	55	47
29/98	Troms	16/16	82	68	63
30/98	Troms	15/14	131	122	131
31/98	Troms	17/16	148	128	173
34/95	Sarek	12/11	33	17	30
37/95	Sarek	15/9	34	—	—
49/96	Sarek	16/16	59	37	62
53/96	Sarek	10/10	39	39	53
56/96	Sarek	10/10	195	195	186
57/96	Sarek	10/10	75	75	68
58/96	Sarek	10/10	91	91	95
63/97	Sarek	15/15	70	63	79
65/97	Sarek	13/13	56	53	63
Females					
03/96	Troms	43/32	81	71	77
05/96	Troms	21/20	36	27	36
07/96	Troms	23/21	126	100	97
11/96	Troms	22/21	65	44	62
14/96	Troms	22/21	120	120	109
15/96	Troms	21/20	122	121	113
19/97	Troms	31/25	72	68	60
32/98	Troms	25/23	154	96	141
33/98	Troms	23/22	75	65	73
13/93	Sarek	26/17	76	31	42
44/96	Sarek	21/20	171	111	158
46/96	Sarek	22/19	129	53	93
55/96	Sarek	10/10	68	68	59
62/97	Sarek	10/10	54	54	34
64/97	Sarek	15/15	71	61	68

^aIndicates year of radio-collaring.

^bTwo numbers of fixes are given because all fixes were used with 100% MCP; only independent fixes were used with 95% MCP and the kernel method.

predictions and the results of earlier studies (Banci 1994), a greater proportion of males (100%) than females (69%) dispersed, but the difference was not statistically significant. However, when the sample size is small, biologically interesting conditions may be missed because statistical tests are unlikely to give statistically significant results (Thomas and Juanes 1996). Sedentary females could, of course, disperse later in life. However, the animals were followed for 3–5 years, which should have minimized this risk. We documented one case of a female of unknown age that dispersed after reproduction a minimum of 56 km from the site where she was radio-marked. Except for four females that shifted range to a neighbouring territory and one old female who was not able to defend her territory, this is the only documentation of a female that dispersed after reproduction during monitoring for approximately 113 adult female-years (unpublished data).

The retirement (because of mortality or shifting territory) of adult females from established home ranges had an effect on the dispersal behaviour of young females. Such retirement was followed by occupation by a young female in six cases, by sedentary daughters in four cases, and by dispersing females in two cases (Table 1). The timing of this “occupation” corresponded well to the availability of vacant territories. Genovesi et al. (1997) found a similar pattern in the stone marten (*Martes foinea*): a neighbour rapidly occupied the vacant territory when an adult died. In our study areas, hunting resulted in vacant female territories. However, in theory there might also be some flexibility within the intra-sexual territorial system before sexual maturity. Juveniles and subadults can be incorporated into their parents’ home range in keeping with the resource-dispersion hypothesis (Macdonald 1983). In years with good prey availability, the primary individual has excess resources and may therefore allow its offspring to remain in the natal area to exploit the resource surplus (von Schantz 1984). When prey availability declines, the juveniles must disperse. When they reach sexual maturity, the individuals may be forced out irrespective of resource availability. By sexual maturity, most individuals (83%) in this study had dispersed.

Young male wolverines are probably not able to defend territories in their natal area and the competition from adult males forces them to leave. They become “satellites,” using large areas. According to Copeland (1996), subadults were forced to disperse because of social pressure or competition

for resources. Magoun (1985) suggested that reproductive competition influences dispersal. Gardner (1985) and Banci (1987) found that the appearance of adult males seemed to influence the dispersal of immature males and their establishment of home ranges.

Legal and illegal hunting was the most important cause of mortality for both female and male adult wolverines during the study period (unpublished data). This would probably have led to vacant male territories, as well as vacant female territories, within the distribution area during the study. However, assuming there were male territory vacancies, no effect on dispersal was seen among males, of which none became sedentary. Male home ranges are about three times larger than female home ranges in our study areas (unpublished data). Consequently, if we assume a sex ratio of unity in the wolverine population (Landa et al. 1998b), there should be more nonresident adult males than females searching for a vacant territory. This might result in stronger competition for male territories than for female territories and therefore less possibility of young inexperienced males competing with adults to take over a natal territory.

The dispersal pattern could also be linked to population trends and density. Wolff (1997) suggested that dispersal should be inversely density-dependent in territorial species because territoriality at high densities can impede immigration and make it difficult for juveniles to leave their natal area. This trend was found in the red fox (*Vulpes vulpes*). The proportion of male red foxes that dispersed was inversely related to population density, probably because low density resulted in fewer interactions with conspecifics (Allen and Sargeant 1993). Künkele and von Holst (1996) suggested that dispersal of female European wild rabbits (*Oryctolagus cuniculus*) could be associated with the presence of vacant territories nearby. Dispersing females could thereby immediately attain a high status. Gese and Mech (1991) found a connection between population trends and dispersal rate in Minnesota wolves (*Canis lupus*). Both yearlings and pups dispersed at relatively higher frequencies when the population was increasing or decreasing than during a more stable phase. This was probably due to variations in the size of the prey base and the availability of vacant territories and mates (Gese and Mech 1991).

Even though the population density is high in parts of the wolverine distribution area in Scandinavia (e.g., our study areas), there are many vacant areas where competition for resources and mates is lower. A large proportion of the mountainous area in Scandinavia may therefore offer the potential for recovery of the wolverine population, as well as opportunities for successful dispersal, which might lead to a high dispersal rate.

Based on the characteristics observed in this study, competition for resources (good-quality territories) seems to explain the dispersal pattern observed in female wolverines. The dispersal pattern for young males is best explained by the mate-competition hypothesis.

Distance moved

In contrast to our prediction, no significant difference in dispersal distance was found between the sexes. However, 51 km for males and 60 km for females are likely to be underestimates, because radio contact is lost to a greater

extent with long-distance dispersers than with those that remain within the study area. Altogether, 8 of 11 males and 6 of 9 females died or were lost after dispersal, the latter probably being a result of long-distance dispersal, illegal hunting, or a combination of the two.

The median dispersal distance for most mammals is relatively short, usually much shorter than 10 home-range diameters (Shields 1982). Although our results show that wolverines can disperse for long distances, few dispersed more than 5 home-range diameters (Figs. 2 and 3). Waser (1985) proposed a model in which the animals should move to the first uncontested home range they encounter and no farther. Uncontested sites arise through death or because adults shift their territory. Agreement with this model can be taken as evidence that competition for resources and mates is the primary determinant of juvenile dispersal. The distance that dispersers move within an area where food is not in short supply is probably determined by their social status and the availability of vacancies and mates in nearby areas (Gese and Mech 1991). The population density in Scandinavia is discontinuous (Landa et al. 1998b) and therefore the variation in dispersal distances is probably high. Individual variation in dispersal behaviour, density of humans, and patchiness of the appropriate habitat may also explain variations in dispersal distance (Boyd and Pletscher 1999).

The capacity for dispersal is interesting as it indicates the ability to travel between subpopulations and thereby to contribute to the recovery of the species. Our data show dispersal distances of up to 178 km and that both sexes can disperse long distances. Copeland (1996) reported two males dispersing 168 and 199 km, and Gardner (1985) relocated a 3½-year-old male 378 km from where it was radio-collared. Dispersing individuals in northwestern Alaska may have travelled as far as 300 km (Magoun 1985). Obviously, both sexes have the capacity to establish themselves far away from their natal areas, thereby ensuring recolonization and gene flow between subpopulations. The large proportion of vacant wolverine habitats is most likely explained by factors other than low dispersal capacity. If turnover in the population is high, owing to harvest, the result could be a higher proportion of sedentary females and a lower female dispersal rate, thus reducing the rate of recolonization. There are indications that illegal hunting is less important in the core of the study areas than outside the study areas, which would influence the dispersal pattern in these areas (Landa et al. 1999).

Exploratory movements

It is too simple to regard dispersal as representing a single decision made by a juvenile to leave its natal area. A dispersing individual may be one whose foray ends in success (Waser 1996). Exploratory movements were observed in eight cases in this study. Only 25% of the dispersing individuals showed predispersal movement patterns, but this is likely to be an underestimation because individuals may have made undetected exploratory movements. The time of exploratory movements and dispersal coincides with the time of year when weather and light conditions prohibit regular and frequent radio-tracking, sometimes resulting in periods without radio-tracking. Moreover, individuals that travelled outside their natal area and died were regarded as dispersers in our

study. These movements could well have been exploratory. However, most of the exploratory movements were initiated close to the average time of dispersal, indicating that exploratory movements are just failed dispersals. Furthermore, it may be that conditions are favourable for true dispersal in our study areas, resulting in few exploratory movements. Messier (1985) observed that yearling wolves initiated, on average, three extraterritorial forays per year. He interpreted these as predispersal forays (failed dispersal), with low prey abundance and age as predominant factors influencing these movements. Thus, such movements may be made in order to survive through a temporary failure of resources. They could also be a way of assessing territory vacancy (Messier 1985). Van Ballenberghe (1983) also reported that dispersing wolves showed a common pattern of one or more extraterritorial trips.

Home-range analyses

Home ranges of adult male wolverines are typically larger than those of adult females (Banci 1994; Landa et al. 1998a), but because differences in home-range size between the sexes are connected with reproduction and mating systems (Sandell 1989), no difference is expected before sexual maturity. We predicted that juveniles would use the same area as their mothers during the summer months, but we found no evidence for that in earlier studies. In agreement with our prediction, the summer home range area of juveniles is comparable to that of denning females during the same time period in this study. This is also in concordance with our results on age of dispersal.

Summer home ranges in this study were larger than those previously reported from Alaska and Snøhetta in south-central Norway. However, the sample size was small in both cases. In Alaska, three juvenile males had an average summer home range of 49 km² (May–August, 100% MCP) (Magoun 1985). At Snøhetta, two juvenile males also had an average summer home range of 49 km² (April–September, 95% kernel) (Landa et al. 1998a).

Among carnivores, there is extensive intraspecific variation in home-range size. This could be affected by the dispersion of food or variation in food availability (Gittleman and Harvey 1982; Macdonald 1983). Resource dispersion may therefore set the limits of territory size in a carnivore society (Macdonald 1983).

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References

Allen, S.H., and Sargeant, A.B. 1993. Dispersal patterns of red foxes relative to population density. *J. Wildl. Manag.* **57**: 526–533.

- Arnemo, J.M., Dypsund, P., Berntsen, F., Schulze, J., Wedul, S.J., Ranheim, B., and Lundstein, L. 1998. Bruk av implanterbare radiosendere på store rovdyr. [Use of intraperitoneal radio-transmitters in large carnivores.] [In Norwegian with English summary.] *Nor. Vet. Tidss.* **110**: 799–803.
- Banci, V. 1987. Ecology and behaviour of wolverine in Yukon. M.Sc. thesis, Simon Fraser University, Burnaby, B.C.
- Banci, V. 1994. Wolverine. In *The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine in the western United States*. U.S. For. Serv. Gen. Tech. Rep. RM-254. pp. 99–123.
- Banci, V., and Harestad, A.S. 1988. Reproduction and natality of wolverine *Gulo gulo* in Yukon. *Ann. Zool. Fenn.* **25**: 265–270.
- Björvall, A., Franzén, R., Nordkvist, M., and Åhman, G. 1990. Renar og rovdjur. Rovdjurens effekter på rennæringen. Naturvårdsverket förlag, Solna, Sweden.
- Boyd, D.K., and Pletscher, D.H. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. *J. Wildl. Manag.* **63**: 1094–1108.
- Canadian Council on Animal Care. 1993. Guide to the care and use of experimental animals. Vol. 1. 2nd ed. Canadian Council on Animal Care, Ottawa, Ont.
- Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* **63**: 215–244.
- Copeland, J.P. 1996. Biology of the wolverine in central Idaho. MS thesis, University of Idaho, Moscow.
- Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.* **30**: 1183–1192.
- Dobson, F.S., and Jones, W.T. 1985. Notes and comments. Multiple causes of dispersal. *Am. Nat.* **126**: 855–858.
- Faul, F., and Erdfelder, E. 1992. GPOWER: a priori, post-hoc, and compromise power analyses for MS-DOS (computer program). Department of Psychology, Bonn University, Bonn, Germany.
- Gardner, C.L. 1985. The ecology of wolverines in southcentral Alaska. MS thesis, University of Alaska, Fairbanks.
- Gauthreaux, S.A., Jr. 1978. The ecological significance of behavioural dominance. In *Perspectives in ethology*. Vol. 3. Edited by P.P.G. Bateson and P.H. Klopfer. Plenum Press, New York. pp. 17–54.
- Genovesi, P., Sinibaldi, I., and Boitani, L. 1997. Spacing patterns and territoriality of the stone marten. *Can. J. Zool.* **75**: 1966–1971.
- Gese, E.M., and Mech, L.D. 1991. Dispersal of wolves *Canis lupus* in northeastern Minnesota, 1969–1989. *Can. J. Zool.* **69**: 2946–2955.
- Gittleman, J.L., and Harvey, P.H. 1982. Carnivore home range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* **10**: 57–63.
- Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Grundsten, C. 1997. The Laponian area: a Swedish world heritage site. Swedish Environmental Protection Agency, Fälth's Tryckeri AB, Sweden.
- Haglund, B. 1966. De stora rovdjurens vintervanor. [Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow.] [In Swedish with English summary.] *Viltrevy*, **4**: 81–309.
- Harris, S., Cresswell, W.J., Forde, P.G., Trehwella, W.J., Woollard, T., and Wray, S. 1990. Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mammal Rev.* **20**: 97–123.
- Howard, W.E. 1960. Innate and environmental dispersal of individual vertebrates. *Am. Midl. Nat.* **63**: 152–161.
- Krebs, J.R., and Davies, N.B. 1997. Behavioural ecology: an evolutionary approach. 4th ed. University Press, Cambridge.

- Künkele, J., and von Holst, D. 1996. Natal dispersal in the European wild rabbit. *Anim. Behav.* **51**: 1047–1059.
- Landa, A., and Andersen, R. 1999. Jervens økologi, konflikter og tiltak. Sluttrapport til Norges forskningsråd, Norwegian Institute for Nature Research, Trondheim.
- Landa, A., Strand, O., Linnell, J.D.C., and Skogland, T. 1998a. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Can. J. Zool.* **76**: 448–457.
- Landa, A., Tufto, J., Franzén, R., Bø, T., Lindén, M., and Swenson, J.E. 1998b. Active wolverine *Gulo gulo* dens as a minimum population estimator in Scandinavia. *Wildl. Biol.* **4**: 159–168.
- Landa, A., Lindén, M., and Kojola, I. 1999. Final draft plan for the conservation of wolverines (*Gulo gulo*) in Europe. The Council of Europe T-PVS (98) 27 (revised), Strasbourg.
- Landa, A., Tufto, J., Andersen, R., and Persson, J. 2001. Aktive ynglehi hos jerv som bestandsestimator basert på nye data om alder for første yngling. Norwegian Institute for Nature Research, Trondheim.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science (Washington, D.C.)*, **241**: 1455–1459.
- Lidicker, W.Z., Jr., and Stenseth, N.C. 1992. To disperse or not to disperse: who does it and why? *In Animal dispersal: small mammals as a model. Edited by N.C. Stenseth and W.Z. Lidicker, Jr. Chapman and Hall, London.* pp. 21–36.
- Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature (Lond.)*, **301**: 379–384.
- Magoun, A.J. 1985. Population characteristics, ecology and management of wolverines in northwestern Alaska. Ph.D. thesis, University of Alaska, Fairbanks.
- Magoun, A.J., and Copeland, J.P. 1998. Characteristics of wolverine reproductive den sites. *J. Wildl. Manag.* **62**: 1313–1320.
- McShea, W.J., and Madison, D.M. 1992. Alternative approaches to the study of small mammal dispersal: insights from radiotelemetry. *In Animal dispersal: small mammals as a model. Edited by N.C. Stenseth and W.Z. Lidicker, Jr. Chapman and Hall, London.* pp. 319–332.
- Mech, L.D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis.
- Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* **63**: 239–245.
- Miljøverndepartementet. 2001. Regjeringens miljøvernpolitikk og rikets miljøtilstand. Stortingsmelding No. 24 (2000–2001).
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**: 223–249.
- Mundry, R., and Fischer, J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect *P* values: examples from Animal Behaviour. *Anim. Behav.* **56**: 256–259.
- Myrberget, S., and Sørungård, R. 1979. Fødselstidspunkt og kullstørrelse hos jerv. [Time of birth and litter size in wolverines.] [In Norwegian with English summary.] *Fauna*, **32**: 9–13.
- Powell, R.A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. *Z. Tierpsychol.* **50**: 153–165.
- Pusey, A., and Wolf, M. 1996. Inbreeding avoidance in animals. *Trends Ecol. Evol.* **11**: 201–206.
- Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**: 295–299.
- Påhlsson, L. 1984. Naturgeografisk regionindelning av Norden. Nordiska ministerrådet, Stockholm.
- Rausch, R.A., and Pearson, A.M. 1972. Notes on the wolverine in Alaska and the Yukon territory. *J. Wildl. Manag.* **36**: 249–268.
- Ryvarden, L. 1997. Norges nasjonalparker. 3. utgave. Universitetsforlaget, Oslo.
- Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. *In Carnivore behaviour, ecology, and evolution. Edited by J.L. Gittleman. Cornell University Press, Ithaca, N.Y.* pp. 164–182.
- Shields, W.M. 1982. Philopatry, inbreeding and the evolution of sex. State University of New York Press, Albany.
- Swihart, R.K., and Slade, N.A. 1985. Testing for independence of observations in animal movements. *Ecology*, **66**: 1176–1184.
- Thomas, L., and Juanes, F. 1996. The importance of statistical power analysis: an example from Animal Behaviour. *Anim. Behav.* **52**: 856–859.
- Van Ballenberghe, V. 1983. Extraterritorial movements and dispersal of wolves in southcentral Alaska. *J. Mammal.* **64**: 168–171.
- von Schantz, T. 1984. Spacing strategies, kin selection, and population regulation in altricial vertebrates. *Oikos*, **42**: 48–58.
- Waser, P.M. 1985. Does competition drive dispersal? *Ecology*, **66**: 1170–1175.
- Waser, P.M. 1996. Patterns and consequences of dispersal in gregarious carnivores. *In Carnivore behaviour, ecology, and evolution. Vol. 2. Edited by J.L. Gittleman. Cornell University Press, Ithaca, N.Y.* pp. 267–295.
- Weaver, J.L., Paquet, P.C., and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conserv. Biol.* **10**: 964–976.
- White, G.C., and Garrott, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego.
- 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.
- Worton, B.J. 1987. A review of models of home range for animal movement. *Ecol. Model.* **38**: 277–298.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**: 164–168.