

Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment

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Abstract: We compared the use of space and habitat by wolverines, *Gulo gulo*, and arctic foxes, *Alopex lagopus*, on the Snøhetta plateau and surrounding mountains in south-central Norway. The arctic foxes used smaller annual home ranges than the wolverines, whose home ranges were among the largest yet reported for the species. In both species, resident males used larger home ranges than resident females. Arctic foxes used a much narrower, and higher, range of altitudes than wolverines, always above the tree line. Wolverines used lower altitudes in winter than in summer. Female wolverines showed pronounced seasonal peaks in their use of the peripheral areas of their home ranges. Both species showed an ability to cross at least some transportation corridors (road, rail, human settlements) in the area. The habitat available at Snøhetta appears suitable for arctic foxes and does not explain the failure of the population to recover during 67 years of protection. Because of predation on domestic sheep, wolverines will probably be confined to a series of core conservation areas (CCA). At present densities (0.28–0.36 wolverines per 100 km²), the CCA surrounding Snøhetta can contain from 36 to 50 wolverines.

Résumé : Nous avons comparé l'utilisation de l'espace et de l'habitat chez le Carcajou, *Gulo gulo*, et chez le Renard arctique, *Alopex lagopus*, du plateau Snøhetta et des montagnes environnantes dans le centre-sud de la Norvège. Les renards sont confinés à des domaines vitaux annuels plus restreints que les carcajous dont les domaines dans la région sont les plus grands jamais observés chez cette espèce. Chez les deux espèces, les résidents mâles ont des domaines plus étendus que les résidents femelles. Les renards fréquentent une gamme beaucoup plus étroite et plus élevée d'altitudes que les carcajous, toujours au-dessus de la ligne des arbres. Les carcajous se tiennent à des altitudes plus basses en hiver qu'en été. Les carcajous femelles utilisent les zones en périphérie de leurs domaines vitaux beaucoup plus fréquemment en certaines saisons. Les deux espèces se sont avérées capables de traverser au moins certains corridors de transport (routes, voies ferrées, agglomérations) dans la région. L'habitat disponible sur le plateau semble tout à fait adéquat pour les Renards arctiques et l'échec des efforts de protection de l'espèce pendant 67 ans reste inexpliqué. À cause de la prédation qu'ils exercent sur les moutons domestiques, les carcajous devront probablement être confinés à un réseau de zones de conservation (Core Conservation Areas, CCA). Aux densités actuelles, (0,28–0,36 carcajou par 100 km²), la zone CCA qui entoure Snøhetta peut contenir de 36 à 50 carcajous.

[Traduit par la Rédaction]

Introduction

Both arctic foxes, *Alopex lagopus*, and wolverines, *Gulo gulo*, have wide circumpolar distributions in tundra and tundra-taiga zones, respectively. Although the two species have been relatively poorly studied, neither is regarded as critically endangered throughout most of their large range, and in many areas they are harvested for their valuable fur (Ginsberg and Macdonald 1990; Banci 1994). In Norway, both species are confined to more or less discrete alpine areas (effectively habitat islands) surrounded by boreal forest. They both exist at low population levels in Norway, and are presently absent from

many alpine areas that they have occupied previously (Landa and Skogland 1995). Overharvesting for fur and to control predation on livestock and semidomestic reindeer, *Rangifer tarandus*, are the main historical reasons for the original decline of the arctic fox and wolverine, respectively. For both species the decline stems from the last decades of the 1800s and the first decades of this century (Bevanger 1992; Hersteinsson et al. 1989). Following the introduction of protection (1973 and 1982 for southern and northern Norway, respectively), wolverine populations have generally increased in density and distribution (Kvam et al. 1988; Bevanger 1992; Landa and Skogland 1995) and have been moved from vulnerable to rare in the IUCN Red List classification for Norway. In contrast, despite having been protected since 1930, arctic foxes have failed to respond to protection and are still classified as vulnerable (Haglund and Nilsson 1977; Strand et al. 1996).

Although the reasons for the failure of arctic foxes to respond to protection are debated (Hersteinsson et al. 1989), it is clear that the species is not limited by humans now, as there is no harvest or any other conflict with humans that might affect its survival in Norway. In contrast, wolverines are increasingly involved in conflicts with humans because of their predation on free-ranging domestic sheep in summer (Landa and Tømmerås 1996; Aanes et al. 1996). This has led to

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administrative limits, based on the degree of social acceptance of wolverine depredation, being imposed on their potential distribution as determined by intrinsic ecological factors and habitat availability. In 1994, three core conservation areas (CCA) were established to help maintain stable populations, one in south-central Norway and two in the north of Norway along the border with Sweden and Finland. The two northern CCAs were abolished by the Norwegian Parliament in June 1997.

When planning the management and conservation of species in fragmented landscapes, the movement patterns, home-range sizes, and dispersal abilities of the species are of critical importance for determining their population density, the carrying capacity of each fragment, and the ability of individuals to travel between subpopulations. Similarly, habitat selection by the species is critical for determining the proportion of each fragment that can be regarded as a suitable habitat. In this study, information on home-range sizes of and habitat selection by arctic foxes and wolverines was collected to determine the suitability of part of the southern Norwegian alpine ecosystem (centred on the Snøhetta and neighbouring plateaus) as habitat for these alpine carnivores. Additionally, for wolverines, we examined the relationship between the spatial scales of movement and habitat use relative to the size of the southern CCA surrounding Snøhetta and the two national parks in the same area.

Study area

The southern Norwegian CCA consists of 13 505 km² on state-owned and private land, extending over parts of four counties with separate wildlife management administrations (Fig. 1). At least three partly distinct subareas can be defined (Snøhetta (4400 km²), Rondane (4850 km²), and Reinheimen (4200 km²)), each with a wild reindeer population. These are high plateaus with peaks above 2000 m asl, separated by steep valleys dominated by mountain birch (*Betula pubescens*) woodland with Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies*) at the lowest altitudes. The valleys also contain railways, roads, summer dairy farms, permanent settlements, and clusters of recreational cabins. This separation is extreme between Reinheimen and the other two subareas (Fig. 2). Other upland plateaus adjoin the CCA on all four sides (Fig. 2) and are similarly separated by valleys containing settlements and transportation corridors. The climate is subject to a greater oceanic influence in the west, where the tree line is at about 800 m, and is more continental in the east, where the tree line is at about 1000 m. The main human activities in all subareas are hiking, cross-country skiing, reindeer hunting (autumn), and free-range sheep grazing (summer); part of the Snøhetta area is a military training area. Two National Parks, Dovrefjell (256 km²) and Rondane (580 km²), lie within the borders of the CCA. Plans exist for these to be merged to form a single park up to 6000 km² in size.

We carried out most of our studies on the Snøhetta plateau between 1990 and 1995. This subarea contains the only reproducing populations of wolverines and arctic foxes in southern Norway, as well as one of the most genetically pure populations of wild reindeer remaining in Scandinavia (Røed 1985).

Methods

Capturing and radio-collaring

In total, 25 arctic foxes were captured in baited box traps made of wire netting. Seventeen were cubs captured at their natal den in summer and 8 were adults captured in winter. All these individuals were

trapped in a system of three adjacent territories. In winter, traps were checked daily and in summer they were generally under continuous observation from a blind. The foxes were manually restrained while a radio collar was fitted. Ten wolverines were caught in baited box traps made of wood or stone, 1 was captured using padded leg-hold traps (Soft-Catch™), and 3 cubs were captured by hand in or near natal dens in spring. Traps were connected to a radio-alarm system that allowed immediate response. Wolverines were drugged with ketamine hydrochloride, alone or mixed with Domitor. Adult foxes and wolverines were equipped with a collar-mounted radio transmitter (150–250 g, Telonics, Mesa, Arizona, U.S.A., and Televilt International, Lindesberg, Sweden). Juvenile foxes and 1 juvenile wolverine were fitted with radio transmitters mounted on expanding collars (50–70 g, Televilt International) and 2 juvenile wolverines were equipped with intraperitoneally implanted transmitters (Telonics). Age and sex were determined on the basis of size, tooth development and wear, and external examination of testicles and teats.

Radio-tracking and analysis

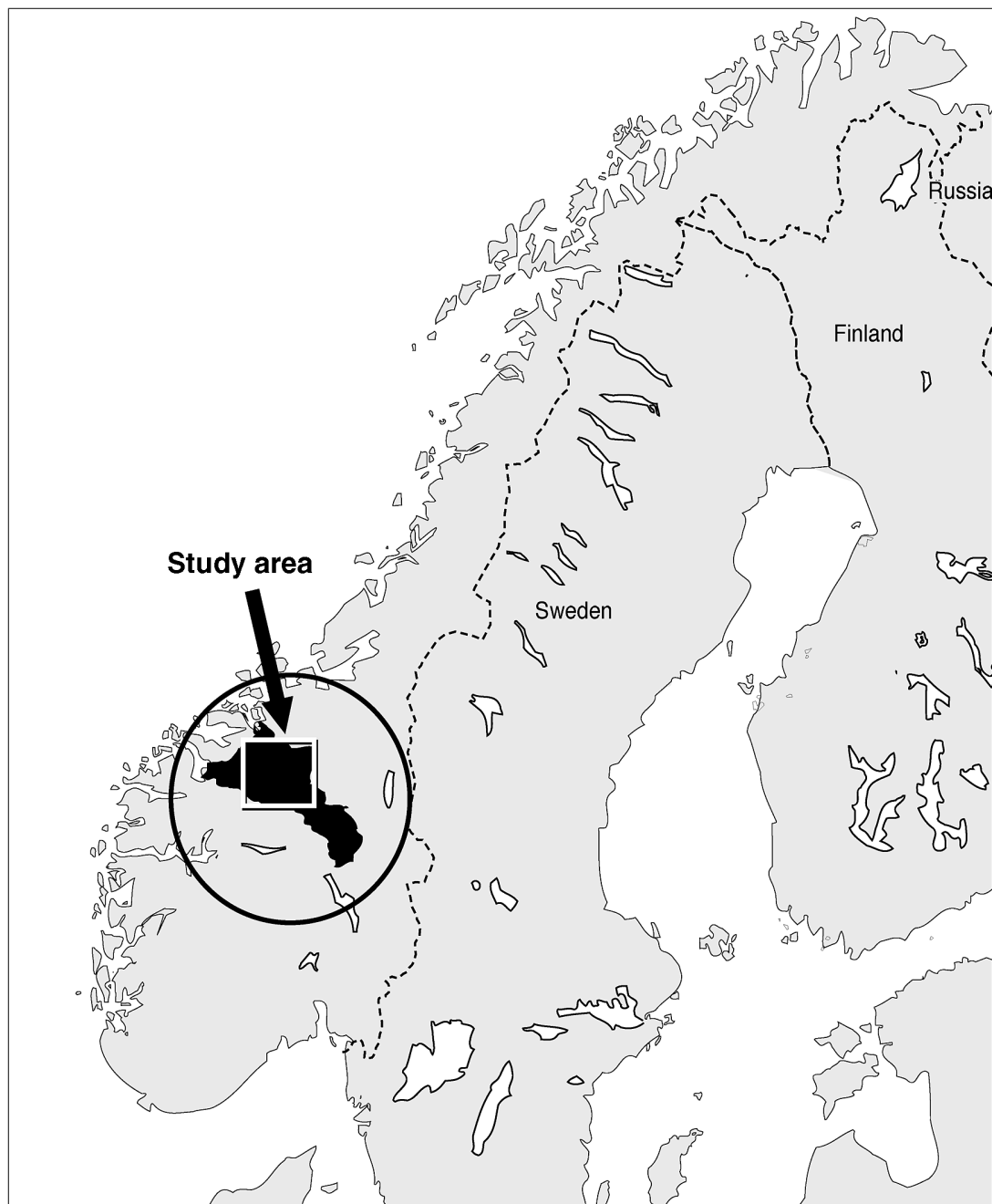
Individuals were radio-tracked both on the ground and from the air. Because of the distances covered by wolverines, ground tracking was really only practical for the arctic foxes and denning female wolverines, and usually consisted of intensively following one animal as far as possible. We aimed to monitor animals from the air at weekly intervals throughout the year. However, extreme weather conditions, especially in winter, meant that radio-tracking was often more irregular. As a result, several home ranges were calculated on the basis of small sample sizes that probably did not represent the total range used; these should therefore be regarded as minimum ranges. No statistics were performed on any home range calculated from fewer than 10 points.

Data were analysed using the computer programs RANGES v (Robert Kenward, Institute of Terrestrial Ecology, Wareham, U.K.), SPSS, and EXCEL. Home ranges were measured using the outer convex polygon method so that data would be comparable to those from other studies, and, for comparison, the 95% kernel method in order to remove strong outlier effects (Worton 1987; Harris et al. 1990). Only independent tracking points (no more than one per day) were used to calculate kernel ranges, whereas all points were used to calculate outer convex polygons. Statistics were only performed on the outer convex polygon areas. Because of the small number of individuals available for home-range analysis and the resulting low power of all statistical tests, we have avoided separating “significance” at the <0.05 level and “trends” at the <0.1 level. Instead, we simply present the exact probability value and state the direction of the result for values between 0.1 and 0.01. Readers can then make their own judgement.

Two seasons were recognised, summer (May–September) and winter (October–April). For arctic foxes, the summer season corresponds to the denning period during which cubs are born and weaned, whereas for wolverines the summer corresponds to the period after cubs have emerged from dens and to the free-range grazing season for sheep (June – mid-September). Two categories of arctic fox were recognised, residents and floaters. Residents were those pairs of individuals that remained stable within a single territory. By comparison, “floaters” did not occupy a stable home range, were unpaired, and were often found within other territories. It should be noted that in some cases an individual could be a resident during the denning period and become a floater during winter (its annual range would therefore be classified as that of a floater).

The risk of a resident animal being found outside a CCA is proportional to its relative use of the peripheral parts of its range. To investigate seasonal movement patterns of wolverines within their home ranges, we calculated an activity radius, which is the linear distance between each independent tracking point and the geographical centre of each individual’s annual home range (arithmetic mean). These radii are presented as monthly means of all radiolocations for the following three classes: adult males, resident females (included

Fig. 1. Location of the Snøhetta study area in the southern wolverine core conservation area in Norway.



one yearling occupying a stable home range), and two sibling male cubs.

Habitat use

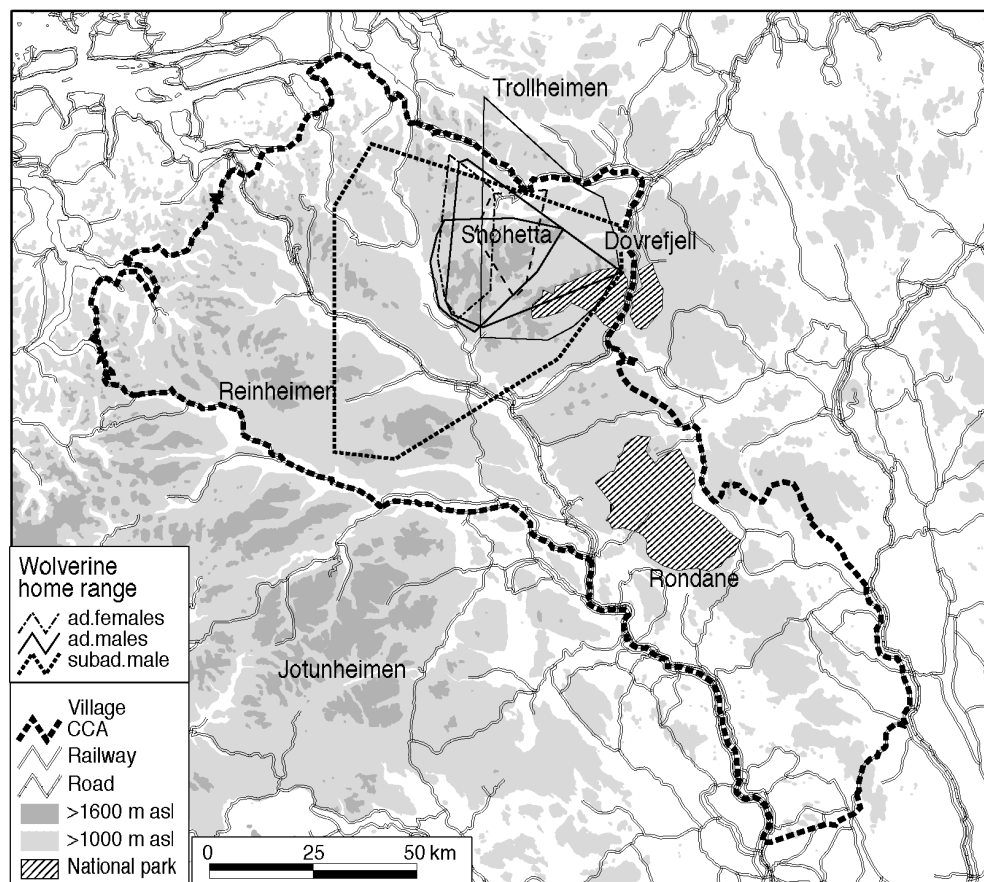
Since habitat changes with altitude, we used altitude as an indirect measure of habitat. The altitude of each independent tracking point was read manually from 1 : 50 000 maps. Altitude use by all individuals of each species in each season was combined, so for the purposes of analysis, the individual location was regarded as an independent sample (following Whitman et al. 1986). Differences between means of altitude use were compared using the Mann–Whitney *U* test (*U* statistic) and the distributions of altitude use were compared using the Kolmogorov–Smirnov two-sample test (*z* statistic) in SPSS for Win-

dows. To compare the altitudes of radio-tracking locations with the altitudes available at Snøhetta, 2571 systematic points were read from 1 : 50 000 maps of the area.

Monitoring of the arctic fox population

In many areas, including Scandinavia, arctic foxes use large dens excavated in sand and gravel for reproduction (MacPherson 1969; Østbye et al. 1978). These are often very large, obvious structures and may be used over decades or even centuries (MacPherson 1969). Dens within the three adjacent territories where the radiotelemetry study was carried out were monitored each year from 1989 to 1996 (Strand et al. 1996). In addition, an increasing number of other dens on the Snøhetta plateau were monitored each year. The dens were

Fig. 2. Annual home ranges of wolverines in the Snøhetta and surrounding plateaus relative to the size of the existing Dovrefjell and Rondane National Parks and the wolverine core conservation area (CCA).



checked for signs of arctic fox activity during the mating season (March–April) and during the period when cubs should be present (July–August). In summer, any dens that showed signs of activity were observed for at least 24 h in an attempt to count the number of cubs and adults present. A minimum number of arctic foxes present per year was determined from the number of radio-collared animals plus the known number of unmarked animals associated with radio-collared animals.

Monitoring of the wolverine population

The wolverine population at Snøhetta has been monitored in two different ways since 1979. Firstly, a system of transects was covered on the same day, using snow scooters in winter. The information obtained was used to calculate a minimum number of individuals. This method has been used to produce 9 population estimates between 1979 and 1995. Secondly, data on natal dens have been collected from the Snøhetta plateau since the reestablishment of wolverines in 1976–1979 (Landa and Tømmerås 1996; Landa et al. 1997).

Results

Arctic fox home ranges

Arctic fox home ranges were permanently centred around a central den or series of dens. Socially, the animals were organised in mated pairs, or a mated pair with additional non-reproducing adults (O. Strand, unpublished data). Resident

males used larger home ranges than resident females (Table 1), as both annual home ranges (49 ± 27 vs. 28 ± 12 km² (mean $\pm$ SE); $t = 1.98$, $df = 11$, $p = 0.07$) and denning home ranges (45 ± 42 vs. 16 ± 6 km²; $t = 2.4$, $df = 17$, $p = 0.03$). Individuals used significantly smaller home ranges during the denning period than during the whole year (paired t test, $t = 3.7$, $df = 11$, $p = 0.003$). In addition to the resident individuals, there were a number of floaters, both juveniles and sexually mature foxes of both sexes. They used home ranges that were larger than those of all resident foxes, both throughout the year (160 ± 32 km²; $t = 9.7$, $df = 15$, $p < 0.001$) and during the denning period (136 ± 68 km²; $t = 5.1$, $df = 20$, $p < 0.001$).

Wolverine home ranges

Wolverine home ranges were always much larger than arctic fox home ranges (Table 1 vs. Table 2). Adult females with newborn young used temporary dens for a few months during late winter. Otherwise, wolverines did not use any central-place structure. Adult males used larger home ranges than resident females (adult females plus one resident subadult) both during the whole year (663 ± 194 vs. 274 ± 122 km²; $t = 3.01$, $df = 5$, $p = 0.03$) and during the summer (627 ± 333 vs. 274 ± 143 km²; $t = 2.2$, $df = 9$, $p = 0.057$). Although the difference between annual and summer range use was not as pronounced as for arctic foxes, individual wolverines used smaller ranges

Table 1. Arctic fox home ranges (km²) during the whole year (annual) and during the denning (summer) period (100% minimum convex polygon (MCP) and 95% kernel methods).

ID	Year	Annual		No. of fixes	Denning period		No. of fixes
		MCP	Kernel		MCP	Kernel	
Resident males							
5	1991	—		—	27	16	45/19
5	1992	65	44	17/17	39	28	14/14
5	1994	—		—	19	9	10/10
37	1992	62	52	15/15	60	40	12/12
38	1991	60	34	37/37	34	8	29/15
38	1992	—		—	12	26	6/6
49	1995	9	3	36/36	6	3	30/30
Resident females							
27	1991	47	14	52/30	9	3	37/15
27	1992	22	11	19/14	22	10	14/14
27	1993	14	4	12/12	9	4	9/9
28	1990	—		—	21	5	88/17
28	1991	49	25	71/40	20	17	48/19
28	1992	24	11	18/18	16	9	15/15
29	1990	—		—	17	7	81/9
29	1991	21	16	18/15	12	9	11/8
29	1992	27	15	21/21	16	7	16/16
39	1990	—		—	10	7	41/5
39	1991	32	18	32/29	29	19	15/12
39	1992	—		—	14	9	15/15
54	1995	17	6	36/36	9	4	30/30
119	1993	49	31	7/7	44	28	5/5
Floaters							
5	1991	161	42	64/38	—		—
5	1993	206	154	16/16	133	62	12/12
5	1994	132	80	16/16	—		—
27	1990	—		—	65	39	128/23
38	1993	—		—	201	236	10/10
49	1993	—		—	94	74	9/9
115	1995	143	84	35/35	143	81	30/30

Note: Two numbers of fixes are given because of the different sample sizes of fixes used for the two methods; only independent fixes were used with the kernel method.

during summer than during the whole year (paired *t* test, *t* = 2.148, *df* = 6, *p* = 0.075).

Two sibling cubs implanted with transmitters during the denning period in May used an area of 61 km² during the summer. The mother was not collared, so it was not possible to determine whether she also used such a restricted home range.

Seasonal variation in wolverine activity radii

Male and female wolverines showed pronounced and different seasonal variations in their activity radii (Fig. 3). Despite the apparent peak in February–March, the monthly variation in activity radii was not significant for the adult males (Kruskal–Wallis ANOVA, $\chi^2 = 15.01$, *df* = 11, *p* = 0.182). In contrast, the variation in resident female activity radii was highly significant (Kruskal–Wallis ANOVA, $\chi^2 = 44.24$, *df* = 11, *p* < 0.001), implying that the late-winter decrease and late-autumn increase in activity radii reflect a real biological

Table 2. Wolverine home ranges (km²) during the whole year (annual) and during the summer period (April–September) (100% minimum convex polygon (MCP) and 95% kernel methods).

ID No.	Year	Annual		No. of fixes	Summer		No. of fixes
		MCP	Kernel		MCP	Kernel	
Adult males							
02	1991	502	230	26/15	420	145	22/11
02	1992	942	564	26/24	427	376	14/14
05	1994	568	382	45/35	425	333	34/25
07	1994*	—	—	—	1281	642	36/29
07	1995	641	437	53/47	563	388	45/39
11	1995	—	—	—	646	408	47/24
Subadult males							
09	1995	3617	2433	34/33	3504	2784	24/24
Cubs (male)							
12	1995	—	—	—	74	53	71/43
13	1995	—	—	—	47	44	47/35
Adult females							
01	1991†	273	198	38/32	241	142	22/20
04	1993‡	—	—	—	194	167	33/30
08	1994‡	—	—	—	513	647	43/29
08	1995‡	397	139	45/44	284	125	32/31
Subadult females							
01	1990	153	124	33/21	141	115	27/15

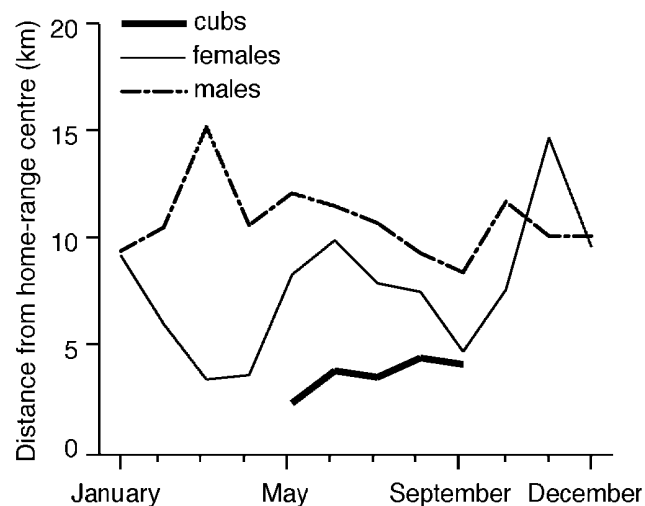
Note: Two numbers of fixes are given because of the different sample sizes of fixes used for the two methods; only independent fixes were used with the kernel method.

*Home range includes two excursions to a nearby subarea (Trollheimen) in 1994.

†Did not give birth.

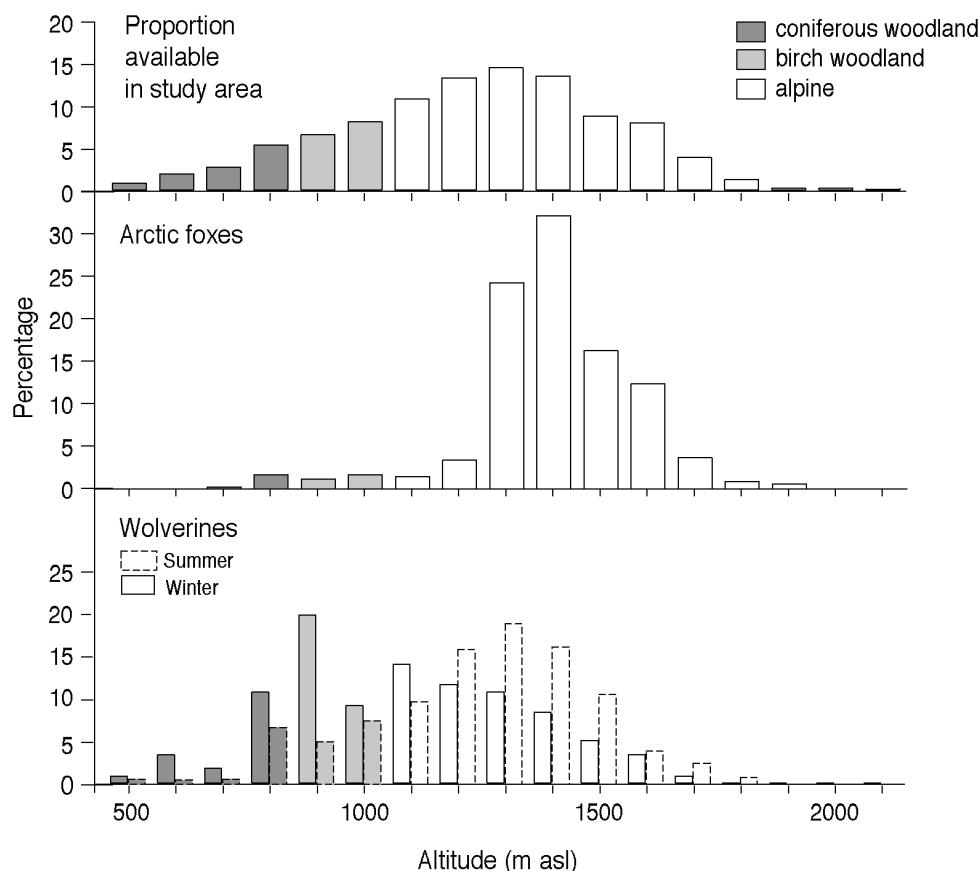
‡Had cubs, but lost them in May–June.

Fig. 3. Monthly variation in the mean activity radii (distance from the geographical centre of the annual home range) of different classes of wolverines in the Snøhetta subarea.



pattern of movement. The seasonal increase in cub activity radii was also significant (Kruskal–Wallis ANOVA, $\chi^2 = 18.08$, *df* = 4, *p* = 0.001).

Fig. 4. Altitude use by wolverines and arctic foxes at Snøhetta, based on the distribution of radio-tracking locations compared with the proportion of land available at different altitudes within the study area.



Comparative habitat selection

Arctic foxes used a distribution of altitudes that did not differ between winter (1471 ± 275 m asl) and summer (1459 ± 178 m asl; $U = 45221$, $p = 0.16$; $z = 1.14$, $p = 0.15$). The combined data show that arctic foxes made greater use of high-altitude areas than expected, given their availability (Fig. 4) ($U = 477084$, $p < 0.001$; $z = 9.93$, $p < 0.001$). Arctic foxes used significantly higher altitudes and a narrower range of altitudes than wolverines (Fig. 4) (1443 ± 252 vs. 1229 ± 269 m asl; $U = 74686$, $p < 0.001$; $z = 6.94$, $p < 0.001$). Arctic foxes were very rarely found within any forested habitats; almost all radio-locations were in the treeless alpine zones.

Wolverines showed a significant difference in altitude use in winter (1117 ± 270 m asl) and summer (1266 ± 258 m asl; $U = 14371$, $p < 0.001$; $z = 2.87$, $p < 0.001$) (Fig. 4). In winter, wolverines made greater use of low-altitude zones than expected, given their availability (1117 ± 271 vs. 1264 ± 298 m asl; $U = 106962$, $p < 0.001$; $z = 3.1$, $p < 0.001$). In summer, altitudes were used as expected from their availability (1266 ± 258 vs. 1265 ± 298 m asl; $U = 460603$, $p = 0.95$; $z = 1.2$, $p = 0.1$). Generally, a very broad range of altitudes was used, spanning the high alpine zone, the low alpine zone, the birch woodland, and even the coniferous woodland.

Comparative den site use

Twenty arctic fox dens that have been used for reproduction

during the last century are known on the Snøhetta plateau. Their mean altitude is 1285 ± 105 m asl (range 1090–1500 m) and all were located above the tree line in the alpine zone. These dens were large structures dug into sandy deposits and showed signs of repeated use over decades or even centuries. All were on flat ground or gently sloping hillsides.

Ten natal wolverine dens were found during the study (9 in Snøhetta and 1 in the neighbouring Rondane subarea). Their mean altitude was 1120 ± 125 m asl (range 960–1300 m). Two were located in the birch woodland, four on the border between birch woodland and the low alpine zone, and four in the treeless low alpine zone. All were temporary structures with vertical entrances dug into snowdrifts in steep, stony valley sides. Only 2 of the 10 dens were within 10 km of the edge of the CCA.

Estimate of arctic fox population

During 1989–1996, reproduction was only demonstrated to have occurred in the three territories where animals were radio-collared, despite monitored of a total of 17 other dens during spring and summer. From this monitoring and what was known from the numbers of radio-collared animals, we determined minimum population sizes for the three territories of between 5 and 24 (including weaned cubs) in various years during the study. At most, 2 or 3 other non-reproducing individuals were present in the other dens.

Estimate of wolverine population

In the first year of monitoring (1979), there was an estimated minimum of 7 wolverines in the Snøhetta area. This steadily increased to 14 in 1984 and varied between 11 and 16 until 1992. In 1995 there was an absolute minimum of 13 and an assumed minimum of 17 individuals (Landa and Tømmerås 1996; Landa et al. 1997). During the 10-year period up to 1995, winter density varied between 0.28 and 0.38 wolverines per 100 km² (12–17 in 4400 km² at Snøhetta).

Movement between the subareas

Young arctic foxes of both sexes travelled beyond their natal home ranges during their first 6 months of life. Six radio-collared cubs were recorded at maximum distances of between 20 and 40 km from their natal dens, and 2 more were recorded at least 10 km from their natal dens. Of these 8, only 1 left the Snøhetta plateau; he moved to the neighbouring subarea of Rondane. However, all the foxes with which contact was maintained returned home to co-occupy the natal den with their parents (O. Strand, unpublished data).

An adult male wolverine twice travelled to the neighbouring alpine area of Trollheimen (Fig. 2). Although less than 20 km long, these journeys necessitated crossing a deep valley with coniferous woodland and a main road. They were made in the mating season of 1994. An uncollared yearling female was killed by a lorry while crossing the same valley in spring 1996. A young collared male dispersed from Snøhetta to Reinheimen in 1994. This journey also required crossing a deep, wooded valley with a railway line, settlements, and a main road. During the monitoring period, he travelled widely throughout a 3617-km² area and reached a maximum distance of 25 km from the edge of the Snøhetta area (Fig. 2). Tracks in snow have also revealed regular movements between the three adjoining subareas of Snøhetta, Knutshø, and Rondane. These are separated by roads and a railway line, but by few settlements, and the alpine habitat is virtually continuous.

Discussion

Ecology of wolverines and arctic foxes at Snøhetta compared with other study sites

This is the first study to apply radiotelemetry to arctic foxes in an alpine environment, as most arctic fox studies have taken place in coastal tundra areas (Hersteinsson and Macdonald 1982; Birks and Penford 1990; Prestrud 1992). The sizes of home ranges in Snøhetta during the denning period were within the range of existing data, being comparable to the mean of 21 km² reported for breeding females in Alaska (Eberhardt et al. 1982), though smaller than values from Svalbard (40–55 km²; Prestrud 1992) and larger than those from Iceland (9–19 km²; Hersteinsson and Macdonald 1982) and Greenland (10–14 km²; Birks and Penford 1990). Few other studies have presented annual home ranges (for an exception see Hersteinsson and Macdonald (1982), whose values were only slightly larger than the denning-period home ranges in this study). Published dispersal distances are only available from ear-tag returns. Although these have shown the ability of foxes to travel from western Alaska to eastern Canada and from Siberia to Alaska (i.e., straight-line distances of over 1000 km; Eberhardt and Hanson 1978; Garrot and Eberhardt

1987), they have not given an unbiased picture of mean dispersal distances. The tendency for mature individuals to remain at the denning site during winter was also found for foxes in Alaska and Iceland (Hersteinsson and Macdonald 1982; Eberhardt et al. 1983). No comparative data are available on altitude use. However, arctic foxes are always found north of, or higher than, the tree line (Garrott and Eberhardt 1987).

The wolverine home ranges observed in Snøhetta are within the upper part of the range previously described from Alaska, the Yukon Territory, and Montana (Hornocker and Hash 1981; Magoun 1985; Whitman et al. 1986; Banci and Harestad 1990; Banci 1994) and preliminary results from a study in northern Sweden (Lindén et al. 1996). The home ranges could be large either because the population is still establishing and has not yet become saturated (e.g., Ream et al. 1985) or the area may have a low carrying capacity (Landa and Skogland 1995). As in these other studies, males had much larger home ranges than females. The seasonal switch to lower altitudes in winter was also seen in larger studies of wolverines in Alaska and Montana (Hornocker and Hash 1981; Whitman et al. 1986) and is probably due to greater availability of small prey and carrion in the low-lying areas in winter. The natal dens (snow tunnels in steep slopes) were typical of wolverines living in alpine areas (Myrberget 1968; Pulliainen 1968; Banci 1994; Lee and Niptanatiak 1996). The limited data available indicate that in the present study area, the same denning areas were used in consecutive years, implying that there are relatively few suitable denning areas (Landa et al. 1997).

The density of wolverines in Snøhetta was lower than that reported at most North American study sites (Hornocker and Hash 1981; Magoun 1985; Becker 1991; Banci 1994). Again, this is probably due to the population being of recent origin and not yet stabilised, although it could also be due to a low carrying capacity (Landa and Skogland 1995). The Snøhetta area supports a large population of wild reindeer, although it is not clear how much of this is available to wolverines as carrion in the absence of larger predators like wolves (Landa and Skogland 1995; Landa et al. 1997).

Comparative ecology of wolverines and arctic foxes

Despite differing in body size (arctic foxes 3–4 kg, wolverines 8–18 kg) the species share many food habits, feeding on rodents (*Microtus* spp., *Lemmus* spp., *Clethrionomys* spp.), hares (*Lepus timidus*), birds, and carrion (Landa et al. 1997; Myhre and Myrberget 1975; Magoun 1987; Garrott and Eberhardt 1987). They differ in that wolverines possess the ability to kill large prey, although it is felt that their predation on wild reindeer is limited. Both species show increased reproduction in years with high rodent numbers (Angerbjörn et al. 1995; Myrberget and Sørungård 1979; Landa et al. 1997). Social systems also differ between mustelids and canids, mustelids being more solitary (Powell 1979; Moehlman 1989; Sandell 1989). This study has shown that wolverines and arctic foxes use different altitudes within the Snøhetta plateau and use space at different spatial scales (cf. Tables 1 and 2). Whereas wolverines weigh about 5 times as much as arctic foxes, they used home ranges that were approximately 10–20 times larger. Wolverines therefore appear to have relatively large energy requirements (e.g., McNab 1989), which they apparently satisfy by roaming over comparatively vast home ranges (Hornocker and Hash 1981; Weaver et al. 1996).

Arctic foxes also differed from wolverines in being permanently attached to a series of dens and remaining in the same area for the whole year, whereas wolverines switched their activity from high-altitude areas in summer to lower areas in winter. The result was that wolverines used a much broader niche (alpine, subalpine, and woodland zones) than arctic foxes, which confined their activity to a narrow range of alpine habitats, probably because they are more constrained by inter-specific interactions at lower altitudes (Hersteinsson and Macdonald 1992).

Implications for conservation and management of arctic foxes

Although arctic foxes use only a narrow range of habitats, their relatively small home ranges imply that a relatively large population of arctic foxes could occupy an area that might contain only a few wolverines. Within the Snøhetta plateau, there is theoretically room for many more arctic foxes than are found there today. As a rough estimate, almost 50% (or 2200 km²) of the Snøhetta plateau lies within the range of altitudes favoured by arctic foxes (data from Fig. 4). The three study territories only covered approximately 100–150 km² in total, and many dens that have been used in the recent past are now empty. Clearly, a lack of space or dens does not explain the present low numbers of foxes in Snøhetta. Whereas juveniles have shown an ability to cross from Snøhetta to the neighbouring Rondane subarea, no individuals are yet known to have crossed the deeper valleys to the north or south. Until further data become available, it is difficult to say whether these valleys present a barrier to dispersal. Further research on arctic foxes must concentrate on identifying the reason for the failure of the population to recover during 67 years of protection despite the availability of apparently suitable habitat (Hersteinsson et al. 1989).

Implications for conservation and management of wolverines

Because the level of the conflict between wolverines and domestic sheep is so high (Landa and Tømmerås 1996; Aanes et al. 1996), there is likely to be little tolerance of wolverines outside conservation areas. Moreover, the high cost of improved husbandry methods required to reduce predation will limit the area over which they can be applied (Linnell et al. 1996; Mysterud et al. 1996). Clearly, the existing national parks in the region are far too small for wolverine conservation (Fig. 2), but their planned amalgamation will create a single park of 6000 km² that will be adequate for around 20 wolverines at existing densities. If surrounding private lands can also be successfully incorporated into the conservation area (Maehr 1990; Mills 1991), there would be room for between 36 and 50 resident wolverines within the CCA. Even our limited data show that wolverines are able to cross the deep valleys that separate several of the alpine areas within the CCA, therefore it is realistic to expect that the CCA could be managed as a single ecological unit.

The success of a conservation area as a refuge from differential management outside it depends on the likelihood of animals that are usually resident inside the area being harvested or controlled outside it (Knick 1990). Knowledge of the seasonal patterns of home-range use can help when harvest and (or) control operations are being planned, so that loss of resi-

dents which live near the border can be minimised. The present licensed wolverine harvest in Norway is restricted to the period 1 October – 15 February. The larger home ranges (and therefore activity radii) of males will place them at greater risk of crossing a border than females as they travel in search of mates. Although the midwinter increase in length of activity radii was not significant, it is likely that males do travel more during this period at the onset of the mating season (Rausch and Pearson 1972; Mead et al. 1991) and might therefore be at greater risk. For females, the opposite is true, as this is the season when they are most stable in the middle of their range following the onset of embryo development and their attachment to natal-den sites (Rausch and Pearson 1972; Banci and Harestad 1988, 1990; Lee and Niptanatiak 1996). All the known wolverine denning areas in Snøhetta are far enough from the edge of the CCA to make it unlikely that females with a natal den inside the CCA will be found outside the CCA during the denning (and late harvest) period. Although the long activity radii in late autumn – early winter do not correspond to any specific period of the reproductive cycle (Mead et al. 1991), they may be related to the search for good denning sites or winter areas with abundant food resources to allow fat deposition (Pond et al. 1994). Clearly, this is a period when females will be at greatest risk of being shot outside the CCA. Ideally, control or harvest should occur during late summer and early autumn, when animals are closest to their home-range centres. This also fits the peak timing of wolverine predation on sheep (Linnell et al. 1996) and means that control at this time is most likely to remove the offending individual.

It appears that the CCA is able to maintain a population of wolverines (36–50) as long as any future harvest avoids draining animals from it. The long-term viability of the population in this CCA will clearly depend on the level of contact between it and the larger populations to the north, and the ability of sheep farmers to adopt new husbandry practices (Linnell et al. 1996) within the CCA. North American experience indicates that wolverine populations have intrinsically low resilience and are vulnerable to disturbance (Weaver et al. 1996). Consequently, the CCA should be closely monitored so that downward trends in the population can be detected in time and appropriate action taken.

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