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In this article we describe 77 arctic fox *Alopex lagopus* dens in Vindelfjällen, northern Sweden, with regard to distribution, morphology and fox use. The density of dens in the area was 1/21 km^2 and dens were more spaced than random. The dens were situated at a mean altitude (± SD) of 915 m a.s.l. ± 74, were on average 3.5 km ± 1.88 from the nearest tree line, had a mean number of 44 den openings ± 32 and a mean area of 277 m^2 ± 237. During the 21-year study period, 31 dens were used by arctic foxes and 10 by red foxes *Vulpes vulpes*. Number of den openings, den area, altitude and distance to the nearest tree line explained 36% of arctic fox den use ($P < 0.001$) and 21% of red fox use of arctic fox dens during the study period ($P = 0.01$). Arctic foxes used dens at higher altitude ($P = 0.03$) and further away from forest than did red foxes ($P = 0.03$), and tended to breed in dens with more openings ($P = 0.08$). Arctic foxes used some breeding dens more frequently than others ($P = 0.002$). Among the breeding dens, both den use and litter size were positively related to den area (den use: $P = 0.04$; litter size: $P < 0.001$). Successful arctic fox breeding dens in Sweden thus appear to be characterised by large size and many openings, and they are situated far away from forest at relatively high altitudes.

Key words: Alopex lagopus, Fennoscandia, interspecific competition, red fox, Vulpes vulpes

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The arctic fox *Alopex lagopus* is a small canid that inhabits most arctic land areas above the tree line, including islands far away from the mainland (Preble & McAtee 1923, Lavrov 1932, Chesemore 1975, Hersteinsson 1984, Prestrud 1992a). As in most other canids, the use of dens is of significant importance during the breeding season (Sheldon 1992), and arctic foxes generally use the same den throughout a breeding season, unless disturbed (Angerbjörn, Ströman & Becker 1997). Arctic foxes breed in two types of dens, viz. dens excavated in tundra soil and dens situated in rocky areas, the latter mostly along coastlines (Lönnberg 1927, Macpherson 1969, Chesemore 1975, Anthony 1996, Prestrud 1992b). Although dens in rocky areas may be difficult to detect (Prestrud 1992c, Nielsen, Pedersen & Klintgaard 1994), dens in tundra areas are gen-

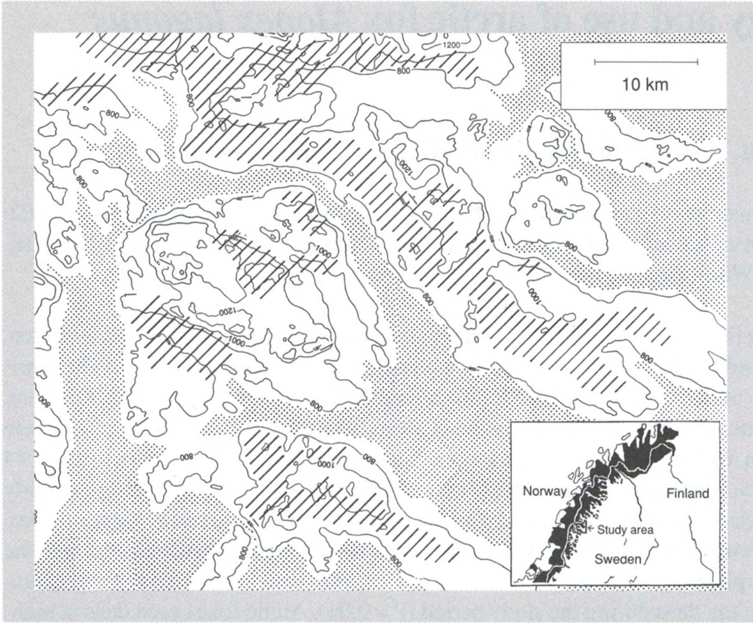

Figure 1. Location of the study area in northern Sweden. Dens are located in the hatched areas, and the grey areas indicate forests. In the inserted map, mountain tundra is shown in black.

erally large with conspicuous lush vegetation and hence easily detectable (Chesemore 1969, Macpherson 1969, Garrott, Eberhardt & Hanson 1983, Smits, Smith & Slough 1988, Smith, Smits & Slough 1992). Because of this, den surveys have been used as a reliable census tool for arctic fox populations in tundra areas (Angerbjörn, Tannerfeldt, Bjärvall, Ericson, From & Norén 1995).

On the Fennoscandian peninsula (Norway, Sweden, Finland), the arctic fox population has not yet recovered from a drastic decline caused by over-hunting more than a century ago, and is currently threatened with extinction (Hersteinsson, Angerbjörn, Frafjord & Kaikusalo 1989, Angerbjörn et al. 1995, Frafjord & Rofstad 1998, Löfgren & Angerbjörn 1998). Suggested reasons for this lack of recovery are demographic and genetic problems resulting from very low fox numbers (below 100 individuals), a lack of large predators leaving carcasses, an absence of lemming peaks, and competition from a northerly expanding red fox *Vulpes vulpes* population (Hersteinsson et al. 1989, Löfgren & Angerbjörn 1998, Linnell, Strand & Landa 1999, Angerbjörn, Tannerfeldt & Lundberg 2001, Elmhagen, Tannerfeldt & Angerbjörn 2002, Tannerfeldt, Elmhagen & Angerbjörn 2002). Red foxes have been observed to take over arctic fox dens for breeding, although arctic foxes in some cases have returned to dens that have been used by red foxes (M. Tannerfeldt & A. Angerbjörn, unpubl. data). In the present study we describe the distribution and morphology of arctic fox dens in Vindelfjällen, northern Sweden, investigate what characteristics affect den use by arctic and red foxes, and if den characteristics are correlated with arctic fox litter size. Finally, to explore the relative quality of Swedish arctic fox dens, we compare den characteristics from our study area with previously published data from North America, Siberia, Norway, Greenland and Svalbard.

Study area

The study area which is situated in the Vindelfjällen Nature Reserve and adjacent areas in northern Sweden (66°10'N, 16°10'E; Fig. 1) covers 1,600 km^2 of mountain tundra, mainly situated within the low alpine vegetation zone, and is dominated by dry heath, grass heath and dry fen. Middle and high alpine parts are relatively small, with the highest peak reaching 1,642 m a.s.l. The tree line is situated at about 750 m a.s.l., and the study area is intersected by 200 km^2 of river valleys with birch *Betula* spp. and coniferous forests, which are not a favourable habitat for arctic foxes. There is no permafrost in the area, but summers are short with snowmelt in June and first snow in September. Most geomorphological formations are of glacial origin, with subglacially engorged eskers, kames and other hummocky glacifluvial accumulations as common geomorphological structures above the tree line (Ulfstedt 1977). Potential predators of the arctic foxes in the area are red fox, wolverine *Gulo gulo*, golden eagle *Aquila chrysaëtos* and white-tailed eagle *Haliaeëtus albicilla*.

Methods

The data were gathered from 1980 through 2000 in a long-term research project investigating arctic fox ecology (Angerbjörn, ArvidSon, Norén & Strömgren 1991, Angerbjörn et al. 1995, Angerbjörn et al. 1997, Tannerfeldt, Angerbjörn & ArvidSon 1994, Tannerfeldt 1997). Den positions were taken using Global Positioning System (GPS) and dens were plotted on a topographic map (1:100,000, contour interval 20 m), from which altitudes and distances to the nearest tree line were estimated. We estimated the gradient of the slopes where each den was excavated by applying a 1-km transect to the map in the direction of the slope with the den in the centre. The gradients of these transects were estimated using the map elevation contours. The density of dens in the area was calculated by dividing the number of dens by the total area above the tree line in the study area. At each den, the number of non-collapsed den openings was counted, and the area covered by the den (hereafter referred to as den area) was estimated as a two-dimensional surface between the four most spaced den openings. For dens situated in slopes, the general aspect of the slope was estimated to the nearest 45 degrees using a handheld compass. Also the orientation of the den itself was estimated, i.e. expressed as the general aspect of the majority of the surface area of the den.

Active dens were observed for up to seven days to determine occupying species and to estimate litter size. Only the first litter size estimate of each season, which was done when the cubs were 4-6 weeks old, was included in the analyses. To avoid bias in the number of observed arctic fox litters, we calculated a standardised number of litters born in each den, by dividing the number of litters observed by the number of breeding seasons each particular den had been inhabited. We used this standardised number of breeding attempts in analyses of breeding frequency.

The spatial distribution of dens was compared to random following Clark & Evans (1954), and the aspects of slopes and dens were compared to uniform using Rayleigh's tests corrected for grouping (Batschelet 1981). For non-random distributions, we used a V-test to test for the general direction. Dens in slopes without reliable estimates and dens on level ground were excluded from the analyses of slope aspect, and dens without reliable aspect estimates and dens without any particular orientation were excluded from the analyses of den aspect. We used logistic regression to test if den openings, den area (m^2), altitude and distance to the nearest tree line could be used to separate dens used and not used for breeding by arctic foxes (breeding dens vs non-breeding dens). The same analysis was conducted to separate dens used and not used by red foxes. To compare den characteristics between dens used by arctic and red foxes we used Tukey HSD post-hoc test on an ANOVA containing the same variables as in the logistic regressions. Den area and altitude were log transformed in the analyses. The frequency of breeding attempts in different dens was compared to a uniform distribution using a χ^2-test. To test if den characteristics affected the frequency with which arctic foxes used different natal dens, we conducted a backward stepwise multiple regression, using den openings, den area and altitude as predictors, controlling for the effect of den. Only natal dens were included in the analysis, and dens inhabited less than four years were excluded to avoid bias due to infrequent use. We also conducted a backwards stepwise multiple regression on the effect of den characteristics on litter size. We used the same predictors as in the previous analysis, but here we also controlled for lemming abundance and feeding regime (Tannerfeldt et al. 1994). Lemming abundance was indexed as either high or low, based on the number of observed lemming winter nests and presence of lemming predators (Angerbjörn et al. 2001). Several feeding experiments have been carried out in the study area (Angerbjörn et al. 1991, Tannerfeldt et al. 1994), and supplementary feeding has also been used in the conservation strategy for the arctic fox (Löfgren & Angerbjörn 1998). Hence, we coded each breeding attempt with regard to the litter being supplementary fed or not (including all feeding regimes, i.e. summer, winter or all-year feeding). In the multiple regression models, den area was log transformed due to a strongly skewed distribution.

All statistical analyses were carried out in STATISTICA ´99 (Statsoft Inc., Tulsa, OK), the level of statistical significance was set at 0.05 and all P-values are two-tailed.

Results

Distribution and morphology

We located 77 dens in the study area, and after 21 years of survey this can be considered the total number of dens present. All dens had the typical characteristics of arctic fox dens. No dens originally dug by red foxes were used for breeding by arctic foxes. Red foxes used dens dug by both arctic and red foxes for breeding. All dens were found in glacifluvial ridges or terrace formations. The study area had a density of 1 den / 21 km^2, and the mean nearest-neighbour distance between dens was 2.9 km (SD = 1.6 km; range: 0.9-11.5 km). The distribution was more widely spaced than random ($R = 1.25$, $P < 0.05$). The mean altitude of the dens was 915 m a.s.l. (SD = 74; range: 760-1,160 m), and the dens were on average 3.5 km from the nearest tree line (SD = 1.88; range: 0.4-11 km). Most dens (87%) were situated in slopes, with a mean gradient of 11.3 degrees (SD = 7.16 degrees; range: 1-30 degrees). For all dens combined, the aspects of the slopes where dens were situated were not uniformly distributed ($N = 59$, $Z = 3.93$, $P = 0.002$), but were predominantly facing south ($N = 59$, $V = 12.38$, $P = 0.02$; Fig. 2A). For breeding dens only, the

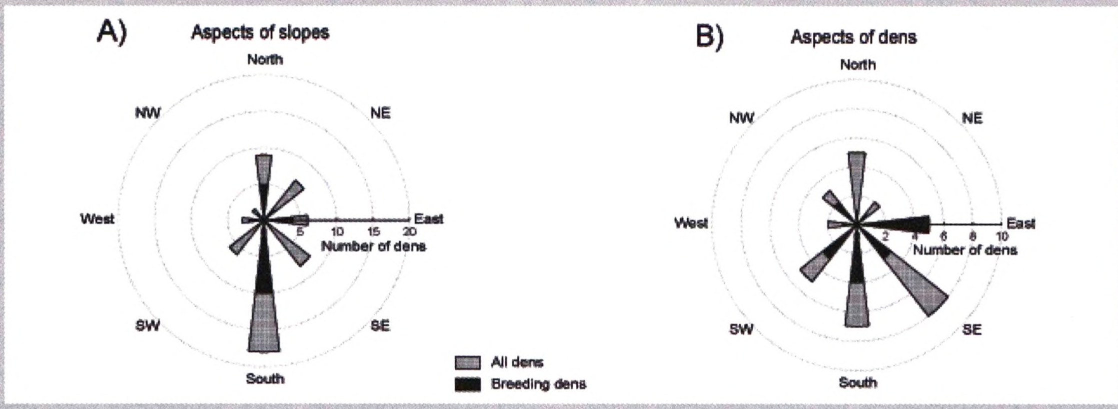

Figure 2. Frequencies of aspects of slopes (A) and dens (B) for all dens pooled and for breeding dens, i.e. dens used for arctic fox breeding during the study period. Aspects are pooled in 45° intervals. For A) the aspects of slopes for all dens are significantly different from uniform (N = 59, Z = 3.93, P = 0.002), but not for slopes of breeding dens (N = 25, Z = 0.71, P = 0.49). For B) the aspects of all dens showed a tendency to differ from uniform (N = 37, Z = 2.22, P = 0.099), but not for breeding dens (N = 20, Z = 1.95, P = 0.15).

slopes were not significantly different from uniform (N = 25, Z = 0.71, P = 0.49; see Fig. 2A). The aspects of the dens themselves were not significantly different from uniform, although there was a tendency for all dens combined to differ from uniform (all dens: N = 37, Z = 1.39, P = 0.099; breeding dens: N = 20, Z = 1.95, P = 0.15; see Fig. 2B). The mean number of den openings was 44 (SD = 32; range: 10-147) and mean den area was 277 m^2 (SD = 237 m^2; range: 20-1,085 m^2). Den area was positively related to the number of den openings ($F_{1,72}$ = 37.1, R^2 = 0.33, P < 0.001; y = 87.8 + 4.30x; Fig. 3).

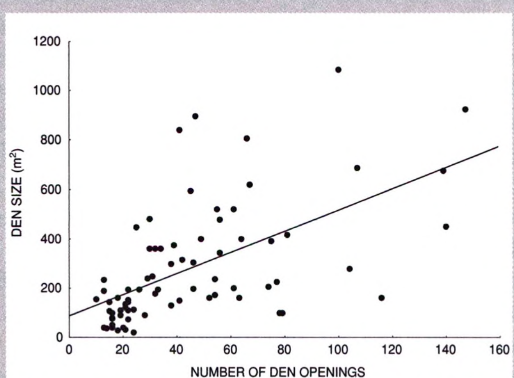

Figure 3. Den area (in m^2) as a function of the number of den openings in 74 arctic fox dens in northern Sweden. The fitted regression line is statistically significant ($F_{1,72}$ = 37.1, R^2 = 0.33, P < 0.001; y = 87.8 + 4.30x).

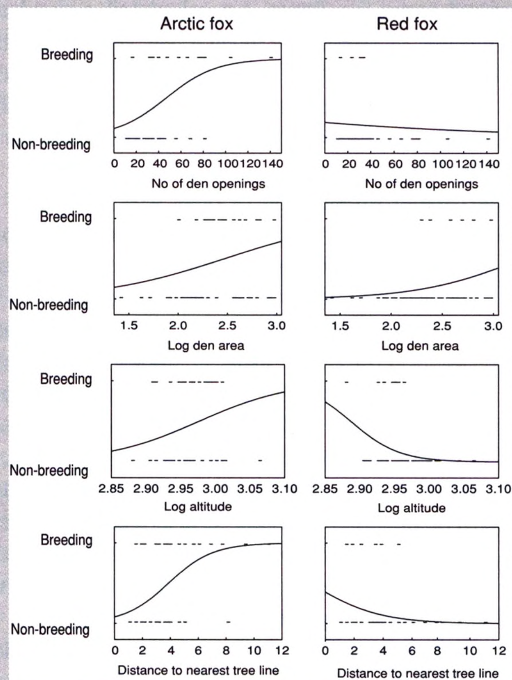

Figure 4. Logistic regressions of arctic fox dens coded as either non-breeding or breeding dens, both for arctic and red foxes based on total number of den openings, log-transformed den area (in m^2), log-transformed altitude and distance to nearest tree line as predictors. The total model, including all predictors explained 36% of arctic fox and 21% of red fox den use (arctic fox: χ^2 = 22.6, df = 3, P > 0.001; red fox: χ^2 = 12.9, df = 4, P = 0.01). For arctic fox, only den openings had a statistically significant partial effect on arctic fox den use (t = 2.24, df = 63, P = 0.03), but distance to nearest tree line showed a tendency for a partial effect (t = 1.85, df = 63, P = 0.07). For red foxes, den area was the only factor with a significant partial effect (t = 2.08, df = 62, P = 0.04).

Den use

During the 21-year study period, 31 dens were used for arctic fox breeding, and 10 dens were used for red fox breeding. The logistic regression including den openings, den area, altitude and distance to the nearest tree line explained 36% of arctic fox den use ($\chi^2 = 27.4$, df = 4, $P < 0.001$; Fig. 4). However, only the number of den openings had a statistically significant partial effect on arctic fox den use (t = 2.24, df = 63, P = 0.03). Distance to the nearest tree line showed a tendency for a partial effect (t = 1.85, df = 63, P = 0.07). For red foxes, the same logistic regression, including the number of den openings, den area, altitude and distance to the nearest tree line explained 21% of their use of arctic fox dens ($\chi^2 = 13.1$, df = 4, P = 0.01; see Fig. 4). For red foxes, den area was the only factor with a significant partial effect (t = 2.08, df = 62, P = 0.04). Arctic foxes used dens at higher altitude (P = 0.03) and further away from the forest than the dens used by red foxes (P = 0.03), and tended to breed in dens with more den openings (P = 0.08). The mean frequency of breeding attempts was 1 litter / 8 years (SD = 1 litter / 5 years; range: ½-1/17). Some breeding dens were used more than others ($\chi^2 = 87.4$, df = 30, $P < 0.001$). Within breeding dens, a standardised number of arctic fox litters was positively related to den area ($R^2 = 0.14$, ß = 0.38, P = 0.04), and was the only variable kept in the final regression model ($F_{1, 27} = 4.62$, $R^2 = 0.15$, P = 0.04; Table 1). After controlling for the effect of supplementary feeding and lemming abundance, arctic fox litter size was also positively related to den area ($R^2 = 0.20$, ß = 0.60, $P < 0.001$; see Table 1). Den area, den openings and lemming abundance were all included in the final regression model on arctic fox litter size ($F_{1, 55} = 4.10$, $R^2 = 0.24$, P = 0.048).

Table 1. ß- and partial R^2- values of predictors used in stepwise multiple regressions on standardised number of litters in natal dens (number of litters / number of years inventoried) and litter size. Only log den area remained in the final model of standardised number of litters ($F_{1, 25} = 4.69$, $R^2 = 0.12$, P = 0.04), whereas log den area, den openings and lemming abundance were included in the final model of litter size ($F_{1, 55} = 4.10$, $R^2 = 0.24$, P = 0.05)

Factor	Included (+) or excluded (-)	ß	Partial R^2	P
Standardised number of litters				
Log den area	+	0.38	0.14	0.04
Den openings	-	-0.02	< 0.01	0.92
Altitude	-	0.15	0.03	0.43
Distance to tree line	-	0.06	< 0.01	0.88
Den	-	0.01	< 0.01	0.99
Litter size				
Log den area	+	0.60	0.20	< 0.001
Den openings	+	-0.27	0.04	0.16
Altitude	-	0.07	0.01	0.63
Distance to tree line	-	-0.07	0.01	0.60
Den	-	0.05	0.00	0.76
Fed or unfed	-	-0.01	< 0.01	0.94
Lemming abundance	+	0.29	0.10	0.03

Discussion

All dens in our study were burrows in glacifluvial sand or silt, which may be a suitable material for den construction. However, we observed that foxes had started expanding several dens, but had given up, probably because of unsuitable substrate. For stable den construction, arctic foxes seem to need sorted material of more or less specific grain size. The dens in our area are located at rather restricted positions in the geomorphological formations, probably where the stratum has the most preferable texture. We did not include rock dens in our study. Rock dens are rare in the area and have never been observed as breeding dens, but rather as resting sites and for food storage. The foxes dig dens in south-facing slopes, and seem to orient the dens towards the south or southeast. A southerly orientation has been found in other areas as well (Chesemore 1969, Smits et al. 1988, Prestrud 1992c), and probably reflects early snowmelt and warmer microclimate in south-facing positions. On Svalbard, dens were predominantly located in moderately rugged terrain with sparse snow cover (Eide, Nellemann & Prestrud 2001). However, the uniform distribution of breeding dens indicates that microclimate has no effect on the suitability of the site after the den has been constructed.

Our study area had a higher density of dens than high arctic tundra plains, but lower than that which has been found on some arctic islands (Table 2). However, on these islands fox densities are often considerably higher than on the adjacent mainland. The fact that the dens in our study area were more dispersed than random agrees with patterns found in several other areas (Macpherson 1969, Prestrud 1992c). However, both random (Fine 1980) and clumped patterns (Anthony 1996) have been observed. Arctic foxes are strictly territorial during the breeding season (e.g. Angerbjörn et al. 1997, Strand, Landa, Linnell, Zimmermann & Skogland 2000). Hence, the wide dispersal of dens may result from territoriality and avoidance of intraspecific competition.

Swedish arctic fox dens are among the largest reported (see Table 2). This may in part be explained by the lack of permafrost, which is regarded as one of the most important limitations to excavation of dens (Bannikov 1970). Macpherson (1969) categorised arctic fox dens from "youthful" to "senile", depending on the number of fresh and collapsed entrances. The word "senile" suggests that there is a definite end to the use of a particular den. However, although dens may be permanently abandoned if they have been excavated by other animals, such as wolves *Canis lupus* or bears *Ursus arctos* (Macpherson 1969), most dens are probably only abandoned for a number of years. This may be to avoid a heavy parasite load (i.e. Butler & Roper 1996) or to let den structures stabilise. Some dens may also be used continuously, although specific parts of the burrow system are left to collapse (M. Tannerfeldt & A. Angerbjörn, pers. obs.). The largest dens must have been in use for a long period of time. Thus, most dens in our study area should be excavated to the maximal extent that each particular site allows. Macpherson (1969) suggested an average life-span of 330 years for each den. In fact, well situated den sites may have been in use for thousands of years.

Arctic foxes clearly prefer some dens to others. In our study area, each territory comprises several arctic fox dens, yet the largest ones are preferred. Thus, there is no evidence that dens are large from frequent use due to non-den related factors, but rather that large dens are preferred because of their size. The large size of Swedish dens compared to dens in other areas thus implies that dens in this study area are of a comparatively high quality. The relation between litter size and den area illustrates that large dens may have benefits compared to smaller dens. The most important benefit of large den size is probably predator avoidance, since large and complex dens provide an increased number of options for escape routes. Dens used by arctic foxes were situated at higher altitudes and further away from the forest than dens used by red foxes. Similar patterns have also been observed in Norway (Linnell et al. 1999). As in the present study, Linnell et al. (1999) only included former arctic fox dens, indicating that red foxes have taken over previous arctic fox breeding areas.

To conclude, Swedish arctic fox dens are among the largest reported for the species, and our study area has a relatively high density of dens compared to most high arctic areas. As large dens seem to be favoured by arctic foxes, the dens in our study are of comparatively high quality. Successful breeding dens for arctic foxes in Sweden appear to be characterised by large size and many openings, and they are situated far away from forest at relatively high altitudes.

Table 2. Distribution and physical characteristics of arctic fox dens in North America, North Siberia, Svalbard, West Greenland and Scandinavia. [a] Mean ± SD; values in parentheses indicate total range. [b] Includes 'den complexes', presumably with several dens.

Area	Site	Habitat	Geographic region	Den type	Latitude	No. of dens	Density (dens / km^2)	No of den openings [a]	Den area [a] (m^2)	Source
North Alaska	Prudhoe Bay and Colville River Delta	Coastal tundra	Arctic	Burrows	70°N	38-50	1/12 and 1/34	33 (1 - 85)	256 (1 - 625)	Garrott et al. 1983, Eberhardt et al. 1983
North Alaska	Teshekpuk lake area	Coastal tundra	Arctic	Burrows	70°N	50		4 (1 - 26)	30 (1 - 100)	Chesemore 1969
North Canada	Herschel Island	Coastal tundra	Arctic	Burrows	69°N	17	1/3	20 ± 14	123 ± 122	Smits et al. 1988
North Canada	Yukon coastal plain	Coastal tundra	Arctic	Burrows	69°N	25	1/102	19 ± 9	130 ± 116	Smits et al. 1988
West Alaska	Yukon-Kuskokwim delta	Coastal tundra	Sub-arctic	Burrows	61°N	11	1/4.7	5 ± 3 (2 - 10)		Anthony 1996
North Siberia	Wrangel Island	Coastal tundra	Arctic	Burrows	70°N	41		31 (5 - 67)	70 (15 - 220)	Dorogoi 1987
Svalbard	Nordenskiöldland	Coastal area	Arctic	Combined rock/burrows	77°N	59	1/13	10 ± 9 (1 - 35)	52 ± 76 (2 - 630)	Prestrud 1992b
West Greenland	Disko Island	Coastal area	Arctic	Combined rock/burrows	69°N	17		18 ± 18 (1 - 63)	196 (3 - 1134)	Nielsen et al. 1994
Norway	Hardangervidda	Mountain tundra	Subarctic	Burrows	60°N	31		(1 - 40)	(10 - 50000) [b]	Østbye, Skar,Svalastog & Westby 1978
Sweden	Vindelfjällen	Mountain tundra	Subarctic	Burrows	66°N	77	1/21	44 ± 38 (10 - 147)	277 ± 237 (20 - 1085)	Our study

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