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Terrain structure and selection of denning areas by arctic foxes on Svalbard

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Abstract We examined the relationship between the distribution of arctic fox dens and the occurrence of rugged terrain on Svalbard, Norway, using indices of terrain ruggedness (TRI) based on contour characteristics from topographic maps in 240 grid cells, each 4 km^2. The distribution of rugged terrain co-varied with occurrence of arctic fox dens. Moderately rugged terrain (TRI = 1.5–3.0) constituted only 21% of the total study area, but contained 77% of all natal dens recorded in the study area. Large clusters (8–36 km^2) of moderately rugged terrain were generally preferred for location of den sites compared to smaller scattered clusters of rugged terrain. The importance of rugged terrain is discussed in relation to snow cover, exposure, soil conditions and distribution of prey species. This simple and non-invasive analysis of terrain ruggedness may be used to predict the distribution of potential arctic fox denning areas across landscapes.

Introduction

The arctic fox (*Alopex lagopus*) has a wide circumpolar distribution. It inhabits the treeless northern tundra regions, most arctic islands and the alpine region of Scandinavia. Arctic foxes breed in underground dens. It is assumed that such dens are necessary for successful breeding, providing pups with vital shelter from adverse weather conditions, as well as protection from predators (Chesemore 1969; Macpherson 1969; Østbye et al. 1978; Eberhardt et al. 1983; Prestrud 1992a). Dens are also used for shelter during winter (Eberhardt et al. 1983). Although a large number of dens may be available in an area, most dens where pups are born are old, large and well developed (Østbye et al. 1978; Prestrud 1992b; Anthony 1996), and may have been in use for centuries (Macpherson 1969). This indicates that some dens are of particular value for rearing pups, and it is assumed that the availability of such sites is limited (Macpherson 1969; Garrott et al. 1983; Smits et al. 1988).

Arctic foxes may be disturbed by nearby human activity close to dens. Human visits at dens resulted in movement of 35% of fox families within 24 h of the disturbance incident (Prestrud 1992b). Foxes could also be adversely affected by more obvious human impacts, such as physical destruction of dens and habitat loss or fragmentation due to development. With the rapidly expanding arctic tourism industry and demands for coal, oil and gas resources, the relatively undisturbed Arctic has in recent years come under increasing pressure (Kaltenborn and Emmelin 1993; UNEP, in press). Thus there is an urgent need to develop simple techniques to predict critical habitats for wildlife prior to larger encroachments in undisturbed areas. As availability of good dens may be a limiting factor for reproduction in arctic foxes, selection of such sites may dominate other components of habitat selection (Orians and Wittenberger 1991). Understanding distribution patterns of arctic fox dens across landscapes could thus be important for future prediction of arctic fox denning areas at larger regional scales (Smits and Slough 1993). This could raise the possibility of identifying key areas, beyond intensively studied arctic fox populations.

Physical characteristics of arctic fox dens have been described in several parts of the species range. In tundra plains of Siberia (Danilov 1961), Alaska (Chesemore 1969; Eberhardt et al. 1983; Garrott et al. 1983;

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Anthony 1996), Canada (Macpherson 1969; Smits et al. 1988; Smith et al. 1992), mountainous Scandinavia (Østbye et al. 1978) and Greenland (Nielsen et al. 1994), most dens are located in pingos, mounds, eskers, river banks or moraine, of fluvial or glacial origin. In contrast, most dens in the mountainous archipelago of Svalbard are found under boulders, in screes or in crevices in bedrock (Prestrud 1992a; Frafjord 1997). Arctic fox dens are typically found on south-facing slopes (Chesemore 1969; Østbye et al. 1978; Smits et al. 1988; Prestrud 1992a) with shallow snow cover (Prestrud 1992a), characterised by soils with good drainage capability, greater depth to the permafrost and higher soil temperatures (Chesemore 1969; Østbye et al. 1978; Smits et al. 1988). All these factors form local descriptions of denning conditions, but provide no indication of the regional availability. Little is known about factors that determine availability of good denning areas at larger scales, although terrain structure is often discussed (Danilov 1961; Chesemore 1969; Østbye et al. 1978; Garrott et al. 1983; Smits et al. 1988; Prestrud 1992a; Smith et al. 1992). Smits and Slough (1993) attributed differences in population density between two areas in the Yukon Territory to differences in the availability of landforms suitable for arctic fox dens. So far however, no studies have assessed directly the influence of terrain structure.

In this paper, we examine the relationship between arctic fox dens and the occurrence of rugged terrain (TRI).

Study area

Arctic fox den sites have been mapped in a study area of approximately 1,000 km^2 in Svalbard, Norway (Fig. 1). The Svalbard archipelago (62,700 km^2, 60% covered by permanent snow and ice) is located between 74 and 81°N, and 10 and 30°E. The study area is bounded by the shoreline of Isfjorden and the surrounding glaciated mountain ranges (Fig. 2). Two large valleys, Adventdalen and Sassendalen, cut through the study area. The landscape is mountainous and moderately glaciated, with all summits below 1,000 m. Vegetated areas reach

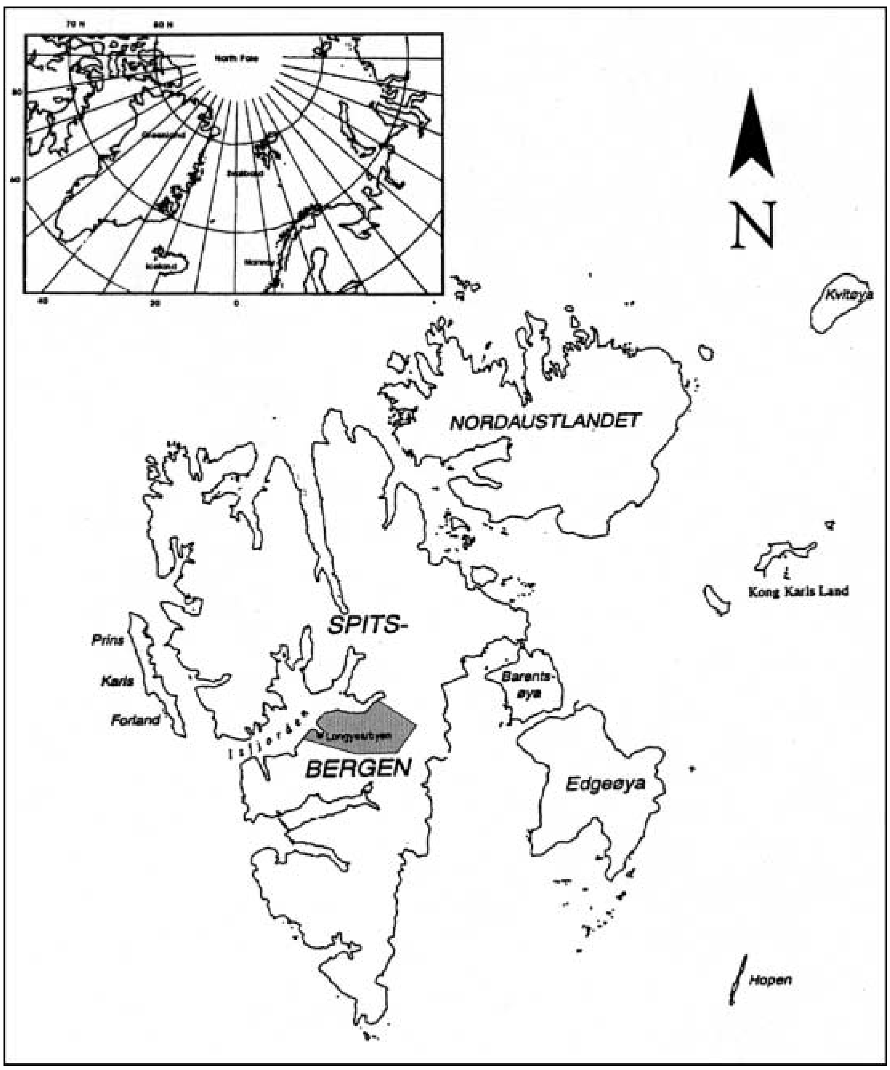

Fig. 1 The study area on Nordenskiöldland, Svalbard, Norway

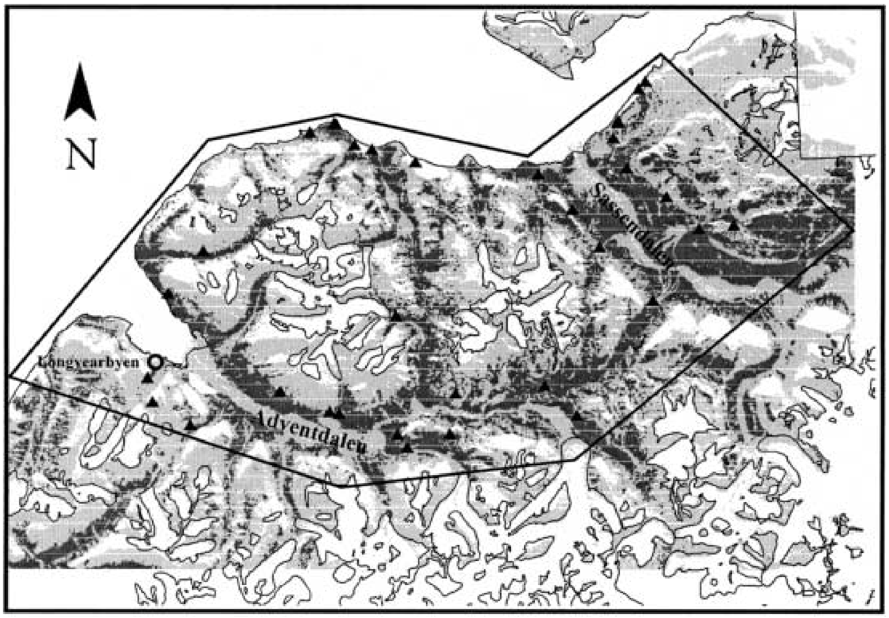

Fig. 2 Map of the study area, indicating vegetated (given in *green*), non-vegetated (given in *grey*) and glaciated areas (given in *white*), and location of arctic fox natal den sites (▲)

500 m.a.s.l. The bedrock consists of sedimentary rock except for rare magmatic intrusions of diabase along the shoreline (Major and Nagy 1972). The topographic relief is mainly a result of erosion of sedimentary rock, and the landscape is dissected by numerous small valleys. Scree covers the lower hill slopes. The flat valleys are covered by marine, fluvial and glacial deposits.

In the summer months large seabird colonies, dominated by fulmar (*Fulmarus glacialis*), Brunnich's guillemot (*Uria lomvia*) and little auk (*Alle alle*), are found along the coast. Pink-footed geese (*Anser brachyrhynchus*) and barnacle geese (*Branta leucopsis*) breed in large colonies in the inland river canyons. Two endemic subspecies – a bird, Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*) and a mammal, Svalbard reindeer (*Rangifer tarandus plathyrhynchus*) – along with the arctic fox, are resident throughout the year.

Longyearbyen, the largest settlement on Svalbard with its 1,200 inhabitants, is situated in the southwestern corner of the study area.

Materials and methods

The arctic fox dens used in this study have been mapped earlier and their physical characteristics have been described in detail (see Prestrud 1992a, b). Dens were located by systematic ground surveys searching eskers, moraines, riverbanks, boulders, screes and large blocks of stone, from sea level up to an altitude of 450–600 m (Prestrud 1992a). During recent fieldwork, in 1997–1999, three additional den sites were found in the same area. Prestrud (1992b) classified dens into three categories: natal dens, assumed natal dens and shelters. A den was identified as natal if live or dead pups were observed at the den at least once during the breeding season. The dens were surveyed during the breeding season (10 June to 25 July) over two periods (1982–1989 and 1997–1999). Some of the dens have been reclassified according to the above classification. Analyses carried out in this study consider only dens classified as "natal dens" ($n = 34$, see Fig. 2), hereafter referred to as "dens".

The exact geographical position of dens was determined with a Global Positioning System (GPS) receiver. All locations were marked on a topographic map (scale 1:50,000; contour interval 25 m) with original Universal Transverse Mercator (UTM) gridlines at 500-m intervals, dividing the study area into regular quadrats (grid cells).

The terrain ruggedness index (Nellemann and Thomsen 1994; Nellemann and Fry 1995) was used for analysis of terrain structure. TRI was derived from a 1:50,000 topographic map. As recommended for studies of habitat use within landscapes, all analyses were done at a mesoscale (in this study 1,000 km^2), with 25-m contour intervals (Nellemann 1997), which imply that small topographical features such as eskers and moraines will not be detected. In order to identify the influence of scale on habitat use (Morris 1987; Nellemann 1997), the TRI was calculated at 2 levels: 1 × 1 km (904 quadrats) and 2 × 2 km (240 quadrats). No larger quadrats were used, as most valleys were less than 3 km wide. Within each quadrat, a transect with a fixed length was placed across the centre. Four transect lines were drawn through the centre of each quadrat. The transect giving the highest TRI value was used for that quadrat. An index of ruggedness (TRI) can be defined by the following equation:

$$\text{Terrain ruggedness index (TRI)} = (\text{TNC} \times \text{TNF})/(\text{TNC} + \text{TNF})$$

where TNF is the total number of changes in aspect along the transect and TNC is the number of contour lines intercepted along the same transect (for details, see Nellemann and Fry 1995). A flat terrain may receive the same index value as a very steep slope, if no changes in aspect occur along the transect. A rugged, horizontal landscape may also receive greater values than a smooth, steep slope. The highest index values are obtained in areas characterised by broken country, both steep and rugged, with many changes in aspect. Due to statistical limitations and the relatively small sample size, the TRI was grouped into only four equally spaced categories, from low topographic heterogeneity to high topographic heterogeneity: (0.0–<1.5, 1.5–<3.0, 3.0–<4.5, 4.5–>). Because no den sites were found above 400 m altitude in the study area (Prestrud 1992a), all analysis of habitat use includes only quadrats below 400 m: 1 × 1 km ($n = 598$), 2 × 2 km ($n = 158$). A quadrat is considered to be above 400 m when more than 50% of the square is above 400 m.

To test if the spatial configuration of rugged terrain (cluster size) had any effect on selection of denning area, a second level of use/availability analyses were performed. Clusters of preferred terrain were identified from the topographic map, by adding neighbouring squares with TRI values 1.5–< 3.0 to form larger clusters (size 1–9 quadrats or 4–36 km^2). Only dens found in the preferred TRI class were used ($n = 26$) in this analysis. Due to a relatively small sample size, clusters were categorised into two classes only: cluster size 1 (4 km^2, $n = 10$) and cluster size 2 and upwards (8–36 km^2, $n = 9$).

Statistical analyses were performed using SIGMASTAT. Habitat selection was evaluated by comparing utilisation of a habitat relative to its availability. Use of terrain ruggedness and clusters in relation to availability was tested for significance using the chi-square goodness-of-fit test and the Bonferroni z-statistics (Neu et al. 1974; Byers et al. 1984). Yates correction was used when there were only two categories (Fowler et al. 1998). P-values less than 0.05 were considered to be statistically significant.

Results

Location of arctic fox dens was significantly different from random ($\chi^2 = 30.6$, $df = 3$, $P < 0.01$) at the level of 2 × 2 km quadrats. At the level of 1 × 1 km quadrats, we found no relationship between terrain ruggedness and distribution of dens ($\chi^2 = 1.9$, $df = 3$, $P > 0.05$). In the following analysis, only data at the 2 × 2 km level are considered.

Moderately rugged terrain (TRI = 1.5–< 3.0) was used significantly more than expected from availability, while areas with low topographic heterogeneity (TRI 0.0–< 1.5) and areas with highly rugged terrain (TRI 3.0, >) were avoided for dens (Table 1). Of the arctic fox dens, 77% ($n = 26$) were found in the preferred terrain class, which composed 33% of the area below 400 m. a.s.l. and 21% of the entire study area.

The observed spatial distribution of arctic fox dens and moderately rugged terrain is illustrated in Fig. 3.

Arctic fox use of clusters with moderately rugged terrain deviated from random ($\chi^2 = 19.3$, $df = 1$, $P < 0.01$). The largest clusters of moderately rugged terrain were preferred for dens (Table 2). Dens were found in 20% of the clusters of 4 km^2, while in 89% of larger clusters. Clusters of 8 km^2 and larger (in total 42 quadrats) composed 27% of the area below 400 m.a.s.l. and 18% of the entire study area. 71% ($n = 24$) of the dens occurred within these clusters of moderately rugged terrain.

Discussion

Arctic foxes on Svalbard preferred moderately rugged terrain for location of dens. This probably reflects the fact that moderately rugged terrain offers better physical conditions for den location. The relationship between rugged terrain and features known to determine arctic fox den location are further discussed.

Arctic fox dens are often located in areas with low accumulation of snow and early snowmelt (Macpherson 1969; Østbye et al. 1978). Prestrud (1992a) found that the extent of bare ground was significantly higher at the

Table 1 Use and availability of terrain by arctic foxes for location of 34 dens in Svalbard (significant preference +; significant avoidance −)

Terrain ruggedness index (TRI)	Natal den sites ($n = 34$) given in proportions			
	Observed p_i	Expected p_{io}	95% Bonferroni intervals for p_i	
TRI 0–< 1.5	0.029	0.253	[−0.043; 0.102]	−
TRI 1.5–< 3.0	0.765	0.329	[0.583; 0.946]	+
TRI 3.0–< 4.5	0.088	0.266	[−0.033; 0.210]	−
4.5, −>	0.118	0.152	[−0.020; 0.256]	0

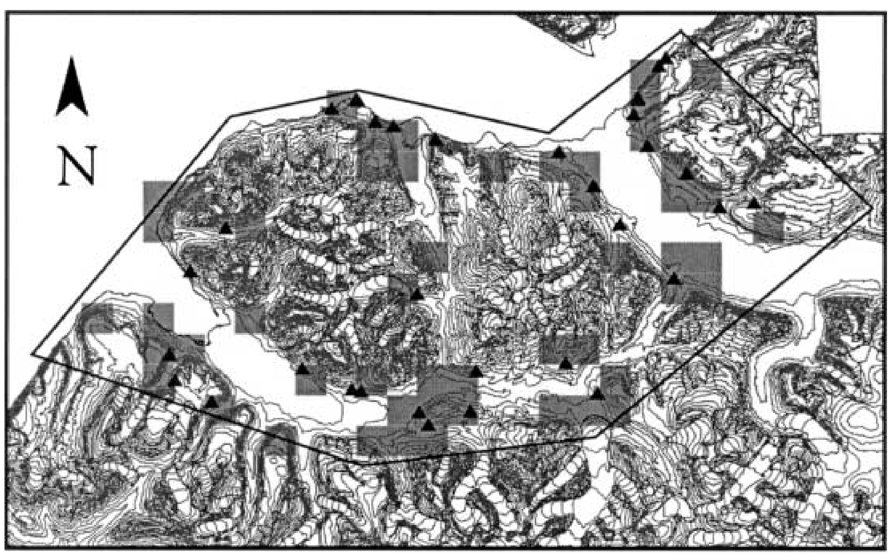

Fig. 3 The observed spatial distribution of arctic fox natal den sites (▲) and moderately rugged terrain, TRI = 1.5–< 3.0 (*grey* area) given in quadrats of 4 km^2

Table 2 Use and availability of clusters of moderately rugged terrain (TRI = 1.5–< 3.0) by arctic foxes for location of 26 den sites in Svalbard (significant preference +; significant avoidance −)

Cluster size of rugged terrain	Natal den sites (n = 26) given in proportions			
	Observed p_i	Expected p_{io}	95% Bonferroni intervals for p_i	
Cluster size 1 (4 km^2)	0.077	0.526	[−0.041; 0.194]	−
Cluster size 2, −> (8–36 km^2)	0.923	0.474	[0.806; 1.041]	+

dens compared with the surrounding areas. Based on satellite images of snow cover in April, a strong positive correlation between TRI and availability of small snow-free areas on exposed ridges was found in the study area (Linn B. Jacobsen, unpublished data). The correlation between sparse snow cover and rugged terrain has also been found in other studies (Uspenskii 1986; Nellemann and Thomsen 1994; Nellemann and Fry 1995; Nellemann 1996). Dens are often located at the top of elevated landforms, which are kept relatively snow free by the wind during most of the winter.

South-facing slopes are greatly preferred by arctic foxes for locating dens (Danilov 1961; Chesemore 1969; Østbye et al. 1978; Smits et al. 1988; Prestrud 1992a). South-facing slopes receive more radiation, which causes a warmer microclimate, earlier snowmelt and thawing of the permafrost (Chesemore 1969; Østbye et al. 1978; Smits et al. 1988; Nellemann and Thomsen 1994). A higher temperature at the den sites than elsewhere was confirmed by Danilov (1961) and Smits et al. (1988). In rugged terrain, the availability of south-facing slopes will naturally be high.

Several studies have documented a preference for locating dens in thick active layers of dry soil with good drainage capability (Danilov 1961; Chesemore 1969; Macpherson 1969; Smits et al. 1988; Anthony 1996). Undulating terrain has larger local variation of soil types and depth to permafrost compared with flat areas (Swanson 1996; Nelson et al. 1997). Ridges and knolls typically consist of warm mineral soil with coarse texture, having a good drainage capability, and a deeper active layer of soil above the permafrost/bedrock (Swanson 1996). Arctic fox dens on Svalbard were primarily found in association with large stones, boulders or crevices in bedrock. Here, entrances could be dug out in the soil under or between large stones or solid rock (Prestrud 1992a). Areas with bedrock and large blocks of stone probably have a greater ground stability, due to the effect of the binding soil, while areas with only unconsolidated material are characterised by higher instability, with erosion and more solifluction of the soil typical of tundra areas with permafrost. Large stones and boulders are concentrated along valley slopes, together with exposed bedrock. Here, historical glacial and present erosion processes make crevices in the bedrock, and release small and large blocks of stones. Such highly eroded valley slopes are associated with large topographic heterogeneity and consequently high TRI values.

In contrast to other arctic tundra areas, relatively few dens used in this study were found in riverbanks, eskers and moraines (see Prestrud 1992a). The limited spread of eskers and moraines on Svalbard is one explanation for this. In addition, the unconsolidated material found in such landforms on Svalbard originates from relatively young and soft bedrock, providing a large component of the fine-grained material in the soil (Ida Lønne, personal communication), resulting in lower drainage capability, higher instability and reduced suitability for digging a den. Thus, when they are given the opportunity, arctic foxes prefer valley slopes with rugged terrain. Absence of lush, green vegetation at dens located in boulders and in between blocks of stone makes them difficult to locate. No studies performed in the mountainous part of the arctic fox range have invested a large effort searching such areas, which might be a reason why this preference has not been documented before.

Spatial and temporal patterns of prey distribution are also important for a predator's choice of denning area. The absence of a relationship between terrain ruggedness and distribution of dens at the small scale (1 × 1 km) confirms that the choice of an area for establishment of a den is dependent on more than just local physical habitat factors. Morris (1987, 1992) emphasised that if a too-small or a too-large scale is applied to habitat studies, one might be incapable of assessing habitat selection. The analysis of the small grid size probably gives a too-variegated picture of terrain to explain the general den distribution patterns. Along the coast, most dens are found in association with large seabird colonies (Prestrud 1992a; Frafjord 1997), where food availability is highly concentrated. As for the inland areas, a higher availability of prey species may explain the fact that arctic foxes preferred the larger clusters of moderately rugged terrain compared to the smaller clusters. This preference also suggests that a minimum amount of preferred habitat is needed to find an area potentially suitable for reproduction. Availability of terrain features has been suggested as an important factor explaining distributions of many species. Due to a prolonged period of snowmelt, caused by accumulation of snow in depressions, rugged terrain has an elongated and relatively large availability of high-quality forage (Nellemann and Thomsen 1994), which should attract several herbivorous species. Throughout the Arctic, spring migrating geese seek patches of snow-free areas on ridges and slopes, both for grazing (Fox et al. 1991; Frafjord 1993) and breeding (Frafjord 1990;

Stickney and Ritchie 1996; Alsos et al. 1998). In this study, most dens in Sassendalen were found in close proximity to breeding colonies of geese. Two-thirds of the breeding geese were found within a radius of 1 km from an active fox den (unpublished data). Interpretation of the results from Unander and Steen (1985) suggests that the distribution of territorial male Svalbard rock ptarmigan could be explained by the distribution of rugged terrain. Snow bunting (*Plectrophenax nivalis*) and purple sandpiper (*Calidris maritima*) also show an attraction to early snow-free patches (Summers and Underhill 1996). Within the circumpolar region, areas characterised by rugged terrain are found to be important feeding grounds for arctic ungulates during winter and spring (Nellemann 1997). Reindeer that die from natural causes during winter on Svalbard are often found in such broken country (N. Tyler, personal communication), and reindeer carcasses constitute an important part of the arctic fox year-round diet (Prestrud 1992c).

Smits and Slough (1993) explained regional differences in den densities in the Canadian Arctic by differences in terrain and availability of landforms. Densities of natal dens range from 1 den pr. 4.7 km^2 in the coastal tundra of Alaska (Anthony 1996) to 1 den pr. 24 km^2 in our study area (Prestrud 1992b). Densities of litters change with the lemming cycles (Angerbjörn et al. 1999) or are stable and low in areas where rodents are absent, as in our study area. Litters are more widely spaced than random, implying that territorial behaviour also influences the distribution of dens (Macpherson 1969; Prestrud 1992b). Inside arctic fox home ranges, there are commonly several dens that may be used as natal dens. Litters are often moved between these dens or even split between them (Eberhardt et al. 1983; Prestrud 1992b; Smits and Slough 1993; Anthony 1996; Landa et al. 1998). Although arctic foxes in our study area change their use of habitat throughout a summer season, and the variations in habitat use between individual foxes are considerable, the general picture is that they exhibit a great preference for topographically heterogeneous habitats (unpublished data).

The present study has demonstrated that there is a strong relationship between terrain and the distribution of dens. The terrain ruggedness index integrates several factors important for arctic fox habitat selection. The TRI may therefore become a simple predictor, providing information as to where good arctic fox denning areas can be found on Svalbard. The extent to which this index, based on ordinary topographic maps, could be used as a tool to identify arctic fox denning areas in other parts of the species range needs however, to be tested and reconfirmed by additional studies. The TRI has been proved effective for mapping high-level use areas for arctic ungulates, e.g. the mountainous areas of central Norway and the flat polygonated tundra on the north slope of Alaska (Nellemann 1997). It must be emphasised that the calculation of the TRI needs to be adjusted to the specific characteristics of the region in question affecting the choice of contour intervals and quadrat size. In flat tundra areas where most arctic fox populations are found, one could not operate on such a coarse resolution as done in this study area, which constitutes mountainous terrain. More detailed topographic maps, with contour intervals in the range 5–15 m, would serve better for analysing the terrain structure in open tundra landscapes. This smaller scale would reveal smaller bluffs, ledges, terraces, hills or elevated landforms such as eskers and moraines, important for den location. If the exact position of arctic fox dens is needed for further management action to be taken, the suggested method could not fully replace traditional ground or aerial surveys. It would, however, easily pick out focus areas, making these surveys more efficient, especially in localities where ground surveys are the only option.

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