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ORIGINAL PAPER

Finding the right home: distribution of food resources and terrain characteristics influence selection of denning sites and reproductive dens in arctic foxes

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Abstract We examined 83 arctic fox (*Alopex lagopus*) dens on Bylot Island (Canada) during the summers of 2003–2005, to determine how arctic foxes select a denning site among potential sites, and a breeding den among existing dens. We compared denning sites to random locations in a 425 km^2 study area (landscape scale) and to other potential denning sites in a 100 m radius (local scale). Dens were located on mounds or in slopes and were closer to streams than expected. Sites with low snow cover in spring, high ground temperature, high depth to permafrost, and steep and southerly exposed slopes were preferred. Of the 83 dens, 27 were used at least once for reproduction from 2003 to 2005. We show with a resource selection function analysis that an attractive force (distribution of food resources) and an apparently repulsive one (presence of other dens in the vicinity) affected selection of dens for reproduction. We generate testable hypotheses regarding the influence of food and social factors on the denning ecology of arctic foxes.

Introduction

Understanding the process of habitat selection is a fundamental goal in animal ecology. Various factors can influence habitat use by individuals, but the general assumption is that individuals select habitats where their fitness is maximized in accordance to the activity they need to perform. For many carnivorous mammals, access to a den is essential for successful breeding and cub rearing (Moehlmann 1989; Tannerfeldt et al. 2003). The location of these dens is rarely random but often based on factors such as the ease of escape from predators (Ruggiero et al. 1998; Slough 1999) or the proximity of available food resources (Pruss 1999; Arjo et al. 2003). In the arctic tundra, arctic foxes (*Alopex lagopus*) excavate dens where they give birth to cubs and rear them until the mid-summer weaning period (Macpherson 1969). Access to a den is believed to be essential for successful reproduction, but they can also be used as shelters during winter or summer (Prestrud 1992a). Physical characteristics of arctic fox dens have been described throughout most of the species' range (Chesemore 1969; Macpherson 1969; Garrott et al. 1983; Smits et al. 1988; Prestrud 1992b; Nielsen et al. 1994), but few studies have considered the influence of environmental characteristics on their spatial distribution (Eide et al. 2001). Habitat components such as distance to water sources, vegetation height or distance to a road have been shown to influence the location of den sites in other carnivores (Ruggiero et al. 1998; Pruss 1999; Henner et al. 2004). Identifying factors influencing habitat selection can provide important clues on the ecology, physiology as well as on constraints to which a given species is exposed.

Our first objective was to determine environmental characteristics influencing den site selection by an arctic mammal, the arctic fox. Eide et al. (2001) have

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demonstrated the influence of landscape heterogeneity on the selection of denning areas by arctic foxes in Svalbard. Other topographical and micro-climatic characteristics such as altitude, slope inclination and orientation, snow cover, or presence of streams and other water bodies, have been suggested to influence the location of arctic fox dens (Chesemore 1969; Macpherson 1969; Garrott et al. 1983; Smits et al. 1988; Prestrud 1992b; Nielsen et al. 1994). However, to our knowledge, the actual selection for these variables has never been studied through a utilisation/availability analysis. Considering the low productivity of the arctic tundra, food resource distribution may also be an important driving force for the selection of an adequate denning area. Due to the difficulties of measuring the distribution and abundance of food in space and time, no study has considered the influence of food resources on the location of arctic fox dens. Eide et al. (2004) did, however, show that the size of arctic foxes' home range varies according to the distribution and predictability of food resources. In this study, we investigated the importance of topography, micro-climate and food resource distribution on the selection of denning sites by arctic foxes at two spatial scales. At the landscape scale, we evaluated the influence of topography, water bodies, surrounding habitat and the distribution of lemmings and nesting geese, the two main prey items of arctic foxes. At a micro-scale, we assessed the influence of snow cover, substrate type, slope aspect and inclination, and soil depth and temperature.

Despite a relatively high abundance of dens excavated by arctic foxes throughout the tundra, only a small proportion of those are repeatedly used for reproduction (Prestrud 1992a; Anthony 1996). The criteria used to select dens for reproduction are unclear. Assuming that an individual selects a den to maximize its fitness, reproductive dens should differ from non-breeding dens in some characteristics of importance to reproducing arctic foxes. Identifying these variables should allow for a better understanding of the constraints to which arctic foxes are exposed during reproduction. The second objective of this study was therefore to identify environmental features used by arctic foxes when choosing a reproductive den. Again, we evaluated the relative importance of topography, micro-climate and the distribution of food resources.

Materials and methods

Study area

We worked on the south plain of Bylot Island (73°N, 80°W), Nunavut, Canada (Fig. 1) during summers of 2003–2005. The area is characterized by large upland mesic plateaus, covering ca. 90% of the landscape (Masse et al. 2001), intersected by several valleys with lowland moist habitats. This is the most important breeding site of the greater snow goose (*Chen caerulescens atlantica*) with more than 55,000 breeding individuals (Reed et al. 2002). Many other migrating bird species nest in the area but their density is relatively low compared to snow geese (Lepage et al. 1998). Two species of lemmings are present: the brown lemming (*Lemmus sibericus*), which prefers wetlands and feeds largely on graminoids (Gauthier et al. 1996; Negus and Berger 1998), and the collared lemming (*Dicrostonyx groenlandicus*), which prefers drier habitats and feeds primarily on *Dryas* and other forbs (Rodgers and Lewis 1986). The abundance of both lemming species is generally comparable except in years of peak abundance when brown usually outnumber collared (Gruyer 2007). Total lemming abundance throughout the study area peaked in 2004 but was low and moderate in 2003 and 2005, respectively (Gruyer 2007). The arctic fox is the main terrestrial predator of the system. It preys mainly on lemmings but also feeds on snow goose eggs and chicks, especially when rodent populations drop (Bety et al. 2001).

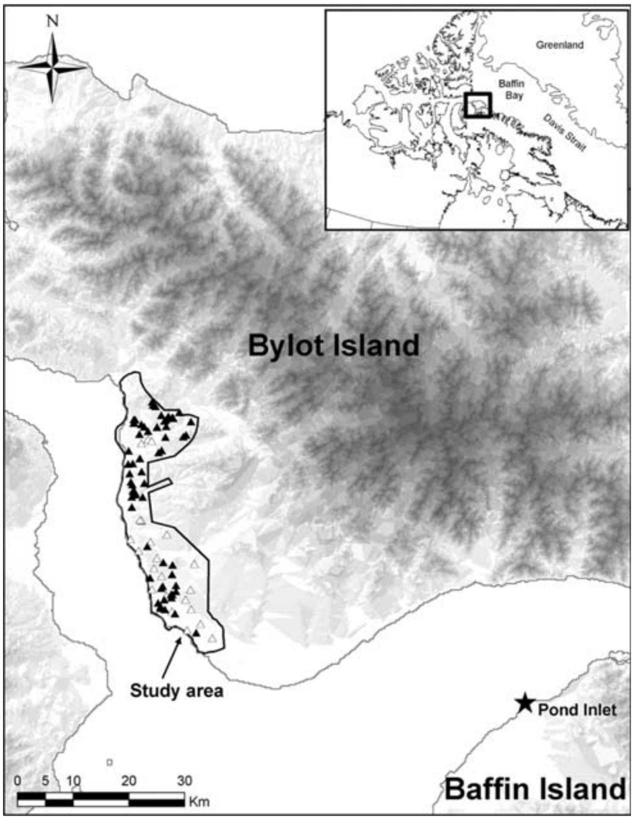

Fig. 1 Topographical map of Bylot Island (73°0′N, 80°0′W), Nunavut, Canada, with location of study area and arctic fox breeding (*white triangles*) and non-breeding (*black triangles*) dens

More than 40 dens had been found opportunistically on the south plain of Bylot Island between 1993 and 2002 and were already known at the start of the study. In the summer of 2003, we performed an extensive search for dens by foot and snowmobile to complete the survey throughout the study area. We covered an area of approximately 60 km of coastline that extended between 4 and 15 km inland, depending on the relief. The surveyed area totalled approximately 425 km^2 (Fig. 1). It was delimited to the west by the sea, and to the north and east by polar semi-deserts where preliminary exploration showed that dens where either rare or absent. Logistic constraints prevented us from surveying the area to the south. To minimize the risks of including arctic hare burrows in our analysis, only structures with more than one entrance were considered as arctic fox dens. Field work performed in subsequent years indicated that virtually all dens ($n = 83$) in the study area had been found by 2003.

Landscape characteristics of denning sites

Each den was positioned using a global positioning system (GPS) receiver (±5 m) and its surrounding environment was first described at a coarse landscape level. Topographic heterogeneity was evaluated using the terrain ruggedness index (TRI) proposed by Nellemann and Fry (1995). The TRI was derived from a 1:50,000 topographic map (with 20 m contour intervals) at two different scales (1 × 1 km and 2 × 2 km). The whole study area was divided into quadrats (of either 1 × 1 km, $n = 448$ or 2 × 2 km, $n = 131$), within which four transects of a fixed length (1 or 2 km) were positioned in a rosette, centered in the quadrat, at 45° intervals. The TRI was calculated for each transect using the following equation:

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

where TNC is the total number of contour lines intercepted by the transect and TNF is the total number of changes in aspect (ups and downs) along the transect (Nellemann and Fry 1995). For each quadrat, the transect with the highest index value was retained. Each den was assigned the TRI of the quadrat in which it was located. Aspect and slope inclination were measured with a GPS and clinometer, respectively. The habitat surrounding the den (100 m radius) was visually classified as xeric, mesic, or moist according to the dominant habitat class. Distance to closest coastline, lake and stream were measured on a digitalized map of the area using ArcGIS (ESRI® ArcMapTM9.0)

Two variables were used to estimate food resource distribution at the landscape scale. The first one was the distance to the main snow goose breeding colony of Bylot Island. Since 1991, several hundred adult females are marked with plastic neck-collars annually during brood-rearing (Gauthier et al. 2001). Each year, systematic searches of collared females on nests are conducted throughout the colony and the position of each nest is recorded using a GPS. Assuming that collared geese are distributed randomly in the colony, we calculated a cross-validated (LSCV) fixed 95% kernel (Seaman and Powell 1996) of the position of their nests from 2000 to 2005, using the ArcView (ESRI®, ArcView GISTM 3.2a) animal movement extension (Hooge et al. 1999), to map the average extent of the whole colony. We then measured the distance separating dens from the closest edge of the colony with ArcGIS and used it as an index of goose availability for foxes.

Second, an index of lemming habitat quality (ILHQ) was derived from signs of utilisation left by lemmings, in order to reflect lemming availability to foxes. The study area was classified into ten habitats based on vegetation communities and topographical features: graminoid wet meadow, moist meadow, moist shrub tundra, mesic tundra, graminoid mesic tundra, shrub-heath tundra (dominance of *Cassiope*), shrub-heath tundra (dominance of *Dryas*), stream edge, moist polygons and mesic polygons (S1 in Electronic supplementary material; see Duclos et al. 2006 for detailed habitat description). Lemming's relative use of each habitat was estimated through counts of lemming burrows and faeces. Although faeces can be deposited in both summer and winter, burrows are predominantly used in summer (Predavec and Krebs 2000), and thus our index of lemming habitat quality should reflect more summer than winter habitat use. The measures were taken during the summer of 2005, a year of moderate lemming abundance following the peak of 2004. Since both faeces and burrows were observed to persist for multiple years, the derived index represents a multi-annual average use by lemmings of each habitat category.

We sampled ten sites per habitat. Sampling sites were chosen in the field by selecting throughout the study area patches of at least 3,000 m^2 of uniform habitat, to avoid influence of other surrounding habitats. For each sampling site, we positioned two parallel transects (20 m apart) on which three 1.5 × 1.5 m quadrats were located 20 m apart. We estimated the number of lemming faeces within each quadrat. A thorough search for scats was performed, by moving vegetation or other obstacles, to minimise bias in counts due to variation in detectability between habitats. We counted lemming burrows in six 40 m^2 quadrats (2 × 20 m) adjacent to the quadrats used to estimate faeces. The total N per habitat for both faeces and burrows is thus 60 quadrats (10 sites × 2 transects × 3 quadrats). For each site, the mean numbers of scats and burrows were transformed to values constrained between 0 and 1. This was accomplished by dividing the mean number of faeces or burrows of site i by the highest value obtained across all sites. The value for faeces and burrows were then added up for each site to obtain a value between 0 and 2 representing lemming utilisation of the site. An index of lemming habitat use (ILHU) was then created for each habitat category by calculating the mean value for all sampled sites in the habitat. Using a digital vegetation map (Duclos et al. 2006) and aerial photographs of Bylot Island, we then measured the proportion occupied by each of the ten habitats within a 0.5, 1 and 2 km radius around fox dens using ArcGIS. An index of lemming habitat quality (ILHQ) was then assessed for each den, at these three scales, by summing the product of the proportion occupied by each habitat (P_i) by its index of lemming habitat use (ILHQ = $\Sigma(P_{\mathrm{i}} * \mathrm{ILHU}_{\mathrm{i}})$).

To determine whether arctic foxes *select* for particular environmental characteristics when establishing their den, we also measured each variable at random locations ($n = 92$) within the study area. We compared characteristics of den locations to those of random locations using two-sample *t* tests or Mann–Whitney *U* tests, depending on the normality of the variable. *G* tests were used to compare nominal variables.

Local characteristics of denning sites

Preliminary observations showed that most dens were excavated in natural ridges and/or in slopes of 10° or more (95% of dens satisfied at least one of these conditions). Therefore, we assumed that the presence of at least one of these features was essential for the establishment of a den. Sites with such characteristics (hereafter called "potential denning sites") were abundant in the study area and did not appear limiting. To determine the importance of micro-climatic and micro-topographic features on the selection of a denning site, we compared den characteristics with those of nearby potential denning sites. In the field, we randomly selected two to four potential denning sites, depending of their availability, within a 100 m radius of each studied den using a table of random angles and distances. For each den and potential site, we sampled the same variables as follows. We measured height of ridges, by averaging maximum height on each side, and/or the inclination and orientation of the slope using a clinometer and GPS, respectively. We estimated ground snow cover in a 10 m radius (<5%, 5–25%, 25–50%, 50–75%, ≥75%) at the beginning of June. We classified the substrate as sand, loam, gravel, rock or a combination of these. Finally, we measured ground temperature (5 cm below surface) and depth of loose soil (depth to permafrost or rocky substrate) at five random locations on the den and its periphery. We compared heights of ridges and ground temperatures using paired sampled *t* tests. We applied Wilcoxon signed-rank tests to compare snow cover (using the median of each class of cover), slope aspect and inclination, as well as depth of loose soil because data were not distributed normally. Finally, we used the *G* test statistic to compare substrate types between dens and potential den sites. In this case, categories with significant differences were identified using Bonferoni 95% interval. Table 1 summarizes the complete set of variables measured at each den.

Comparisons of reproductive and non-breeding dens

From 2003 to 2005, we visited 83 dens at least twice during the summer (mid-June and -July) to check for signs of fox presence. Reproductive effort of foxes varied greatly among years with few litters born in 2003 ($n = 4$) compared to 2004 ($n = 15$) and 2005 ($n = 9$). Dens where cubs were observed at least once during this period were classified as "reproductive dens", while those with no reproduction observed during the three years of the study were classified as "non-breeding dens". Since arctic foxes have been observed to move their litter between dens during the rearing period, reproductive dens were further divided into "natal" (cubs observed at beginning of breeding season) or "rearing" (movement of litter directly observed or cubs only appeared late in the breeding season) dens. To determine if any variable could explain the different utilisation made of these three categories of dens, we compared environmental characteristics of each set of dens using ANOVAs or Kruskal–Wallis tests, depending on the normality of the data, followed by Dunn's multiple comparison tests.

Second, we used resource selection function (RSF) analysis (Manly et al. 1993) to determine the relative importance of each variable in distinguishing between reproductive and non-breeding dens. Since the movement of a litter from its natal den to another rearing den may be prompted by disturbances such as our visits or the trapping conducted at dens during a concurrent study, rearing dens were excluded from this analysis and only natal dens were considered as reproductive dens. We used binary logistic regression to estimate the resource selection probability functions (RSPF) which took the form:

$$W^{*}(x) = \{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n)\}/ \\ \{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n)\}$$

where $W^{*}(x)$ is the probability of a den being used for reproduction for a given combination of variables (x_i) and their coefficients (β_i). We only included in the models variables that were not strongly correlated to each other (Pearson correlation <0.7) and for which measurements were repeated at most dens. SNOW was therefore

Table 1 Description of habitat variables measured at dens

Variable	Description
ALTITUDE	Elevation above sea level (m)
TRI_1KM	Terrain ruggedness index at 1 × 1 km scale
TRI_2kM	Terrain ruggedness index at 2 × 2 km scale
SNOW	Ground snow cover in 10 m radius (<5, 5–25, 25–50, 50–75, >75%)
HEIGHT	Height of ridge averaged over both sides
EXPO_EW	East-west component of slope exposition
EXPO_NS	North-south component of slope exposition
INCLINATION	Degree of inclination of slope (°)
HABITAT	General habitat in 100 m radius (moist, mesic or xeric)
SUBSTRATE	Substrate (sand, loam, gravel, rock or combination)
TEMP	Ground temperature at 5 cm
DEPTH	Depth of loose soil (depth to permafrost or rocky substrate)
DISTCOAST	Distance to closest coastline (km)
DISTDEN	Distance to closest den (km)
DISTSTREAM	Distance to closest stream (km)
DISTLAKE	Distance to closest lake (km)
NBDEN_1kM	Number of dens present in a 1 km radius
NBDEN_3KM	Number of dens present in a 3 km radius
NBDEN_5kM	Number of dens present in a 5 km radius
GEESE	Minimal distance to edge of goose breeding colony (km)
LEMM_500M	Index of lemming's habitat quality in 0.5 km radius
LEMM_1KM	Index of lemming's habitat quality in 1 km radius
LEMM_2KM	Index of lemming's habitat quality in 2 km radius

eliminated for RSF analysis because of missing values for many dens, while TRI_2KM, LEMM_1KM and NBRDEN_5KM were removed because of multicollinearity with other variables. Finally, to avoid eliminating important variables through this preliminary screening, the two following pairs of correlated variables (ALTITUDE/INCLINATION and DISTDEN/EXPO_EW) were retained, but only one variable from each pair was used at a time in a given model to respect the condition of independence of variables.

We performed multiple logistic regressions (MLR), using forward and backward stepwise approaches, to do a preselection of the best variables allowing for discrimination of the two classes of dens. Different models were then built and evaluated using Akaike's information criterion (AIC) to select the best, while most parsimonious, RSF models. Due to our small sample size, we used the second-order AIC (AICc) (Burnham and Anderson 2002). McFadden's Rho-squared statistic was also calculated for each model to assess model performance. McFadden's Rho-squared is intended to mimic *r*-squared used in linear regression (Steinberg and Colla 2004) but tends to have lower values. According to Hensher and Johnson (1981), values between 0.20 and 0.40 should be considered very satisfactory. The discriminatory power of each model was also evaluated through receiver operating characteristic (ROC) curves analysis (Pearce and Ferrier 2000). According to Pearce and Ferrier (2000), the area under ROC curves represents an adequate estimation of the discrimination performance of a model. Estimated by the *c*-statistic, ROC values between 0.7 and 0.8 are considered acceptable while values between 0.8 and 0.9 are considered excellent discrimination (Hosmer and Lemeshow 2000). The area under the curve was evaluated using the Mann–Whitney *W* statistic approach proposed by Hanley and McNeil (1982).

Results

Index of lemming habitat use

The ILHU varied according to habitat type (Kruskal–Wallis test statistic = 40.499, $P < 0.001$) but habitat categories did not always differ significantly from each other. Of the ten habitat categories, stream edge was the most heavily used by lemmings while lemming scats and burrows were almost totally absent in graminoid wet meadows (Fig. 2). While faeces may be underestimated in some wet habitats due to faster degradation compared to dry habitat, we believe that this bias is small because faeces were still found in relatively high abundance in most wet habitats (MST, MM, SE) compared to dryer ones (GMT, MT, SHTD, SHTC).

Landscape characteristics of den sites

We compared the environment surrounding 83 fox dens to that surrounding 92 random sites (Table 2). First, we confirmed the strong selection for mounds. Furthermore, dens were located on steeper slopes than random sites and were also located closer to streams than expected. Finally, neither slope orientation, terrain ruggedness, distance to lakes, surrounding habitat (moist, mesic or xeric), distance to coastline, distance to goose colony nor lemming habitat quality influenced the location of arctic fox dens.

Local characteristics of denning sites

Comparison of characteristics of dens with those of potential denning sites revealed that snow cover on dens

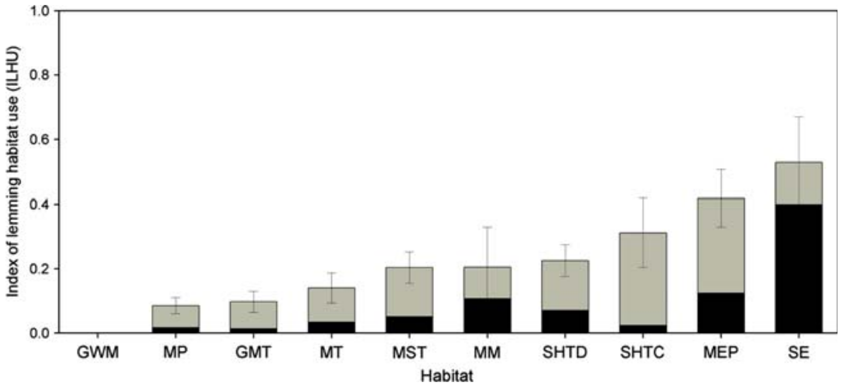

Fig. 2 Index of lemming habitat use (ILHU) for the ten habitats recognized on the south plain of Bylot Island, Nunavut, Canada. Mean ± standard errors are given. Relative contribution of scat abundance (*dark gray*) and burrow abundance (*light gray*) to total index is illustrated. *GWM* graminoid wet meadow, *MP* moist polygons, *GMT* graminoid mesic tundra, *MT* mesic tundra, *MST* moist shrub tundra, *MM* moist meadow, *SHTD* shrub-heath tundra (Dryas), *SHTC* shrub-heath tundra (*Cassiope*), *MEP* mesic polygons, and *SE* stream edges

was lower than on other potential sites, while ground temperature and depth of loose soil were significantly higher at dens (Table 3). Dens were also usually located on steeper slopes than other potential sites and had a more southerly orientation, but there were no significant differences in the height of mounds selected by arctic foxes. Finally, dens were preferentially excavated in sandy substrate while loam was avoided despite its relatively high availability in the ecosystem.

Comparisons between reproductive and non-breeding dens

We compared 83 dens (20 natal, 7 rearing and 56 non-breeding) which were monitored over three consecutive years (2003–2005). Natal dens were closer to the goose breeding colony than non-breeding dens and were farther away from another den than non-breeding or rearing dens (Table 4). The number of dens in a 1, 3 and 5 km radius

Table 2 Comparison of environmental variables between arctic fox dens (n = 83) and random sites (n = 92) on the south plain of Bylot Island, Nunavut, Canada

Variables	Den sites Mean ± SE	Random sites Mean ± SE	Statistic value	*P*
Sites located on mounds (%)	31	1	33.1[a]	<0.001
Slope inclination (°)	18.2 ± 1.5	3.6 ± 0.8	1,112	<0.001
N/S exposition (1.0 = N/–1.0 = S)	–0.21 ± 0.10	–0.11 ± 0.14	909	0.726
E/W exposition (1.0 = E/–1.0 = W)	–0.19 ± 0.08	–0.46 ± 0.09	673	0.070
Terrain ruggedness index (1 km)	1.06 ± 0.10	1.11 ± 0.07	3,626	0.452
Terrain ruggedness index (2 km)	2.12 ± 0.16	2.22 ± 0.15	3,434	0.603
Surrounding habitat (% of sites)				
Moist	12%	16%		
Mesic	84%	81%	0.185[a]	0.911
Xeric	4%	3%		
Distance to closest stream (km)	0.19 ± 0.02	0.22 ± 0.02	4,536	0.032
Distance to closest lake (km)	1.15 ± 0.10	1.05 ± 0.11	3,341	0.154
Distance to coastline (km)	3.82 ± 0.26	4.14 ± 0.29	3,988	0.611
Distance to goose colony (km)	14.7 ± 1.2	11.9 ± 1.13	3,363	0.174
Lemming habitat quality (0.5 km)	0.170 ± 0.005	0.180 ± 0.004	4,030	0.526
Lemming habitat quality (1 km)	0.181 ± 0.005	0.191 ± 0.003	4,079	0.436
Lemming habitat quality (2 km)	0.183 ± 0.004	0.186 ± 0.003	3,929	0.740

Mean ± SE are given. Sites are compared using Mann–Whitney *U* tests (*U*) unless mentioned otherwise

[a] *G* test statistic (*G*)

Table 3 Comparison of environmental variables between arctic fox dens and potential denning sites in a 100 m radius around the den, on the south plain of Bylot Island, Nunavut, Canada

Variables	Den sites Mean ± SE	Potential sites Mean ± SE	Statistic value	*df*	*P*
Height of mound (m)	1.31 ± 0.36	0.84 ± 0.12	1.72^{a}	8	0.124
Ground temperature (°C)	8.6 ± 0.3	7.4 ± 0.3	5.10^{a}	77	<0.001
Depth of loose soil (cm)	32.3 ± 0.6	27.7 ± 0.7	5.29	76	<0.001
Slope inclination (°)	21.6 ± 1.5	17.7 ± 0.6	3.03	57	0.002
N/S exposition (1.0 = N/–1.0 = S)	–0.26 ± 0.11	–0.06 ± 0.08	–2.04	42	0.042
E/W exposition (1.0 = E/–1.0 = W)	–0.09 ± 0.09	–0.24 ± 0.07	1.38	42	0.167
Snow cover (%)	17.9 ± 5.7	40.3 ± 7.2	–2.62	17	0.009
Substrate (% of sites)					
Sand	39%*	15%*			
Loam	34%*	66%*			
Gravel	1%	0%			
Loam + Sand	9%	3%	32.6^{b}	6	<0.001
Loam + Gravel	9%	9%			
Sand + Gravel	6%	6%			
Loam + Rocks	1%	1%			

Mean ± SE are given. Sites are compared using Wilcoxon signed-rank test (*W*) unless mentioned otherwise. Values with asterisk (*) differed significantly according to Bonferonni 95% interval

[a] Paired *t* test statistic (*t*)

[b] *G* test statistic (*G*)

Table 4 Comparison of environmental variables between natal (n = 20), rearing (n = 7) and non-breeding (n = 56) arctic fox dens on Bylot Island

Variables	Natal dens Mean ± SE	Rearing dens Mean ± SE	Non-breeding dens Mean ± SE	Test statistic	*P*
Distance to closest stream (km)	0.14 ± 0.04^{ab}	0.06 ± 0.03^{a}	0.23 ± 0.03^{b}	8.05	0.018
Distance to goose colony (km)	7.33 ± 1.78^{a}	13.64 ± 3.51^{ab}	17.46 ± 1.5^{b}	10.0	0.007
Lemming habitat quality (0.5 km)	0.208 ± 0.006^{a}	0.224 ± 0.005^{a}	0.173 ± 0.006^{b}	17.7	<0.001
Lemming habitat quality (1 km)	0.200 ± 0.006^{a}	0.208 ± 0.009^{a}	0.175 ± 0.005^{b}	13.7	0.001
Lemming habitat quality (2 km)	0.192 ± 0.007^{a}	0.203 ± 0.011^{a}	0.175 ± 0.004^{b}	14.4	0.001
Distance to closest den (km)	1.62 ± 0.24^{a}	0.63 ± 0.32^{b}	0.74 ± 0.09^{b}	12.3	0.002
Number of dens in 1 km radius	1.0 ± 0.4^{a}	2.6 ± 0.7^{ab}	2.6 ± 0.4^{b}	7.00	0.003
Number of dens in 3 km radius	4.8 ± 0.7^{a}	6.1 ± 1.1^{ab}	9.0 ± 0.5^{b}	18.2	<0.001
Number of dens in 5 km radius	11.8 ± 1.3^{a}	13.1 ± 2.4^{ab}	16.4 ± 0.5^{b}	12.8	0.002

Mean ± SE are given. Variables are compared using Kruskall–Wallis test. Values with the same letter on the same line do not differ significantly ($P > 0.05$, Dunn test)

was significantly lower around natal dens than around non-breeding ones (Table 4). Finally, rearing dens were closer to a stream than non-breeding dens and both natal and rearing dens were located in better lemming habitats than non-breeding dens at all scales (Table 4).

Our index of lemming habitat quality was clearly variable across the study area (S2 in Electronic supplementary material). Lemming's habitat quality around reproductive (natal and rearing) dens (1 km radius) was positively correlated to the distance separating the den from the goose colony (Fig. 3). Reproductive dens located far away from the colony were thus located in higher quality lemming habitats than those located close to the colony. Figure 3b shows that virtually all dens located both far away from the colony and in poor lemming habitats were not used for reproduction.

Seventy-six dens (20 natal and 56 non-breeding) were used to build the resource selection functions. Nine variables

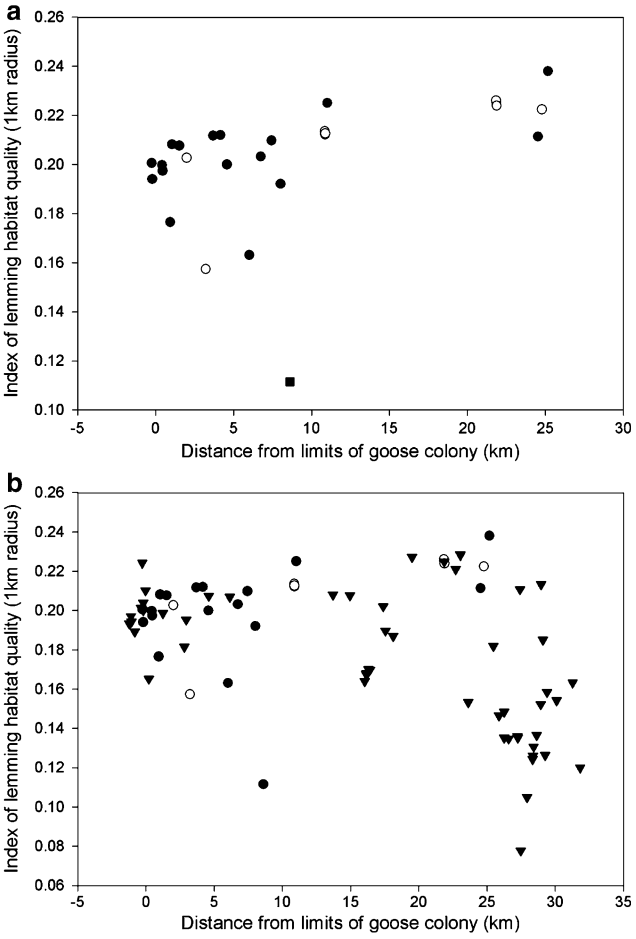

Fig. 3 **a** Correlation between distance to the goose colony and lemming's habitat quality around reproductive dens (1 km radius). Natal dens are illustrated by *black circles* and rearing dens by *white circles*. One outlier is illustrated by the *black square symbol*. With outlier included $n = 27$, Pearson $r = 0.454$, $P = 0.017$; with outlier excluded, Pearson $r = 0.633$, $P = 0.001$. **b** Correlation between distance to the goose colony and lemming's habitat quality around all dens (1 km radius). Natal dens are illustrated by *black circles*, rearing dens by *white circles* and non-breeding dens by *black triangles*; $n = 83$, Pearson $r = -0.419$, $P < 0.001$

were retained through the forward and backward stepwise approach: GEESE, NBDEN_3KM, LEMM_500M, LEMM_2KM, EXPO_NS, DISTCOAST, DISTDEN, DISTSTREAM and TRI_1KM. Table 5 summarizes the six best models obtained. All six models had a ΔAICc lower than 2.0, suggesting substantial evidence for each of them (Burnham and Anderson 2002). The most parsimonious model (model 1) allowing for discrimination of the two sets of dens included three variables (distance to the goose breeding colony, number of dens present in a 3 km radius, and lemming's habitat quality in a 500 m radius) linked through the following equation:

$$W^{*}(x) = \{\exp(V)\}/\{1 + \exp(V)\}$$

where

$$V = -2.393 - 0.074(\text{GEESE}) - 0.375(\text{NBDEN\_3KM}) + 24.2(\text{LEMM\_500M})$$

According to this model, the probability of a den being used for reproduction increases with lemmings habitat quality around it, while it decreases as its distance to the colony and the number of dens in a 3 km radius increase. These three variables were all retained in the top six models, which strongly suggests that they were the most important variables explaining the selection of reproductive dens by arctic foxes. This model had a high discriminatory power as its likelihood of correctly classifying a den as reproductive, within a pair of reproductive and non-breeding dens, was 88.5%. Three additional variables were retained in the other five top models: distance to closest coastline (negative effect as distance increases), distance to closest den (positive effect as distance increases), and north/south component of slope exposition (negative effect as exposition becomes northward).

Table 5 Variables retained in the model with the sign of the effect, second order Akaike's information criterion (AICc), McFadden's rho squared (MF) and receiver operating characteristics curve *c*-statistic (ROC) for the six top logistic models discriminating between reproductive (natal) and non-breeding arctic fox dens on Bylot Island, Nunavut, Canada

	Models variables	AIC_c	ΔAIC_c	MF	ROC
1	–GEESE, –NBDEN_3KM, +LEMM_500M	62.56	0.000	0.384	0.885
2	–GEESE, –NBDEN_3KM, +LEMM_500M, –DISTCOAST	62.99	0.124	0.405	0.902
3	–GEESE, –NBDEN_3KM, +LEMM_500M, +DISTDEN	63.03	0.468	0.405	0.895
4	–GEESE, –NBDEN_3KM, +LEMM_500M, +GEESE x LEMM_500M	63.28	0.722	0.402	0.894
5	–GEESE, –NBDEN_3kM, +EXPO_NS, –DISTCOAST, +LEMM_2KM, +DISTDEN	64.03	1.472	0.444	0.921
6	–GEESE, –NBDEN_3KM, +LEMM_500M, –EXPO_NS, –DISTCOAST	64.43	1.876	0.411	0.905

See Table 1 for description of model variables

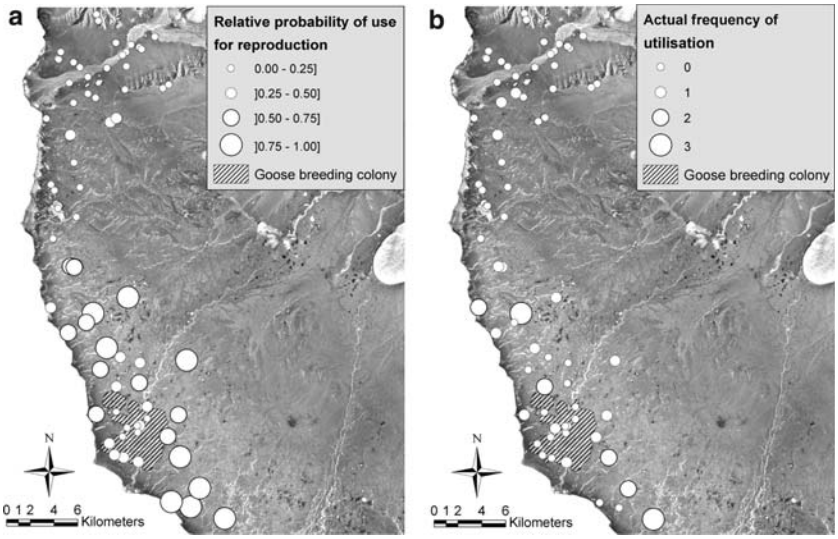

Fig. 4 Use of dens by arctic foxes on the south plain of Bylot Island, Nunavut, Canada. **a** Probability of use of dens for reproduction according to the most parsimonious model selected (see results and Table 5) and **b** observed frequency (number of years) of utilisation of dens by arctic foxes for reproduction between 2003 and 2005

We used the most parsimonious model (model 1) to predict the probability of reproduction at each den of the study area (Fig. 4a) and compared it with the actual frequency of utilisation of each den by reproductive arctic foxes (i.e. number of years the den was used for reproduction from 2003 to 2005) (Fig. 4b). According to the model, dens located inside the limits of the goose colony usually had a lower probability of use than those located in its periphery, which was consistent with field observations. Comparison of both figures shows that only seven dens had a high predicted probability of utilisation (>50%) but were not actually used as natal dens between 2003 and 2005. Of those seven dens, four were actually rearing dens while only three dens were truly never used for reproductive purpose during the study period. While most natal dens had a high predicted probability of use, five out of the 20 natal dens were used more often than predicted by the model. Finally, when plotting the actual frequency of utilisation of a den for reproduction against the probability predicted by our model (Fig. 5), we can see that highly used dens usually have a higher probability predicted by our model, confirming the high accuracy of our model in predicting arctic fox use of a den for reproduction.

Discussion

Selection of denning sites

Few landscape variables explained the spatial distribution of fox dens on Bylot Island. The availability of favourable topographical structures, such as ridges and slopes, and the proximity of streams, were the only features clearly selected by arctic foxes.

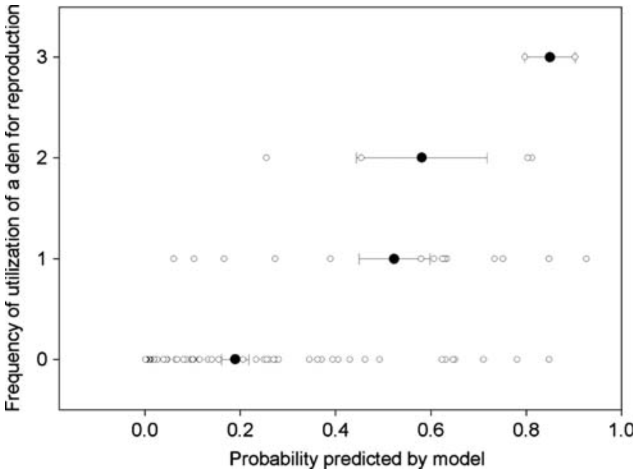

Fig. 5 Frequency (number of years) of utilisation by arctic foxes of each den as a natal den, between 2003 and 2005, compared with the probability of utilisation predicted by the most parsimonious model (model 1, see Table 5). Mean probabilities with standard errors are illustrated for each category of frequency

According to Tannerfeldt et al. (2003), the permafrost layer in the arctic tundra represents a physical barrier for arctic foxes trying to dig new dens in spring. Den sites may then be limited to areas where the active layer is sufficiently deep and where soil conditions allow burrowing. Ridges and mounds typically consist of warm mineral soil with coarse texture, are well drained, and have a deep layer of soil over the permafrost or bedrock (Swanson 1996). Terrains with steep slopes should also be well drained and thus reduce the formation of permafrost. Our analysis at the local scale further highlighted the high importance of aspect and inclination of slope on the selection of a specific denning site by foxes. The prevalence of arctic fox dens on southerly rather than on northerly exposed slopes has often been reported (Chesemore 1969; Garrott et al. 1983; Smits et al. 1988; Dalerum et al. 2002), and is believed to be linked to the warmer microclimate associated with southerly exposed locations. The southerly orientation and steep slope of denning sites may be responsible for their lower snow cover, higher soil temperature and higher depth to permafrost compared to other nearby potential sites. Furthermore, considering the high permeability of sand (Gluyas 2005), selection of sites with sandy rather than loam substrate may also provide a better drainage of the site, allowing for a faster warming of the ground, reducing the formation of permafrost and thus allowing for an easier digging. The combination of these criteria may therefore result in a deep active layer allowing arctic foxes to excavate sufficiently large structures for an efficient protection from hazardous weather or even for potentially giving birth and rearing a litter.

The utilisation of streamside cutbanks for denning is a common phenomenon in arctic foxes (Chesemore 1969; Macpherson 1969; Smits et al. 1988). In our study area, 35 out of 83 dens (42%) were located directly along the banks of rivers, streams or temporary water channels. We suggest two non exclusive hypotheses to explain this observation. First, the good drainage found on the slopes along water channels may provide good ground stability, easy digging, and a reduction of flooding risks. Second, stream sides were the most heavily used habitats by lemmings (Fig. 2). Choosing a site near a stream could thus ensure that a reliable source of food is present nearby.

Neither lemming's habitat quality nor distance to the goose colony affected the distribution of dens. Considering the large energy expenditure related to reproduction, we expected a greater influence of parameters associated with food resources. However, from 1993 to 2005, only 42% of existing dens had a record of reproduction (Gauthier et al., unpublished data). Other studies also found a proportion of reproductive dens varying between 23 and 55% in their research area (Prestrud 1992a; Anthony 1996; Dalerum et al. 2002). This suggests that arctic foxes dig out a large number of dens but only use some of them for reproduction. Hence, the criteria used by foxes to select sites for the excavation of a new den may differ from those used to select a reproductive den.

Selection of reproductive dens

Food resource distribution seems to be the major criterion influencing the selection of reproductive dens by arctic foxes. Food resources clearly affect cub survival, as was demonstrated by Tannerfeldt et al. (1994) through a supplementary feeding experiment. Surprisingly, although the importance of food resources on the dynamic of arctic fox populations is widely recognized (Angerbjorn et al. 1995; Kaikusalo and Angerbjorn 1995; Tannerfeldt and Angerbjorn 1998; Angerbjorn et al. 1999; Roth 2003), the influence of food resource distribution on the selection of reproductive dens had never been demonstrated.

The positive association between lemming's habitat quality around reproductive dens and distance to the goose colony suggests that arctic foxes trade off between these two food sources and may need to maximize the availability of at least one of them when selecting a reproductive den. As distance separating the den from the colony augments, it may become increasingly important to be located in a good lemming habitat to fulfill the alimentary requirements of a growing litter. The fact that the relation between distance to the colony and quality of lemming habitat around the den is positive for reproductive dens but becomes negative when considering all dens (Fig. 3) suggests that this result is not due to a biased distribution of high quality lemming habitats far away from the goose colony. It actually reinforces the idea that foxes breeding far away from the colony select dens located in the best lemming habitats, even though such sites are scarcer.

Although dens closer to the goose colony had a higher probability of being used for reproduction according to our model, dens located inside the limits of the colony were rarely used by reproducing foxes. The intensive exploitation of this extremely aggregated resource by several foxes, as well as the high density of geese present, may increase disturbance, intraspecific competition for food, as well as risks of predation for cubs, thus reducing the potential fitness of foxes reproducing inside the colony. For a territorial species such as the arctic fox (Tannerfeldt et al. 2003), it may become impossible to defend a territory and raise a litter in such a food rich area. The territoriality of arctic foxes could also explain the lower number of dens present around reproductive dens (i.e. the third variable retained in all top models). Two alternative hypotheses could explain this observation. First, reproducing arctic foxes may avoid areas with high density of dens, thereby reducing intraspecific competition as well as energy investment for defending the territory against potential neighbours. However, the causal relationship may also be opposite, and the scarcity of dens around reproductive dens could be a consequence of the strong territoriality of reproducing foxes. Since reproductive dens are repeatedly used over time, the regular presence of territorial foxes at those dens may deter other foxes from digging new dens in their vicinity.

Few dens with no record of reproduction had a high predicted probability of use (>50%) according to our top model. This suggests that this simple model accurately predicts the selection of reproductive dens by arctic foxes. Furthermore, the fact that the most heavily-used dens also had a high probably of utilisation predicted by our model further reinforces its high adequacy. However, considering that a few dens selected by reproducing foxes had a very low probability of use predicted by our model, this suggests that some additional variables may be missing in our top model. For example, a secondary variable retained in other models was the minimal distance to coastline. Marine resources have been shown to represent up to 70% of arctic fox diet in coastal areas (Angerbjorn et al. 1994). The proximity of a den to the coastline may thus provide additional food sources, such as seals, seabirds or other marine wildlife, and could thus compensate for the poor lemming habitat or the high distance of a den from the goose colony. Although some variables may be absent from our top model to accurately explain den site use by reproducing foxes, the 88.5% discriminatory power of this model suggests that food resource distribution and territoriality are probably the most important parameters influencing den selection by reproductive arctic foxes.

Conclusion

We suggest that topography and micro-climate are the main factors influencing den site selection by arctic foxes. The presence of permafrost under a very thin layer of active soil may be the dominant factor limiting the excavation of new dens. Selection of sites with early snowmelt, southerly exposition and good drainage increases the chance of having a deep active layer over permafrost, and thus represent favourable conditions for the excavation of a den. However, the large number of non-breeding dens suggests that foxes dig out many dens wherever physical characteristics of the site allow it, but only those located in areas with sufficient food resources and far enough from other dens are used for reproductive purpose. Hence, despite the high abundance of dens in the arctic tundra, high quality dens suitable for reproductive purpose may still be limited. The growing occurrence of red foxes in the high arctic (Marsh 1938; Macpherson 1964; Chirkova 1968) may therefore represent a potential threat for arctic fox populations through competition for adequate reproductive dens (Killengreen et al. 2007). Monitoring of fox communities and studies of preferences of both species in term of reproductive dens are required to evaluate the potential impacts of red foxes' range expansion on arctic fox populations.

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ELECTRONIC SUPPLEMENTARY MATERIAL

S1: Floristic and environmental description of the 10 habitats recognized on the south plain of Bylot Island, Nunavut, Canada (adapted from Duclos et al. 2006).

Habitat type	Description
Habitat classification based mostly on vegetation	
Graminoid Wet Meadow	Flat microtopography dominated by mosses and graminoids (*Dupontia fisheri*, *Eriophorum scheuchzeri*)
Moist Meadow	Hummocky or flat microtopography dominated by graminoids *(Eriophorum sp., Carex spp., Arctagrostis latifolia)*, dwarf-shrubs *(Salix arctica*, *Dryas Integrifolia*), and mosses
Moist Shrub-Tundra	Hummocky microtopography dominated by dwarf-shrubs (*S. arctica*, *Salix reticulata*,*D. integrifolia*), mosses, and lichen
Mesic tundra	Hummocky microtopography dominated by mosses, graminoids (*A. latifolia*, *Luzula* spp), and dwarf-shrubs (*S. arctica*, *Cassiope tetragona*)
Grass Mesic Meadow	Flat microtopography dominated by graminoids (*Alopercus alpinus*, *A. latifolia*, *Luzula nivalis*), dwarf-shrubs (*S. arctica*) and mosses.
Shrub Heath Tundra (*Dryas)*	Flat or hummocky dry microtopography dominated by dwarf-shrub (*D. integrifolia*, *Salix* spp), and lichen
Shrub Heath Tundra (*Cassiope*)	Hummocky or flat dry microtopography dominated by dwarf-shrub (*C. tetragona*, *Salix* spp), mosses and graminoids (*A. latifolia*, *Carex* spp., *Luzula* spp.,*E. triste*)
Habitat classification based mostly on topography	
Moist Polygons	Polygons with concave or flat center usually filled with graminoid wet meadow and rims dominated by moist shrub tundra
Mesic Polygons	Polygons with convex or flat center covered by mesic tundra and separated by deep and narrow water canals
Stream edge	Twenty-meter area on each side of streams

S2: Variations in index of lemming's habitat quality (ILHQ) throughout study area on the south plain of Bylot Island, Nunavut, Canada. Each category of ILHQ regroups 20% of the total area. Arctic fox reproductive dens (white triangles) and non-breeding dens (black triangles) are illustrated.