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Microhabitat utilisation, home ranges, and movement patterns of the collared lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic

Martin Predavec and Charles J. Krebs

Abstract: We investigated patterns of home ranges, movements, and microhabitat use of the collared lemming (*Dicrostonyx groenlandicus*) on Kent Peninsula, Northwest Territories. Eleven animals were fitted with radio collars and intensively radio-tracked for 2 months. Males and females differed in their home ranges and movement patterns. Males moved, on average, 47.4 m and females 10.5 m in a 2-h period. Corresponding to the larger movements, males had larger home ranges than did females and the degree of overlap was greater in males. In both sexes activity was centred on burrows, but this was more evident in females. Collared lemmings differentially used available microhabitats, preferring areas with larger hummocks, a larger number of burrows, and greater cover of *Salix lanata*. It is suggested that this pattern of microhabitat use is related to reducing detection and capture by predators. Collared lemmings appear to be highly conservative in their patterns of habitat use and home ranges across their distribution.

Résumé : Nous avons étudié les domaines vitaux, les déplacements et l'utilisation des microhabitats chez le Lemming variable (*Dicrostonyx groenlandicus*) dans la péninsule de Kent, Territoires du Nord-Ouest. Onze lemmings ont été munis de colliers émetteurs et suivis par radio pendant 2 mois. Les domaines et les patterns des déplacements ne sont pas les mêmes chez les mâles et les femelles. Les mâles se déplacent en moyenne de 47,4 m en 2 h et les femelles de 10,5 m. En conséquence, les mâles ont des domaines plus grands que les femelles et le chevauchement est plus important chez les mâles. Chez les deux sexes, l'activité est centrée autour les terriers, et ceci est plus apparent chez les femelles. Les lemmings utilisent différemment les microhabitats disponibles préférant les zones à buttes plus importantes, au nombre de terriers plus élevé et à couverture de *Salix lanata* plus étendue. Il est probable que ce choix de microhabitat soit relié à des propriétés de réduction de détection et de capture par les prédateurs. *Dicrostonyx groenlandicus* semble un animal très conservateur quant à l'utilisation de l'habitat et au choix de domaines dans toute sa répartition.

[Traduit par la Rédaction]

Introduction

Like other lemming species, collared lemmings, *Dicrostonyx groenlandicus*, are often characterised by the cyclic nature of their population fluctuations, and much work has focussed on recording and explaining these cycles (for a review see Stenseth and Ims 1993). Despite the large volume of work carried out on the various lemming species, relatively little attention has been paid to aspects of their basic biology, such as diet, home ranges, and habitat use, particularly in North American species.

To date only four published studies have investigated home ranges in the collared lemming (Brooks and Banks 1971; Rodgers and Lewis 1986*b*; Brooks 1993; Blackburn et al. 1998) and three have looked at habitat use (Batzli et al. 1983; Pitelka and Batzli 1993; Morris et al. 2000). The most comprehensive of these studies is that by Brooks (1993), based at Churchill and Eskimo Point in Manitoba. These studies have shown that males generally have larger home ranges than do females and this is likely to be associated with their polygamous mating system. Home ranges appear to contract as the population density increases and at peak population density there is little difference in home-range size between the two sexes (Brooks 1993). Collared lemmings are generally found in relatively dry habitats such as ridges and hummocks and also those with an abundance of low willow shrubs. How applicable, however, are the results from these previous studies to all populations of collared lemmings? The collared lemming has the most northern distribution of any rodent (Hall 1981) and is found across the Canadian High Arctic. Can we make generalisations about basic aspects of their biology across their entire range? Further, previous studies were largely not concerned with the activity of animals within home ranges, or with specific microhabitats that made up the general habitat used by the animals.

In this study, intensive radio-tracking was used during the increase phase of a population cycle to investigate movements, home-range sizes, and microhabitat use in the col-

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Table 1. Variables and their units used in estimating microhabitat use by collared lemmings, together with the reasoning for each variable.

Variable	Units	Reasoning
Water	A scale of 1–10 (1 = dry bare rock and 10 = a tundra pond)	Water strongly influences the distribution of potential food plants for collared lemmings, which are generally thought to use relatively dry habitats (Pitelka and Batzli 1993)
Topography	Maximum height of hummocks (cm)	Observations suggest that collared lemmings use spaces between hummocks as runways, with larger hummocks possibly providing more protection from predators
Salix arctica, *S. lanata*, *S. reticulata*, sedges, *Dryas integrefolia*, mosses, herbs, lichens	Percent ground cover in 10% categories	These were the major groups of plants present in the area, many of which are food items for collared lemmings (Rodgers and Lewis 1986*a*)
Pedicularis spp.	Number of plants	A major plant group found in the area
Burrows	Number of intact burrow entrances in the area	Collared lemmings readily use already constructed burrows both as shelter and as natal nests (Brooks 1993)

lared lemming, and the results were compared with those from past studies in other regions.

Materials and methods

Study area, trapping, and radio-tracking

The study was carried out at the Walker Bay Research Station on Kent Peninsula in the Northwest Territories (108°6′W, 68°21′N). The area is characterised by a combination of dry hummocky mixed tundra with codominant ground and dwarf willows and herbs, and mesic mixed tundra with codominant shrubs and grasses.

Animals were trapped on a 270 × 270 m trapping grid consisting of 100 Longworth traps, with each trap station 30 m from the next. Traps were baited with fresh apple and had been locked open during the previous winter. Trapping took place between July and August 1995. During this time 11 animals (7 females and 4 males) were fitted with radio collars (Biotrack SS-2 and SS-1). Collars had a mean mass of 3.5 g and were attached using electrical cable ties. The mean mass of animals was 71 g and so the masses of the collars were within the acceptable 5% range. All animals were adult and reproductively active. During the study, all animals captured that were above the acceptable mass for a collar had a collar attached.

Regular position fixes were taken for each animal between 10 July and 9 August 1995. During either 10- or 14-h shifts starting at 8 a.m. or 6 p.m., positions were recorded for animals every 2 h, thus covering all time periods of the day. In total there were 18 separate shifts spread over the period of the study. For the first location fix of a shift the exact position of an animal on the grid was found and recorded relative to adjacent trap stations and if necessary marked using a coloured survey flag. For subsequent fixes during a shift it was firstly determined from a distance whether or not the animal was above ground and secondly whether or not it was moving. If the animals was in roughly the same position as at the first fix, this was confirmed by triangulation from at least 50 m away to minimise disturbance of the animal. If the animal had moved, the exact position was once again determined and again if necessary marked using a flag. If an animal could not be detected on the trapping grid, the surrounding area was searched for a distance of 100 m on all sides of the grid and if the animal was still not detected, it was recorded as having left the grid for that time period. Given the extent of the searches, the shallowness of the burrows, and the reliability of the transmitters, we are confident that animals not detected on the grid were in fact absent and not simply present and undetectable.

Animals' movement patterns

A recorded movement of an animal was taken to be any change in location between two sequential 2-h fixes, the straight-line distance between the two positions being the distance moved. Alternatively, if the animal was not detected on the grid, whereas it had been at the previous fix, or visa versa, it was again recorded as having moved, and the straight-line distance to the nearest edge of the grid was taken as the distance moved. To distinguish between movements within a burrow system and movements between burrows, only movements longer than 10 m were considered to be true movements. Frequency distributions of moves made by males and females in each 2-h period were compared using a χ^2 test, whereas mean movement distances were compared using a Mann–Whitney U test of ranks.

Home ranges

All data were used for calculating home ranges. The minimum convex polygon was used to calculate home ranges after subsequent fixes were found to be statistically non-independent (Swihart and Slade 1985). To check whether enough fixes had been obtained to reliably show the true home-range sizes, the area of the minimum convex polygon was calculated with fixes sequentially removed. The range was considered a reliable estimate if in a plot of home-range size against the cumulative number of fixes the curve reached an asymptote, which occurred, on average, after 30 fixes. The area and maximum length of the distributions were calculated, and means were compared for males and females by means of unpaired t tests.

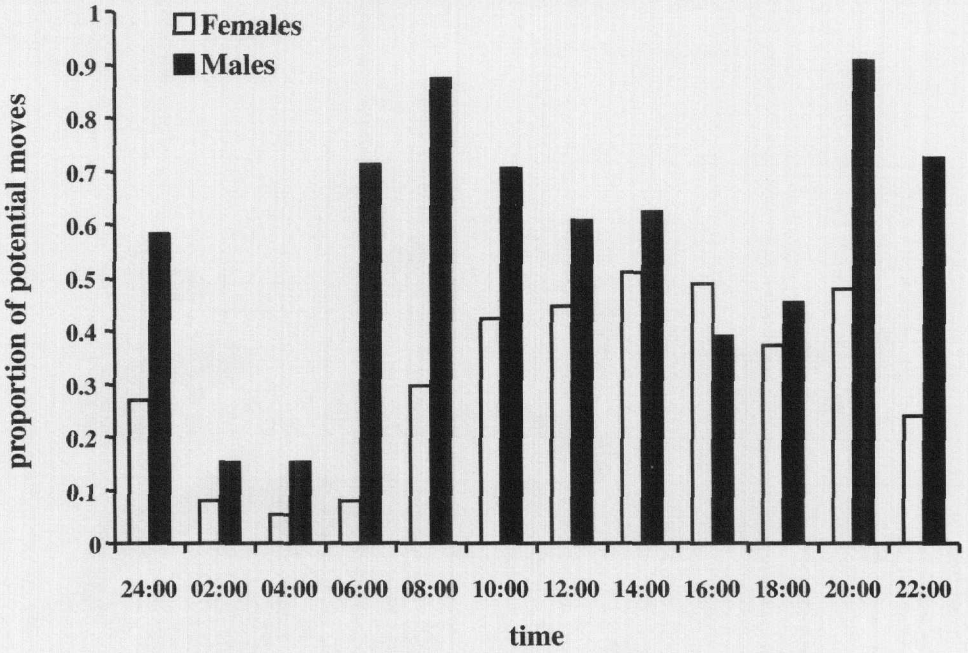
Microhabitat use

At each new position fix for an animal, 12 habitat variables were measured in a 2 by 2 m quadrat centred on the location. Measurements were taken either at the time of the position fix if the animal was in a burrow or at a later date if the animal was above ground, so as not to disturb the animal's activity. The senior author measured all variables to reduce variation. Variables, with their units and reasoning, are given in Table 1.

To determine the abundance of microhabitat variables, the same 12 habitat variables were measured on a grid of 361 points, with each measurement point 15 m from the next.

Data were analysed using discriminant function analysis comparing used and available microhabitat types. Only the first location fix for a single individual in a particular location was used, in order to reduce potential bias due to an individual animal. Data from all individuals were combined. Prior to the analysis, data were tested for the assumptions of normality and the presence of outliers that can greatly influence the outcome of the discriminant analysis (Tabachnick and Fidell 1996). Where necessary, transformations of the original data were made. The analysis was run on both the complete function, including all variables, and using a forward-stepping method, with a p-to-enter of 0.15, to obtain a reduced function. In both cases a jackknifed classification matrix was

Fig. 1. The proportion of potential moves actually made by male and female collared lemmings. A recorded movement of an animal was taken to be any change in location greater than 10 m between two sequential 2-h fixes.



calculated. To test the validity of the function a cross-validation technique was used. All original cases were assigned randomly to two groups; 65% of cases fell into a learning sample and 35% fell into a test sample. The learning sample was used to estimate the classification functions and then the resulting functions were used to classify the test sample. All analyses were carried out using SYSTAT version 9.0 (Wilkinson 1989).

Results

Movements

Male collared lemmings moved much larger distances than did females (89.8 m ± 57.9 (mean ± 1 SD) and 36.0 m ± 23.6, respectively; Mann–Whitney *U* test on ranks, $U = 2716$, $p < 0.0001$). The largest single movement recorded for a male during a 2-h period was 290 m compared with the largest for a female of 131 m. Males did not move during 46% of the paired fixes compared with 65% in females. Both sexes made the fewest movements between 02:00 and 04:00 (Fig. 1). Males showed two peaks in movements, at 08:00 and 20:00, whereas female activity peaked once, at 14:00. There is a significant difference between the distributions of timing of movements between males and females (Fig. 1; $\chi^2 = 79.19$, $p < 0.001$).

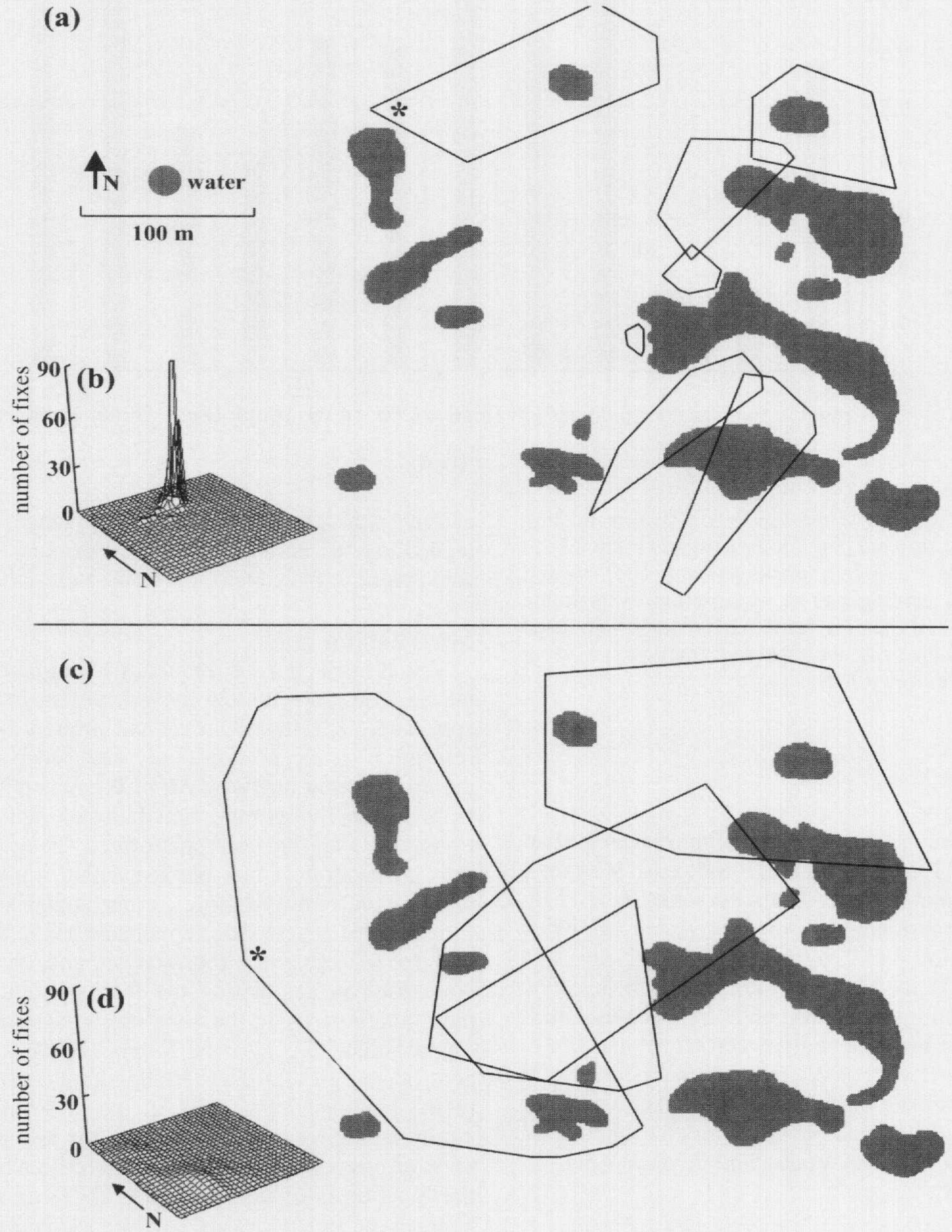
Home ranges

Males' home ranges were much larger than those of females in terms of both area and maximum length (23 984 ± 13 387 m^2 (mean ± 1 SD) for males, 3 514 ± 2 666 m^2 for females ($t = 3.0$, df = 10, $p < 0.05$), and 241 ± 91 m for males, 99 ± 52 m for females ($t = 3.45$, df = 10, $p < 0.01$), respectively (Figs. 2*a* and 2*c*)). Males showed a much greater degree of overlap in their home ranges than did females (the mean proportion of ranges overlapping was 0.43 ± 0.35 and 0.05 ± 0.04 for females. The patterns of space use within the activity ranges also differed: males tended to spread their activity across most of the activity range, whereas females tended to concentrate their activity around 1 or 2 burrows located close to the edge of the home ranges (Figs. 2*b* and 2*d*).

Microhabitat use

Visual inspection of frequency histograms for the 12 habitat variables showed that herbs, mosses, lichens, *Pedicularis* spp., and *Salix reticulata* all had limited distributions at the resolution of the present study and hence were not used in the discriminant analysis. All of the remaining variables apart from water, topography, and burrows had skewed distributions and were arcsine-transformed. Even after transformation, inspection of box plots revealed a number of outliers, which were removed from further analysis (Tabachnick and Fidell 1996). There thus remained 303 "available" cases and 229 "used" cases for the analysis and 65% of these cases were used in calculating the learning functions. The complete function, using the 8 variables, was strongly significant (approximate $F_{[3,350]} = 59.6$, $p < 0.0001$). Eighty-four percent of all cases in the learning sample were classified correctly, but this fell to 81% in the jackknifed classification. Applying the resulting function to the test sample resulted in 85% of cases being classified correctly, which suggests that the function is relatively robust. The 4 most important variables in the function were burrows, *Salix lanata*, topography, and grass. The forward-stepping function resulted in the inclusion of 5 variables and this was again strongly significant (approximate $F_{[3,350]} = 59.6$, $p < 0.0001$). Eighty-four percent of the learning-sample cases were classified correctly using the resulting function and this dropped by only 1% with the jackknifed classification. Eighty-eight percent of the test cases were classified correctly using the function, again suggesting a robust fit. The reduced function, including only 5 variables, was as robust as the complete model. The 5 variables included were burrows, *S. lanata*, topography, grasses, and sedges. Where animals were located, there

Fig. 2. Home ranges of seven female (*a*) and four male collared lemmings (*c*) at Walker Bay, Kent Peninsula, Northwest Territories. Home ranges were drawn using minimum convex polygons. An asterisk indicates the home ranges that are shown as utilisation distributions for a single female (*b*) and a single male (*d*). Surface plots were rendered using a kernel smoothing technique.



was a larger number of burrows, greater hummock size, a higher percent cover of *S. lanata* and grasses, and a lower percent cover of sedges (Table 2).

Discussion

This study looked at three measures of movement: mean distance, percentage of potential moves made, and the timing of moves. All three factors showed remarkable similarity to the findings of previous studies based at Churchill and Eskimo Point (Brooks and Banks 1971; Brooks 1993). The earlier studies showed that males moved, on average, 69 m and females 37 m (90 and 36 m, respectively, in the present study), and that males did not move on 51% of occasions and females on 71% (47 and 72%, respectively, in the present study). Both studies showed a reduction in the proportion of potential moves made between 02:00 and 06:00 and between 14:00 and 18:00, although these reduced movement

Table 2. Comparison of the 5 variables used in the reduced discriminant function.

Variable	Available	Used
Burrows	0.44±1.11	3.25±2.97
Topography (cm)	17.77±11.15	27.97±9.11
Salix lanata (%)	3.77±7.71	24.47±33.32
Grasses (%)	3.18±4.25	6.78±5.85
Sedges (%)	36.57±28.90	19.28±16.56

Note: The data shown are not transformed, although in the analysis, *S. lanata*, grasses, and sedges were all arcsine-transformed. Values are given as the mean ± standard deviation; $n_{\text{available}}$ = 303 and n_{used} = 229. See Table 1 for an explanation of the variables.

times were shorter in the present study and the afternoon reduction was not as dramatic. A number of factors may explain the overall pattern in the timing of movements and the differences between males and females. Firstly, females must remain in the burrow to suckle and protect young. Males, on the other hand, must move around to find females for mating and this may explain the extended activity period for males and the greater proportion of potential moves made. During the time of the study there was 24 h of daylight and so it is hard to relate light patterns to the activity of the animals, particularly the decline in activity between 02:00 and 06:00. However, it has been suggested that predators such as Arctic foxes are most active at night (Frafjord 1994), and lemmings may time their activity so as to reduce the risk of predation (Brooks 1993). It must be pointed out, however, that at the study site, many avian predators are active during the daytime peak of lemming activity (D. Wilson, personal communication).

The patterns of home-range areas were also very similar to those found in past work, but the exact sizes of home ranges were slightly different. In the present study, estimated density was 1.9/ha during the increase phase of the population cycle (Blackburn et al. 1998; Wilson et al. 1999), which is a similar to the density found during the peak phase by Rodgers and Lewis (1986*b*). However, differences between the home ranges of males and females in the present study were much greater than that found by Rodgers and Lewis (1986*b*). Females' home-range sizes were 15% of males' in the present study, whereas in the earlier work they were 86% at the same population density, although over all 3 years of the previous study they covered 45% (Rodgers and Lewis 1986*b*). The 15% difference is very similar to that shown by Brooks (1993), although the home ranges of both males and females in the present study were, on average, three times larger than those in the previous work (Brooks 1993). However, Brooks (1993) showed that as the population density increased, differences between the sizes of males' and females' home ranges disappeared, which may explain the discrepancies between the present study and that of Rodgers and Lewis (1986*b*).

Home ranges of adults in the present study were also significantly larger than those of juveniles at high densities in the same population (approximately 100 m^2; Blackburn et al. 1998). What is not clear is whether the differences can be attributed to changes in population density or to the different stages of maturity. Juveniles' home ranges are similar in size to those of adult females at high density at Eskimo Point and Churchill and the home ranges of collared lemmings have been shown to contract with increasing population density (Brooks 1993).

Although the home ranges in the present study were relatively large, use of the total area within home ranges was not uniform and usage differed between males and females. Females tended to concentrate their activity at any one time around a single burrow, and since all the females were reproductively active, it is likely that these burrows contained young. As in earlier studies, females' burrows were located towards the edge of the activity range and it has been suggested that this may make it harder for predators to locate burrows relative to the main foraging areas (Brooks 1993). Females did move burrows, but infrequently. Males, on the other hand, used multiple burrows and regularly moved between them, covering a much larger area than did the females. Males showed a similar degree of overlap of home ranges to that found in past work, whereas the degree of overlap for females was much less (5% in present study compared with 32% in previous work; Rodgers and Lewis 1986*b*). However, the earlier study combined 3 years of data and hence three different population densities. Nevertheless, Brooks (1993) found no overlap in females' home ranges. Overlap in male–male and male–female home ranges occurred at very close time scales. On a number of occasions males were located in the same burrow as females and they would remain together for up to 8 h. Spatial overlap between males did occur within the same day, but they were never located within the same burrow system. Female–female overlap did not appear to occur on the same temporal scale. Although home ranges did overlap spatially, boundaries appeared to be strictly maintained at any one time. On two separate occasions females moved burrows and hence moved the centre of activity within their home ranges. Within 48 h, a female from an adjacent home range then shifted her activity to centre on the recently vacated burrow. It is known that juveniles remain at the natal burrow for up to 10 days after the mother has departed (Brooks 1993). Given the timing of the move of the females, it is likely that the arrival of the new female resulted in the killing of any juveniles in the burrow (see Mallory and Brooks 1978). Hence, although there appears to be a small degree of overlap in the females' home ranges, it is likely that they strictly maintain and defend the boundaries of their activity ranges. Males, on the other hand, possibly because of the large size of their activity ranges, seem not as able to maintain range boundaries. However, male collared lemmings are known to be aggressive in captivity (Bowen and Brooks 1978), yet in the present study not many individuals were captured with scars resulting from intraspecific encounters. It is likely that if two males encounter one another, fighting will occur, but given the sizes of the home ranges in the present study and the relatively low density of animals, encounters between males are likely to be infrequent.

The pattern of microhabitat use found in the present study corresponds to the broader scale pattern of habitat use found in other studies of the same species and population. Morris et al. (2000) demonstrated that collared lemmings showed a preference for hummock habitat, which was described as containing high hummocks and having vegetation dominated by prostrate and taller shrubs, forbs, sedges, and grasses. However, the pattern of habitat use was density-dependent, and collared lemmings moved into suboptimal habitats when the population density increased and when *Lemmus lemmus* moved into the preferred hummock habitat. This general pattern of habitat use has been found in other studies (e.g., Pitelka and Batzli 1983). In the present study, collared lemmings differentially used areas with high hummocks, high percent cover of plants, including *S. lanata*, and numerous burrows; there are a number of possible explanations for this pattern of usage. Firstly, plants such as *S. lanata* are an important food item for collared lemmings during winter months, when they live in subnivean spaces (Predavec et al. 2000), yet the importance of this food item is reduced in summer months, when the present study was carried out. Secondly, collared lemmings are regularly subject to predation, and a number of predators are present in the study area, including snowy owls (*Nyctea scandiaca*), short-eared owls (*Asio flammeus*), pomarine jaegers (*Stercorarius pomarinus*), and Arctic foxes (*Alopex lagopus*) (Wilson et al. 1999). The 3 most important variables involved in microhabitat selection, namely burrows, *S. lanata*, and hummocks, may all be related to providing protection from predators, in terms of both avoiding detection and evading capture. Previous studies have suggested that mortality from predation may be as high as 50% (Wilson et al. 1999), hence any mechanism that reduces the chance of predation will be advantageous. In future studies it would be interesting to see whether or not the pattern of microhabitat selection is density-dependent as is overall habitat selection. Mortality studies (Wilson et al. 1999) suggest that the percentage of mortality due to predation increases at the peak of the population cycle and during the decline phase, when animals are likely to be in suboptimal habitats (Morris et al. 2000). This pattern suggests that habitat and microhabitat selection are likely to be important factors in collared lemming mortality.

When the results of the present study are compared with those of previous studies from other regions, it appears that the collared lemming is highly conservative in terms of patterns of habitat use, movements, and home ranges. Future studies should concentrate on comparing these factors at different stages of the population cycle to elucidate their role in driving population fluctuations.

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