Diet overlap of collared lemmings and tundra voles at Pearce Point, Northwest Territories

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We used a combination of faecal pellet analysis and feeding enclosure trials to determine the diets of collared lemmings (*Dicrostonyx kilangmiutak*) and tundra voles (*Microtus oeconomus*) at Pearce Point, Northwest Territories, and we looked for evidence of exploitative competition between the two species. Voles preferred monocotyledons (*Carex* and *Eriophorum* spp.) and lemmings preferred *Dryas integrifolia*. We found that there was little overlap in the natural diets of the two species, but that overlap was increased experimentally when both species were forced to forage in the same habitats. However, food preferences generally did not change. The diet of collared lemmings at Pearce Point was similar to that found in all other studies except those done in Alaska, where *Dryas* is uncommon. We conclude that exploitative competition for food is unlikely to be an important factor in interspecific relations between collared lemmings and tundra voles.

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Les résultats de l'analyse des boulettes fécales et d'expériences dans des enceintes fermées nous ont permis de déterminer le régime alimentaire de Lemmings variables (*Dicrostonyx kilangmiutak*) et de Campagnols nordiques (*Microtus oeconomus*) à Pearce Point, dans les Territoires du Nord-Ouest. Nous avons examiné les probabilités de compétition entre les deux espèces dans leur exploitation du milieu. Les campagnols préfèrent les monocotyles (*Carex* et *Eriophorum* spp.), alors que les lemmings consomment de préférence *Dryas integrifolia*. Nous avons constaté qu'il y avait peu de chevauchement entre les régimes alimentaires naturels des deux espèces, mais que le chevauchement augmentait lorsque les deux espèces étaient forcées de chercher leur nourriture dans les mêmes milieux. Cependant, de façon générale, les préférences alimentaires ne changeaient pas. Le regime alimentaire des Lemmings variables de Pearce Point était semblable à celui signalé dans toutes les autres études, sauf en Alaska où *Dryas* est une plante rare. Nous concluons que la compétition pour la nourriture ne constitue probablement pas une composante importante des relations interspécifiques entre les Lemmings variables et les Campagnols nordiques.

[Traduit par la rédaction]

Introduction

Collared lemmings (*Dicrostonyx kilangmiutak*) and tundra voles (*Microtus oeconomus*) are the two most abundant microtines occurring at Pearce Point, Northwest Territories. Several observations suggest that there might be competition between these species. First, the geographic distributions of tundra voles and collared lemmings overlap in a strip along the northern coasts of Eurasia and western North America. Within this broad area they are ecologically separated at the local level, showing distinct habitat segregation in the summer months. Tundra voles prefer wet sedge meadows where cover is abundant (Tast 1966; Batzli and Jung 1980). Collared lemmings favour drier upland tundra characterized by heath plants and sparse sedges (Watson 1956; Krebs 1964; Fuller et al. 1975). Despite these habitat preferences, both species are able to utilize the same foods, suggesting that some competition may be occurring (Batzli and Jung 1980). Secondly, although there is clear evidence that collared lemmings cycle in the eastern Canadian Arctic, where tundra voles do not occur (Krebs 1964; Parker 1974), no such trends have been documented west of Bathurst Inlet, where the distributions of the two species overlap. It is possible that compensatory interactions between voles and lemmings may be preventing large cyclic fluctuations (Pitelka 1957).

Competition can be divided into two main forms: exploitative and interference. Interference competition involves defence of a space containing an essential resource, while exploitative competition involves direct competition for the resource in question (Miller 1967). This study was designed to test the hypothesis that exploitative competition for food is occurring between collared lemmings and tundra voles. If this hypothesis is true, diet overlap of the two species should be large. A potential for exploitative competition need not be realized if the two species segregate by habitat. Using faecal pellet analysis, we attempted to measure both the summer and winter diets of tundra voles and collared lemmings. To complement these results we measured the diets of animals foraging within experimental enclosures. With this information we examine diet overlap and test the hypothesis of exploitative competition.

Study area

Research was conducted at Pearce Point, Northwest Territories (69°49′N, 122°43′W), along the northwestern coast of mainland Canada between 30 May and 1 September 1990. The area is characterized by tall dolomite cliffs along the coast that support high summer densities of rough-legged hawks (*Buteo lagopus*), a specialized microtine predator, and peregrine falcons (*Falco peregrinus*), mainly an avian predator, as well as a variety of terrestrial predators including foxes (*Alopex lagopus* and *Vulpes vulpes*) and ermine (*Mustela erminea*).

Between the cliffs and rocky outcrops are patches of suitable microtine habitat that can be divided into two main types. The drier heath tundra is typical of coarse, shallow, slightly calcareous soils and is characterized by short sedges (*Carex* spp.) and *Dryas integrifolia*, an evergreen shrub, and by several species of herbs and willow that occur as minor components (Ritchie et al. 1987). This type of association can be found on exposed upper slopes and ridges and in upland tundra locations. It appears to be good habitat for the collared lemming and is similar to areas on Banks Island that support large numbers of collared lemmings. The second habitat consists of mesic to wet meadows with

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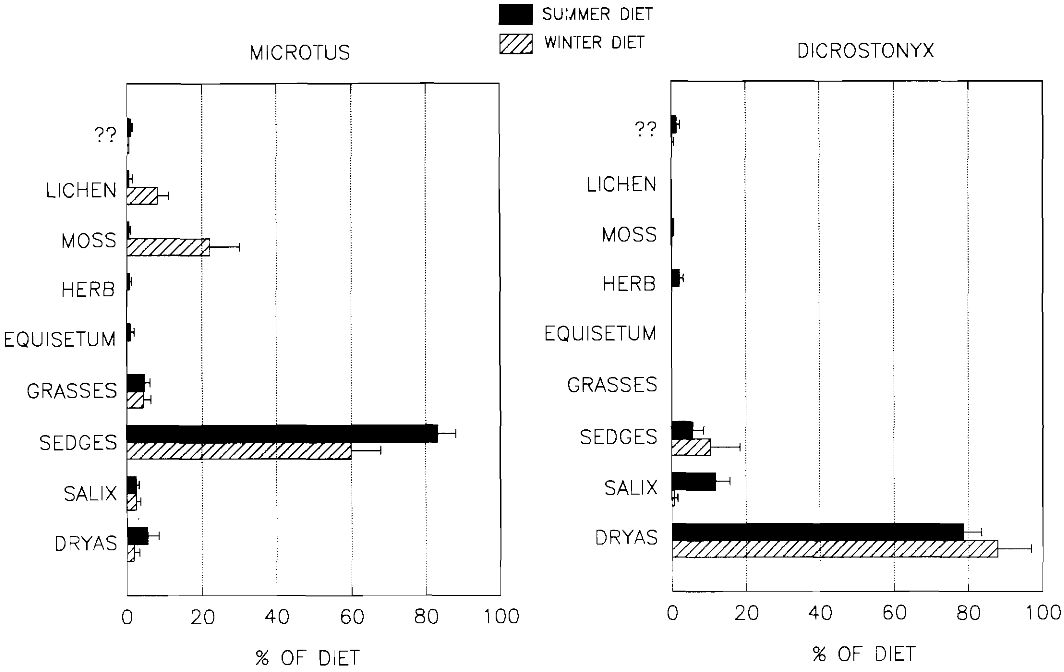

FIG. 1. Summer and winter diets of *Microtus oeconomus* and *Dicrostonyx kilangmiutak* at Pearce Point, N.W.T., as determined from faecal pellet analysis (*Microtus*: summer $n = 62$, winter $n = 25$; *Dicrostonyx*: summer $n = 79$, winter $n = 20$). Error bars represent 95% confidence intervals. "Sedges" were *Carex* and *Eriophorum* spp.; ??, unknown.

much taller sedges (*Carex* spp.) and cotton grasses (*Eriophorum* spp.), often growing over a surface mat of mosses. These communities are located in low, flat areas where drainage is poor, usually around the margins of ponds or streams or at the borders of tundra polygons. A description of similar communities in the nearby Melville Hills region is given by Ritchie et al. (1987). These wet meadows at Pearce Point appear to be a good habitat for the tundra vole, which reaches densities of 50–100/ha in some years (C.J. Krebs, unpublished data).

Methods

Natural diets

Faecal pellet samples representing the winter diet were collected in early spring 1990 on four study areas. Collections were made from wooden nest boxes and Longworth traps locked open through the previous winter, as well as from winter latrines. Faecal pellets of each species were readily distinguishable by their distinctive size. Those of *Dicrostonyx* were 2–5 mm in length and 1–2 mm in diameter; those of *Microtus* were 5–10 mm in length and up to 3 mm in diameter. From mid-June to September 1990, samples were collected from animals in hand during trapping sessions on six study areas and preserved in separate vials containing 75% ethyl alcohol.

To identify cuticular fragments in the faecal samples, we collected typical specimens of all the common plants in the study area throughout the summer. Replicas of the epidermis from both the abaxial and adaxial surfaces of leaves, stems, and flowers were obtained following methods outlined by Rodgers (1984). Photomicrographs of these replica preparations were taken with a 35-mm camera using transmitted light.

Microscope slides of faecal samples were prepared using modifications of existing techniques (Clarke 1960; Hansson 1970). Each faecal sample was treated with 85% lactic acid and placed in a boiling water bath to remove fat, gastric juices, and many of the small unidentifiable cells of leaf mesophyll. Separation of fragments was achieved by gentle teasing with a stirring rod. Two slides were prepared from each sample.

Observer training for faecal analysis was based on the preparation of test slides for all the common plant species, with the assistance of Dr. Art Rodgers, who has analyzed lemming diets from the eastern Arctic with these techniques (Rodgers 1984). In this study plant fragments were not identified to species but only to broad plant groups. Errors of identification were thus minimized.

Analysis of the faecal preparations was carried out under low magnification (× 100) with a compound microscope. Randomly chosen transects were tranversed until 40 plant fragments had been examined on each of two slides, for a total of 80 fragments. We attempted to identify all of the fragments along the transect by comparing epidermal structures with those in the reference collection. The frequency of occurrence of each fragment type was recorded. Tests of 10 samples showed no significant differences in the frequency of occurrence of plant species between pairs of slides (χ^2; $p > 0.05$ in all cases). Consequently, data from paired slides were pooled for further analysis.

Enclosure diets

Since voles and lemmings are often habitat segregated in summer, it is interesting to ask how much their diets would overlap if they were confined to the same habitat. To determine this we measured the diet within small experimental enclosures. Four 1 × 1 m enclosures constructed of 1/4-in. hardware cloth were used to facilitate direct observations of *D. kilangmiutak* and *M. oeconomus* feeding in a natural habitat. Enclosures were replicated twice in each of two habitats, *Dryas* upland (dry) and sedge hummock (wet). Only one rodent species was tested in each enclosure. Percent cover of different plant species in each enclosure was estimated.

Feeding trials were carried out from 28 July to 15 August 1990. Animals caught in Longworth live traps were placed in an enclosure for 20 min. Sample sizes are given in Figs. 2 and 3. All species of plants eaten were recorded in a frequency table, with each bite recorded as a single observation. Individual plants of rare species that had been eaten during a trial were replaced before the next animal was introduced, to maintain a consistent species composition. Each animal was observed in both habitat types.

Food preferences

The availability of forage must be known in order to calculate most food preference indices. To collect these data we carried out visual cover estimates in 200 random 0.25-m^2 quadrats located on two study areas. One site (Water Lake) contained primarily lemmings, while the other (Caribou – Second Valley) contained only voles. We used both Manly's α and the rank-preference method to calculate food preferences (Krebs 1989, pp. 396–397). Our visual cover estimates

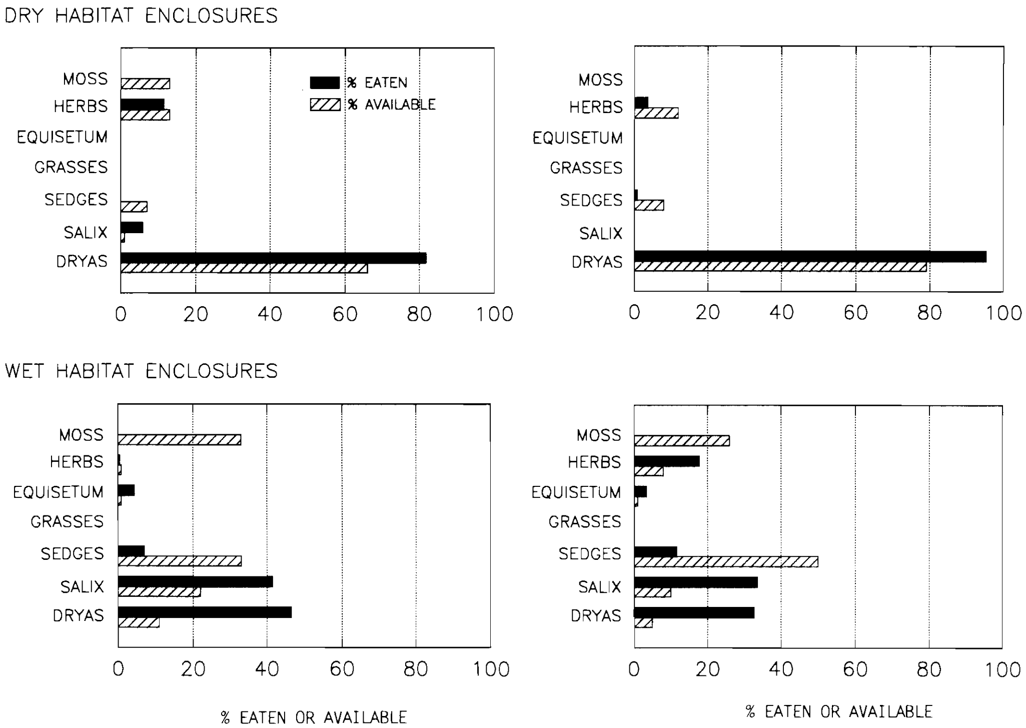

FIG. 2. Comparison of forage availability and summer diet of *Dicrostonyx kilangmiutak* in four 1 × 1 m enclosures, two located in dry habitats (n = 8 and 5) and two in wet habitats (n = 11 and 7). "Sedges" were *Carex* and *Eriophorum* spp.

were highly correlated with clip samples from the same study areas collected by D. Reid (unpublished data).

Diet overlap

The Morisita–Horn index of overlap (Krebs 1989, p. 385) was used to estimate diet overlap between lemmings and voles. Standard errors were obtained using 200 bootstrap replications. To determine whether estimates were biased by sample size, rarefaction curves were calculated for both winter faecal analysis and the analysis of enclosure diets. Overlap estimates were plotted against sample size, and the infection point where the curve became level indicated when an adequate sample size had been reached. Calculations were performed using the program NICHE (D. Schluter, University of British Columbia, Vancouver).

Results

Natural diets

Summer

Faecal pellet analysis indicated that the summer diet of both tundra voles and collared lemmings was composed predominantly of one food type (Fig. 1). While collared lemmings ate mainly the evergreen shrub *D. integrifolia* (78.5 ± 3.5%; 95% confidence interval), tundra voles consumed primarily sedges (*Carex* and *Eriophorum* spp.) (83.2 ± 4.9%). Minor food types of lemmings in summer included *Salix* spp. (11.7 ± 2.8%) and sedges (5.6 ± 1.9%). Rare components included herbs, mosses, Graminae, *Equisetum* spp., and lichen. These species were also rare components of the voles' summer diet, which included *D. integrifolia* as its only minor component (5.5 ± 3.8%).

Winter

The winter diet of lemmings (Fig. 1) showed a 10% increase in the amount of *D. integrifolia* and a near doubling of the amount of sedges compared with the summer diet. The amount of *Salix* and other rare species in the diet decreased to nearly zero. The winter diet of *M. oeconomus* showed a 30% decline in the amount of sedges, and mosses became a major component. Lichens became a minor component (Fig. 1). Mosses and lichens formed a negligible part of the summer diet of *M. oeconomus*.

Enclosure diets

The diet of lemmings foraging in enclosures placed in dry habitats (Fig. 2) was quite similar to that of lemmings foraging naturally (Fig. 1), despite altered forage availabilities within these enclosures. However, this was not true of lemmings foraging in enclosures placed in wet habitats (Fig. 2). Under these conditions, *Salix* spp. and *Dryas* were eaten in similar quantities, both plant types comprising between 35 and 45% of the diet. The amount of *Equisetum* consumed in wet enclosures approached 5% compared with only 0.1% in the natural summer diet.

The diets of voles in enclosures of both habitat type (Fig. 3) showed several differences from the natural diet. The amount of sedges eaten was nearly halved. In the enclosures where *Dryas* was available, the proportion consumed approached or exceeded that of sedges. The proportion of herbs eaten in enclosures placed in dry habitats was almost 20 times that eaten naturally, and a similar increase in consumption occurred for *Equisetum* spp. in wet habitats.

Preferences

Both the rank preference and Manly's α preference indices obtained from faecal pellet sampling indicated that collared lemmings foraging naturally preferred *Dryas*, followed by *Salix* spp. Manly's α values for all other food types were much smaller, indicating these are chosen less than the two major foods. The least preferred food types were mosses and lichens (Table 1).

Voles foraging naturally preferred grasses (Table 1). Manly's α ranked sedges as the second most preferred food, followed distantly by herbs. This result differed from that obtained by

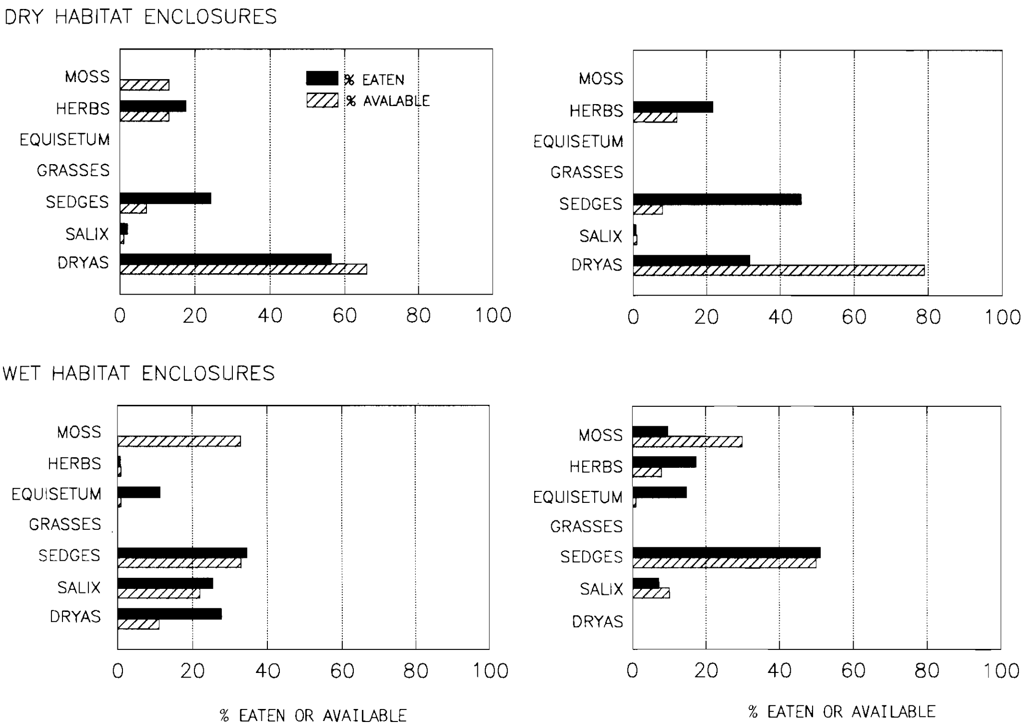

FIG. 3. Comparison of forage availability and summer diet of *Microtus oeconomus* in four 1 × 1 m enclosures, two located in dry habitats ($n = 8$ and 5) and two in wet habitats ($n = 11$ and 7). "Sedges" were *Carex* and *Eriophorum* spp.

TABLE 1. Dietary preferences of *Dicrostonyx kilangmiutak* and *Microtus oeconomus* as inferred from faecal pellet sampling

Plant species	Rank-preference index[a]	Manly's α[b]
Dicrostonyx		
Dryas integrifolia	1	0.795
Salix spp.	2	0.151
Graminae	3	0.014
Herbs	4	0.016
Equisetum spp.	5	0.007
Carex and *Eriophorum* spp.	6	0.014
Lichens	7	—
Mosses	8	0.003
Microtus		
Graminae	1	0.385
Salix spp.	2	0.049
Carex and *Eriophorum* spp.	3	0.379
Dryas integrifolia	4	0.061
Herbs	5	0.086
Equisetum spp.	6	0.030
Mosses	7	0.010

[a] Numbers 1–8 represent high to low preference. Vertical lines indicate tied ranks.
[b] Large to small values represent high to low preference.

the rank-preference method, which gave *Salix* spp. as the second most preferred food, followed by sedges.

For the enclosure feeding trials, both preference indices revealed *Carex* as one of the two least preferred foods of lemmings in every enclosure regardless of habitat type. Five of eight index calculations show *Dryas* to be the most preferred food, while herbs and *Salix* spp. vie for second place. In one instance *Equisetum* spp. are ranked first and second by Manly's α and rank preference, respectively (Table 2).

For voles foraging in enclosures, the rank-preference index showed sedges to be the most preferred in dry habitats, while herbs were the least preferred. Manly's α values were similar except for placing *Dryas* instead of herbs last in both cases. In wet enclosures sedges ranked in the middle, while *Equisetum* spp. were placed first in three of four calculations (Table 2).

Ingestion rates

Ingestion rates are highly variable and the variance is related to the mean. Box–Cox transformation analysis (Krebs 1989, p. 451) indicated a logarithmic transformation was the best statistical method of stabilizing the variances. A nested ANOVA on these data showed that there were no statistical differences between the dry and wet habitats in ingestion rates ($F = 0.670$, df = 1, $\alpha = 0.05$, $p = 0.42$); however, rates did appear to decrease when individuals were foraging in their nonpreferred habitat (wet for lemmings, dry for voles). The mean ingestion rate was 1.18 ± 0.135 (SE) bites/min, and for voles ($n = 25$) 1.64±0.291 bites/min for lemmings ($n = 31$); median ingestion rates were 1.10 and 1.20 bites/min, respectively, for these two species. These are low ingestion rates, which reflects the artificial nature of the enclosures.

Diet overlap

The natural diets of collared lemmings and tundra voles show little overlap regardless of season: 0.131 ± 0.049 (SE) in winter and 0.143 ± 0.026 in summer. However, overlap is much larger (0.539 ± 0.092) when calculated from the enclosure diets of the two species. This increase in overlap is due almost entirely to the increase in voles' consumption of *Dryas* and herb species. The Morisita–Horn index of overlap was used for these comparisons.

TABLE 2. Dietary preferences of *Microtus oeconomus* and *Dicrostonyx kilangmiutak* in dry and wet enclosure trials

	Rank-preference index		Manly's α	
Plant species	*Microtus*	*Dicrostonyx*	*Microtus*	*Dicrostonyx*
Wet enclosure 1				
Dryas integrifolia	1	1	0.149	0.373
Equisetum spp.	2	2	0.673	0.397
Carex spp.	3	5	0.062	0.019
Herbs	4	4	0.047	0.044
Salix spp.	5	3	0.068	0.166
Mosses	6	6	—	—
Wet enclosure 2				
Equisetum spp.	1	4	0.763	0.206
Herbs	2	3	0.128	0.159
Carex spp.	3	5	0.055	0.015
Dryas integrifolia	4	1	—	0.409
Salix spp.	5	2	0.037	0.210
Mosses	6	6	0.017	—
Dry enclosure 1				
Carex spp.	1	4	0.452	—
Salix spp.	2	1	0.261	0.109
Dryas integrifolia	3	3	0.111	0.155
Herbs	4	2	0.176	0.736
Mosses	5	5	—	—
Dry enclosure 2				
Carex spp.	1	3	0.654	0.062
Salix spp.	2	4	0.092	—
Dryas integrifolia	3	1	0.046	0.743
Herbs	4	2	0.208	0.195

NOTE: For explanation of values see Table 1.

Rarefaction curves indicated that a sample size of 10 for both faecal analysis and enclosure experiments was sufficient for obtaining unbiased estimates of diet overlap. However, larger sample sizes were used to increase the precision of the estimates.

Discussion

The observed composition of the summer diet of the collared lemming at Pearce Point corresponds closely to that described by Rodgers and Lewis (1986) for the same species at Igloolik, N.W.T., where *Dryas* composed 77% of the diet, *Salix arctica* 16%, and herbs 7%. Similar to these findings are the observations of Fuller et al. (1975), who found that lemmings on Devon Island, N.W.T., ate *Dryas* (43%), herbs (41%), and *S. arctica* (12%). Watson (1956) and Dunaeva and Kucheruk (1941, cited in Watson 1956, p. 292) also reported utilization of heath plants by *Dicrostonyx* on Baffin Island and in Siberia, respectively. In contrast to these four studies, Alaskan workers have found *Dicrostonyx* diets to contain large amounts of *Salix* spp.: up to 70% at Atkasook, Alaska (Batzli and Jung 1980), and 45% at Barrow, Alaska (Batzli and Pitelka 1983), and few or no heath plants. These results from Alaska reflect the very restricted distribution of *Dryas* in these areas.

There have been several detailed studies on the composition of the diet of *M. oeconomus*. Barkalow (1952) reported harvesting of the grass *Poa pratensis* by tundra voles on Barter Island, Alaska. Tast (1966) stated that tundra voles in northern Finland preferred sedges in both winter and summer, listing the monocots *Carex aquatilis*, *Carex rostrata*, and *Eriophorum angustifolium* as the principal species eaten. However, no quantitative data were given in either case. Batzli and Jung (1980) found that the summer diet of tundra voles near Atkasook was composed of 50–70% monocotyledons (Graminae being as important as *Carex* spp.), 20–30% *Salix* spp., and 0–10% various herbs. Batzli and Henttonen (1990) found that tundra voles ate mostly sedges in northern Alaska. Batzli and Lesieutre (1991) showed that *Carex bigelowii* and *Eriophorum* spp. were highly palatable to tundra voles in the laboratory, and voles grew better when fed these species. Our results are similar to these findings in that monocotyledons predominated in the diet (87%). However, *Carex* and *Eriophorum* spp. were used much more than Graminae (83 vs. 5%), and *Salix* spp. were utilized least (3%). Whereas *Dryas* was the second most abundant food type in the summer diet of voles at Pearce Point, it was not used at all by voles at Atkasook, where it is rare.

Rodgers and Lewis (1986) attribute differences in the diets of *Dicrostonyx* between localities to variations of forage abundance in different sites. Much of the habitat at both Atkasook and Barrow is composed of moist to wet meadows in which *Dryas* occurs rarely if at all, whereas *Salix* spp. are much more abundant. The forage availability, and hence diet composition, is reversed at both Igloolik and Pearce Point, where there is an abundance of heath tundra and much less willow.

Both this study and that of Rodgers and Lewis (1986) found that herbs composed a smaller proportion of the diet than was found by Fuller et al. (1975). This is probably due to the methods used in these three studies rather than to availability. Fuller et al. (1975) used feeding craters to determine the species eaten, whereas in the other two studies the method used was faecal analysis, which has several potential sources of bias. One of the main problems with these techniques is that they can cause underestimation of the amount of herbaceous dicots, which have more easily digested cell walls than mosses and graminoids, which are much more resistant to digestion (Hansson 1970; Batzli and Cole 1979; Holechek et al. 1982). Batzli and Pitelka (1971) suggested that herbs were underrepresented by two-thirds in the diet of *Microtus californicus*. Neal et al. (1973) found that sedges and dicots were underestimated by 50% in the diet of *Microtus pennsylvanicus*. No correction factors have been proposed for *Dicrostonyx*.

Diet-selection processes in voles seem to be governed primarily by forage availability rather than preference. Although voles preferred Graminae (Table 1), this food type was rare in the diet, and the more abundant but less preferred *Carex* and *Eriophorum* spp. were the main components. Batzli and Jung (1980) present similar data. They found that the use of minor species in the diet of *M. oeconomus* depended on their availability, and the percentage in the diet increased linearly with availability; however, this was not true of *Carex*, for which availability had no influence on the amount consumed. This last point might explain why *Carex* was most preferred by voles in the dry habitat enclosures, but ranked third in preference when the voles foraged in wet habitat enclosures. Since preference indices take into account the amount consumed versus the amount available, voles will appear to prefer a food that makes up a constant proportion of the diet when percent availability is less than percent consumption, as is the case with *Carex* in dry habitats, over a food for which percent availability is greater than percent consumption.

Two of our results appear to conflict with the finding of Batzli and Jung (1980) that *Carex* makes up a constant proportion of the diet of *M. oeconomus*. One is that the percentage of monocotyledons in the diet in summer appears to be nearly halved when voles forage in enclosures. A probable explanation for this result is that the enclosures did not contain *Eriophorum* spp. because of the difficulties these plants presented for making observations. *Eriophorum* likely composes the balance of monocot species in the diet in the wild.

The second conflicting result is that the proportion of monocotyledons in the winter diet decreases by almost 30% and is replaced by mosses. In preparation for winter, monocots in the Arctic divert nutrients to underground stores, causing a reduction of up to 90% in the aboveground biomass available in the summer (Batzli and Pitelka 1983). According to the findings of Batzli and Jung (1980), consumption of *Eriophorum* in summer increases with availability, whereas that of *Carex* spp. does not. If the same occurs in winter, the reduction in monocot availability in winter should influence consumption of *Eriophorum*, but not of *Carex*. The decrease that we observed in the proportion of monocotyledons present in the winter diet could be due solely to a decrease in *Eriophorum*, while the amount of *Carex* remains constant. Alternatively, the reduction in aboveground biomass of *Carex* prior to winter may be so great that the amount in the diet is actually reduced.

Tast (1966) reported that *M. oeconomus* in northern Finland continued to feed on sedges throughout the winter by burrowing into moss hummocks to reach the nutrient-rich bases of monocotyledonous species. This is made possible by the spongy peat turf on which they occur. At Pearce Point winter burrowing would be difficult, since the ground lacks a deep peat base. To compensate for this, voles appear to increase their utilization of mosses during the winter. This seasonal change in foraging behaviour is quite similar to patterns observed in brown lemmings (Batzli and Jung 1980; Batzli and Pitelka 1983; Rodgers and Lewis 1986).

The analyses of natural diets has allowed us to reject the null hypothesis that exploitative competition for food is occurring between collared lemmings and tundra voles at Pearce Point. Overlap of the natural diets of these two species is small in both summer and winter, and the most preferred food of each ranks low in the other's diet.

However, this lack of overlap does not allow us to reject completely the hypothesis of competition. These species could still be involved in interference competition, i.e., competition for space. For example, lemmings may be competitively excluding voles from favoured habitat, forcing them to subsist on dissimilar diets because of altered forage availability in marginal habitats. This would explain both the increase in diet overlap and the large changes in vole (but not lemming) diet composition observed when both species were forced to utilize the same habitats in the enclosure experiments.

A possible alternative explanation for this phenomenon that does not implicate competition involves two factors, habitat selection and diet selection. First of all, voles may select habitat on the basis of a quality other than food (e.g., cover). Birney et al. (1976) discussed the importance of cover to *Microtus* populations and proposed a model to explain how cover might regulate vole populations. Batzli and Lesieutre (1991) showed that tundra voles in northern Alaska selected habitats on the basis of the abundance of high-quality foods and not on the basis of cover. Secondly, diet-selection processes in voles may be governed primarily by forage availability.

Tundra voles at Pearce Point may select their habitat on the basis of both high-quality food and cover, and both these factors are consistent with our data. If both factors are involved in habitat selection, one would expect to find the diet of *M. oeconomus* to be composed of mainly *Carex* and *Eriophorum* spp., since these plants are the dominant vegetation in habitats providing any significant amount of cover in the barren tundra ecosystems around Pearce Point. If animals select their habitat in this way and are then placed in a different environment (such as the dry habitat enclosures), one might expect that the diet would change somewhat to reflect the new availabilities, as indeed we have observed.

The food types an animal is able to use are still ultimately determined by long-term metabolic requirements. If animals are unable to exploit the food plants in a particular habitat efficiently, it may be impossible for them to live there. This could explain the different diets of collared lemmings and tundra voles. The presence of high-quality food is thus necessary for habitat selection (Batzli and Lesieutre 1991), and tundra voles would not be expected to colonize dry heathland habitats even if cover were artificially provided. The geographic distribution of the tundra vole is clearly not restricted by the range of its preferred food plants in northern Canada, and factors other than the particular food plants that occur must operate to limit its range.

This is one of the first attempts to watch the foraging behaviour of microtines in their natural habitat (see Belovsky 1984; Batzli et al. 1981). The patterns of forage preference directly observed were very similar to those inferred from other, less direct, techniques like faecal analysis.

In summary, the diets of collared lemmings and tundra voles at Pearce Point are similar to those of populations found elsewhere in similar tundra habitats. Overlap in the natural diets of these two species is small and it does not appear that competition for food is an important factor in relations between the two species.

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