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Comparative Winter Habitat Use and Associations among Herbivores in the High Arctic

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ABSTRACT. We studied winter habitat use and interspecific associations among large- and medium-sized herbivores on southeastern Victoria Island, Arctic Canada, by documenting the deposition of feces in relation to vegetation. Associations between ptarmigan (*Lagopus* spp.), arctic hares (*Lepus arcticus*), caribou (*Rangifer tarandus*), and muskoxen (*Ovibos moschatus)* were assessed using the Jaccard Index (JI) and χ^2 at two scales, i.e., with 1 m^2 and 1 ha as sampling units. JI values for species pairs were greater at the larger scale, but χ^2 revealed significant (positive) associations only at the smaller scale and only between arctic hares and caribou and between arctic hares and ptarmigan. Comparative use of habitats was described with respect to vegetation by canonical correspondence analysis (CCA). Ptarmigan and muskoxen were most strongly correlated with lowland vegetation and caribou with upland vegetation; arctic hares were intermediate. CCA also indicated rather wide separation in the multivariate space, further suggesting distinct patterns of habitat use. The results imply that these species were segregated in their use of resources in this High Arctic environment.

Key words: arctic hare, caribou, habitat selection, interspecific relationships, multivariate, muskox, niche, ptarmigan, spatial scale

RÉSUMÉ. On a étudié l'utilisation de l'habitat hivernal et les associations biotiques parmi les grands et moyens herbivores du sud-est de l'île Victoria située dans l'Arctique canadien, en étudiant l'emplacement des crottes par rapport à la végétation. À l'aide de l'index Jaccard (IJ) et de χ^2 à deux échelles (c.-à-d. en prenant 1 m^2 et 1 ha comme unités d'échantillonnage), on a évalué les associations entre le lagopède (*Lagopus* spp), le lièvre arctique (*Lepus arcticus*), le caribou (*Rangifer tarandus*) et le boeuf musqué (*Ovibos moschatus*). Les valeurs de IJ pour les paires d'espèces étaient plus élevées à grande échelle, mais χ^2 ne montrait des associations notables (positives) qu'à petite échelle et seulement entre le lièvre arctique et le caribou ainsi qu'entre le lièvre arctique et le lagopède. On a décrit l'utilisation comparative des habitats en rapport avec la végétation par analyse de correspondance canonique (ACC). Le lagopède et le boeuf musqué étaient corrélés le plus fortement avec la végétation des basses-terres et le caribou avec celle des hautes-terres; le lièvre arctique se situait au milieu. L'ACC montrait aussi une séparation relativement importante dans l'espace à plusieurs variables, ce qui laisse suggérer des modèles distincts d'utilisation de l'habitat. Les résultats indiqueraient qu'il existait pour ces espèces une ségrégation dans l'utilisation des ressources au sein de cet environnement extrême-arctique.

Mots clés: lièvre arctique, caribou, sélection de l'habitat, interactions biotiques, à plusieurs variables, boeuf musqué, habitat spécifique, lagopède, échelle spatiale

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INTRODUCTION

The concept of niche continues to occupy a central position in ecological thought (Pianka, 1994; Liebold, 1995). Increasingly, niche has become linked to the study of competition and comparative resource use among species. Nonetheless, this branch of ecology has, at times, been encumbered by the sheer complexity of ecological systems (Connor and Simberloff, 1986; Begon et al., 1990). The Arctic may therefore prove to be a valuable study area. Because of the relatively simple ecological structure of high-latitude environments, the Arctic may represent the best testing ground for describing ecological relationships (Klein and Bay, 1994) and testing ecological theory (Caughley and Gunn, 1993).

Amongst the numerous conceptualizations of niche, Hutchinson's model, which portrays a species space as multidimensional hypervolume along several environmental axes, is perhaps the most common (Pianka, 1994). Multivariate statistics may therefore be particularly useful for describing niche (Shugart, 1981). Recently, canonical correspondence analysis (CCA) has been found to be effective in extracting the relationships between two multivariate data

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sets (ter Braak, 1987; Palmer, 1993). For the study of niche, CCA could be applied to two sets of data, one comprising the species of interest and the other, the environmental variables.

Univariate approaches have also been used to describe interspecific interactions. Many indices are available to quantify the associations between species on the basis of their presence or absence in sampling units (Ludwig and Reynolds, 1988). Nonetheless, as is the case for many ecological phenomena, the strength and direction of these associations may depend on the spatial scale at which we view them (Wiens, 1989). To date, little regard has been given to the degree to which interspecific associations might vary with scale.

In this study, we documented the relationships among four medium- to large-bodied herbivore species and their correspondence to vegetation, on southeastern Victoria Island in the Canadian High Arctic. Using the presence of fecal pellets, we compared winter habitat use by arctic hares (*Lepus arcticus*), ptarmigan (*Lagopus* spp.), caribou (*Rangifer tarandus*), and muskoxen (*Ovibos moschatus*). With the exception of lemmings (*Dicrostonyx torquatus* and *Lemmus sibiricus*), these species constituted the entire guild of herbivores during winter in the study area.

METHODS

We carried out the fieldwork in the vicinity of Wellington Bay and Ferguson Lake (69°25′N, 106°15′W; Fig. 1). The area was characterized by willow-sedge meadows, *Dryas* uplands, raised beaches, and numerous small lakes. Bliss (1990) classified the area as "polar semi-desert," part of the "High Arctic zone." Elevation varied from 0 to 150 m above sea level. Our observations suggested moderate population densities of herbivore species. Both caribou and muskoxen had increased in numbers in the three decades that had preceded the study (Ferguson and Gauthier, 1992; D. Kaomayok, pers. comm. 1992). All species resided in the study area throughout the year except the caribou, which were present only from October to early June.

Sampling was carried out from 22 July to 13 August 1991 and from 28 July to 18 August 1992, concurrently with a detailed study of plant communities (Schaefer and Messier, 1994). We used a hierarchical, stratified random design. Within each stratum (i.e., a 1 km^2 Universal Transverse Mercator square), a random point was selected using a 1:50 000 topographic map and a grid overlay of points 0.2 km apart. Here a 100 × 100 m site was established. Within each site, six 1 m^2 quadrats were located randomly.

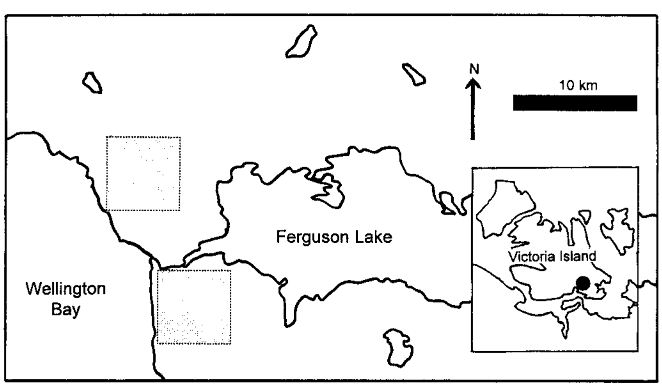

FIG. 1. The study area (indicated as shaded blocks) on southeastern Victoria Island, Northwest Territories, Canada.

For vegetation, within each quadrat, sixteen 25 × 25 cm contiguous plots were analysed. In each small plot, we estimated the aerial coverage of plants (usually by genus), using the classes 1%, 5%, 10%, 20%, 30%, ... 100%. For graminoids, we estimated total aerial coverage in addition to determining the presence of species in the 1 m^2 quadrat. We included data on the most common lichen in the area, *Cetraria cucullata*. For habitat use, we documented the presence of any feces (i.e., single pellets or groups) in each 1 m^2 quadrat. For caribou and muskoxen, only winter feces were found; the season of fecal deposition by ptarmigan and hare could not be differentiated. Two sites were excluded because the random points landed on lakes; at another, no observations on graminoids were taken. Thus, in all, 69 sites were analysed.

Nomenclature for the flora follows Porsild and Cody (1980). Voucher specimens were submitted to the W. P. Fraser Herbarium, University of Saskatchewan, Saskatoon.

We conducted the analysis of interspecific association on two scales, i.e., using each 1 ha site and each 1 m^2 quadrat as the sampling units. Following the recommendation of Ludwig and Reynolds (1988), we employed the Jaccard Index to test the strength of interspecific association between all possible pairs of herbivore species and the chi-square statistic to test for independence among species. The Jaccard Index is a measure of the proportion of sampling units where both species occur in relation to the total number of sampling units containing at least one of the species (Ludwig and Reynolds, 1988). To maintain a conservative error for the six pairwise associations at each scale, we applied a Bonferroni-corrected α of $0.05/6 \approx 0.01$.

To describe the relationships of animal species with the flora, we used canonical correspondence analysis (CCA). CCA is a robust technique for extracting the relationships between two multivariate data sets (Palmer, 1993), in this case, vegetation and herbivore feces. CCA provides maximum separation of species (i.e., the herbivores) and sites as constrained by the environmental (i.e., floral) variables. All default settings in CANOCO version 3.10 (ter Braak, 1990) were followed. For the analysis, we used the data from each 1-ha site as the sampling unit and retained *Cetraria cucullata* and all Spermophyta with frequencies greater than 30% across the sites (Fig. 2). For each 1 ha site, we used the mean coverage values of plant species (except graminoid species), and the frequency (i.e., across the 1 m^2 plots, range: 0 to 6) of feces and graminoid species.

RESULTS

Our results indicated rather distinct use of the study area by the four species. The Jaccard Index— which varies between

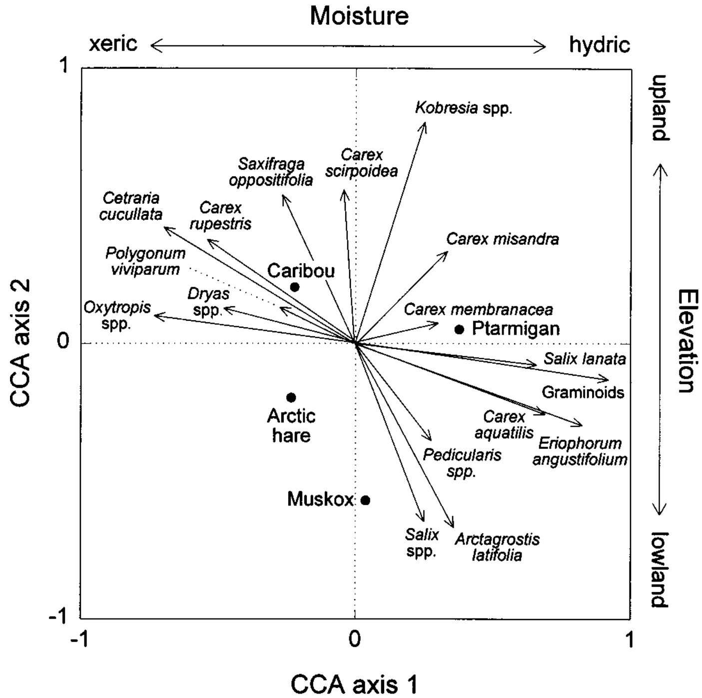

FIG. 2. First two axes of canonical correpondence analysis (CCA) as a biplot of floral variables and herbivore habitat use. The centroid for each herbivore species is indicated. The scale for the vegetation arrows is 2:1.

0 and 1, with higher values indicating stronger associations—revealed weak to moderate associations between species pairs at both scales. Associations were invariably stronger at the larger scale (Table 1). Nonetheless, only two associations indicated a lack of species independence, and both involved arctic hares. This species was positively associated with both ptarmigan and caribou, but only at the smaller scale (Table 1).

The interpretation of multivariate results, using CCA, are straightforward and largely graphical (ter Braak, 1987; Palmer, 1993). In the present case (Fig. 2), floral variables are represented by arrows, each of which displays an axis. By projecting each herbivore species onto the axis, we can estimate the species rank for that variable.

The first CCA axis captured 30.0% of the variance in the species data, and appeared to be related to moisture levels across the study area (Fig. 2). The second CCA axis, which captured 18.6% of this variance, largely depicted elevational differences. Ptarmigan were most closely associated with willow-sedge meadows, including erect willow (*Salix lanata)*, water sedge (*Carex aquatilis*), cotton sedge (*Eriophorum angustifolium*), and overall graminoid abundance. Muskoxen exhibited similar although weaker relationships to these flora and were most strongly associated with prostrate willows (*Salix* spp.) and the grass *Arctagrostis latifolia*. Caribou, on the other hand, were correlated to upland flora, including the sedge *Carex rupestris,* the lichen *Cetraria cucullata*, and purple saxifrage (*Saxifraga oppositifolia*). Arctic hares appeared intermediate between caribou and muskoxen (Fig. 2).

The multivariate results were generally consistent with the univariate analysis, indicating considerable separation among species. The centroid for each herbivore species resided in a separate quadrant of the two-dimensional ordination diagram

TABLE 1. Interspecific associations between arctic herbivores at two spatial scales as determined by the Jaccard Index. Significant associations from χ^2 tests are indicated (* = significant, Bonferroni-corrected α of 0.01).

	Scale = 1 m²			Scale = 1 ha		
	Caribou	Muskox	Ptarmigan	Caribou	Muskox	Ptarmigan
Arctic Hare	0.21*	0.07	0.17*	0.30	0.17	0.31
Caribou	–	0.08	0.13	–	0.15	0.42
Muskox	–	–	0.11	–	–	0.11

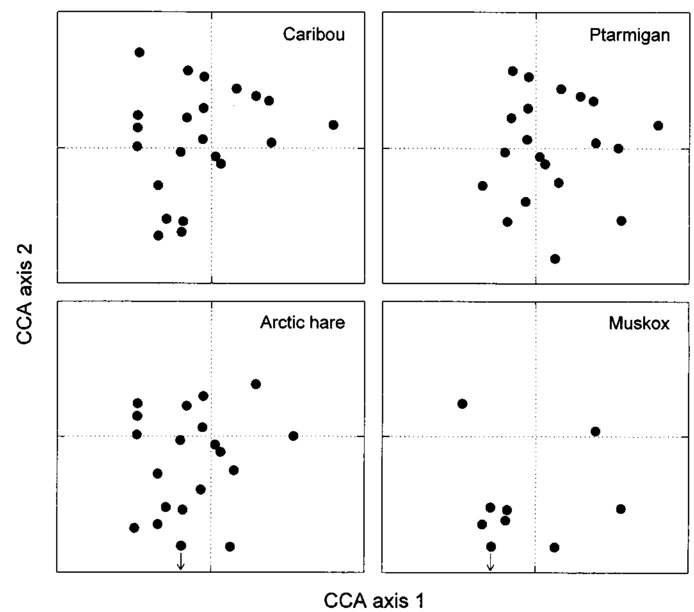

FIG. 3. The first two axes of canonical correspondence analysis (CCA) as a plot of each 1 ha site with the presence of herbivore feces. The lowest datum for muskox and arctic hare is an outlier on CCA axis 2.

(Fig. 2), with arctic hares and caribou in closest proximity. Examination of the individual sampling sites also showed that niche overlap, where present, involved ptarmigan with arctic hares and caribou more than other species pairs (Fig. 3).

DISCUSSION

The distribution of fecal groups has been widely used in wildlife ecology as an indicator of resource use by herbivores (e.g., Thomas and Edmonds, 1984; Adamczewski et al., 1988; Nault et al., 1993). The technique appears to carry reasonable validity (Edge and Marcum, 1989). Indeed, our results on herbivore–vegetation relationships are generally consistent with previous studies of habitat selection and diets of ptarmigan (West and Meng, 1966; Weeden, 1969; Klein and Bay, 1991), arctic hares (Parker, 1977; Klein and Bay, 1991), and caribou (Adamczewski et al., 1988) in the Arctic. For muskoxen, our observations were complemented by independent, direct measurements at feeding sites and craters during winter (Schaefer and Messier, 1995b). The present findings concur that muskoxen tend to be positively associated with their dominant forage plants, such as *Carex aquatilis*, *Eriophorum* spp., and *Salix* spp., although these relationships indicated by fecal groups were weaker than those observed directly (Schaefer and Messier, 1995b).

The description of herbivore niche solely on the basis of vegetation may neglect other significant environmental axes. Indeed, niche has come to be regarded as a conceptual space incorporating all environmental factors impinging on a species (Begon et al., 1990; Liebold, 1995). Nonetheless, we have documented previously that the vegetation of the study area is correlated to topographic, edaphic, and nival variables (Schaefer and Messier, 1994, 1995a). In light of this redundancy, additional environmental variables are unlikely to add substantial new information, and hence are equally unlikely to enhance the separation amongst species. On the other hand, our observations omit other potential avenues for niche partitioning, such as temporal separation in resource use or selection for particular dietary species (Klein and Bay, 1991).

As indicated by the univariate analyses of association, species occurrences were largely independent across both spatial scales. Studies of other herbivore communities have also documented little overlap in resource use, particularly during winter (Wydeven and Dahlgren, 1985; Gordon and Illius, 1989; Klein and Bay, 1994). Our study suggests, however, that the magnitude of the associations is sensitive to spatial scale. The tendency for associations to increase in strength at the larger scale (Table 1) is consistent with the suggestion by Wiens (1989) that ecological patterns seem more predictable at larger scales. We have also noted that the magnitude of floral–nival correlations in the study area is amplified as the scale of observation is increased (Schaefer and Messier, 1995a).

In ecology, niche has become closely linked to interspecific competition, but inferring process from pattern must be done cautiously. Numerous authors (Begon et al., 1990; Gunn et al., 1991; Sinclair, 1991) have noted the impracticality of trying to verify that species compete by demonstrating niche overlap. Nevertheless, interspecific competition—particularly between muskoxen and caribou—continues to occupy a prominent place in the literature (e.g., Wilkinson et al., 1976; Vincent and Gunn, 1981; Thomas and Edmonds, 1984; Gunn et al., 1991; Staaland and Olesen, 1992). Few studies have documented significant overlap in resource use between these ungulates (cf. Parker, 1978), which corresponds well with the species' disparate foraging strategies (Klein, 1992). Our results agree with this pattern. We suggest, nonetheless, that descriptive studies of niche are unlikely to resolve such issues. In the end, rigorous examination of interspecific competition is likely to require an experimental approach (Begon et al., 1990).

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