Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden

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Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden

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We studied seasonal migration of individually radio-collared moose *Alces alces* in a partially migrant population in northern Sweden. First, to investigate habitat selection at the level of individuals, we examined use vs availability of habitat characteristics within seasonal ranges. Second, to investigate what habitat characteristics migrants use to select these seasonal ranges, we contrasted the characteristics of summer and winter ranges of individual migrants. Third, to investigate why some moose migrate whereas others do not, we contrasted the snow conditions and the composition of the vegetation in the seasonal ranges of 36 migrant and 30 resident moose. At the level of habitat selection within a range, moose selected areas which had less mire, clear-cut and field habitats, as well as less snow. At the level of the entire range, migrants and residents had rather similar range compositions and differed only in migrants having less field habitats in their winter ranges; the proportion of Scots pine *Pinus sylvestris* stands, Norway spruce *Picea abies* stands, mire, deciduous, and clear-cut forest habitats did not differ, nor was there a difference in snow depth. Similarly, within the group of migrants, we detected no differences in habitat composition or snow depth between the summer ranges they just left, and the winter ranges they moved to. Snow quality (as indexed by the depths to which moose sank) did not differ between the two seasonal ranges of migrants, but calves sank less deeply in ranges of migrants than in ranges of residents, suggesting that snow quality may play a role in the selection of ranges by moose or their decision to migrate/remain resident. Thus, habitat composition and snow depth were important at lower levels of habitat selection, but differences among home ranges were not dramatic. The observation that snow quality differed significantly between ranges of residents and migrants suggests that future studies of migration might profitably investigate snow quality.

Key words: Alces alces, habitat composition, moose, partial migration, snow depth, snow quality, ungulate

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Most migration studies have considered the conspicuous long-range seasonal movements of birds, but mammal migration has also been the subject of considerable scrutiny (for reviews see Baker 1978, Rankin 1985, Dingle 1996). Animal populations which exhibit partial migration present a unique opportunity to understand the causes of migratory behaviour (Lundberg 1988, Kaitala, Kaitala & Lundberg 1993). Such populations may allow us to better understand the general phenomenon of migration by contrasting individual animals that migrate to others in the same geographic area which do not.

Some moose *Alces alces* populations across Europe, Asia and North America have been reported to be migratory (LeResche 1974, Pulliainen 1974, Hauge & Keith 1981, Cederlund, Bergström & Sandegren 1989, Sweanor & Sandegren 1988, 1989, Sandegren & Sweanor 1988, Andersen 1991a, Ballard, Whitman & Reed 1991, Cederlund & Sand 1992). For brevity we will follow many previous authors and use the labels 'migrant' and 'resident' to refer to the seasonal movement patterns of moose. However, migration is better viewed as a continuous phenomenon, where 'migrant' or 'resident' are the end points of the continuum representing movement distance (LeResche 1974, Sweanor & Sandegren 1989). The distance between the summer and winter ranges of migrant moose varies considerably (LeResche 1974, van Ballenberghe 1977, Ballard et al. 1991). Note, however, that even the smallest movements are properly termed 'migration' if there is a clear shift between non-overlapping ranges, regardless of how close these might have been. LeResche (1974) called the distance needed to achieve such a change in habitats an 'ecological distance'. Like Dingle (1996), we define migration as a shift between habitats, but one must keep in mind that the labels 'migrant' and 'resident' represent a continuum of seasonal movements from zero ('resident') to long distances ('migrants').

Factors which have been suggested to influence migration in moose fall into two inter-related groups: food and snow (e.g. Coady 1974, Pulliainen 1974, Peek, Urich & Mackie 1976, Sandegren, Bergström, Cederlund & Dansie 1982). Snow directly decreases the accessibility of food resources by burying (Schwab, Pitt & Schwab 1987), and deep snow increases the cost of locomotion for foraging (Coady 1974, Telfer & Kelsall 1979, 1984, Bunnell, Parker, McNay & Hovey 1990, Sæther, Solbraa, Sødal & Hjeljord 1992). Many studies have suggested that moose migrate to areas with less snow for winter (e.g. Kelsall & Prescott 1967, Coady 1974, Sweanor & Sandegren 1985, Bergström & Hjeljord 1987, see Mysterud, Bjørnsen & Østbye 1997 for an excellent review for cervids in general). Other relevant aspects of snow conditions beside snow depth *per se* might involve the quality of the snow (i.e. snow density and hardness; Kelsall & Prescott 1967, Bunnell et al. 1990). Snow quality affects the depth to which an animal sinks into the snow, and could therefore be considered 'effective snow depth' with respect to locomotion (although not with respect to burying food). Effective snow depth affects the amount of energy needed for locomotion (LeResche 1974, Bunnell et al. 1990), so both snow depth and snow quality might thus be important in habitat choice.

In order to better understand the migratory behaviour of moose, we evaluated the summer and winter ranges in an area where the population is partially migratory. During different seasons, moose consume different food plants (e.g. Thompson & Vukelich 1981, Sandegren et al. 1982, Bergström & Hjeljord 1987) which generally grow in different habitats (Belovsky 1981) and thus may influence the migratory behaviour of moose. Based on published studies (e.g. Cederlund & Okarma 1988, Sæther & Andersen 1990, MacCracken, van Ballenberghe & Peek 1993), we evaluated the composition of moose ranges with respect to the abundance of Scots pine *Pinus sylvestris* stands, Norway spruce *Picea abies* stands, deciduous areas, mires, clear-cuts, lakes and agricultural fields. In addition, we considered snow depth and snow quality. By comparing the characteristics of seasonal ranges of individually radio-marked migrants and residents, we hope to better evaluate the underlying causes of this behaviour and understand why some, but not all, moose choose to migrate. How do the ranges of residents differ from those of migrants? How do the winter ranges of individual migrants differ from the summer ranges these individuals have just left? Finally, within their ranges, how do moose select habitats? Other authors have noted that conclusions reached by considering the 'average' animal may differ from that which result from a study of the decisions actually made by individuals (e.g. Chesson 1978, Ritchie 1988, 1990, Ball 1994). In a partially-migrant population, some moose decide to migrate whereas others do not; an 'average' moose may not exist so we must study the decisions made by individuals.

Previous studies have noted whether a moose population in a given area is migratory or not. Similarly, several studies have compared the characteristics of summer and winter areas. However, even though the decision to migrate or not is made by individual moose, we can find no published study which examines this individual decision making. For example, do individuals actually move to winter areas where there is less

snow than in the summer ranges they have just left? Only year-round studies of marked moose can examine this individual decision making. Finally, understanding the seasonal movements of moose has considerable economic importance: during winters in Scandinavia moose sometimes aggregate and cause severe damage to regenerating pines (Lavsund 1987).

Material and methods

Study area

The study area is in the middle boreal zone of northern Sweden (Ahti, Hämet-Ahti & Jalas 1968), in the county of Västerbotten, 64°12'N, 20°45'E (Fig. 1). Scots pine and Norway spruce dominate the forest, but are interspersed with birch *Betula* spp., aspen *Populus tremula*, rowan *Sorbus aucuparia* and willows *Salix* spp. The field layer mainly consists of bilberry *Vaccinum myrtillus*, lingonberry *Vaccinum vitis-idaea*, crowberry *Empetrum* spp. and heather *Calluna vulgaris*. Mires, clear-cuts and agricultural fields are also present. Vegetation on mires is dominated by willow, dwarf birch *Betula nana*, sedge *Carex* spp. and grasses of the order *Poaceae*. Forests are typically logged with a rotation period of 80-100 years. Elevation varies within 0-380 m a.s.l. At the coast, the ground is covered by snow 140-160 days of the year, and the median snow depth on 31 January is 40 cm. For the more inland part of our study area, the figures are 160-180 days and 50-60 cm, respectively (Ångström 1974). Moose density during the study period was 0.7-0.9 moose/km^2 as estimated by aerial helicopter surveys (J.P. Ball & K. Wallin, unpubl. data).

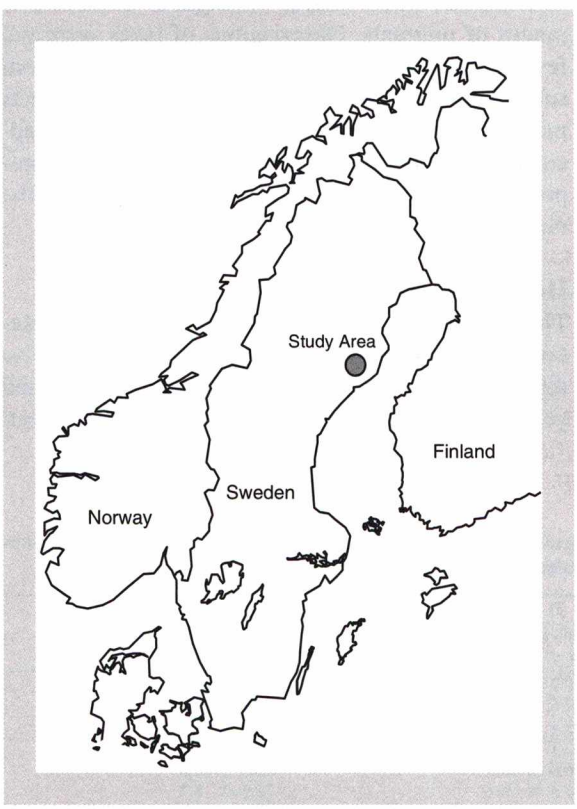

Figure 1. The study area in which the home ranges of 36 migrant and 30 resident radio-collared moose were studied during January 1993 - April 1997.

Home ranges

We immobilised both adult and young moose during late winter (January-March) with Ethorphine and Xylazine (Sandegren, Pettersson, Ahlqvist & Röken 1987) using a dart gun (Model 1M, Daninject) from helicopters. Each animal was marked with a radio collar (Televilt International, Lindesberg, Sweden) and unique ear-tags. The locations of radio-collared moose (25 males and 41 females) were determined by triangulation from roads every 7-21 days between 26 January 1993 and 14 April 1997 (N = 6,428 radio locations; median = 61 locations/moose). The centroids of the home ranges were calculated using the adaptive kerneling (Worton 1989) option of the program Tracker (Camponotus AB, 1994). Distance between summer and winter ranges was defined as the straight-line distance between the centroids of the ranges.

Classification of migrant and resident moose

We classified a moose as migratory if the minimum convex polygons (White & Garrott 1990) for its winter and summer areas during consecutive years did not overlap. Of the moose 36 were migrants and 30 were residents. Each individual moose was studied during only one of the three years of our study in case it migrated one year but not another. The average distance between seasonal ranges of migrant moose was 22 km ± 14 (mean ± SD).

Home range composition

To evaluate the composition of each moose's home range, we performed systematic line-transect sampling every 100 m along the 1.5 km sides of a triangle centred on the centroid (Manly, McDonald & Thomas 1993) of that moose's range (N = 44 points/range). The proportion of pine stands, spruce stands and stands dominated by deciduous species was estimated along the transects, together with the proportion of clear-cuts, mires, fields and lakes. Clear-cuts were defined as areas where the trees had been harvested, but any vegetation was still so short that it was primarily covered

by snow. For pine, we considered stands between five and 30 years of age because (although it varies with site productivity) the maximum browse production of pine is between 15-20 years (Bergström & Hjeljord 1987), and pines in this area older than 30 years are too tall for moose to browse. Pines younger than five years are so short that they are covered by snow and not available to moose. Stand age was estimated by counting whorls of pine. Spruce is rarely eaten by moose (e.g. Bergström & Hjeljord 1987), but when the trees are old enough they form a closed canopy and provide shade in summer (Thompson & Vukelich 1981, Schwab & Pitt 1990) and reduced snow depth in winter (Kelsall & Prescott 1967). We therefore restricted our analysis to spruce older than 70 years, which is approximately when they form a closed canopy in our area.

Snow depth and quality

We measured depth of snow in the year-round ranges of residents, and in winter and summer ranges of migrant moose. We assessed both ranges of a given migrant on the same day so our comparison of snow depth in winter vs summer ranges is not confounded by snowfall events. At the occurrence of every moose track encountered along the transects, (hereafter 'track sites'), we measured the depths of the tracks from the top of the snow layer down to the bottom of the footprint. We also noted whether the tracks were made by an adult moose or by a calf, because foot loading is much greater for adults than for calves (Kelsall & Prescott 1967). In soft snow, adults may sink all the way to the ground whereas in hard snow calves may not sink at all, so we used the sinking depths of calves and adults as two complementary indices of snow quality ('effective snow depth'). To test if moose selected areas with certain characteristics within their range, the same variables measured along the transects were also measured at track sites.

Statistical analysis

We used the means of individual summer or winter ranges and we used a given moose in only a single year to avoid pseudoreplication (Hurlbert 1984) so the unit of independence is the individual moose winter or summer range. Parametric tests were not used because residual analysis (Tabachnick & Fidell 1983) revealed that few variables satisfied the necessary assumptions and some data could not be transformed to satisfy these assumptions. The Wilcoxon Matched-Pairs Signed rank test (Siegel 1956) was used to test the paired values of the variables at summer and winter ranges of migrant moose, and between track sites and the overall ranges. The Mann-Whitney U-test (Siegel 1956) was used to test differences between the ranges of migrants and resident moose. All tests were done with the program JMP® (SAS Institute 1995).

Results

Details of statistical tests are presented in the following three sections, but a summary of the results is given in Table 1 to provide an overview of year-round ranges of residents, winter ranges of migrants and summer ranges of migrants. Observations of lakes were too few for statistical analysis and were thus omitted from subsequent mention. Note however, that this reflects more the paucity of lakes in our study area than inadequate sampling intensity; we recorded habitat composition every 100 m along 459 km of transects in the ranges of the 66 moose.

Home range composition

The composition of summer ranges regarding vegetation seemed to be similar for all moose. There were no differences between the summer ranges of migrants and year-round ranges of residents (Mann-Whitney U-test:

Table 1. Mean values and standard deviations (SD) of variables relating to snow depth (first three in cm) or habitat composition (%) within the ranges of resident and seasonally migrant moose in northern Sweden during 1993-1997.

	Migrants (N = 36)		Residents (N = 30)
Variables	Summer ranges (mean ± SD)	Winter ranges (mean ± SD)	Year-round ranges (mean ± SD)
Snow depth, cm	62.4 ± 14.2	62.0 ± 15.9	55.8 ± 12.0
Adult sinking depth, cm	25.1 ± 13.6	27.6 ± 14.2	30.1 ± 12.1
Calf sinking depth, cm	14.2 ± 12.5	13.4 ± 5.5	26.2 ± 12.8
Mire, %	1.5 ± 1.5	2.1 ± 1.8	1.4 ± 1.3
Pine, %	49.5 ± 14.5	46.6 ± 16.0	48.0 ± 10.4
Spruce, %	23.8 ± 13.0	21.4 ± 7.7	22.2 ± 5.3
Deciduous, %	16.8 ± 0.8	14.8 ± 7.9	19.6 ± 9.7
Clear cut, %	0.4 ± 0.6	0.4 ± 0.6	0.3 ± 0.3
Field, %	0.5 ± 0.8	0.3 ± 0.6	0.6 ± 0.7

P > 0.17 for pine stands, spruce stands, mire, deciduous, clear-cut and field habitats).

Comparing the summer to winter ranges of individual migrants, we found no differences in the amount of pine, spruce, deciduous and clear-cut habitats (Wilcoxon Matched-Pairs Signed Ranks test: P > 0.22 for all). There were, however, trends for the winter ranges of migrants to have more mire (P = 0.10) and less field habitats (P = 0.16) than their summer ranges.

When comparing winter ranges of migrants to the year-round ranges of residents, there was a significant difference in the occurrence of field habitats (Mann-Whitney U-test: P = 0.02), with residents having a higher proportion of fields within their ranges. Mire tended to be more common in winter ranges of migrants than in the year-round ranges of residents (P = 0.13) and deciduous habitats tended to be less common (P = 0.09). Pine, spruce and clear-cut did not differ between winter ranges of migrants and year-round ranges of residents (P > 0.37 for all).

In contrast to habitat selection at the level of the entire range listed above, moose rather strongly selected habitat types within their ranges. Compared to their entire home range, moose avoided areas of mire, clear-cut and field (Wilcoxon Matched-Pairs Signed Ranks test: P = 0.001, 0.001 and 0.003, respectively; Table 2). There was a tendency for moose to use the areas within their ranges which had more pine and more spruce (Wilcoxon Matched-Pairs Signed Ranks test: P = 0.14 and 0.15, respectively; see Table 2). Within a home range, areas of deciduous trees were neither selected nor avoided (Wilcoxon Matched-Pairs Signed Ranks test: P = 0.97; see Table 2).

Thus, summer ranges were similar for all moose, and the winter ranges of migrants were not different from the summer ranges they left. The winter ranges of migrants had less agricultural fields than did residents' ranges, but overall they did not seem to differ dramatically. However, within an individual's range during winter, moose showed a strong preference to utilise sections of their ranges which had less mire, clear-cut and agricultural field habitats than was available within their range.

Table 2. Comparison of snow depth (cm) and habitat characteristics (%) at used vs available areas within home ranges of individual moose in northern Sweden (N = 66 moose: 36 migrants and 30 residents).

	Used areas (mean ± SD)	Available areas (mean ± SD)
Snow depth	51.50 ± 18.42	59.20 ± 14.51
Mire	0.12 ± 0.23	0.18 ± 0.16
Pine	6.84 ± 1.98	6.69 ± 1.45
Spruce	5.13 ± 1.96	4.14 ± 1.86
Deciduous	1.89 ± 1.46	1.70 ± 0.90
Clear-cut	0.01 ± 0.02	0.04 ± 0.05
Field	0.01 ± 0.08	0.04 ± 0.06

Snow depth

At the 44 systematic sampling points per range, we recorded individual snow depths ranging within 0-130 cm. Note however, that the average snow depth at the level of the 102 ranges (30 resident, 36 migrant winter ranges plus 36 migrant summer ranges) varied within 35-100 cm (mean = 59.2 cm). We found no evidence that individual migrants moved to ranges with less snow than the ranges they left (Wilcoxon Matched-Pairs Signed Ranks test: P = 0.64, N = 36).

When comparing migrant winter ranges to year-round ranges of residents, we similarly found no difference in snow depth, although here there was a trend for residents to have less snow in their ranges than did migrants (56 vs 62 cm, respectively; Mann-Whitney U-test: P = 0.08).

In contrast to habitat selection at the level of the entire range, snow depth did influence habitat selection by moose within their range: moose selected areas with less snow than the average available over their entire range (51.5 vs 59.2 cm; Wilcoxon Matched-Pairs Signed Ranks test: P = 0.04; see Table 2).

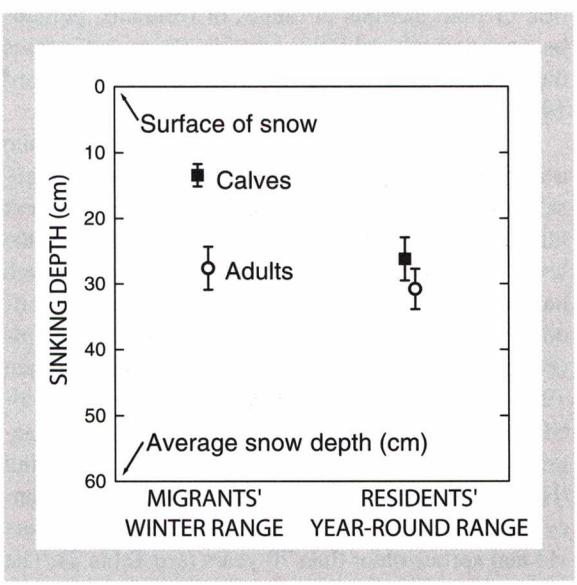

Figure 2. Snow quality differences between the winter ranges of migrants and resident moose during the winters of 1993-1997. The depths (means ± standard error) to which adult and moose calves sank into the snow are shown. Note that the reversed y-axis indicates the depth down from the snow surface, and that the bottom of the y-axis indicates the mean snow depth of 60 cm.

Snow quality

Neither sinking depths of calves nor adults differed between winter and summer ranges of migrants (Wilcoxon Matched-Pairs Signed Ranks test: $P > 0.43$ for both).

Turning now to a comparison of winter ranges of migrants and year-round ranges of residents, there was a significant difference in snow quality as indexed by the sinking depths of calves. At winter ranges of migrants, calves (but not adults) sank significantly less than at year-round ranges of residents (13 cm vs 26 cm, respectively; Mann-Whitney U-test: $P = 0.007$ for calves; 28 vs 30 cm, $P = 0.41$ for adults; Fig. 2).

Discussion

Home range composition

If migration is currently adaptive, we should detect some differences in the moose's environment. One possibility is that both migrants and residents use similar areas during a given season, but then migrants move to areas which are better in some way during the other season, whereas residents utilise a 'compromise' range year round.

In our study, we found little evidence that migration serves to move moose between areas which differ strongly in the composition of their vegetation (see Table 1), with the exception that there was a higher proportion of field habitats in ranges of residents, perhaps because agricultural fields provide grains and grasses during early and late summer (Bergström & Hjeljord 1987, Histøl & Hjeljord 1993).

At a lower level of habitat selection we noted quite a different pattern: during winter, moose strongly selected parts within their range where there was less mire, clear-cut and fields than what was available at the level of the entire range (see Table 2). Although such habitats may be important during the snow-free period by providing graminoids and other palatable plants (Bergström & Hjeljord 1987, Heikkilä & Härkönen 1993, Histøl & Hjeljord 1993), they might be avoided during winter when snow covers the ground vegetation. Open areas also provide less shelter from wind (Histøl & Hjeljord 1993). We also observed a tendency for moose to utilise areas with more pine 5-30 years old and spruce older than 70 years (see Table 2). The general importance of pine as winter moose food in Scandinavia is well known (e.g. Bergström & Hjeljord 1987, Histøl & Hjeljord 1993); our results are also in accordance with those of Histøl & Hjeljord (1993), who reported that pine-dominated forests are likely to be winter habitats of migrating moose, regardless of snow depth. The tendency to use old spruce stands in winter is probably due to the fact that the closed canopy reduces snow depth and therefore the energetic cost of locomotion.

Although Histøl & Hjeljord (1993) reported that during winter, migrant moose used habitats of a lower quality, and pine forests more often than resident moose did, we found no such pattern (see Table 1). Perhaps any differences in winter habitats of migrants and residents may not lie in the abundance of any single habitat type, but in the total amount of available food, as suggested by Pierce & Peek (1984). Alternatively, resources in our moderately flat, forested area may be relatively uniformly distributed, since agriculture and intensive forestry has created a checkerboard-like patchwork of habitats and vegetation types that often are geographically close.

Snow depth

Many previous studies have reported that snow depths of 40-50 cm are associated with moose leaving their summer range (Nasimovich 1955 in Pulliainen 1974, Coady 1974, Pulliainen 1974, van Ballenberghe 1977, Sandegren, Bergström & Sweanor 1985). Our range of snow depths spanned this 'critical depth' nicely, but we found no difference between summer and winter ranges of migrants (see Table 1). Thus, snow depth *per se* did not influence the choice of winter range made by migratory moose in our study. Similarly, when comparing winter ranges of migrants to the year-round ranges of residents, we found no significant difference in snow depth (in fact, migrants' winter areas had slightly more snow than did residents, see Table 1). This trend is in the opposite direction of what might be expected if a benefit of migration was a winter range with less snow than that experienced by a non-migrating animal. Thus, our analysis does not support the idea that migrants benefit by selecting winter ranges with less snow than residents. Note however, that we do not suggest that snow depth *per se* is unimportant to moose ecology. At the lowest level of habitat selection, i.e within a home range, we did detect a significant over-use of areas with reduced snow depth (see Table 2), suggesting that moose use different criteria to select habitat at different levels (e.g. selection of a home range vs selecting where to feed within that home range).

Snow quality

The analysis indicated there was no difference in the sinking depths of calves or adults between seasonal ranges of migrants (see Table 1 and Fig. 2). However,

calves (but not adults) sank significantly less deeply into the snow at the winter ranges of migrants than at the year-round ranges of residents (see Table 1 and Fig. 2). In the snow conditions we experienced, it was apparently only the sinking depths of calves that was sensitive enough to reveal small differences in snow quality - adults, with their heavy foot loading (Kelsall & Prescott 1967) evidently being too crude a measure for the soft snow conditions we experienced.

The significant difference in the sinking depths of calves we found suggests that there may be a difference in snow quality between ranges, and that migrants may be selecting winter ranges where the effective snow depth is less. Since the cost of locomotion is affected by both snow depth (Bunnell et al. 1990) and snow quality (Coady 1974, LeResche 1974, Bunnell et al. 1990), it is perhaps not surprising that snow quality could be important for moose deciding whether to migrate or remain resident.

Differences in snow quality may arise from several causes and moose may also be responding to one of the other factors. For example, the density of vegetation may affect the compaction of snow by wind, and the differences in snow quality may also reflect something as simple as one home range on a slope facing south vs another range facing north. The tracks we measured for sinking depth were made under many different weather conditions, and this would have increased the variability of our snow quality estimates (and thus reduced our statistical power). It is therefore quite interesting that in spite of this variability, we did detect significant differences in sinking depth. Overall, our results suggest that snow quality could be involved in the habitat selection decisions made by moose.

General discussion

If migration has a cost, then movement between seasonal ranges should involve a positive change in some aspect of the habitat if migration is adaptive. In our study, we found little evidence that migration was strongly related to differences in the composition of the vegetation in different ranges, and most importantly, individual moose did not move to winter areas having less snow than the summer areas they left (see Table 1). However, when evaluating habitat selection at a lower level (Forbes & Theberge 1993, Mysterud et al. 1997), we found that moose utilised areas within their ranges with less snow than their range had on average (see Table 2). Like Bunnell et al. (1990) and Histøl & Hjeljord (1993), our results suggest little direct influence of snow depth *per se* on moose migration, but still highlights the importance of snow depth to habitat selection at a smaller scale. Overall, our results suggest that in our area, snow quality may be more relevant to migration than snow depth *per se*, and we recommend that future studies evaluate this possibility using direct measures of snow quality (e.g. the ramsonde (Ager 1965) or the snow penetrometer (Klein, Pearce & Gold 1950)).

Perhaps migration is adaptive for an individual, but not necessarily every year, since snow depth and condition vary among winters. However, if migration has little or no cost, then a moose might migrate every year even if it only benefited some years. The migratory patterns of moose can be maintained through several generations (Sweanor & Sandegren 1989, Andersen 1991a, b), and several authors have reported that the philopatric behaviour of moose is resistant to change (in part to cultural inheritance between mother and offspring; Cederlund, Sandegren & Larsson 1987, Sweanor & Sandegren 1989, Andersen 1991a,b, Takahasi 1998, Whitehead 1998). Therefore, migration in a given year may be non-adaptive due to annual differences in snow conditions, or if food availability is altered.

Another aspect of habitat choice is population density. Perhaps moose choose to winter in areas where population numbers are higher, and where they can benefit from other moose by walking in each others' tracks in order to reduce the cost of locomotion (Pennyquick 1975, Telfer & Kelsall 1979). In areas where snow is deep, this reduction in energy cost might thus be more important than avoiding competition for food.

For long-lived animals like moose, it may not be easy to determine if migration is currently adaptive, adaptive in only some years with particular snow conditions, or even presently maladaptive. Overall though, studies like ours on the decisions made by individual moose (incorporating direct investigation of snow quality) seem to be the best way to shed further light on this interesting and economically important phenomenon.

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