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## Site fidelity of female caribou at multiple spatial scales

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### Abstract

Studies of site fidelity have been hampered by arbitrary designations of spatial scale and the lack of null models for comparison. We generated null expectations of fidelity at different scales from the distribution of radio-tracked animals in a population. We applied the models to space use of satellite-tracked caribou (*Rangifer tarandus caribou*), the most vagile nonvolant terrestrial animal, from populations representing sedentary and migratory ecotypes. We compared distances between consecutive-year locations of adult females to expectations based on the total range and seasonal range of each population. At the scale of the total range, sedentary and migratory caribou displayed remarkably similar philopatry, despite a 30-fold difference in size of their population ranges, from time of calving (late May) to breeding (late October). The most intense fidelity occurred during post-calving when, on average, sedentary and migratory females returned to as near as 6.7 km and 123 km, respectively, of locations occupied the previous year. At the scale of the seasonal range, the ecotypes differed. Sedentary caribou still displayed fidelity from calving to breeding; migratory caribou exhibited fidelity only during late autumn. For migratory, but not sedentary caribou, inter-year distances during winter were negatively correlated with age, implying that older females were more philopatric. We conclude that reproductive activities delimit the season of fidelity of female caribou of both ecotypes, and that scale-dependent ecotypic differences in fidelity may reflect different factors of population limitation. A spatially-explicit approach to site fidelity is essential for synthesizing patterns across studies.

### Introduction

Site fidelity, the tendency of animals to remain in or return to a particular space, is an important feature for gauging the effects of human activity on animal movement (White and Garrott 1990). Site fidelity of birds and mammals has continued to receive considerable attention (e.g., Linnell and Andersen 1995; Van Dyke et al. 1998; Irons 1998; Phillips et al. 1998; references in Lindberg and Sedinger 1997; and Robertson and Cooke 1999). A persistent obstacle to evaluation and the synthesis of patterns, however, has been the lack of appropriate null models to derive expectation and permit comparison. Fidelity has been measured as the

relative changes in the space use within one population (e.g., Van Dyke et al. 1998; Flynn et al. 1999) or, more commonly, as the proportion of animals returning to a specific site or range (e.g., Berry and Eng 1985; Ramsay and Stirling 1990; Lewis et al. 1996; Irons 1998; Phillips et al. 1998; Flynn et al. 1999). Despite the voluminous literature, broadly generalizable patterns have been elusive (Robertson and Cooke 1999) because most studies have been conducted in an area of arbitrary size (cf. Garrott et al. 1987; Fancy and Whitten 1991) and at one spatial scale (cf. Lindberg et al. 1998). Conclusions about fidelity, like many ecological patterns, may be sensitive to the scale of observation (Wiens 1989).

We devised null models of site fidelity from the distribution of radio-tracked animals in the population, couched in a hierarchy of spatial scales. We defined fidelity as the propensity for consecutive-year locations of an individual to be closer together than random pairs of locations from the radio-tracked population, bounded by its distribution over a specified time. For our study of woodland caribou (*Rangifer tarandus caribou*) from Labrador and Québec, we identified two periods for random expectation, i.e., the season and year, which translated into null models nested at two spatial extents (Figure 1). The approach allowed us to extract scale-explicit patterns and make comparisons between populations. For caribou, the most vagile nonvolant terrestrial animal (Bergman et al. 2000), range fidelity has been described for the calving period (Brown and Theberge 1985; Gunn and Miller 1986; Fancy and Whitten 1991) but not during other critical points of the year, such as breeding, when gene flow is mediated (Greenwood 1980).

Our study populations represented two caribou ecotypes, migratory and sedentary, that differed in their life-histories and demography. Ecotypic identifications of *Rangifer* have been founded on the relative extent of movements and the spatial dispersion of females at parturition (Bergerud 1988, 1996). Migratory caribou display long-distance movements and the aggregation by adult females at traditional calving grounds (Gunn and Miller 1986); sedentary caribou exhibit lower mobility and the over-dispersion of females at parturition (Brown and Theberge 1985; Bergerud et al. 1990). These behaviors have been interpreted as contrasting strategies to minimize predation risk, especially by wolves (*Canis lupus*; Bergerud 1988, 1996). Demographically, too, the ecotypes tend to differ. Predation has generally been regarded as a more severe limiting factor for populations of the sedentary caribou (Bergerud and Elliot 1986; Seip 1992; Rettie and Messier 1998; Schaefer et al. 1999), whereas food represents the functional limitation for migratory caribou (Messier et al. 1988; Couturier et al. 1990; Crête and Huot 1993). Because scale-inconsistencies in space-use may reflect differences in the prevailing limiting factors at various scales (Power 1984; Folt et al. 1998; Rettie 1998), we predicted that site fidelity, construed as a strategy to minimize predation risk, would differ between these ecotypes when viewed on different scales.

## Methods

### Study area

The range of sedentary caribou, the Red Wine Mountains herd, spanned approximately 25,000 km<sup>2</sup> in central Labrador (Figure 1). Tundra vegetation occurred at higher elevations (>700 m), and was dominated by grasses, sedges, mosses, lichens, and low shrubs. At lower elevations, a mosaic of forest, peat bogs, streams, shallow ponds, and lakes occurred. Here, open conifer-lichen forest was dominated by black (*Picea mariana*) and white spruce (*P. glauca*), occasionally mixed with balsam fir (*Abies balsamea*), and ground cover of lichens and low shrubs. Stands of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and willow (*Salix* spp.) occurred along river valleys (Schaefer et al. 1999).

The range of the migratory ecotype, the George River herd, covered 700,000 km<sup>2</sup> of Labrador and northern Québec (Figure 1). Most of the area north of 58°N in Québec and 56°N in Labrador was tundra dominated by mosses, graminoids, and lichens. Lower latitudes comprised forest tundra and open lichen woodland. The canopy was dominated by black and white spruce and tamarack (*Larix laricina*), with common shrubs represented by dwarf birch (*Betula glandulosa*) and willows (Hearn et al. 1990).

During the study, the George River herd, 600,000 to 800,000 animals, was the largest caribou population in the world (Couturier et al. 1996). From 1989 to 1997, the Red Wine Mountains herd declined from approximately 740 to 150 animals (Schaefer et al. 1999).

### Data collection and preparation

We carried out the study from June 1986 to March 1998 for migratory caribou, and May 1993 to March 1998 for sedentary caribou. We captured adult ( $\geq 1$ -year-old) females using chemical restraint agents, administered by darts fired from a helicopter. We deployed satellite-tracked (Service Argos, Landover, Maryland, USA) ultra high frequency Platform Terminal Transmitters (PTTs; Telonics, Mesa, Arizona, USA.). PTTs had 3- or 4-day transmission cycles. We replaced or removed PTTs prior to battery exhaustion. In total, we tracked the movements and activity of 40 and 16 females for at least 1 year each from the migratory and sedentary herds, respectively.

We extracted a lateral incisor at time of capture. Age at last birthday (estimated as 1 June) was es-

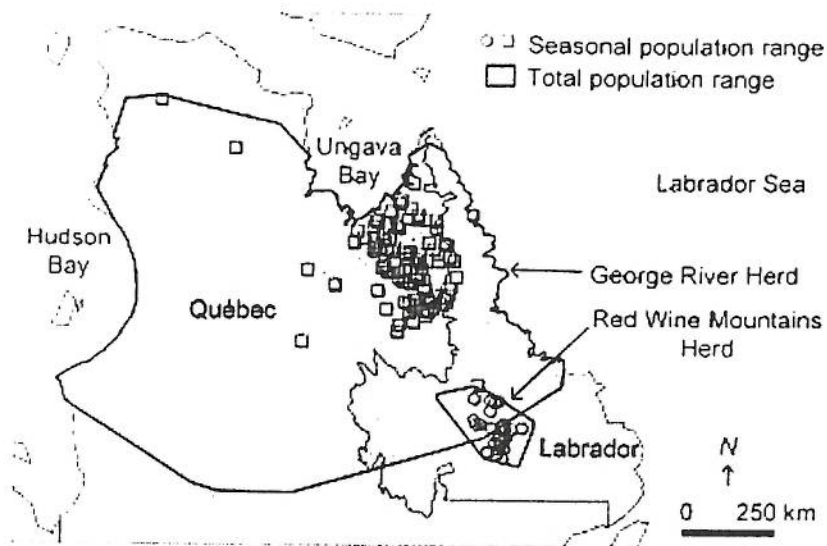


Figure 1. Study area of migratory George River caribou and sedentary Red Wine Mountains caribou. Scales for the assessment of fidelity are shown: total population range and examples of the seasonal (i.e., 6–9 June) population range. All animal locations are shown for the seasonal ranges. For clarity, minimum convex polygons (excluding coastal waters) represent the total ranges.

timated by counting annuli in the dental cementum (Matson's, Milltown, Montana, USA). To determine parturition status, we observed most females each year by helicopter near the time of parturition. For migratory caribou, checks were conducted 28 May to 26 June for presence of distended udder, calf, and antlers. Females with at least one of these characteristics were deemed parturient (Whitten 1995). For sedentary females, during 1994–1995, checks were conducted once in early June, and during 1996–1997, every 3 days from late May to early June. Because udder distention was obscured in forested sedentary range, we used the presence of a calf to characterize a female as parturient.

We selected the PTT location with the best quality class (NQ; Keating et al. 1991) during each transmission period as provided by Service Argos. We discarded locations with  $NQ < 0$  due to their inherent imprecision (Keating et al. 1991). For the remaining data, we calculated Keating's  $\xi$ , an indicator of potentially erroneous locations, determined by successive vectors of animal movement (Keating 1994). We deemed the upper 5% of  $\xi$  values as indicating potentially erroneous data. Following Rettie and Messier (1998), we retained such locations only if each could be confirmed by another nearby (<1 km) location from Service Argos within the same trans-

mission period; otherwise, the location was discarded and replaced with another location during the same period, subject to the same criteria. The total number of locations per animal ranged from 104 to 504.

#### Data analyses

For the observed pattern, we computed distances between paired locations of an individual, obtained 1 year apart, for each 4-day period during the annual cycle, beginning with the first calendar day. We retained the animal as sampling unit. For cases of more than one observation during a 4-day period (i.e., from radio-collars on a 3-day duty cycle), we used the average of the multiple distances during the 4-day period. We created a year-long profile of each caribou herd by plotting the mean distance between consecutive-year locations against time of year.

To derive the null expectations, we extended the approach of Garrott et al. (1987), using the population of radio-collar locations, to two spatial scales (Figure 1). We defined the total population range as the space denoted by locations of all radio-collared animals during all portions of the annual cycle; we defined the seasonal population range as the space denoted by locations of all radio-collared animals during a specific portion (i.e., 4 days) of the annual cycle.

For the smaller scale, seasonal population range, distances were calculated between all possible pairs of locations within each 4-day period for any location at least 1 year apart. For the larger scale, distances were computed between random pairs of locations during any period of the annual cycle from any year of radio-tracking. In this case, an extreme number of pairwise computations were possible; therefore, we randomly chose a subsample of 100 locations, calculated the mean distance between all possible pairs, and repeated the procedure until the estimate of the mean appeared to stabilize ( $n = 20$ ).

Because of the large number of comparisons at each scale, we maintained a conservative experiment-wise error rate, using  $\alpha = 0.01$  for each test. For each empirical mean during each 4-day period, we calculated a 99% confidence interval and denoted site fidelity as occurring when the null value was outside this confidence interval. At the scale of the total population range, where subsampling of locations was necessary to derive the null model, we performed two-sample *t*-tests for each 4-day period. To make comparisons between ecotypes, we computed the ratio of observed to expected distances for each 4-day period at each scale.

To examine the effect of reproductive status on fidelity, we compared, in any two consecutive years, the inter-year distances of females with a calf in both years versus those of females that did not have a calf in at least one year. We computed inter-year distances shortly after the peak of calving (i.e., 29 May to 1 June, and 14 June to 17 June for sedentary and migratory caribou, respectively). Because observations of reproductive status were not available for all animals in all years, only 19 migratory and 10 sedentary caribou qualified for analysis. We used a 2-way ANOVA to examine the effects of herd and reproductive status on inter-annual distance.

To test for the effect of age on fidelity, we computed inter-year distances of females at three contrasting points of the annual cycle: winter (1–4 March), calving (17–20 June), and breeding (3–6 October). To retain the animal as sampling unit, we selected the final complete year of data for individuals with at least 3 years of tracking. We regressed inter-year distance against age for each of these periods in the annual cycle.

Unless otherwise noted,  $\alpha = 0.05$ . Variables are reported as  $\bar{x} \pm 1$  SE. Statistical analyses were performed using SAS (SAS Institute Inc., Cary,

N.C., USA). Distances were calculated using MapInfo (MapInfo Corp., Troy, N.Y., USA.).

## Results

Female caribou displayed varying degrees of site fidelity, contingent on time of year, spatial scale, and ecotype. A pronounced annual cycle was evident for both ecotypes (Figure 2). For sedentary caribou, the mean distance between consecutive-year locations of individuals during winter was about 50 km, but after the onset of calving (late May), females displayed attraction to sites occupied the previous year. This distance declined to as low as 6.7 km in August. Comparisons to null models at both scales were consistent, indicating philopatry from late May to late October (Figure 2A,B).

Migratory caribou also displayed a distinct annual rhythm (Figure 2). During winter, average distances between consecutive-year locations of individuals were 400–450 km. As calving time approached in mid-May, these distances declined rapidly, attaining a minimum of 123 km during early July. For migratory caribou, fidelity was highly dependent on scale of the null model. At the larger scale, the total population range, migratory caribou were philopatric from early May to late November, encompassing the two periods of reproduction (parturition and breeding) and the intervening summer season (Figure 2C). In contrast, the smaller-scale seasonal null model implied that fidelity was absent during these times of year but present during late fall and early winter (Figure 2D).

The ratio of observed to expected distances across scales and ecotypes (Figure 3) indicated remarkable similarity between sedentary and migratory females at the larger scale, although the ecotypic patterns tended to diverge during summer and early fall. On the smaller scale, however, the ecotypes contrasted sharply during the period of May to October. The pattern exhibited by the sedentary ecotype was largely immutable across scales, whereas for the migratory ecotype, the pattern was strongly scale-dependent. There was little difference between observation and expectation for migratory caribou at the smaller scale (Figure 3).

We found no influence of parturition status on fidelity at calving time. During early June, the mean inter-year distances of sedentary and migratory females with calves in two consecutive years ( $23.1 \pm 3.1$  km and  $96.5 \pm 28.1$  km, respectively)

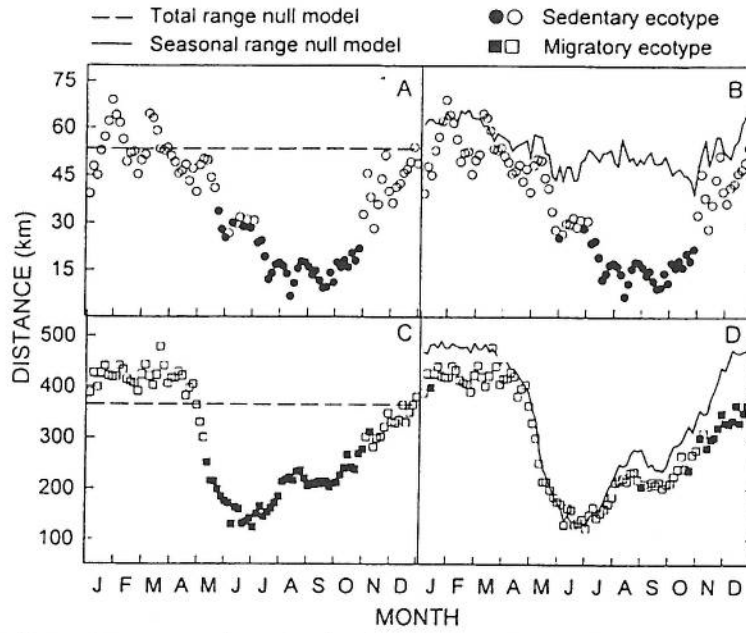


Figure 2. Site fidelity (distances between consecutive-year locations of individuals) of sedentary (A, B) and migratory (C, D) female caribou in relation to null models at two spatial scales. Closed symbols represent values significantly different ( $p < 0.01$ ) than those of the respective null model.

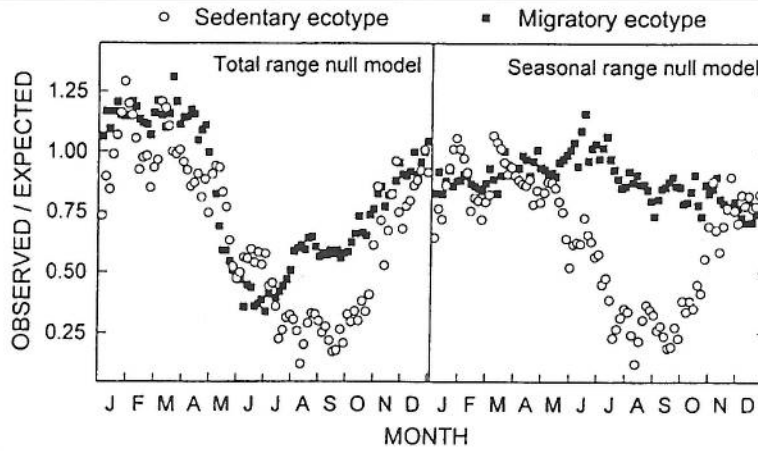


Figure 3. Ratio of observed and expected distances (between consecutive-year locations of individuals) for sedentary and migratory female caribou in relation to null models at two spatial scales.

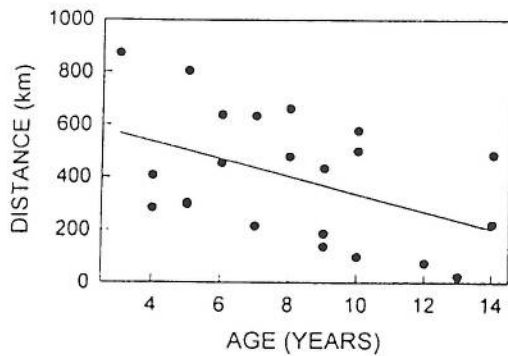


Figure 4. Distance between consecutive-year locations of individual adult female migratory caribou as a function of age.

were not statistically distinguishable from those lacking a calf in one or two years ( $55.6 \pm 27.4$  km and  $102.3 \pm 17.0$  km, respectively;  $F = 0.61$ ; 1, 25 d.f.;  $p = 0.443$ ). For sedentary caribou, there was no effect of age on inter-annual distances during winter ( $F = 2.74$ ; 1, 4 d.f.,  $p = 0.174$ ), calving ( $F = 0.98$ ; 1, 4 d.f.,  $p = 0.378$ ), or breeding season ( $F = 3.32$ ; 1, 4 d.f.,  $p = 0.166$ ). For migratory caribou, there was no effect of age on inter-annual distances during calving ( $F = 0.05$ ; 1, 23 d.f.,  $p = 0.828$ ) or breeding season ( $F = 0.01$ ; 1, 18 d.f.,  $p = 0.916$ ). However, for migratory caribou, inter-year distance during winter was inversely correlated with age (Figure 4;  $r^2 = 0.209$ ,  $F = 5.28$ ; 1, 20 d.f.,  $p = 0.032$ ), a relationship not confounded by year of study ( $F = 1.34$ ; 1, 20 d.f.,  $p = 0.261$ ).

## Discussion

Fidelity to a particular space has been proposed to confer individual ecological benefits, such as familiarity with resources and avoidance of predators (Greenwood 1980). Biotic and abiotic environments exhibit gradients across many scales (Bell et al. 1993; Schaefer and Messier 1994). We can anticipate, therefore, that as animals move further afield, they will encounter increasingly novel habitats and potentially experience reduced fitness. For caribou, patterns of space-use have been regarded as responses to the risk of predation (Bergerud 1988, 1996; Rettie 1998). We surmise that site fidelity may confer reduced predation risk to females and their calves, although this notion has not been tested. Indeed, the purported ecological benefits

to individuals have rarely been demonstrated in any species to date (Lindberg and Sedinger 1997).

Most studies have treated site fidelity as a discrete variable: an animal returned to a pre-defined location or did not. Synthesizing patterns across these studies has been hindered by the designation of how close an individual must return to its previous location, an arbitrary decision that can obscure comparisons between populations and species (Lindberg and Sedinger 1998; Robertson and Cooke 1999). Fidelity has been denoted as the percentage of animals returning to a specific range or site (e.g., Cameron et al. 1986; Edge et al. 1985; Festa-Bianchet 1986; Johnson et al. 1993; Irons 1998; Phillips et al. 1998) or the frequency distribution of between-year distances of animals returning to a given area (e.g., Berry and Eng 1985; Brown and Theberge 1985; Ramsay and Stirling 1990; Lewis et al. 1996). For both approaches, defining an area has been variable. For example, investigations of winter philopatry of waterfowl have ranged in extent from less than  $1 \text{ km}^2$  to nearly  $10,000 \text{ km}^2$  (Robertson and Cooke 1999). Even within species, patterns can differ sharply with scale. White-tailed deer (*Odocoileus virginianus*), for instance, displayed only moderate fidelity to their winter range, but at a larger scale, animals tended to reside in the same wintering yard each year (Tierson et al. 1985). A distinct advantage of our approach is the capacity to allow tracking of individuals at any scale. The organism defines the various spatial extents of study (Schaefer and Messier 1995; Folt et al. 1998), thus remedying the effects of arbitrary notions of scale.

As noted by Schneider (1994), computing the ratio of one quantity to another constitutes scaling. Ratios of observed and expected inter-year distances (Figure 3) provide common, scale-explicit currencies for comparison across populations. Using this metric, we conclude that large-scale expressions of site fidelity by female caribou were strikingly similar between ecotypes despite a nearly 30-fold difference in the spatial extent of these populations (Figure 1). Return to traditional calving grounds has been regarded as one of the most consistent behaviors of migratory caribou (Gunn and Miller 1986), fidelity which has been considered stronger than to other portions of the annual range (Valkenburg and Davis 1986). Our results corroborate this observation but indicate, in broader perspective, that parturition represents only the initiation of fidelity which is sustained until the autumn breeding season (Figure 2). The two seasons of reproduction thus delimit the period of large-scale fidelity of both caribou

ecotypes. For many species, site fidelity appears more common during the breeding, than non-breeding, season (Greenwood 1980; but see Myers et al. 1988; Robertson and Cooke 1999). White-tailed deer, for example, display greater tenacity to summer than winter ranges (Tierison et al. 1985; Dusek et al. 1989; Aycrigg and Porter 1997; Van Deelen et al. 1998).

On the large scale of the population range, the most notable contrast between ecotypes occurred during post-calving to breeding (mid-July to late October) when inter-year distances were less for the sedentary ecotype. This difference is consistent with the notion that site fidelity may be diminished for more gregarious species. The maintenance of established patterns may be prone to association with conspecifics (Festa-Bianchet 1986; Bergerud 1996). Indeed, the less intense fidelity for migratory, compared to sedentary, caribou during summer and early fall might be linked to the social and competitive influences, in particular, aggregation in response to insect harassment (Toupin et al. 1996) and scramble competition for summer forage (Manseau et al. 1996).

Philopatry of migratory caribou is a highly scale-dependent pattern. Fidelity to calving and summer range disappeared when viewed at the smaller scale, corroborating earlier suggestions (Fancy and Whitten 1991; Bergerud 1996) that females are philopatric to their traditional calving grounds, but not to precise locations within these grounds. The pattern for sedentary caribou, on the other hand, persisted across scales, indicating consistent site fidelity from calving to breeding periods, regardless of the extent of our observations.

One of the insights of a hierarchical approach is the capacity to search for scaling consistencies or 'domains' (Wiens 1989) potentially indicative of consistency in the factors of population limitation (Power 1984; Folt et al. 1998; Rettie 1998). For caribou, minimization of predation risk to females and calves has been regarded as the dominant underlying cause of space use of both ecotypes (Ferguson et al. 1988; Bergerud 1996). Assuming that site fidelity by female caribou represents a strategy to minimize predation risk, our analysis underscores previous studies indicating ecotypic differences in the dominant factors of population limitation. Migration to calving grounds appears to provide an effective means to escape the direct effects of predation, as caribou space away from their less mobile predators (Fryxell et al. 1988; Bergerud 1996). This, in turn, has resulted in the migratory George River herd to become regulated by

competition for high-quality summer forage (Messier et al. 1988; Couturier et al. 1990; Crête and Huot 1993). At a small scale, these caribou may largely decouple themselves from predation risk. Foraging opportunities have become a more salient limitation within the calving and summer range (Fancy and Whitten 1991; Manseau et al. 1996). On the other hand, the scale-invariant philopatry of the sedentary ecotype indicates a single domain. This pattern accords with the pervasive and consistent limiting effects of predation on these forest-dwelling populations (Seip 1992; Bergerud 1996; Rettie and Messier 1998; Schaefer et al. 1999).

Site fidelity is also expected to have genetic consequences for populations. Breeding philopatry, in particular, may have a strong influence on the genetic structure of populations; it may heighten genetic divergence between populations (Greenwood 1980; Robertson and Cooke 1999). Consistent with the philopatric nature of adult females, electrophoretic analysis of Red Wine Mountains and George River herds indicates genetic discreteness (van Staaden et al. 1995), although the natal philopatry of *Rangifer* has not been documented.

A major question in animal ecology is the degree to which individuals vary in their expression of fidelity and the factors influencing these differences. Age appears to be a significant influence on fidelity of migratory caribou during winter (Figure 4), a pattern consistent with other species (e.g., Garrott et al. 1987; Dusek et al. 1989; Switzer 1997; Lindberg et al. 1998). Similarly, for many animals, reproductive success is often linked to subsequent site fidelity (Switzer 1997; Flynn et al. 1999). For both sedentary and migratory caribou, however, we failed to find an association between parturition status and strength of calving site fidelity (Brown and Theberge 1985). Because of the high mortality rate of calves (Bergerud 1996; Schaefer et al. 1999), however, recruitment may better approximate the reproductive success of females. We surmise, therefore, that success at calf recruitment may represent a more sensitive determinant of calving site fidelity for female caribou.

Site fidelity and spatial scale are inexorably linked. A recent synthesis (Robertson and Cooke 1999) has called for greater incorporation of scaling as a component of fidelity studies. We agree. Hierarchical approaches, using explicit organism-defined scales, will be required if conclusions about site fidelity are to be more than study-specific. We believe that our approach represents an advance in this direction.

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