Female site fidelity of the Mealy Mountain caribou herd (Rangifer tarandus caribou) in Labrador

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Abstract: The Mealy Mountain caribou population of southeastern Labrador is listed as threatened. Site fidelity - the philopatric tendency of an animal to remain in or return to the same site - has often been suspected in sedentary caribou like the Mealy Mountain, but rarely has been examined. Philopatric behaviours are important because fidelity sites may then receive priority protection from human disturbance. To describe and document site fidelity for the Mealy Mountain herd, satellite telemetry data from 12 collared adult females during three years was examined. The mean distance between locations in consecutive years of tracking the individual caribou was calculated and an annual profile of site fidelity generated. This profile illustrated that the lowest inter-year distances occurred during calving, when caribou returned to within 3.9 km (2005-06) and 11.5 km (2006-07) of the previous year’s location, and during post-calving, when the mean distance was 7.7 km (2005-06). Spring snow depths were substantially greater in 2007 and appeared to weaken calving site fidelity. This spatial information may serve as a basis for detecting anthropogenic effects on woodland caribou.

Key words: anthropogenic effects; calving; Labrador; philopatry; snow.

Introduction

The Mealy Mountain Caribou Herd (MMCH) is a woodland caribou (Rangifer tarandus caribou) population inhabiting 24 000 km2 in southeastern Labrador (Otto, 2002), an example of the forest-dwelling, sedentary ecotype. Like other woodland caribou populations, they migrate short distances of only 50-150 km; females “space out” at calving time; and they are either solitary, or form small groups, depending on the season (Seip, 1992; Mallory & Hillis, 1998). They are late-successional specialists of the boreal forest and are generally found in mature coniferous forests of North America (Miller, 1982; Ahiti & Hepburn, 1967). Since the 1800s, their numbers have greatly declined and their range in North America has diminished, leaving them confined to even more northerly portions of their range (Bergerud, 1974a; Miller, 1982). Many forest-dwelling populations,
along with the MMCH, are listed as threatened by the Committee on the Status of the Endangered Wildlife in Canada (COSEWIC) due to predation, disease, and habitat loss that is potentially caused by forest fires, the expansion of human settlements, and land development (Armitage & Stopp, 2003; Schaefer & Pruitt, 1991; Seip, 1992; Thomas & Gray, 2002).

Although the MMCH population has fluctuated in the past (Bergerud, 1967), recently it has been stable or slightly increasing to approximately 2600 caribou (Otto, 2002; Schmelzer et al., 2004). The most significant threats to the caribou herds in Labrador, including the MMCH, are thought to be illegal hunting and developments such as hydroelectric, commercial forestry, highways and snowmobile trails (Roberts et al., 2006). Development increases human access and disturbance and may fragment the landscape.

Due to the threatened status of forest-dwelling MMCH caribou, it is of the utmost importance to understand the ecological processes and patterns that can assist in devising management strategies to promote their survival and recovery. Site fidelity is the tendency of an animal to remain in or return to the same site. If site fidelity is displayed by individual caribou, those sites, or habitats selected for comprising those sites, may be of particular importance to protect from human access and disturbances. Site fidelity is known to occur in a number of birds and mammals, including caribou (Ferguson & Elkie, 2004; Greenwood, 1980; Metsaranta, 2002; Schaefer et al., 2000; Schieck & Hannon, 1989). It is most common in polygamous mammals where breeding dispersal is male-biased. Adult males gain little from being philopatric so they are more likely to disperse (Greenwood, 1980). It has been suggested that female philopatry has evolved mainly to enhance the cooperative potential among breeding individuals within social groups to eliminate female dispersal cost (Chesser & Ryman, 1986).

Caribou are most commonly faithful to their calving grounds, although some herds have been known to return to the same post-calving, breeding and wintering grounds (Brown & Theberge, 1985; Gunn & Miller, 1986; Ferguson & Elkie, 2004; Schaefer et al., 2000). Along with habitat selection, site selection implies that an animal evaluates available habitats and chooses the one with the highest quality and stability (Switzer, 1993). This selection is viewed as hierarchical process in which an organism first chooses a general place to live (a home range) and then makes subsequent decisions about the use of different patches, the search modes it employs, and its responses to specific objects that it encounters (Johnson, 1980). By being philopatric, the animal may gain benefits such as a familiarity with resources and a reduction in predation risk (Greenwood, 1980; Schaefer et al., 2000; Rettie & Messier, 1998).

Although fidelity is poorly understood in the MMCH, studies in an adjacent Labrador woodland caribou herd, the Red Wine Mountains caribou, found adult females were highly philopatric to calving and especially post-calving sites (Brown & Theberge, 1985; Schaefer et al., 2000). This knowledge is important because those sites and seasons are now recognized and might be used to protect the herd from human disturbance. Further, since female caribou are highly sensitive and avoid human disturbance (Armitage & Stopp, 2003; Banfield, 1974; Cameron et al., 1979; Chubb & Keith, 1992; Cowan, 1974; Miller & Broughton, 1974; Harrington & Veitch, 1992), changes in site fidelity might be useful to gauge human disturbance and habitat changes.

Satellite telemetry was used to document site fidelity of adult female Mealy Mountain caribou. It was predicted that site fidelity would be displayed by the MMCH and would be most prominent during calving and post-calving seasons, that the degree of fidelity would differ between years, and that this difference may be governed by annual variation in snow cover.

In order to test these hypotheses, 12 female caribou from the MMCH were collared and satellite telemetry was used to pinpoint their locations on 4-day cycles. Because it has been suggested that the MMCH is divided into a mainland subpopulation and an island subpopulation in which individuals are thought to only inhabit George Island, a 12 km² island located 9 km offshore from the herd’s range (Jeffery et al., 2007), the telemetry data from both of these putative subpopulations were examined closely. To quantify fidelity inter-year distances between previous year locations were computed to examine annual profiles of the tendency to return to the same site (Schaefer et al., 2000). Snow cover data were used to relate the strength of fidelity to snow accumulation, a major influence on the year-to-year patterns of range use by caribou (Bergerud, 1967; Eastland et al., 1989). Home range size and travel rates were also quantified in order to test for correlations with site fidelity.

Materials and methods

Study area

Labrador is a relatively undeveloped landmass consisting of boreal and subarctic ecozones. The study area was comprised of approximately 60% forest, 30% tundra, soil and rock barrens, and 3.5% peatlands (Roberts et al., 2006). Black spruce (Picea marit-
ana) was the most common tree species, while other softwoods included white spruce (Picea glauca) and balsam fir (Abies balsamea), and hardwoods included white birch (Betula papyrifera), trembling aspen (Populus tremuloides), balsam poplar (Populus balsamifera), many willow (Salix) species, which together made a total of 150 species of shrubs and trees (Ryan, 1978). There are 610 species of lichen known to Labrador (Ahiti, 1983). Moose and wolves were present in the study area (Roberts et al., 2006).

Typical total mean annual precipitation in the southern regions of Labrador is 1300 mm, and normal mean temperature, 0 °C (Banfield, 1981; Peach, 1984), with an annual mean snowfall of 300-400 cm (Roberts et al., 2006).

Data collection
On 18 April 2005, 12 female caribou, 8 from the mainland and 4 from George Island, both from the Mealy Mountain herd, were captured using a Coda net gun with 5-m x 5-m nets. The net gun was fired from an A-Star Helicopter that flew in a systematic flight pattern across the herd’s range. GPS satellite hybrid collars (Telonics, Mesa, Arizona, USA) with a lifespan of three years were then fitted onto the animals. Location data via satellite were determined at 4-day intervals from CLS America supplier from 18 April 2005 to 25 June 2007.

Six seasons were established: Winter – 4 December to 3 April, Spring Migration – 4 April to 31 May, Calving – 1 June to 3 July, Post-Calving – 4 July to 7 September, Pre-Breeding – 8 September to 27 October, and Fall Migration – 28 October to 3 December.

Data analysis
All statistical analyses were undertaken using Statistica v.9. One-sample Kolmogorov Smirnov tests were performed in order to confirm normality. All figures were created using Statistica v.9 or Microsoft Excel 2007.

Site fidelity
Longitude and latitude coordinates were converted into radian longitude and latitudes in order to allow for distance between years in kilometres to be calculated. For each individual, the radian location data were paired for every four-day location according to Julian day between consecutive years (2005-2006 and 2006-2007). Locations that were not matched with a consecutive-year location were removed. The distance between consecutive-year locations according to the following formula:

\[ \text{Distance} = \text{ABS}(\text{ACOS}((\text{COS}(Rl1)*\text{COS}(Rl0)) * (\text{COS}(Rl2)*\text{COS}(Rl0)) + \text{COS}(Rl1)*\text{SIN}(Rl0))\] 

Where \( Rl0 \) was the radian longitude of the later year, \( Rl1 \) was the radian latitude of the later year and \( Rl02 \) and \( Rl02 \) were the radian longitude and latitude of the previous year, respectively.

For every 4-day cycle, the mean inter-year distance was calculated for the group of 8 ‘mainland’ females as well as separately for the 4 ‘island’ females from George Island and was used to generate profiles from 18 April to 28 December (2005-06) and 4 January to 25 June (2006-07). Repeated Measures ANOVA’s were performed on the mainland female inter-year distance means for the 2005-06 and 2006-07 year sets. Fisher LSD tests were used to determine where the inter-year distance means for the mainland females differed between months.

Home range size and site fidelity
The annual home ranges size of each of the 8 mainland individuals from 1 June 2005 to 31 May 2006 and 1 June 2006 to 31 May 2007 were calculated by plotting all telemetry locations onto ArcGIS v.9.2. Locations were converted from latitude and longitude (WGS 1984) into UTM (Universal Transverse Mercator; NAD 1927, Zone 21) coordinates. Hawth’s Analysis Tools extension was used to calculate a minimum convex polygon (MCP) for each individual. The MCP areas were plotted against the mean inter-year distances during the calving seasons (1 June to 3 July), 2005-06 and 2006-07, to examine the relationship between home range size and fidelity.

Home range variation between years
The mean home range size for the 8 mainland females from 1 June to 31 May, 2005-06 and 2006-07 was calculated and a paired t-test was performed to determine if there was a significant difference in home range size between years.

Rate of travel
The mean daily rate of travel was calculated for the 8 mainland females from 1 June to 31 May, 2005-06 and 2006-07. A paired t-test was performed to determine if there was a significant difference in the distance travelled per day between years.

Snow cover
Snow cover data for the nearby communities of Happy Valley-Goose Bay and Cartwright were obtained from Environment Canada (Environment Canada, 2008) for April to June, 2006 and 2007. The mean depth of snow-on-the-ground for each month during each year was calculated.
Results

The partial year-long profiles of female caribou fidelity, expressed as the distance between consecutive-year locations between 2005-06 and 2006-07, for the mainland (Fig. 1) and island (Fig. 2) groups, showed that fidelity was greatest during calving and post-calving for the mainland group, but did not appear to be displayed at a seasonal scale in the island group. Therefore the focus was on the mainland group exclusively for all subsequent analyses. During calving, the inter-year distance was only 3.9 km during 2005-06 and 11.5 km during 2006-07. During post-calving the mean inter-year distance was 7.7 km (2005-06). In contrast, fidelity was lowest during winter. Female caribou were, on average, 17.1 km and 19.0 km, in 2005-06 and 2006-07 respectively, from their previous year's location.
Table 1. Mean inter-year distance between month p-values as resulting from Fisher LSD test (2005-06). * represents significant pairwise differences.

| Month | Apr  | May  | Jun  | Jul  | Aug  | Sep  | Oct  | Nov  | Dec  |
|-------|------|------|------|------|------|------|------|------|------|
| April | 0.027* | 0.345 | 0.510 | 0.768 | 0.726 | 0.054 | 0.025* | 0.467 |       |
| May   | 0.003* | 0.771 | 0.513 | 0.200 | 0.006* | 0.003* | 0.102 |       |       |
| June  | 0.006* | 0.715 | 0.316 | 0.013* | 0.005* | 0.172 |       |       |       |
| July  | 0.014* | 0.519 | 0.029* | 0.013* | 0.309 |       |       |       |       |
| August| 0.058 | 0.108 | 0.052 | 0.712 |       |       |       |       |       |
| Sep   | 0.749 | 0.054 | 0.006* | 0.013* | 0.002* | 0.110 |       |       |       |
| Oct   | 0.960 | 0.025* | 0.003* | 0.005* | 0.013* | 0.309 |       |       |       |
| Nov   | 0.120 | 0.467 | 0.102 | 0.172 | 0.309 | 0.704 | 0.210 | 0.110 |       |
| Dec   |       |       |       |       |       |       |       |       |       |

There was a significant difference in mean inter-year distances of mainland females between months in 2005-06 ($F_{24} = 3.4$, $P = 0.009$) and 2006-07 ($F_{35} = 3.5$, $P = 0.012$). Fidelity at calving (June) tended to be significantly different than in fall and early spring (April, October, November, sometimes May) but not post-calving (July, August, September; Tables 1 and 2).

The correlation between the mean inter-year calving distances (km) and the annual home range sizes (km$^2$) was weak for both 2005-06 ($r^2 = 0.123$) and 2006-07 ($r^2 = 0.250$).

Strength of fidelity differed between years. The 2006-07 distances were greater than the 2005-06 distances during the overlapping months of April to June (Fig. 3). In April, caribou in 2005-06 were 3.4 km closer to their previous year site than they were in 2006-07 (Table 3); in May, they were 15.7 km closer in 2005-06 than in 2006-07, and in June, were 7.6 km closer in 2005-06 than 2006-07. These distances were significantly different for May and June, but not April.

The snow depth in Happy Valley-Goose Bay (Fig. 4a) was 67% greater in April and May 2007 than in 2006, i.e., mean snow depth was 40.5 cm in 2006 but 67.7 cm in 2007. Meanwhile, in Cartwright (Fig. 4b) snow depth increased by 204% over the same period. In April of 2006, the mean snow ground cover was 80.8 cm, whereas in 2007 the mean was 245.8 cm. In June, there was no snow in 2006, but in 2007 there was a mean of 1.7 cm. Caribou experienced both greater depth and duration of snow cover during spring 2007.

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Discussion

The degree of fidelity may vary due to the analytical effects of scale (Schaefer et al., 2000). For example, caribou on a large scale may display fidelity to a region, such as an island, and on a finer scale, display fidelity to seasonal calving grounds. Mealy Mountain mainland and island female caribou displayed differences in site fidelity. George Island has an area of 12 km² and is located 9 km off the coast of Labrador, to the east of the herd’s range. It has been suggested that females of the George Island population do not leave the island (Jefferey et al., 2007). Although strongly philopatric at the scale of the whole island, these island females appeared to display an absence of seasonal site fidelity, likely because of the island’s small size. The Mealy Mountain mainland females displayed the expected patterns of fidelity, specifically to calving and post-calving sites. Although caribou have been known to display fidelity to many seasonal sites (Metsaranta, 2002; Schaefer et al., 2000), the most pronounced fidelity for females, including the adjacent Red Wine Mountains Caribou Herd, are to calving and post-calving sites (Brown & Theberge, 1985; Ferguson & Elkie 2004; Schaefer et al., 2000). It has been suggested that site fidelity is beneficial because there is an acquired familiarity with resources and an increase in avoidance of predators (Greenwood, 1980). An animal should respond positively to an environment in which its survival chances and reproductive success increase, such as to a familiar site with a decreased risk of predation (Levins, 1968).

The reproductive success of females in many polygamous ungulates, such as woodland caribou, is limited by their ability to acquire adequate food resources for lactation and calf development (Brown & Mallory, 2007) and minimize the risk of predation (Rettie & Messier, 2000). In Alaskan migratory caribou, the progression of the calving season is highly synchronized with forage plant phenology to ensure sufficient food resources, reducing the energetic burden of lactation (Post et al., 2003). During post-calving seasons, doe milk production, fawn survival, and production rates are highly correlated with mid-summer habitat (White, 1983). Thus, forage supply likely influences both the sites selected for calving and post-calving and female fidelity to those sites.

Since predation is considered the most important proximal factor limiting caribou populations (Brown & Mallory, 2007), and caribou often avoid habitats with increased predation risk (Rettie & Messier, 2000; Bergerud & Page, 1987), suitable habitat not only includes an abundance of forage, but also a reduction in predation. Caribou are most sensitive to harassment by predators and humans during the calving season (Armitage & Stopp, 2003) and most calf mortality occurs during the first six weeks of life (Mahoney et al., 1990). To compensate, females may return year after year to a calving site associated with low predator risk, and some authors have suggested that fidelity occurs as an anti-predator tactic (Rettie & Messier, 1998; Bergerud et al., 1983). Another behaviour exhibited by sedentary woodland caribou, including the MMCH, is that females become solitary during calving, often dispersing along lake shores and on islands in open bogs. This behaviour, too, is considered an anti-predator strategy, as the caribou are ‘spacing out’, i.e., making themselves rare in the midst of predators (Bergerud, 1985; Bergerud & Ballard, 1988). Caribou may be returning to previous year’s sites for the added benefit of predator avoidance. Overall, if a site is recognized to have an adequate forage supply as well as a potential decreased risk of predation, it would seem sensible for an animal to return to such a site, enhancing reproductive success. To date, however, studies have failed to uncover a difference in site fidelity for female caribou with calves versus those without calves, owing perhaps to small sample sizes (Schaefer et al., 2000).

Fidelity may vary due not only to the analytical effects of scale (Schaefer et al., 2000) but also to environmental effects of snow cover (Bergerud 1967). The months of April, May and June displayed differences in which 2005-06 had a stronger degree of fidelity than did 2006-07, although only the months of May and June had differences that were significant.

Habitat selection and fidelity to a particular site may change from year to year depending on many factors such as forage supply, predation, alternative prey abundance, habitat alteration, and other environmental factors (Klein, 1970; Bergerud et al., 1983; Mahoney & Schaefer, 2002; Miller et al., 1985; Ion & Kershaw, 1989). Snow cover is a particularly important factor in the winter ecology of Rangifer (Pruitt, 1959; Bergerud, 1967). Two towns in the vicinity of the herd’s range, Happy Valley-Goose Bay and Cartwright, provided snow depth data for the months leading up to calving (April and May, as well as during the calving season, June). There was substantially less snow in 2006 than in 2007. This coincided with greater calving site fidelity in 2006 and weaker fidelity in 2007, and suggests that snow cover acts as an important environmental component affecting the animal’s return to the same site (Eastland et al., 1989; Bergerud, 1967).

In contrast, home range size and rate of travel did not differ significantly between 2005-06 and 2006-07. This suggests that in response to the increase in snow cover, the MMCH did not respond with respect
to these two features, but possibly instead moved to regions with less snow accumulation. When snow accumulation is great, caribou often display increased inter-year distances from previous locations (Wittmer et al., 2006). Bergerud (1967) discovered that the winter distribution of the MMCH varied between years in relation to snow cover. In years with greater snow accumulation, caribou moved north onto the Mealy Mountains where there was less snow, and moved south in years with little snow. In a separate study, Bergerud & Page (1987) found that just prior to calving; female woodland caribou in British Columbia moved to high elevations, apparently to avoid predators during spring in years when snow accumulation was greater.

Snow cover has been shown to be associated with movement, and has been correlated with predation rates, as well as forage abundance. Deep snow can restrict caribou movements causing an increase in energy expenditure (Wilson & Klein, 1991; Cumming, 1992). In migratory herds, this may prevent cows from reaching calving grounds (Bergerud & Ballard, 1988). Although caribou may have restricted movement in deep snow, their wolf predators may be able to travel on top of the snow crust as they have a lighter foot loading, thus allowing kill rates of other prey such as white-tailed deer to increase (Mech & Frenzel, 1971; Nelson & Mech, 1986). In deep snow years, not only does predation increase, but forage supply may decrease, causing caribou to move to areas with less snow in order to gain access to forage that is more easily available (Wilson, 2000; Bergerud, 1974b; Bergerud & Nolan, 1970; LaPerriere & Lent, 1977; Pruitt, 1979). Habitats selected in deep snow years may change to more closed canopy and irregular terrain (with varying wind speeds) that result in shallower snow depths (Bergerud, 1974b; Brown, 2005).

The findings of this study generate conservation possibilities for the MMCH. With knowledge of site fidelity, which is a predictable year-to-year behaviour, one can adopt strategies to protect sites, or habitats comprising those sites, selected during high fidelity seasons, such as the calving and post-calving. Anthropomorphic habitat disturbances such as roads, seismic lines, and forest harvesting, have been demonstrated to have negative impacts on caribou abundance, distribution, and potentially survival and reproduction (Vistnes & Nellemann, 2008; Lessard, 2005). Caribou are the least tolerant of all ungulates to human disturbances (Mallory & Hillis, 1998). Females and calves are highly vulnerable to disturbance during calving as stillbirths, injuries, cow-calf separation, and physiological depression of lactation can result (Armitage & Stopp, 2003; Banfield, 1974; Cowan, 1974; Miller & Broughton, 1974; Harrington & Veitch, 1992). For example, females are known to be found 2-3 times farther away from clearcuts than males, and are generally more influenced by disturbance than males (Cameron et al., 1979; Chubbs & Keith, 1992). These examples display the vulnerability of caribou during calving and post-calving seasons, suggesting that when they have found a site allowing increased reproductive and survival success, the locations should be protected from anthropomorphic disturbances and development. Because the MMCH and other sedentary herds space out during calving and post-calving seasons as an anti-predator strategy, communal calving grounds do not exist. In order to accommodate protection of sites high in fidelity, an approach that identifies the habitats selected for is ideal. Once identified, habitats associated with high fidelity located in proximity to the home ranges of all individuals, rather than the individual sites themselves, should be protected.

Detecting anthropogenic impacts on caribou is complicated by their longevity and wide-range habitats. Human development and infrastructure will likely increase across the range of the MMCH, and will be associated with a rise in human access to region. It is suggested that site fidelity offers a predictable pattern, which, in light of the probable link to reproductive success, can serve as a sensitive gauge of anthropogenic disturbances. Given the baseline fidelity data, a decrease in the strength of fidelity, specifically by females during calving or post-calving, may be a valuable indicator of the negative effects of disturbance, both natural and human mediated. Evidence of severely weakened fidelity may be associated with compromised reproductive success and have negative consequences for this threatened herd. Conservation actions appropriate to promote the continued existence of the MMCH could be justified based on weakened fidelity. Gathering baseline understanding, as it was done here, is the first step to such conservation actions. Future monitoring of inter-year distances, which may indicate changes in the degree of site fidelity, is recommended.

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