

Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland

J.A. Schaefer and S.P. Mahoney

Abstract: Understanding the relationship between abundance and distribution is central to ecology but may require broad-scale observations, especially for long-lived, mobile animals like caribou (*Rangifer tarandus* (L., 1758)). We tested the link between demography and spatial ecology of Newfoundland caribou, coincident with their numerical growth (1980s, 1990s) and decline (2000s). We analysed site fidelity, rate of movements, timing of migration, and population organization from telemetry observations of more than 600 adult females. Site fidelity was consistent across herds, intensifying near the onset of calving and peaking in late summer, a cycle that may reflect selection for postpartum security. Late-summer fidelity was stronger in the 1980s than 1990s, a trend that reversed itself during the 2000s. Weekly movements were lower in the 2000s, but with no clear differences between the 1980s and 1990s. Timing of migration changed: in the 2000s, spring migration of the Buchans herd occurred 3 weeks earlier and autumn migration 3 weeks later compared with the previous decade, the reversal of a 40-year trend. Herd affinities, revealed by fuzzy membership coefficients, diminished by the 2000s. These changes are consistent with the hypothesis of limitation by summer forage competition. Space use represents a useful gauge of numerical changes in caribou.

Key words: caribou, demography, migration, philopatry, population structure, *Rangifer tarandus*.

Résumé : La compréhension du lien entre l'abondance et la répartition est une notion fondamentale en écologie qui peut toutefois nécessiter des observations à grande échelle, notamment en ce qui concerne les animaux mobiles longévifs comme le caribou (*Rangifer tarandus* (L., 1758)). Nous nous sommes penchés sur la présence éventuelle d'un lien entre la démographie et l'écologie spatiale du caribou de Terre-Neuve durant une période de croissance (années 1980 et 1990) puis de baisse (années 2000) de leur nombre. Nous avons analysé la fidélité au site, la fréquence des déplacements, le moment des migrations et l'organisation de la population à la lumière d'observations télémétriques sur plus de 600 femelles adultes. La fidélité au site était uniforme d'un troupeau à l'autre, s'intensifiant au début de la période de mise bas pour atteindre un maximum à la fin de l'été, ce cycle pouvant refléter une sélection axée sur la sécurité post-partum. La fidélité au site à la fin de l'été était plus forte dans les années 1980 que dans les années 1990, cette tendance s'inversant dans les années 2000. Si les déplacements hebdomadaires étaient moins fréquents dans les années 2000, aucune différence nette n'a été notée entre les années 1980 et 1990. Le moment des migrations a changé : dans les années 2000, la migration printanière du troupeau de Buchans a eu lieu trois semaines plus tôt et la migration automnale, trois semaines plus tard, que durant les années 1990, ce qui constitue une inversion de la tendance des 40 années précédentes. À partir des années 2000, les affinités des troupeaux, indiquées par des coefficients d'appartenance floue, ont diminué. Ces changements concordent avec l'hypothèse voulant que la concurrence associée à l'alimentation estivale joue un rôle limitant. L'utilisation de l'espace constitue un bon indicateur des variations du nombre de caribous. [Traduit par la Rédaction]

Mots-clés : caribou, démographie, migration, philopatrie, structure des populations, *Rangifer tarandus*.

Introduction

One of the great truisms in ecology is that organism abundance and distribution are linked (MacArthur 1972; Gaston and Blackburn 2000). This fundamental relationship is exemplified by species like caribou (*Rangifer tarandus* (L., 1758)) where changes in population size and space use often vary in concert. Numbers of migratory caribou may rise or fall by 100-fold in a few decades (Bergerud 1996; Vors and Boyce 2009; Couturier et al. 2010; Mahoney et al. 2011), swings in demography that may move in tandem with size of the home range (Schaefer and Wilson 2002; Couturier et al. 2010), fidelity to calving grounds (Gunn et al. 2012), and timing of migration (Mahoney and Schaefer 2002). Population structure, too, may be altered (Hinkes et al. 2005).

Space use resides at the heart of caribou ecology. Indeed, this is the most mobile nonvolant, terrestrial animal on the planet (Fancy et al. 1989; Bergman et al. 2000) whose ecotypes are distin-

guished by the space-use strategies of females (Bergerud 1988, 1996). The legendary return of females to traditional calving grounds (Brown and Theberge 1985; Gunn and Miller 1986; Schaefer et al. 2000) sets the stage for population structure. At the same time, switches in herd affiliation by female caribou are not unusual (Boulet et al. 2007; Nagy et al. 2011). Over the long term, whole calving grounds may shift, often associated with population peaks (Bergerud 1996; Hinkes et al. 2005; Taillon et al. 2012). Understanding these patterns is valuable. Changes in space use may precede observations on demographic or habitat changes (Schaefer and Wilson 2002; Faille et al. 2010) and thus could serve as early indicators of numerical change. Nevertheless, long-term, individual-level studies of caribou are still rare (Hinkes et al. 2005; Boulet et al. 2007; Bergerud et al. 2008) and our knowledge of their spatial dynamics is still incomplete.

There is growing evidence that migratory caribou are regulated by summer food (Messier et al. 1988; Crête and Huot 1993;

Received 5 June 2013. Accepted 27 August 2013.

J.A. Schaefer, Department of Biology, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.

S.P. Mahoney, Sustainable Development and Strategic Science, Department of Environment and Conservation, Government of Newfoundland and Labrador, St. John's, NL A1B 4J6, Canada.

Corresponding author: James Schaefer (e-mail jschaefer@trentu.ca).

Couturier et al. 2010), including those in Newfoundland (Mahoney and Schaefer 2002; Mahoney et al. 2011). Over 3 decades, Newfoundland caribou displayed sustained numeric growth ($r = 0.064$; 1975–1997) to an estimated peak of 95 810 animals, followed by abrupt decline to approximately 32 170 animals ($r = -0.099$; 1997–2008) (Mahoney and Weir 2009). These trends have been synchronous across the island (Bergerud 1971; Mahoney et al. 1998, 2011) and have been coupled with the diminished stature of adults, lower juvenile survival, and less time spent on the calving and summer grounds. Such patterns are consistent with the hypothesis of density-dependent competition for summer food (Mahoney and Schaefer 2002; Mahoney et al. 2011). During most of this period, movements of female caribou were monitored with radiotelemetry. We capitalized on this opportunity to improve our understanding of the link between demography and spatial ecology of the genus *Rangifer* Hamilton Smith, 1827.

Here, we documented the geography of changing caribou abundance in Newfoundland, based on radio-tracking of more than 600 adult females during 1980–2010. We quantified some fundamental features of space use—site fidelity, rate of weekly movements, timing of migration, and population structure—with a particular focus on five herds with historic (1980s, 1990s) and recent (2000s) telemetry observations. Under the hypothesis of summer-food regulation, we predicted site fidelity and herd membership of females would decline and movements increase in the face of population growth and intensified forage competition. We also anticipated a shift in timing of migration. Over 4 decades, the Buchans herd displayed a pronounced change in peak migration, leading to a 2-month reduction in annual residency on the calving and summer grounds (Mahoney and Schaefer 2002). With the recent numeric decline and relaxed food competition, we expected a halt or even a reversal to this longstanding trend. We tested these ideas by applying recent quantitative methods: interyear distances to assess site fidelity across the full annual cycle (Schaefer et al. 2000); power laws to determine animal speed under varying relocation intervals (Schaefer and Mahoney 2003); and fuzzy classification to assign individuals to populations (Schaefer et al. 2001; Nagy et al. 2011).

Materials and methods

Study area and populations

Caribou ranges were typically composed of forests of balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), and white birch (*Betula papyrifera* Marshall) and bogs with stunted black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch). Barrens, lakes, ponds, and heaths were also widespread. Forestry activities were the primary human-caused disturbance. In 2000, clearcuts accounted 0.5%–1.2% of each caribou population range.

In most herds, adult female caribou undertook a short (30–100 km) northward migration from their winter ranges to congregate on open calving grounds. Most births occurred mid-May to early June.

Data collection and preparation

During 1980–1997, adult female caribou were live-captured and fitted with mortality-sensing very high frequency (VHF) radio transmitters. Radiotelemetry reconnaissance was carried out approximately fortnightly by airplane, more frequently (roughly every 5 days) during spring and summer. Radiolocations had an accuracy of ≤ 500 m based on repeated blind-test positioning of “dummy” transmitters. More recent (2004–2010, and for the Gros Morne herd, during 1990s) observations were garnered from Argos platform transmitter terminals (PTTs) and global positioning system (GPS) collars. PTTs were programmed to transmit every 2 or 4 days; GPS collars to collect locations every 1, 2, or 4 h. Animals were live-captured and handled in accordance with

Table 1. Sample sizes of radio-collared adult female caribou (*Rangifer tarandus*), by decade, in the analyses of site fidelity and movements of five Newfoundland caribou herds during 1980–2010.

Herd	Decade	Site fidelity	Movements
Buchans	1990s	41	44
	2000s	29	35
Grey River	1980s	52	113
	2000s	39	42
Gros Morne	1990s	24	56
	2000s	10	10
LaPoile	1980s	61	126
	2000s	36	39
Middle Ridge	1980s	36	47
	1990s	31	62
	2000s	22	34

guidelines from the American Society of Mammalogists (Sikes et al. 2011).

Before analysis, we screened the automated telemetry data for errors. For PTTs, we selected the location with the best-quality class for each collar during each transmission period provided by Service Argos. We then calculated ξ , an indicator of potentially erroneous fixes, determined by successive vectors of animal movement (Keating 1994). Based on the distribution of log-transformed ξ values, we deemed extreme locations ($\xi > 6640$ m; 2.2% of the best-quality locations) as erroneous. For the GPS data, we followed Lewis et al. (2007) and eliminated two-dimensional fixes with high dilution of precision (DOP > 5). Finally, to resemble better daytime VHF telemetry, we further reduced these copious data by selecting one GPS fix for each animal each day, closest to 1230 Newfoundland Standard Time (NST) during 0930–1530 NST.

Following Mahoney et al. (2011), we tested for differences among decades, coincident with the growth (1980s), cessation of growth (1990s), and decline (2000s) of these populations. We conducted geographic analyses in MapInfo version 11 (Pitney Bowes Software, Troy, New York, USA), statistical computations in Statistica version 10 (Statsoft, Tulsa, Oklahoma, USA) or SigmaPlot version 12 (Systat Software, San Jose, California, USA).

Site fidelity

We developed a year-long profile of fidelity based on the distances between locations of an individual in consecutive years (Schaefer et al. 2000). Because VHF data were relatively sparse, we set 5 days as the resolution of the analysis. We calculated the distance between any two locations of an individual, separated by 363–367 days, for each 5-day period during the annual cycle, beginning with the first calendar day. We maintained the animal as experimental unit. For cases of >1 observation during a 5-day period, we used the mean of multiple distances during the period. We retained any period represented by ≥ 6 animals (Table 1) and created a year-long profile of each herd by plotting the mean (± 1 SE) distance between consecutive-year locations against time of year. Dates were expressed as the mid-point of a 5-day period.

To test for decadal differences, we focussed on two herds with a nearly continuous profile of fidelity during late summer across ≥ 2 decades, i.e., the Middle Ridge herd (1980s, 1990s, 2000s) and Gros Morne herd (1990s, 2000s). We assembled data on all animals with observations in every 5-day period, 27 July–31 August, and carried out repeated-measures ANOVA. After initial analysis, we noted the residuals failed to assume a normal distribution; we therefore \log_{10} -transformed the data to meet this assumption. For the Middle Ridge herd, ANOVA was followed by post hoc Tukey means tests.

Table 2. Log–log regression statistics of distance travelled (km) versus time (days) for female caribou (*Rangifer tarandus*) from five Newfoundland herds during 1980–2010.

Herd	Decade	Intercept	Slope
Buchans	1990s	0.371	0.573
	2000s	0.008	0.625
Grey River	1980s	0.820	0.313
	2000s	−0.042	0.555
Gros Morne	1990s	0.015	0.518
	2000s	−0.081	0.356
Lapoile	1980s	0.246	0.784
	2000s	0.026	0.626
Middle Ridge	1980s	0.372	0.239
	1990s	0.185	0.462
	2000s	0.165	0.591

Movements and migration

The time between telemetry relocations differed substantially during our study. Because the speed of animal movement is sensitive to temporal resolution (Rowcliffe et al. 2012), we applied power laws to standardize observations to a 7-day interval (Schaefer and Mahoney 2003). For each herd and decade, we assumed a common, underlying movement pattern, although we acknowledge that this approach ignores seasonal variation in caribou pathways. First, we computed the distance between all individual animal locations separated by 3–14 days. This data set contained 843 506 movements from 630 females. We then determined the slope (z) of log–log regressions of distance (Y ; in kilometres) versus time (X ; in days), separately for each herd and decade (Table 2). We then modified each raw observation to a common time scale (X_0) of 7 days by computing an adjusted distance (Y_{ADJ}) with the formula (Thorpe 1975):

$$(1) \quad Y_{ADJ} = 10^K$$

where

$$(2) \quad K = \log Y - z(\log X - \log X_0)$$

We choose a common temporal resolution ($X_0 = 7$ days), a value within the range of data collection, to avoid the dangers of extrapolation. To maintain the animal as experimental unit, we then computed the mean adjusted distance (Y_{ADJ}) for each animal during each 7-day period of the year. Finally, we created a year-long profile of each herd and each decade by plotting the mean (± 1 SE) distance travelled as a function of calendar date. Dates were expressed as the mid-point of each 7-day period. We retained any period represented by ≥ 3 animals (Table 1).

To assess changes in timing of migration, we augmented a previous analysis of the Buchans herd, for which we had long-term observations originating in 1957 (Mahoney and Schaefer 2002). For spring and autumn of 2006–2010, we determined the date of crossing by each female near the southern edge of the herd's calving and summer grounds. Because the annual sample size was modest (range = 4–25 animals), we used the median date each year rather than the mode. To evaluate whether timing changed, we evaluated two competing models of the date of peak migration versus year: linear regression (under the hypothesis of no switch in the long-term trend) against a piecewise, two-segment regression (under the hypothesis of a switch in migrational timing). We did this separately for spring and fall migrations. We compared the two models using Akaike's information criterion for small sample sizes (AIC_c).

Population structure

Similar to Bergerud (1972), we delineated four seasons: spring (precalving, calving, early postcalving, and the early growing season; 1 May–30 June), summer (late postcalving and peak plant biomass; 1 July–30 September), autumn (breeding and after hard frost; 1 October–30 November), and winter (continuous snow cover; 1 December–30 April). We retained all animals with ≥ 3 locations per season and computed the median Universal Transmicator (UTM) coordinates (easting and northing) for each animal for each season. The analysis comprised 529 females ($n = 100$ in 1980s; $n = 80$ in 1990s; $n = 349$ in 2000s). We used the median UTM coordinates of each female during spring, the conventional time of year for delimiting herds (Roffler et al. 2012), in the classification. Median coordinates of females during spring were highly correlated with their median easting ($r > 0.90$) and northing ($r > 0.96$) locations from the other three seasons, indicating high redundancy among seasons.

Following Schaefer et al. (2001), we applied fuzzy c -means clustering to identify populations. We used FuzMe version 3.5c (Minasny and McBratney 2002) to compute membership coefficients for each animal in each group. We set the weighting exponent, m , which determines the degree of blurriness among groups, at a moderate level ($m = 2.0$). We looked for minima in the fuzziness performance index, F' , and the normalized classification entropy, H' , to indicate appropriate numbers of groups (k) from the classification.

To project the resultant populations in space, we assigned each animal to the group where its fuzzy membership coefficient was highest. For each group, we constructed 95% harmonic mean ranges using all median seasonal locations for two subsets of animals—all females in the group and only those females with strong affiliations (i.e., membership ≥ 0.8). To test for changes in the strength of herd affinities, we conducted Kolmogorov–Smirnov (KMS) tests on the individual maximum fuzzy membership coefficients between decades.

Population delineations are likely sensitive to the timing and location of collar deployment (Bethke et al. 1996) and contingent on representative sampling across the study area (Harwood 2009). Indeed, in Newfoundland, there was a shift in the principal season of live captures, from spring in the 1980s and 1990s to winter in the 2000s. To account for this potential confounding influence, we repeated KMS tests by matching season of collar deployment across decades—spring between the 1980s ($n = 45$) and the 2000s ($n = 27$) and winter between the 1990s ($n = 16$) and the 2000s ($n = 197$).

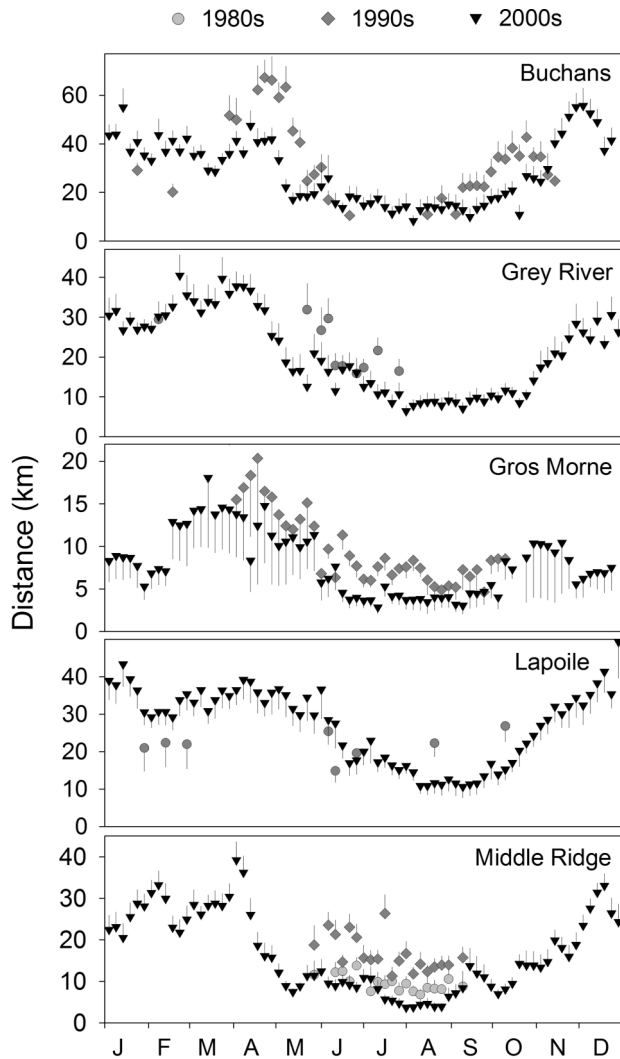
Results

Site fidelity

Female caribou displayed a distinct annual rhythm of fidelity. Continuous telemetry tracking during the 2000s uncovered seasonal patterns that were consistent across herds (Fig. 1). As calving approached (mid-May), site fidelity intensified and became most pronounced postcalving. Although distances varied among herds, the timing of the most intense fidelity, when interyear distances were minimal, was consistently late summer: 1 August for the Grey River and Middle Ridge herds, 6 August for the Buchans herd, and 10 September for the Gros Morne and LaPoile herds. In contrast, females exhibited much weaker philopatry during winter when individuals were typically 35–45 km away from their previous year's location, albeit less (≈ 15 km) for the Gros Morne herd (Fig. 1).

Across decades, the Middle Ridge herd exhibited substantial changes in late-summer fidelity ($F_{[2,43]} = 13.91$, $P < 0.0001$; Fig. 1) during the phases of population growth and decline. Tukey' tests revealed that during the 1980s, females returned, on average, 5.82 km closer to previous year's sites compared with the 1990s ($P = 0.023$). This pattern then reversed itself. During the 2000s, late-summer distances were 7.60 km less than during the 1990s ($P = 0.0001$) and marginally less (1.78 km) than the 1980s ($P = 0.058$). Females from the Gros Morne herd exhibited the same decadal

Fig. 1. Site fidelity of female caribou (*Rangifer tarandus*) from five Newfoundland herds, by decade, expressed as distances between consecutive-year locations of individuals. Values are means \pm 1 SE.



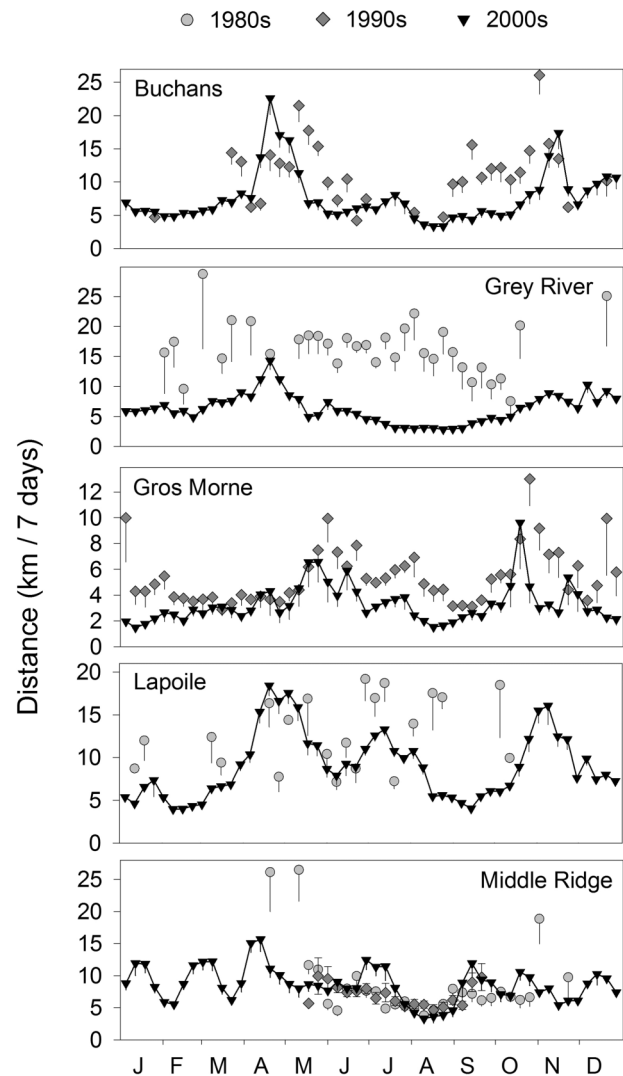
trend—stronger late-summer fidelity in the 2000s (≈ 3.87 km) than in the previous decade (≈ 6.57 km; $F_{[1,15]} = 5.41$, $P = 0.034$; Fig. 1). Historical shifts during other seasons could be interpreted only qualitatively and tentatively because of intermittent VHF monitoring. Nevertheless, patterns were broadly similar (Fig. 1). Compared with previous decades, site fidelity was generally stronger during the 2000s in spring (Buchans and Gros Morne herds) and at calving (Gros Morne and Grey River herds), whereas in winter it appeared weaker (Buchans and LaPoile herds).

Movements and migration

The apparent movements of caribou were sensitive to temporal resolution. The slopes (z) of log-log regressions of the distance travelled versus time were consistently and substantially less than unity (Table 2; $0.239 < z < 0.784$). The power formula removed any scale sensitivity. Once we adjusted observations to common, 7-day intervals for each herd and decade, distance (Y_{AD}) remained only faintly correlated with time between relocations ($0.004 < r < 0.019$).

With the exception of the Middle Ridge herd, weekly movement rates during the 2000s declined relative to the previous two decades (Fig. 2). The magnitude of change, however, was variable among herds and most pronounced for the Grey River herd. For the Gros Morne herd, where automated Argos and GPS telemetry provided continual observations during the 1990s, diminished

Fig. 2. Rate of movement of female caribou (*Rangifer tarandus*) from five Newfoundland herds, by decade, standardized as the distance travelled per 7 days. Values are means \pm 1 SE.



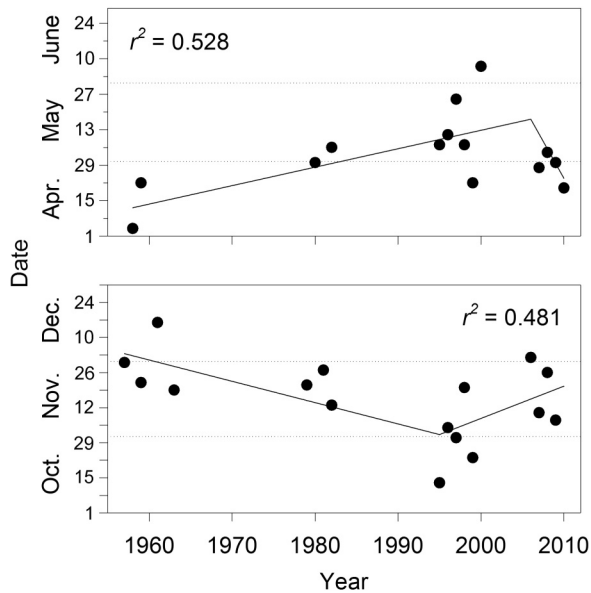
movement in the 2000s was clearly evident across the entire annual cycle (Fig. 2). On the other hand, we discerned no obvious shifts in the Middle Ridge herd with observations during both the 1980s and the 1990s, the period of population growth (Fig. 2).

The Buchans herd exhibited a reversal of a 40-year trend in timing of both spring and fall migrations (Fig. 3). Piecewise, two-segment regression emerged as the superior model over linear regression during both spring (piecewise $AIC_c = 155.6$; linear $AIC_c = 163.0$) and fall (piecewise $AIC_c = 179.9$; linear $AIC_c = 184.7$). Buchans caribou in the 2000s migrated about 3 weeks earlier in spring (12 May in the 1990s, 27 April in the 2000s) and 3 weeks later in autumn (30 October in the 1990s, 18 November in the 2000s) (Fig. 3) compared with the previous decade. Such a switch was also apparent in the change in peak movements in both seasons for the Buchans herd (Fig. 2).

Population structure

Fuzzy classification revealed that Newfoundland caribou could be delineated into herds; F' and H' exhibited several local minima (Fig. 4). Although there was strong rationale for coarse delineations of two and four populations, we choose $k = 8$ because of its comparability with longstanding herd designations (Fig. 5; Mahoney and Weir 2009) and management units, and thus its

Fig. 3. Timing of peak spring and autumn migrations of caribou (*Rangifer tarandus*) in the Buchans herd, Newfoundland, during 1957–2010. Lines of best fit and coefficients of determination were determined from two-segment regressions.



utility in caribou management. There was considerable ambiguity among these groups. The maximum membership coefficients of females were typically much lower than unity (median = 0.755; range = 0.272–0.996; Fig. 6), signifying that many females displayed partial herd affinities.

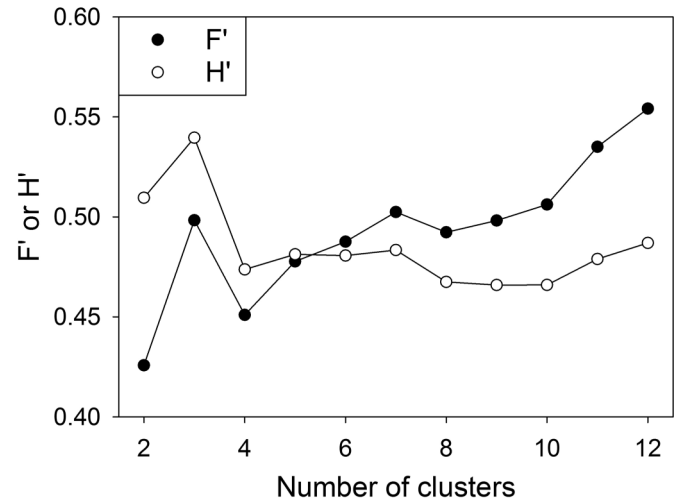
Maximum fuzzy membership coefficients declined from a median of 0.807 in the 1980s, 0.787 in the 1990s, to 0.724 in the 2000s (Figs. 6, 7). There were significant differences from the 2000s versus the 1980s and 1990s (KMS test, $P < 0.025$; Fig. 7), signifying some erosion of herd identities. This pattern persisted when we controlled for season of live capture. Based on spring collar deployments, median fuzzy coefficients were significantly higher in the 1980s (0.863) than in the 2000s (0.664) (KMS test, $P < 0.001$); based on winter deployments, the median was also higher in the 1990s (0.813) than in the 2000s (0.693) (KMS test, $P < 0.025$). These geographic trends were readily apparent in the westward shift of LaPoile herd and southward shift of the Middle Ridge herd in the 2000s relative to earlier decades (Fig. 6).

Discussion

Use of space is fundamental to caribou. Indeed, the primary feature for distinguishing ecotypes is the distribution of parturient females—the strategies of “spacing out” or “spacing away” from predators (Bergerud 1988, 1996). The demographic consequences can be profound. For some populations, migration effectively allows females with calves to escape the regulatory effects of predation. These herds, in turn, appear regulated by summer food, typically revealed by changes in body size, diet quality, juvenile survival, recruitment, and time spent on the summer grounds (Messier et al. 1988; Crête and Huot 1993; Mahoney and Schaefer 2002; Couturier et al. 2010; Mahoney et al. 2011).

Conversely, shifts in caribou distribution and movements can mirror numerical change. The growth and decline of the George River herd, for instance, was reflected in expansion and subsequent shrinkage in the sizes of the population range, calving grounds, and female home ranges (Messier et al. 1988; Schaefer and Wilson 2002; Couturier et al. 2010; Taillon et al. 2012). Timing of movement, too, may vary. The Buchans herd represents a clear example. During the era of sustained growth, during 1957–2000, spring migration became progressively delayed while fall migra-

Fig. 4. Indicators of the appropriate number of groups of Newfoundland caribou (*Rangifer tarandus*) during 1980–2010, based on the fuzzy performance index, F' , and normalized classification entropy, H' .



tion advanced; this represented a shift of 2 months over 40 years (Mahoney and Schaefer 2002), which has abruptly reversed (Fig. 3). Compared with a decade earlier, Buchans caribou in the 2000s spent roughly 6 weeks longer per year on their calving and summer range, a pattern revealed only after a half-century of observations. Hinkes et al. (2005) surmised that even 25 years of monitoring may be insufficient to gain understanding of caribou spatial dynamics.

Other spatial metrics of Newfoundland caribou coincided with their numerical rise and fall. Compared with the 1980s, spring and summer site fidelity deteriorated in the 1990s, then intensified in the 2000s (Fig. 1); rates of movement declined (Fig. 2). The inverse relationship between breeding site fidelity and population density is a reiteration of patterns from other vertebrates (Pyle et al. 2001; Itonaga et al. 2011). We cannot entirely discount, however, the potential confounding influences of changes in technology. For instance, with VHF telemetry in the 1980s and 1990s, we may have failed to detect long-distance movements (Koenig et al. 1996) and thus overestimated site fidelity. Even with massive field effort (for example, nearly 2500 VHF locations from 157 animals in the LaPoile herd), historic data were often too sparse for the assessment of site fidelity. Nevertheless, these shifts are consistent with the hypothesis that Newfoundland caribou are food-limited, a conclusion further supported by decades of morphological change (Mahoney and Schaefer 2002; Mahoney et al. 2011). We surmise that, during the recent population decline, competition for high-quality forages (and the imperative to find them) has diminished, too.

Some behaviours were consistent across populations. Indeed, even though the annual return of female caribou to their calving range is well-known (Brown and Theberge 1985; Gunn and Miller 1986; Roffler et al. 2012), our analysis demonstrates more pronounced philopatry during postcalving (Fig. 1; Schaefer et al. 2000; Popp et al. 2011). Such behaviour may represent the large maternal investment and selection for postpartum security by females for their calves. Indeed, the energetic and fitness costs of lactation exceed those of gestation (Clutton-Brock et al. 1989) and during summer the mortality of calves (<6–8 weeks of age) is high and variable (Mahoney et al. 1990; Bergerud 1996). On the other hand, females displayed little or no tendency to return to specific parts of their winter range (Fig. 1; Schaefer et al. 2000). Such predictability implies the utility of site fidelity as an assay of habitat quality

Fig. 5. Population structure of Newfoundland caribou (*Rangifer tarandus*) during 2004–2010, based on fuzzy classification of females in spring. Open polygons represent population ranges of all members in each herd; stippled polygons represent individuals with membership coefficients ≥ 0.8 .

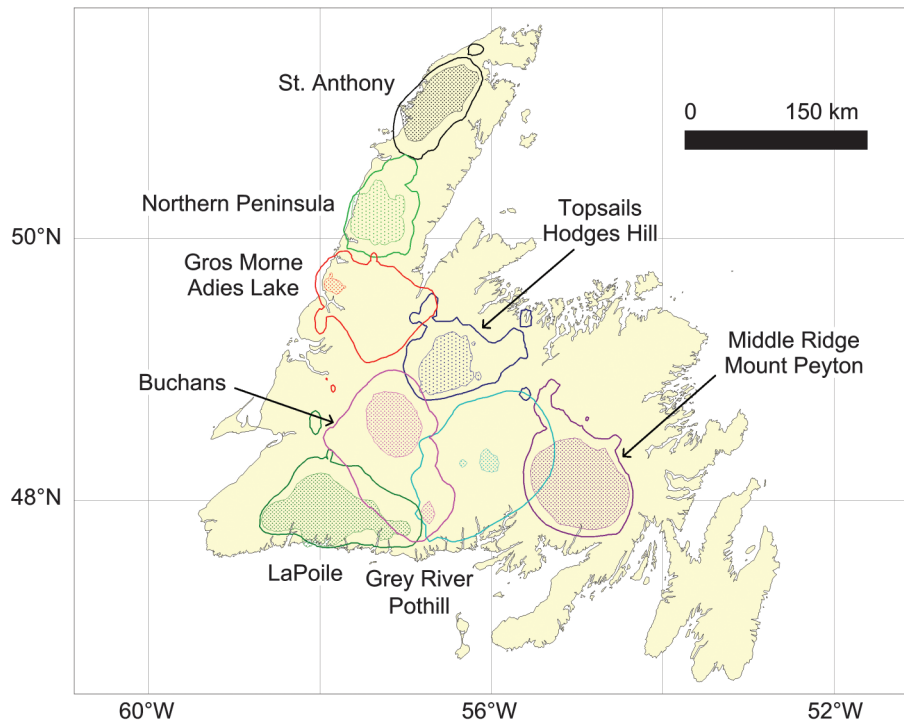
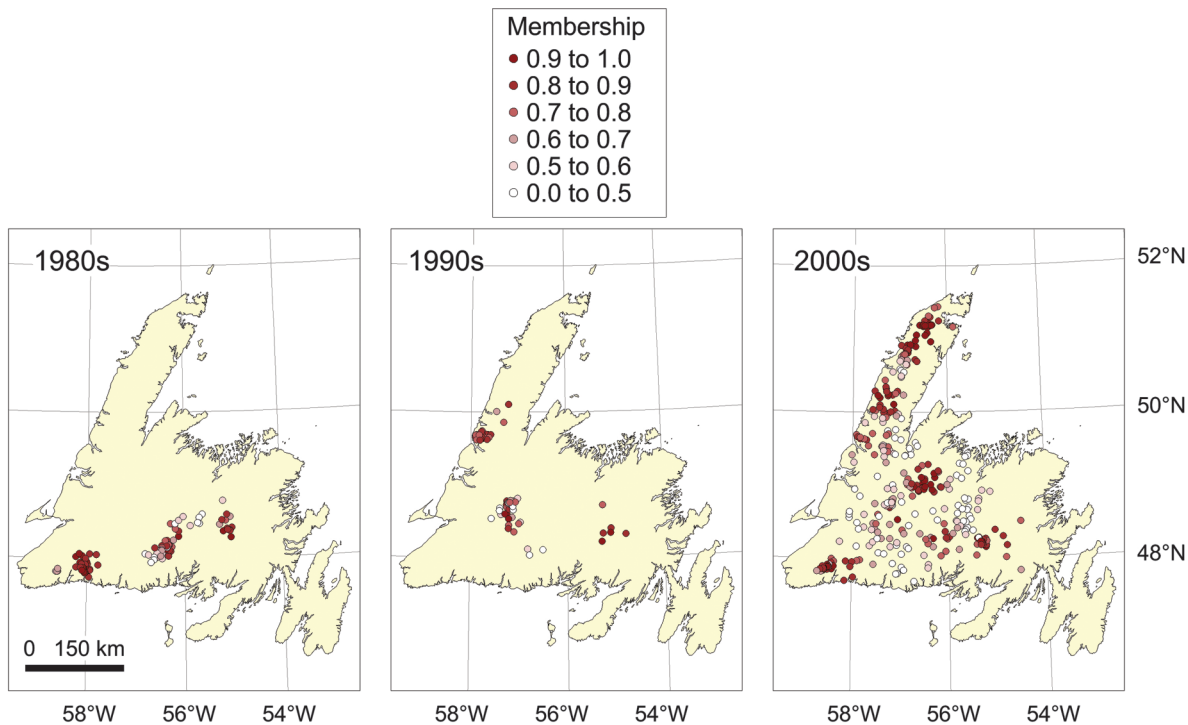


Fig. 6. Median locations of female Newfoundland caribou (*Rangifer tarandus*) in spring during 1980–2010, by decade, depicted by the maximum fuzzy membership coefficient for each individual.

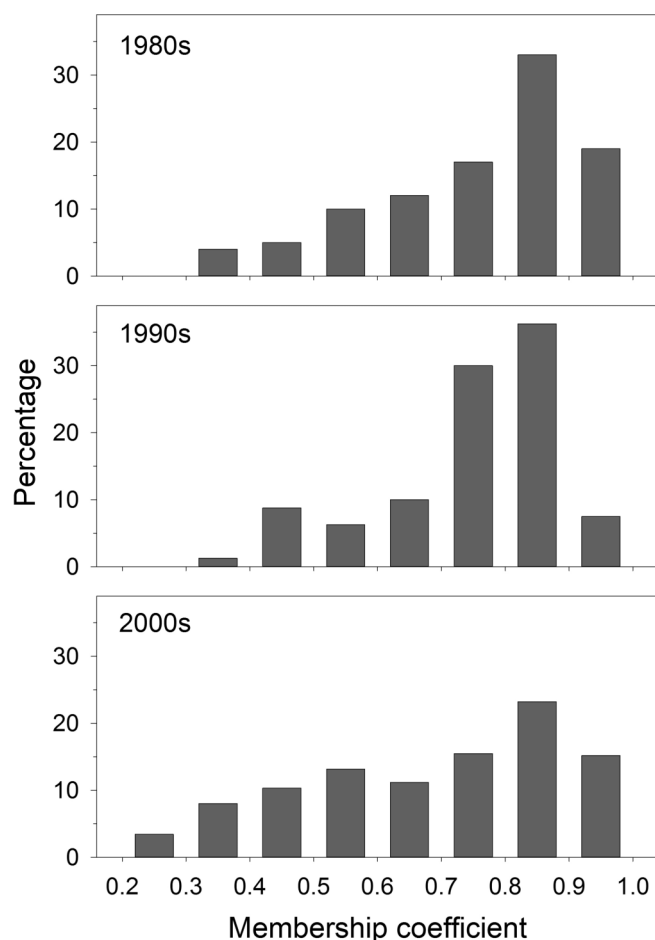


(Faille et al. 2010), which for migratory caribou may be driven by variation in density (Fig. 1; Gunn et al. 2012).

Philopatry underlies population organization. Relationships between individuals are the basis for delineating populations (Harwood 2009), whether genetic, demographic, or geographic

(Wells and Richmond 1995). Population bounds, however, may not be static. Over 3 decades, although population structure in the 2000s remained highly similar to conventional herd delineations in Newfoundland (Fig. 5; Mahoney and Weir 2009), female caribou exhibited lower herd affiliations (Figs. 6, 7). The sparser distribu-

Fig. 7. Maximum fuzzy membership coefficients of female caribou (*Rangifer tarandus*) in Newfoundland during 1980–2000, by decade.



tion of females in spring, detectable as lower herd affinities, may represent a compensatory response to degraded food resources on traditional calving grounds; the recovery of forages may take years (Hansen et al. 2007). Our results add to the growing evidence of long-term shifts in calving grounds, especially when coupled to population peaks (Bergerud 1996; Hinkes et al. 2005; Taillon et al. 2012).

Abundance and distribution, noted Bergerud (1996), are two sides of the same coin. Caribou in Newfoundland exemplify how animal abundance both governs and is governed by animal mobility. Following the population peak, female caribou responded with less movement, stronger site fidelity during summer, and some departure in herd structure from their traditional calving grounds. At least one population reversed a 40-year trend by migrating earlier in spring and later in autumn. Competition for summer forages appears to have relaxed, coincident with declining caribou numbers—a conclusion consistent with the recent improvements in body condition, recruitment, and calf survival (S.P. Mahoney, unpublished data). The similarity of patterns among these populations implies predictability, and hence value in monitoring caribou distribution and movements to detect and understand numerical change.

Acknowledgements

This work was supported by the Newfoundland and Labrador Department of Environment and Conservation and a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to J.A.S. We are grateful to K.P. Lewis for comments on an earlier draft, to two reviewers for their suggestions, and to

the many Wildlife personnel, particularly A.T. Bergerud, whose efforts set the foundation of this work.

References

- Bergerud, A.T. 1971. The population dynamics of Newfoundland caribou. *Wildl. Monogr.* 25: 1–55.
- Bergerud, A.T. 1972. Food habits of Newfoundland caribou. *J. Wildl. Manage.* 36: 913–923. doi:10.2307/3799448.
- Bergerud, A.T. 1988. Caribou, wolves and man. *Trends Ecol. Evol.* 3: 68–72. doi:10.1016/0169-5347(88)90019-5. PMID:21227095.
- Bergerud, A.T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? *Rangifer Spec. Issue No. 9*. pp. 95–116. doi:10.7557/2.16.4.1225.
- Bergerud, A.T., Luttich, S.N., and Camps, L. 2008. *The return of caribou to Ungava*. McGill–Queen's University Press, Montreal.
- Bergman, C.M., Schaefer, J.A., and Luttich, S.N. 2000. Caribou movement as a correlated random walk. *Oecologia*, 123: 364–374. doi:10.1007/s004420051023.
- Bethke, R., Taylor, M., Amstrup, S., and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecol. Appl.* 6: 311–317. doi:10.2307/2269574.
- Boulet, M., Couturier, S., Côté, S.D., Otto, R.D., and Bernatchez, L. 2007. Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. *Mol. Ecol.* 16: 4223–4240. doi:10.1111/j.1365-294X.2007.03476.x. PMID:17784914.
- Brown, W.K., and Theberge, J.B. 1985. The calving distribution and calving-area fidelity of a woodland caribou herd in central Labrador. *In Proceedings of the 2nd North American Caribou Workshop, Val Morin, Que., 17–20 October 1984*. Edited by T.C. Meredith and A.M. Martell. McGill Subarctic Research Station, Schefferville, Que. McGill Subarctic Research Paper No. 40. pp. 57–67.
- Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature*, 337: 260–262. doi:10.1038/337260a0. PMID:2911365.
- Couturier, S., Otto, R.D., Côté, S.D., Luther, G., and Mahoney, S.P. 2010. Body size variations in caribou ecotypes and relationships with demography. *J. Wildl. Manage.* 74: 395–404. doi:10.2193/2008-384.
- Crête, M., and Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Can. J. Zool.* 71(11): 2291–2296. doi:10.1139/z93-321.
- Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H., and Dussault, C. 2010. Range fidelity: the missing link between caribou decline and habitat alteration? *Biol. Conserv.* 143: 2840–2850. doi:10.1016/j.biocon.2010.08.001.
- Fancy, S.G., Pank, L.F., Whitten, K.R., and Regelin, W.L. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. *Can. J. Zool.* 67(3): 644–650. doi:10.1139/z89-093.
- Gaston, K.J., and Blackburn, T.M. 2000. *Pattern and process in macroecology*. Blackwell Science, London.
- Gunn, A., and Miller, F.L. 1986. Traditional behaviour and fidelity to caribou calving grounds by barren-ground caribou. *Rangifer Spec. Issue No. 1*. pp. 151–158. doi:10.7557/2.6.2.640.
- Gunn, A., Poole, K.G., and Nishi, J.S. 2012. A conceptual model for migratory tundra caribou to explain and predict why shifts in spatial fidelity of breeding cows to their calving grounds are infrequent. *Rangifer Spec. Issue No. 20*. pp. 259–267. doi:10.7557/2.32.2.2274.
- Hansen, B.B., Henriksen, S., Aanes, R., and Sæther, B.-E. 2007. Ungulate impact on vegetation in a two-level trophic system. *Polar Biol.* 30: 549–558. doi:10.1007/s00300-006-0212-8.
- Harwood, T.D. 2009. The circular definition of populations and its implications for biological sampling. *Mol. Ecol.* 18: 765–768. doi:10.1111/j.1365-294X.2008.04066.x. PMID:19207257.
- Hinkes, M.T., Collins, G.H., Van Daele, L.J., Kovach, S.D., Aderman, A.R., Woolington, J.D., and Seavoy, R.J. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *J. Wildl. Manage.* 69: 1147–1162. doi:10.2193/0022-541X(2005)069[1147:JOPGOC]2.0.CO;2.
- Itonaga, N., Köppen, U., Plath, M., and Wallschläger, D. 2011. Declines in breeding site fidelity in an increasing population of White Storks *Ciconia ciconia*. *Ibis*, 153: 636–639. doi:10.1111/j.1474-919X.2011.01131.x.
- Keating, K.A. 1994. An alternative index of satellite telemetry location error. *J. Wildl. Manage.* 58: 414–421. doi:10.2307/3809311.
- Koenig, W.D., Hooge, P.N., and Van Vuren, D. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* 11: 514–517. doi:10.1016/S0169-5347(96)20074-6. PMID:21237947.
- Lewis, J.S., Rachlow, J.L., Garton, E.O., and Vierling, L.A. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. *J. Appl. Ecol.* 44: 663–671. doi:10.1111/j.1365-2664.2007.01286.x.
- MacArthur, R.H. 1972. *Geographical ecology*. Harper and Row, New York.
- Mahoney, S.P., and Schaefer, J.A. 2002. Long-term changes in demography and migration of Newfoundland caribou. *J. Mammal.* 83: 957–963. doi:10.1644/1545-1542(2002)083<0957:LTCIDA>2.0.CO;2.

- Mahoney, S.P., and Weir, J.N. 2009. Caribou data synthesis—progress report. Overview of the status of woodland caribou in insular Newfoundland: research methodology, results, interpretations and future projections. Tech. Rep. No. 001. Sustainable Development and Strategic Science, Government of Newfoundland and Labrador, St. John's.
- Mahoney, S.P., Abbott, H., Russell, L.H., and Porter, B.R. 1990. Woodland caribou calf mortality in insular Newfoundland. In *Transactions of the 19th Congress of International Union of Game Biologists*, Trondheim, Norway, 8–13 September 1989. Edited by S. Myrberget. Norwegian Institute for Nature Research, Trondheim. pp. 592–599.
- Mahoney, S.P., Virgl, J.A., Fong, D., MacCharles, A.M., and McGrath, M. 1998. Evaluation of a mark–resighting technique for woodland caribou in Newfoundland. *J. Wildl. Manage.* **62**: 1227–1235. doi:10.2307/3801986.
- Mahoney, S.P., Weir, J.N., Luther, G., Schaefer, J.A., and Morrison, S.F. 2011. Morphological change in Newfoundland caribou: effects of abundance and climate. *Rangifer*, **31**: 21–34. doi:10.7557/2.31.1.1917.
- Messier, F., Huot, J., Le Hénaff, D., and Luttich, S. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. *Arctic*, **41**: 279–287.
- Minasny, B., and McBratney, A.B. 2002. FuzME version 3.5c. Australian Centre for Precision Agriculture, The University of Sydney, Sydney, N.S.W., Australia. Available from <http://sydney.edu.au/agriculture/pal/software/fuzme.shtml> [accessed 5 June 2013].
- Nagy, J.A., Johnson, D.L., Larter, N.C., Campbell, M.W., Derocher, A.E., Kelly, A., Dumond, M., Allaire, D., and Croft, B. 2011. Subpopulation structure of caribou (*Rangifer tarandus* L.) in arctic and subarctic Canada. *Ecol. Appl.* **21**: 2334–2348. doi:10.1890/10-1410.1. PMID:21939065.
- Popp, J.N., Schaefer, J.A., and Mallory, F.F. 2011. Female site fidelity of the Mealy Mountain caribou herd. *Rangifer tarandus caribou* in Labrador. *Rangifer Spec. Issue No. 19*. pp. 87–95. doi:10.7557/2.31.2.1993.
- Pyle, P., Sydeman, W.J., and Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim. Ecol.* **70**: 1088–1097. doi:10.1046/j.0021-8790.2001.00567.x.
- Roffler, G.H., Adams, L.G., Talbot, S.L., Sage, G.K., and Dale, B.W. 2012. Range overlap and individual movements during breeding season influence genetic relationships of caribou herds in south-central Alaska. *J. Mammal.* **93**: 1318–1330. doi:10.1644/11-MAMM-A-275.1.
- Rowcliffe, J.M., Carbone, C., Kays, R., Kranstauber, B., and Jansen, P.A. 2012. Bias in estimating animal travel distance: the effect of sampling frequency. *Methods Ecol. Evol.* **3**: 653–662. doi:10.1111/j.2041-210X.2012.00197.x.
- Schaefer, J.A., and Mahoney, S.P. 2003. Spatial and temporal scaling of population density and animal movement: a power law approach. *Ecoscience*, **10**: 496–501.
- Schaefer, J.A., and Wilson, C.C. 2002. The fuzzy structure of populations. *Can. J. Zool.* **80**(12): 2235–2241. doi:10.1139/z02-184.
- Schaefer, J.A., Bergman, C.M., and Luttich, S.N. 2000. Site fidelity of female caribou at multiple spatial scales. *Landsc. Ecol.* **15**: 731–739. doi:10.1023/A:1008160408257.
- Schaefer, J.A., Veitch, A.M., Harrington, F.H., Brown, W.K., Theberge, J.B., and Luttich, S.N. 2001. Fuzzy structure and spatial dynamics of a declining woodland caribou population. *Oecologia*, **126**: 507–514. doi:10.1007/s004420000555.
- Sikes, R.S., Gannon, W.L., and the Animal Care and Use Committee of the American Society of Mammalogists 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* **92**: 235–253. doi:10.1644/10-MAMM-F-355.1.
- Taillon, J., Festa-Bianchet, M., and Côté, S.D. 2012. Shifting targets in the tundra: protection of migratory caribou calving grounds must account for spatial changes over time. *Biol. Conserv.* **147**: 163–173. doi:10.1016/j.biocon.2011.12.027.
- Thorpe, R.S. 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). *Biol. J. Linn. Soc.* **7**: 27–43. doi:10.1111/j.1095-8312.1975.tb00732.x.
- Vors, L.S., and Boyce, M.S. 2009. Global declines of caribou and reindeer. *Global Change Biol.* **15**: 2626–2633. doi:10.1111/j.1365-2486.2009.01974.x.
- Wells, J.V., and Richmond, M.E. 1995. Populations, metapopulations, and species populations: what are they and who should care? *Wildl. Soc. Bull.* **23**: 458–462.