



## Decades of habitat use reveal food limitation of Newfoundland caribou

JAMES A. SCHAEFER,\* SHANE P. MAHONEY, JACKIE N. WEIR, J. GLENN LUTHER, AND COLLEEN E. SOULLIERE

*Biology Department, Trent University, 1600 W. Bank Drive, Peterborough, Ontario K9L 0G2, Canada (JAS)*

*Sustainable Development and Strategic Science, Department of Environment and Conservation, Government of Newfoundland and Labrador, P.O. Box 8700, St. John's, Newfoundland A1B 4J6, Canada (SPM, JNW, CES)*

*Wildlife Division, Department of Environment and Conservation, Government of Newfoundland and Labrador, Corner Brook, Newfoundland A1A 5J7, Canada (JGL)*

*Conservation Visions Inc., P.O. Box 5489, Station C, St. John's, Newfoundland A1C 5W4, Canada (SPM)*

\* Correspondent: [jschaefer@trentu.ca](mailto:jschaefer@trentu.ca)

Identifying limiting factors is fundamental to understanding and conserving mammals, yet it often requires long-term data for long-lived species. Numerical changes of migratory caribou (*Rangifer tarandus*), for example, may unfold over decades, but few studies have examined habitat use at similar timeframes. We analyzed multiple decades of habitat use by caribou in Newfoundland, Canada, coincident with their numeric growth ( $r = 0.064$  in 1980s, 1990s) and decline ( $r = -0.099$  in 2000s). We examined 2 scales: selection of land cover, based on radiotracking of 520 adult females, and diet, based on microhistological analysis of feces and age-specific tooth wear from jawbones of harvested animals. Caribou responded at both scales. In contrast to previous decades, females during the population decline used proportionally less open coniferous and closed coniferous forests, they used more shrublands (in fall and winter) and barrens, open habitats with greater vascular plant resources. Patterns of selection also changed from nonselection to avoidance of open coniferous forest and from avoidance to nonselection or preference of barrens. The proportion of dietary moss increased at the expense of deciduous shrubs, especially during spring and summer and of ericaceous shrubs, graminoids, and lichens during winter. Teeth of both sexes exhibited premature wear, likely indicative of abrasion from low-quality forages and cropping of foods near the ground. These patterns mirror other responses, including declines in calf weight, female body size, number of male antler points, herd affinities, and time spent on the summer grounds. We surmise that they reflect density-dependent forage limitation of this island population.

Key words: caribou, diet, food limitation, *Rangifer tarandus*, resource selection

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Limiting factors are critical to population ecology and conservation biology. For mammals, especially long-lived species, long-term observations may be pivotal in our understanding (e.g., [Mduma et al. 1999](#); [Owen-Smith 2006](#); [Mason et al. 2014](#)). Indeed, migratory caribou (*Rangifer tarandus*) may be regulated by food ([Crête and Huot 1993](#); [Mahoney and Schaefer 2002](#); [Couturier et al. 2010](#)), but the strength of food limitation is expected to vary on the scale of decades, in concert with drawn out swings in abundance ([Gunn 2003](#); [Bergerud et al. 2008](#)). To our knowledge, apart from a few studies of diet (e.g., [Joly et al. 2007](#)), there have been no analyses of habitat use by caribou at similar timeframes. Moreover, diet occupies just 1 level in a spectrum of scales ([Schaefer and Messier 1995](#); [Mayor et al. 2009b](#)). Examining multiple levels in this

hierarchy may unveil the factors most limiting to populations ([Rettie and Messier 2000](#)).

Newfoundland is a valuable test case. During the past 4 decades, caribou on this island exhibited sustained population growth ( $r = 0.064$ , 1975–1997) followed by decline ( $r = -0.099$ , 1997–2008—[Weir et al. 2014](#)), trends that have been synchronous across the island ([Bastille-Rousseau et al. 2013](#)). This numerical growth has been reflected in declines in female body size, male antler points ([Mahoney et al. 2011](#)), recruitment ([Mahoney and Schaefer 2002](#)), and calf survivorship (Bastille-Rousseau et al., in press; Mahoney et al., in press), as well as shifts in site fidelity, population affinities, timing of migration, and rate of movements ([Schaefer and Mahoney 2013](#)). While the evidence is consistent with density-dependent food

limitation (Bonenfant et al. 2009), a key element—changes in habitat use—has not been examined.

We hypothesized, given the smaller stature of adults (Mahoney and Schaefer 2002; Mahoney et al. 2011) and heightened predation on calves (Mahoney et al., in press), that Newfoundland caribou (especially females) altered their use of habitat at 1 or more spatial scales. At the broad scale, caribou might forage in riskier, but more productive, land cover types, i.e., open habitats where both foods and their major predators (black bears, *Ursus americanus*, and coyotes, *Canis latrans*—Bastille-Rousseau et al., in press; Mahoney et al., in press) are likely more plentiful. At the fine scale, caribou might experience diminished dietary quality, i.e., consumption of low-quality foods (Thomas et al. 1984) and acceleration in tooth wear, indicative of depletion of high-quality forages and cropping of foods close to the ground (Tyler 1986; Skoglund 1988; Kojola et al. 1998).

Here, we draw on several decades of data to test these ideas. We examined the response of Newfoundland caribou at 2 levels: 1) broad-scale selection of land cover types, based on an island-wide land cover classification and radiotracking of 520 adult females since 1980; and 2) fine-scale dietary patterns, derived from microhistological analysis > 2,500 fecal samples since the 1980s and from examination of age-specific tooth wear of > 8,300 jawbones since the 1970s. We focused on comparisons across decades, especially before (1970s–1990s) and after (2000s) the population peak. Under the hypothesis that consistent habitat selection across scales reveals the most important limiting factors (Rettie and Messier 2000), we predicted that these caribou would respond at both scales.

## MATERIALS AND METHODS

**Study area and general methods.**—Land cover in most of Newfoundland was composed of forests of balsam fir (*Abies*

*balsamea*), black spruce (*Picea mariana*), and white birch (*Betula papyrifera*), and bogs containing stunted black spruce and tamarack (*Larix laricina*). Lakes, ponds, heaths, and barrens were widespread. Potential natural predators of caribou included black bears and lynx (*Lynx canadensis*). Wolves (*Canis lupus*) were extirpated in approximately 1922; coyotes arrived on the island in 1985 and preyed on both adult and juvenile caribou (Weir et al. 2014). Moose (*Alces americanus*), an introduced species, were common in forests.

We based our examination of land cover use on a modified Earth Observation for Sustainable Development (EOSD) map generated by unsupervised classification of data from the Landsat Enhanced Thematic Mapper Plus, representing land cover in 2000 (Wulder et al. 2008). The map was recoded by condensing several classes resulting, across the island of Newfoundland, in 10 cover classes with an accuracy of 76.4% (Table 1). In 4 population ranges, denoted as the minimum convex polygon around all caribou radiolocations, 1980–2011, composition of the 5 most common habitat types was highly comparable, although La Poile range had a higher proportion of barrens and lower proportions of water and closed coniferous forests. Land cover was nearly static during the study. Fire is infrequent in the maritime Newfoundland climate (Krezek-Hanes et al. 2011). The largest disturbance was forest harvesting; clear-cuts constituted ≤1.2% of any population range (Table 1). We updated the land cover map by superimposing new cut blocks onto the classified map each year until 2010.

Before 2000, the land cover composition of clear-cuts was unknowable. Indeed, our analysis revealed a substantial change in land cover between existing (pre-2000) cuts and impending (post-2000) cuts, i.e., increased proportions of open habitats (notably open coniferous forests, barrens, shrubs, and non-treed wetlands) at the expense of closed coniferous forests. To deal with this circumstance, we assumed that pre-2000 cutblocks before

**Table 1.**—Land cover composition and area of population ranges for 4 herds of caribou (*Rangifer tarandus*) in Newfoundland, 2000, based on modified Earth Observation for Sustainable Development classification. Entries with 0 are blank.

Attribute	Buchans	Grey River	La Poile	Middle Ridge	Description
Water (%)	13.0	12.2	9.9	10.5	Lakes reservoirs, rivers, streams
Barren (%)	7.4	7.9	13.2	7.0	Bedrock, rubble, talus, blockfield, rubble mine spoils, lava beds
Bryoids (%)			<0.1		Bryophytes and lichens which are ≥20% ground cover or ≥ one-third of total vegetation
Treed wetlands (%)	0.3	0.3	0.3		Water table near surface; majority of vegetation coniferous, broadleaf, or mixed wood
Shrubs and non-treed wetlands (%)	16.4	19.5	24.4	23.7	≥ 20% ground cover which is ≥ one-third shrub
Herbs (%)	0.1	0.1	0.2	0.2	≥ 20% ground cover or one-third of total vegetation is herbaceous
Closed coniferous–mixed wood (%)	9.1	7.9	6.7	8.4	> 60% crown closure; coniferous trees ≥ 75% of total basal area
Open coniferous–mixed wood (%)	52.2	50.8	44.4	48.7	10–60% crown closure; coniferous trees ≥ 75% of total basal area
Closed broadleaf forest (%)	0.1	0.2	0.1	0.4	> 60% crown closure; neither coniferous nor broadleaf trees ≥ 75% of total basal area
Open broadleaf forest (%)	0.1	0.2	0.3	0.3	10–60% crown closure; neither coniferous nor broadleaf trees ≥ 75% of total basal area
Forestry cuts (%)	1.2	0.8	0.5	0.8	Clear-cuts
Area (km <sup>2</sup> )	29,320	21,740	13,390	11,760	Minimum convex polygon around telemetry locations

harvesting would have resembled the composition of impending, post-2000 cutblocks. In our analysis of caribou telemetry observations that preceded a pre-2000 clear-cut, therefore, we substituted this average pre-cut composition within the block.

Similar to Bergerud (1972), we denoted 4 seasons: spring (1 May–30 June), summer (1 July–30 September), autumn (1 October–30 November), and winter (1 December–30 April). We conducted geographic analyses in MapInfo version 11 (Pitney Bowes Software, Troy, New York) and statistical computations in Statistica version 10 (Statsoft, Tulsa, Oklahoma).

**Land cover use.**—During 1980–1997, adult female caribou were live-captured and fitted with mortality-sensing Very High Frequency (VHF) radio transmitters, following guidelines of the American Society of Mammalogists (Sikes et al. 2011). Radiotelemetry reconnaissance was carried out approximately every 2 weeks by airplane, but more frequently (roughly every 5 days) during spring and summer. Radiolocations had an accuracy of  $\leq 500$  m based on repeated blind-test positioning of “dummy” transmitters. More recent (2004–2010) 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 and GPS collars every 1, 2, or 4 h.

Before analysis, we screened the automated telemetry data for errors. For PTTs, we first selected the location with the best quality class for each collar during each transmission period provided by Service Argos. We then calculated  $\xi$ , an indicator of potentially erroneous fixes, determined by successive vectors of animal movement (Keating 1994). Based on the distribution of log-transformed  $\xi$  values, we deemed extreme locations ( $\xi > 6,640$  m) as erroneous; they were omitted. For the GPS data, we followed Lewis et al. (2007) and eliminated 2-dimensional fixes with high dilution of precision ( $DOP > 5$ ). Finally, due to the copious number of GPS locations and to better resemble daytime VHF telemetry, we further reduced these data by selecting 1 GPS fix for each collar each day, closest to 12h30 Newfoundland Standard Time (NST) during 9h30–15h30 NST.

There was a substantial discrepancy in accuracy among VHF, Argos, and GPS telemetry. To remedy this potentially confounding effect, we computed the proportion of land cover types within a 500-m radius circle around each radiolocation (Rettie and McLoughlin 1999). For each herd, decade, and season, we retained any animal with  $\geq 3$  radiolocations. We treated the animal as experimental unit ( $n = 520$ ).

We tested for changes in habitat selection coincident with population growth (1980s, 1990s) and decline (2000s). For each of the 5 most common land cover classes (Table 1), we computed Ivlev’s electivity index,  $E'$  (also known as the forage ratio—Lechowicz 1982), i.e., the ratio of relative use to relative availability in each population range. We computed the average  $E'$  for each animal, substituted  $E' = 0.001$  in instances where  $E' = 0$  ( $\leq 0.7\%$  of cases for any land cover type), and then log transformed the index to better resemble a normal distribution, symmetrical about 0. We tested the null hypothesis,  $\log E' \approx 0$ , with 1-sample  $t$ -tests for each season and period. We used a Bonferroni-corrected  $\alpha$  of  $0.05/40 = 0.00125$  (i.e., 2 periods  $\times$

4 seasons  $\times$  5 land cover types). Given the minor among-herd differences in land cover composition (Table 1) and in habitat selection (Bastille-Rousseau et al. 2015), we pooled the data among 4 herds (Buchans, Grey River, La Poile, and Middle Ridge). For each season, our final dataset had an average sample size of 262 animals (range: 165–339) during 1980s–1990s and 130 animals (range 127–133) during the 2000s.

**Diet.**—Fresh caribou feces ( $n = 2,518$  pellet groups) were collected opportunistically from population ranges during 1987–1988 (1 herd), 1990–1997 (9 herds), and 2010–2011 (3 herds). Plant species and plant groups were identified by microhistological analysis (Washington State University, Wildlife Habitat and Nutrition Lab) with the intent of identifying all plants in diet (< 5% of the diet). For 1987–1997, there were 3 slides per sample, 20 views per slide; in 2010–2011, there were 1 or 2 slides per sample, 25 views per slide. We combined these data into major plant groups. We analyzed the 5 most common groups, representing approximately 85% of the composition of the feces: deciduous shrubs, ericaceous shrubs, graminoids, fruticose lichens, and mosses.

During the study, field sampling was intermittent and dispersed among herds; only the Middle Ridge herd was sampled across decades. Because our analysis risked being confounded by among-herd differences, we used a dual strategy to test for decadal differences. We analyzed data from the Middle Ridge herd alone and complemented this analysis with all other herds in aggregate. For each season, we used 1-way multivariate analysis of variance (MANOVA) to uncover differences among decades. We arcsine transformed the proportional data to better approximate a normal distribution. For the Middle Ridge herd, an average of 81 samples (range: 13–163) was available for each combination of season and decade. For the other herds, an average of 233 samples (range: 153–385) was available for each such combination.

**Tooth wear.**—Caribou jawbones ( $n = 6,881$  males;  $n = 1,443$  females) were submitted voluntarily and annually by licensed recreational hunters beginning in the 1970s. Based on tooth wear and eruption, each specimen was placed into an apparent age class (2, 3, 4–6, 7–9, or  $\geq 10$  years; see Supporting Information S1); true age was determined from annuli in the cementum (Matson’s Laboratory, Milltown, Montana). We anticipated, if caribou experienced greater tooth abrasion, their dentition would resemble a particular tooth wear class at an earlier age. To test this idea, we used 1-way ANOVAs to examine differences in true age among decades, separately for each apparent age class (based on tooth wear) and sex. To account for potential cohort effects (Forchhammer et al. 2001), we classified animals into decade by year of birth. Where ANOVA revealed a significant decade effect ( $P < 0.05$ ), we used post hoc Tukey tests to determine pairwise differences between decades.

## RESULTS

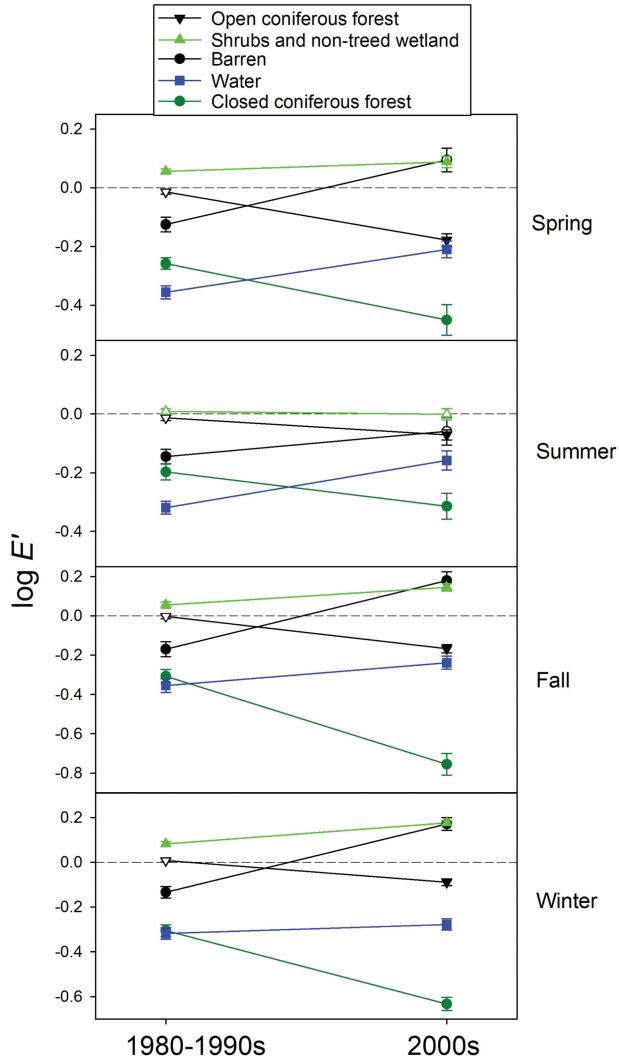
Between the periods of growth (1980–1990s) and decline (2000s), female caribou exhibited substantial shifts in use of land cover types, changes that were generally reiterated across

all 4 seasons (Fig. 1). After the population peak, the proportions of open coniferous and closed coniferous forests near radiocollar locations declined; proportions of shrublands (in fall and winter) and barrens increased. As revealed by use–availability ratios, the direction of selection of some habitats changed, too. In the case of open coniferous forest, females switched from nonselection ( $\log E' \approx 0$ ) to avoidance ( $\log E' < 0$ ), a pattern repeated across all seasons. For barrens, they shifted from avoidance to neutral use in spring and summer and even preference ( $\log E' > 0$ ) in fall and winter (Fig. 1).

Fruticose lichens were a principal food, particularly during fall and winter when they almost always represented half or more of the diet (Fig. 2). During spring and summer, caribou tended to consume a more even distribution of foods, including appreciable portions of graminoids and deciduous shrubs. There were significant differences among decades during each of the 4 seasons ( $P < 0.01$ ; all MANOVA tests); patterns were generally consistent between Middle Ridge and other herds. In

the 2000s, caribou diets showed marked proportional increases in mosses (irrespective of season), decreases in deciduous shrubs (especially during spring and summer), and decreases in ericaceous shrubs, graminoids, and lichens (during winter; Fig. 2).

During most of the study, the apparent age of caribou estimated from tooth wear and eruption corresponded well with their true age determined from annuli in the cementum. This changed during the 2000s (Table 2). The abrupt shift is exemplified by caribou in the 4- to 6-year-old tooth wear class. During the 1970s–1990s, the apparent age of these males and females resembled their true age; during the 2000s, their true age fell to just 3.3 years on average, revealing that teeth were abrading more quickly than in previous decades. We observed similar trends in both sexes in nearly all other classes. Teeth of caribou born in the 2000s appeared older than those born in prior decades (by roughly 0.5–2.5 years; Table 2). There were, however, too few observations in the  $\geq 10$ -year-old class and females in the 2-year-old class during the 2000s to draw reliable inferences.

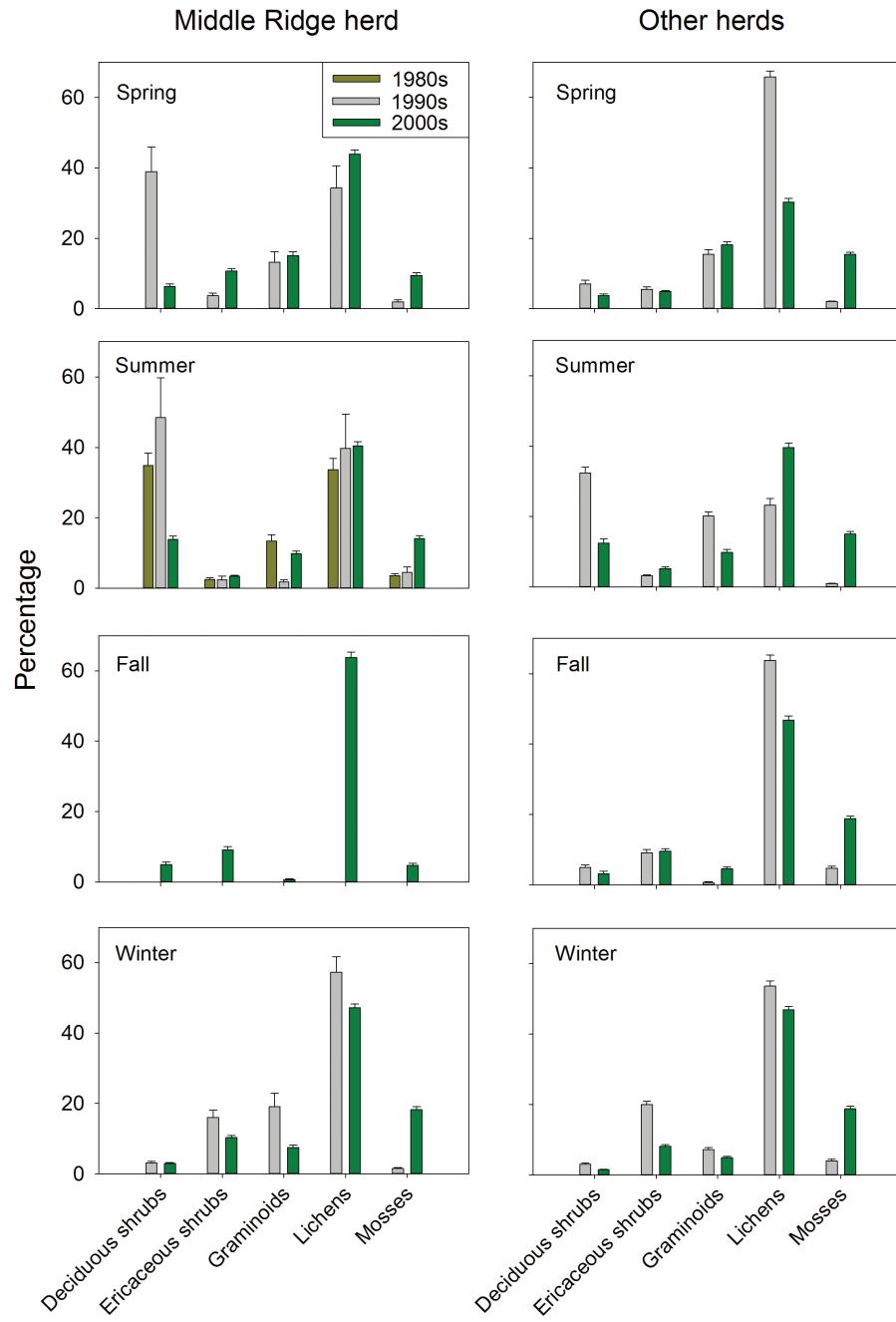


**Fig. 1.**—Electivity indices (mean  $\log E' \pm SE$ ) for the 5 most common land cover types by adult female caribou (*Rangifer tarandus*), Newfoundland, 1980–2011. Values significantly ( $P < 0.00125$ ) different than 0 are indicated by filled symbols.

## DISCUSSION

Habitat is recognized as key to migratory *Rangifer*, reflected in the growing number of studies of habitat use (Sharma et al. 2009; Joly et al. 2010, 2015; Barrier and Johnson 2012; Anderson and Johnson 2014), including those from Newfoundland (Mayor et al. 2009a; Hébert and Weladji 2013; Bastille-Rousseau et al. 2015). Selection for heightened abundance of forage, especially lichens, is a recurrent theme. At the same time, migratory caribou are renowned for swings in numbers, often linked to altered vegetation communities (Manseau et al. 1996; Joly et al. 2007; Newton et al. 2014), diet (Crête and Huot 1993; Joly et al. 2007), body size (Mahoney and Schaefer 2002; Couturier et al. 2010; Mahoney et al. 2011), and space use (Mahoney and Schaefer 2002; Hinkes et al. 2005; Bergerud et al. 2008; Schaefer and Mahoney 2013; Newton et al., in press). Few studies of habitat selection, however, have been conducted at comparable timeframes. Over a 10-year period, Joly et al. (2007) reported changes in winter diet, i.e., an increase in graminoids at the expense of lichens (despite their heightened selectivity), reflective of changes on the landscape and coincident with the decline of the Western Arctic herd in Alaska.

Theory suggests that migratory animals should be regulated by food availability (Fryxell and Sinclair 1988). Moreover, because habitat can be regarded as the suite of resources governing the presence, survival, and reproduction of a population (Caughey and Gunn 1996), it is closely tied to the concept of limiting factors. Accordingly, we anticipated multidecadal, multiscale shifts in habitat use by Newfoundland caribou, consistent with reductions in body size (Morellet et al. 2007). Indeed, caribou responded at both scales. Following the population peak, females exhibited reduced use of closed and open coniferous forests (a switch from nonselection to avoidance), increased use of barrens (a switch from avoidance to nonselection or preference), and shrublands (Fig. 1), i.e., more open habitats that tended to be richer



**Fig. 2.**—Diets of caribou (*Rangifer tarandus*) expressed as percentage composition in feces ( $\pm$  SE) of the Middle Ridge herd and all other herds in Newfoundland, 1987–2011.

in vascular plant biomass (Hébert and Weladji 2013; Bastille-Rousseau et al. 2015). These broad-scale responses, nevertheless, appear to have only partially compensated for diminished food. At the fine scale, caribou during all seasons experienced substantial increases in dietary moss (Fig. 2), a low-digestibility food (Thomas et al. 1984). Both sexes exhibited acceleration in tooth wear, too (Table 2), likely owing to rougher, low-quality diets (Tyler 1986; Kojola et al. 1998) and cropping of vegetation near the ground, leading to ingestion of abrasive soil particles (Skoglund 1988; Loe et al. 2003). Two recent studies of contemporary caribou in Newfoundland (Hébert and Weladji 2013; Bastille-Rousseau et al. 2015) also reported selection by females

for enhanced summer forage resources. Overall, this consistency across studies and across scales (Rettie and Messier 2000) implies food limitation, particularly following the population peak.

Calf mortality has been an important proximate cause of the decline of Newfoundland caribou (Bastille-Rousseau et al., in press; Mahoney et al., in press). Indeed, use of habitat may often represent a compromise between food acquisition and predation risk (Lima and Dill 1990). Whereas Newfoundland caribou may be driven primarily by enhanced foraging opportunities, they appear to have been only marginally successful in reducing encountered risk with coyotes and black bears, important predators, especially on calves (Bastille-Rousseau et al., in press;

**Table 2.**—True age (in years and based on annuli in the cementum) of male and female caribou (*Rangifer tarandus*) by apparent age class (based on tooth wear) and decade of birth in Newfoundland, 1975–2005. For each sex, means with the same superscript are not significantly different between decades ( $P > 0.05$ ). Cells without observations are blank.

Decade	Apparent age class														
	2 years old			3 years old			4–6 years old			7–9 years old			≥ 10 years old		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
<b>Males</b>															
1970s				64	3.58 <sup>a</sup>	1.93	147	4.58 <sup>a</sup>	1.82	228	6.42 <sup>a</sup>	1.82	417	8.12 <sup>a</sup>	1.87
1980s	12	5.67 <sup>a</sup>	1.97	333	3.43 <sup>a</sup>	1.28	920	4.66 <sup>a</sup>	1.52	1220	6.10 <sup>ab</sup>	1.62	997	7.47 <sup>b</sup>	1.82
1990s	162	2.29 <sup>b</sup>	0.80	409	3.27 <sup>a</sup>	1.05	1102	4.49 <sup>a</sup>	1.32	986	5.95 <sup>b</sup>	1.73	455	7.56 <sup>b</sup>	1.85
2000s	33	1.76 <sup>c</sup>	0.79	73	2.51 <sup>b</sup>	0.90	139	3.35 <sup>b</sup>	1.08	40	4.10 <sup>c</sup>	1.08			
<b>Females</b>															
1970s				31	3.58 <sup>a</sup>	1.39	57	4.75 <sup>a</sup>	1.71	63	6.51 <sup>a</sup>	1.98	131	8.09 <sup>a</sup>	2.47
1980s				86	3.16 <sup>a</sup>	1.25	182	4.32 <sup>b</sup>	1.67	181	5.78 <sup>b</sup>	1.97	152	7.78 <sup>a</sup>	2.48
1990s	61	2.18 <sup>*</sup>	0.43	92	3.21 <sup>a</sup>	0.81	225	4.83 <sup>a</sup>	1.75	242	6.74 <sup>a</sup>	2.08	127	8.18 <sup>a</sup>	2.08
2000s	6	2.17 <sup>*</sup>	0.41	31	2.42 <sup>b</sup>	0.89	54	3.30 <sup>c</sup>	1.16	4	4.25 <sup>*</sup>	1.5			

\* 1-way ANOVA not conducted due to small sample size.

Mahoney et al., in press). Early seral stage forests represent habitat for moose, which may serve as alternate prey for these 2 carnivores (Mahoney and Virgl 2003). Females thus appear to be risk-prone foragers (Bastille-Rousseau et al. 2015). For terrestrial mammals, migration often represents a predation-avoidance strategy (Fryxell and Sinclair 1988; Avgar et al. 2014). Most female caribou in Newfoundland aggregate at calving (the distinguishing feature of the migratory ecotype—Bergerud 1988), but migrations on the island may be geographically constrained. These females appear only partially successful at “spacing away” (Bergerud et al. 2008) and escaping the limiting effects of predation on their calves (Bastille-Rousseau et al., in press; Mahoney et al., in press), even in the absence of wolves.

There is growing interest, too, in climate-driven changes in ungulate populations. Climate may have manifold effects on plant growth, vulnerability to predation, and nival conditions; these effects can be manifest in *Rangifer* as variations in calf weight (Weladji and Holland 2003; Couturier et al. 2009), recruitment (Hegel et al. 2010), and population growth (Joly et al. 2011). In Newfoundland, the North Atlantic Oscillation (NAO) had a discernible effect on the jawbone size of females (Mahoney et al. 2011), population trajectories, and their synchrony (Bastille-Rousseau et al. 2013). The effects of population density and climate might also interact (Tyler 2010). Although we did not examine NAO, these companion investigations of Newfoundland caribou (Mahoney et al. 2011; Bastille-Rousseau et al. 2013) also uncovered density effects, consistent with our conclusion.

Ecologists are increasingly aware of the value of long-term investigations. In our study, despite decades of sustained effort, data gaps still existed, along with the potentially confounding variation associated with different animals and different herds. In some cases, such assumptions can be tested (Fig. 2; Bastille-Rousseau et al. 2013). Nevertheless, “recognition of change and understanding the causes of change require long-term investment” (Lindenmayer et al. 2015, p. 214). We believe that our study, in the domain of mammalian population ecology, supports that argument.

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## SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online ([jmammal.oxfordjournals.org](http://jmammal.oxfordjournals.org)). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

**Supporting Information S1.**—Criteria for estimating age of caribou (*Rangifer tarandus*) based on tooth wear and eruption, Newfoundland, 1975–2010.

## LITERATURE CITED

ANDERSON, T. A., AND C. J. JOHNSON. 2014. Distribution of barren-ground caribou during winter in response to fire. *Ecosphere* 5:140.

AVGAR, T., G. STREET, AND J. M. FRYXELL. 2014. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 92:481–490.

BARRIER, T. A., AND C. J. JOHNSON. 2012. The influence of fire history on selection of foraging sites by barren-ground caribou. *Ecoscience* 19:177–188.

BASTILLE-ROUSSEAU, G., J. A. SCHAEFER, S. P. MAHONEY, AND D. L. MURRAY. 2013. Population decline in semi-migratory caribou: Intrinsic or extrinsic drivers? *Canadian Journal of Zoology* 91:820–828.

BASTILLE-ROUSSEAU G., ET AL. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. *Ecography* 38:1049–1059.

BASTILLE-ROUSSEAU, G., ET AL. In press. Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. *Journal of Animal Ecology*.

BERGERUD, A. T. 1972. Food habits of Newfoundland caribou. *Journal of Wildlife Management* 36:913–923.

BERGERUD, A. T. 1988. Caribou, wolves and man. *Trends in Ecology and Evolution* 3:68–72.

BERGERUD, A. T., S. N. LUTTICH, AND L. CAMPS. 2008. The return of caribou to Ungava. *McGill-Queen's University Press*, Montreal, Canada.

BONENFANT, C., ET AL. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.

CAUGHLEY, G., AND A. GUNN. 1996. *Conservation Biology in Theory and Practice*. Blackwell Science, Cambridge, Massachusetts.

COUTURIER, S., S. D. CÔTÉ, R. D. OTTO, R. B. WELADJI, AND J. HUOT. 2009. Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. *Journal of Mammalogy* 90:442–452.

COUTURIER, S., R. D. OTTO, S. D. CÔTÉ, G. LUTHER, AND S. P. MAHONEY. 2010. Body size variations in caribou ecotypes and relationships with demography. *Journal of Wildlife Management* 74:395–404.

CRÊTE, M., AND J. HUOT. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Canadian Journal of Zoology* 71:2291–2296.

FORCHHAMMER, M. C., T. H. CLUTTON-BROCK, J. LINDSTROM, AND S. D. ALBON. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* 70:721–729.

FRYXELL, J. M., AND A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* 3:237–241.

GUNN, A. 2003. Voles, lemmings and caribou: population cycles revisited? *Rangifer*, Special Issue 14:105–111.

HÉBERT, I., AND R. B. WELADJI. 2013. The use of coniferous forests and cutovers by Newfoundland woodland caribou. *Forest Ecology and Management* 291:318–325.

HEGEL, T. M., A. MYSTERUD, T. R. ERGON, L. E. LOE, F. HUETTMANN, AND N. C. STENSETH. 2010. Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. *Journal of Animal Ecology* 79:471–482.

HINKES, M. T., ET AL. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. *Journal of Wildlife Management* 69:1147–1162.

JOLY, K., F. S. CHAPIN, AND D. R. KLEIN. 2010. Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in northwest Alaska. *Ecoscience* 17:321–333.

JOLY, K., M. J. COLE, AND R. R. JANDT. 2007. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in Arctic tundra vegetation. *Canadian Field-Naturalist* 121:379–383.

JOLY, K., D. R. KLEIN, D. L. VERBYLA, T. S. RUPP, AND F. S. CHAPIN. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. *Ecography* 34:345–352.

JOLY, K., S. K. WASSER, AND R. BOOTH. 2015. Non-invasive assessment of the interrelationships of diet, pregnancy rate, group composition, and physiological and nutritional stress of barren-ground caribou in late winter. *PLoS ONE* 10:e0127586.

KEATING, K. A. 1994. An alternative index of satellite telemetry location error. *Journal of Wildlife Management* 58:414–421.

KOJOLA, I., T. HELLE, E. HUHTA, AND A. NIVA. 1998. Foraging conditions, tooth wear and herbivore body reserves: a study of female reindeer. *Oecologia* 117:26–30.

KREZEK-HANES, C. C., F. AHERN, A. CANTIN, AND M. D. FLANNIGAN. 2011. Trends in large fires in Canada, 1959–2007. *Canadian Biodiversity: Ecosystem Status and Trends 2010*, Technical Thematic Report No. 6. Canadian Councils of Resource Ministers, Ottawa, Canada.

LECHOWICZ, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia* 52:22–30.

LEWIS, J. S., J. L. RACHLOW, E. O. GARTON, AND L. A. VIERLING. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. *Journal of Applied Ecology* 44:663–671.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation – a review and prospectus. *Canadian Journal of Zoology* 68:619–640.

LINDENMAYER, D. B., ET AL. 2015. Contemplating the future: Acting now on long-term monitoring to answer 2050's questions. *Austral Ecology* 40:213–224.

LOE, L. E., A. MYSTERUD, R. LANGVATN, AND N. C. STENSETH. 2003. Decelerating and sex-dependent tooth wear in Norwegian red deer. *Oecologia* 135:346–353.

MAHONEY, S. P., AND J. A. SCHAEFER. 2002. Long-term changes in demography and migration of Newfoundland caribou. *Journal of Mammalogy* 83:957–963.

MAHONEY, S. P., ET AL. In press. Woodland caribou calf mortality in Newfoundland: Insights into the role of climate, predation and population density over three decades of study. *Population Ecology*.

MAHONEY, S. P., AND J. A. VIRGL. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Canadian Journal of Zoology* 81:321–334.

MAHONEY, S. P., J. N. WEIR, G. LUTHER, J. A. SCHAEFER, AND S. F. MORRISON. 2011. Morphological change in Newfoundland caribou: Effects of abundance and climate. *Rangifer* 31:21–34.

MANSEAU, M., J. HUOT, AND M. CRÊTE. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *Journal of Ecology* 84:503–513.

MASON, T. H. E., M. APOLLONIO, R. CHIRICHELLA, S. G. WILLIS, AND P. A. STEPHENS. 2014. Environmental change and long-term body mass declines in an alpine mammal. *Frontiers in Zoology* 11:69.

MAYOR, S. J., J. A. SCHAEFER, D. C. SCHNEIDER, AND S. P. MAHONEY. 2009a. The spatial structure of habitat selection: A caribou's-eye-view. *Acta Oecologica* 35:253–260.

MAYOR, S. J., D. C. SCHNEIDER, J. A. SCHAEFER, AND S. P. MAHONEY. 2009b. Habitat selection at multiple scales. *Ecoscience* 16:238–247.

MDUMA, S. A. R., A. R. E. SINCLAIR, AND R. HILBORN. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology* 68:1101–1122.

MORELLET, N., ET AL. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. *Journal of Applied Ecology* 44:634–643.

NEWTON, E. J., K. F. ABRAHAM, J. A. SCHAEFER, B. A. POND, AND G. S. BROWN. In press. Causes and consequences of broad-scale changes in the distribution of migratory caribou (*Rangifer tarandus*) of southern Hudson Bay. *Arctic*.

NEWTON, E. J., B. A. POND, G. S. BROWN, K. F. ABRAHAM, AND J. A. SCHAEFER. 2014. Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biology* 37:715–725.

OWEN-SMITH, N. 2006. Demographic determination of the shape of density dependence for three African ungulate populations. *Ecological Monographs* 76:93–109.

RETTIE, W. J., AND P. D. McLoughlin. 1999. Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology* 77:1175–1184.

RETTIE, W. J., AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.

SCHAEFER, J. A., AND S. P. MAHONEY. 2013. Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. *Canadian Journal of Zoology* 91:767–774.

SCHAEFER, J. A., AND F. MESSIER. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18:333–344.

SHARMA, S., S. COUTURIER, AND S. D. CÔTÉ. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. *Global Change Biology* 15:2549–2562.

SIKES, R. S., W. L. GANNON, 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. *Journal of Mammalogy* 92:235–253.

SKOGLAND, T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos* 51:238–242.

THOMAS, D. C., P. KROEGER, AND D. HERVIEUX. 1984. In vitro digestibilities of plants utilized by barren-ground caribou. *Arctic* 37:31–36.

TYLER, N. J. C. 1986. The relationship between the fat contents of Svalbard reindeer in autumn and their death from starvation. *Rangifer Special Issue* 1:311–314.

TYLER, N. J. C. 2010. Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus* L.). *Ecological Monographs* 80:197–219.

WEIR, J. N., S. F. MORRISON, J. G. LUTHER, AND S. P. MAHONEY. 2014. Caribou Data Synthesis – Progress Report #2. Status of the Newfoundland population of woodland caribou. Technical Bulletin No. 8, Sustainable Development and Strategic Science, Government of Newfoundland and Labrador, St. John's, Newfoundland, Canada.

WELADJI, R. B., AND Ø. HOLAND. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia* 136:317–323.

WULDER, M. A., ET AL. 2008. Monitoring Canada's forests. Part 1: Completion of the EOSD land cover project. *Canadian Journal of Remote Sensing* 34:549–562.

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