Morphological change in Newfoundland caribou: Effects of abundance and climate

Shane P. Mahoney[1], **Jackie N. Weir**[1,*], **J. Glenn Luther**[2], **James A. Schaefer**[3], & **Shawn F. Morrison**[4]

[1]Sustainable Development and Strategic Science, Department of Environment and Conservation, Government of Newfoundland and Labrador, St. John's, NL A1B 4J6.
[2]Wildlife Division, Department of Environment and Conservation, Government of Newfoundland and Labrador, Corner Brook, NL, A1A 5J7, Canada.
[3]Biology Department, Trent University, Peterborough, ON K9J 7B8, Canada.
[4]Dryas Research Ltd., Edmonton, AB, T6C 2R6, Canada.
[*] Corresponding author: jackieweir@gov.nl.ca

Abstract: The demographic and environmental influences on large mammal morphology are central questions in ecology. We investigated the effects of population abundance and climate on body size and number of male antler points for the La Poile and Middle Ridge caribou (*Rangifer tarandus*, L. 1758) herds, Newfoundland, Canada. Across 40 years and 20-fold changes in abundance, adult males and females exhibited diminished stature as indicated by jawbone size (diastema and total mandible length) and the number of antler points at the time of harvest. Associations between jawbone size and population abundance at birth were consistently negative for both herds, both sexes, and all age classes. Large-scale climate patterns, as measured by the North Atlantic Oscillation in the winter prior to birth, were also negatively associated with jawbone size. Declines in male antler size, as measured by the number of antler points, were not well predicted by either abundance or climate, suggesting other factors (e.g., current, rather than latent, foraging conditions) may be involved. We conclude that these morphological changes indicate competition for food resources.

Key words: antler; caribou; climate; Newfoundland; competition; diastema; density; morphology; NAO; forage; nutrition; *Rangifer tarandus*.

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Introduction

Understanding variations in species abundance and life histories remains one of the primary goals in ecology. For large mammals, knowledge of the mechanisms of population limitation and regulation has increased considerably. Particularly well-studied have been migratory caribou and reindeer (*Rangifer tarandus*, L. 1758) where population regulation via food competition in summer (Messier *et al.*, 1988; Couturier *et al.*, 1990; Mahoney & Schaefer, 2002) or winter (Skogland, 1985, 1990) has been linked to patterns of abundance. There is parallel evidence that another highly migratory ungulate, wildebeest (*Connochaetes taurinus*), is also regulated by competition for food resources (Dublin *et al.*, 1990; Mduma *et al.*, 1999). Increased competition for food should be reflected in the body condition and growth of individuals. Thus, a directional change in body size should mirror changes in the availability, abundance or quality of forage resources (but see Coltman *et al.*, 2003) and be related to changes in animal abundance.

During the late 20th century, *Rangifer* around the globe have exhibited remarkable correspondence in population trends (Mallory & Hillis, 1998; Gunn, 2003; Vors & Boyce, 2009). Many migratory herds experienced sustained numerical increases (Skogland, 1985; Fancy *et al.*, 1994), followed in many cases by the cessation of growth (Messier *et al.*, 1988; Mahoney & Schaefer, 2002) and decline (Skogland, 1990). These numerical changes provide valuable opportunities to broaden our understanding of the influence of density-dependent factors, such as resource competition, on population dynamics.

Large-scale climate indices such as the North Atlantic Oscillation (NAO; Hurrell, 1995) are known to affect ungulate population demographics and morphology through their effects on winter severity (Post *et al.*, 1997; Post & Stenseth, 1998; Forchhammer *et al.*, 2002; Mysterud *et al.*, 2003; Helle & Kojola, 2008). Demographics and morphology are also affected by population abundance (Skogland, 1983; Kojola & Helle, 1993; Forchhammer *et al.*, 2001). Population abundance and climate patterns may also interact (Heard & Ouellet, 1994; Aanes *et al.*, 2000). Selective hunting may be discernible both demographically and genetically (Harris *et al.*, 2002; Coltman *et al.*, 2003; Darimont *et al.*, 2009).

The factors that limit and regulate *Rangifer* populations may vary dramatically. For example, in many sedentary populations, caribou appear limited most strongly by predators (Bergerud, 1974; Bergerud & Elliot, 1986; Rettie & Messier, 1998; Wittmer *et al.*, 2005). Caribou co-existing with other ungulates are often regulated by predation at low abundance, well below the abundance that would elicit competition for food (Seip, 1992). In contrast, migratory caribou often experience strong food limitation (Skogland, 1985; Messier *et al.*, 1988; Mahoney & Schaefer, 2002). Herds at high densities exhibit classic signs of density-dependence through reduced juvenile survival (Bergerud, 1971; Skogland, 1985; Mahoney & Schaefer, 2002), lower fecundity and delayed reproductive maturity (Reimers *et al.*, 1983; Skogland, 1983), diminished recruitment (Messier *et al.*, 1988; Couturier *et al.*, 1990; Mahoney & Schaefer, 2002), and smaller stature (Skogland, 1983; Couturier *et al.*, 1990; Mahoney & Schaefer, 2002). Behavioural changes may also occur: dramatic changes in the timing of migration of caribou (*R. t. caribou*, Gmelin, 1788) in Newfoundland have been linked to heightened competition for summer forage (Mahoney & Schaefer, 2002). In particular, the influence of population abundance and environmental conditions during calving can induce long-term variation in life-history characteristics among cohorts within the same population (Forchhammer *et al.*, 2001).

The Newfoundland population of woodland caribou provides an opportunity to test these ideas. It has declined significantly after decades of sustained growth (Bergerud *et al.*, 1983; Mahoney, 2000; Mahoney & Schaefer, 2002). Wolves (*Canis lupus*), the primary predator of caribou (Bergerud, 1996), have been absent from the island of Newfoundland since the 1920's, and as a possible consequence, caribou herds have reached densities higher than elsewhere in North America (Schaefer & Mahoney, 2003). For decades, hunters have submitted jawbones and reported the number of antler points of harvested animals. Skeletal measurements are valuable indicators of trends in herbivore body size because they are resistant to seasonal variability in resource abundance (Høye & Forchhammer, 2006). Antler size, measured as number of points, is also reflective of nutritional status and climate variation (Smith, 1998; Mysterud *et al.*, 2005).

We examined changes in these morphological indices for two Newfoundland caribou herds (La Poile and Middle Ridge herds) across several decades and dramatic changes in population abundance. Such datasets are rare (Gaillard *et al.*, 2000; Wittmer *et al.*, 2005) and allowed us to identify putative limiting and regulating factors which may have contributed significantly to temporal trends in morphology. We anticipated a trend toward diminished size of these caribou – a sign of density-dependence resulting from food competition, consistent with other populations of large, mobile, herbivorous mammals.

Material and methods

Study area

The range of the La Poile caribou herd in southwestern Newfoundland, Canada (47° 44'N, 57° 52'W), was approximately 5000 to 7000 km^2 (Mahoney, 2000) in the early 1990s and was predominately barrens interspersed with partially forested river valleys, rocky outcrops, bogs, fens, and ponds. The coastline was generally rugged, and inland the region showed gentle relief with occasional high summits rising to 650 m above sea level. On the barrens, heath vegetation was characterized by alpine azalea (*Loiseleuria procumbens*), diapensia (*Diapensia lapponica*), pink crowberry (*Empetrum eamesii*) and sheep laurel (*Kalmia angustifolia*). Forested areas were composed of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and occasionally yellow birch (*Betula lutea*). The La Poile herd has been hunted annually since 1965.

The Middle Ridge caribou herd resided in east-central Newfoundland (47° 55'N, 54°48'W). It occupied a range of approximately 9800 km^2 during the late 1980s and early 1990s and has been well-studied (Bergerud, 1971; Chubbs *et al.*, 1993; Mahoney *et al.*, 1998; Schaefer & Mahoney, 2007). The herd's range was comprised of forests dominated by balsam fir, black spruce, and white birch (*B. papyrifera*), as well as bogs containing stunted black spruce and tamarack (*Larix laricina*). Lakes, ponds, heaths, and barrens were common. Human access was limited primarily to the northern portion of the range where forest harvesting (Chubbs *et al.*, 1993) and most hunting occurred. Legal hunting of these caribou has occurred since the early 1970s.

Moose (*Alces alces*), the only other ungulate in the study areas, were widespread in forested areas. Potential predators of caribou included black bears (*Ursus americanus*), lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*). Wolves were extirpated from Newfoundland in approximately 1922, but eastern coyotes (*Canis latrans*) arrived on the island in the late 1980s (Moore & Parker, 1992) and preyed on both adult and young caribou.

Population abundance assessment

Population abundance was assessed intermittently from 1960-2007, following systematic strip, random block, or mark-recapture census procedures (Mahoney *et al.*, 1998; Mahoney, 2000). An evaluation of census procedures (Mahoney *et al.*, 1998) indicated no substantial differences in estimates among fixed-wing, helicopter, and ground re-sighting surveys. In addition, changes in population growth determined from surveys were consistent with estimates from survival-recruitment schedules (Mahoney & Schaefer, 2002; Mahoney, unpubl. data). Census estimates did not control for the geographic area occupied by a herd and we were therefore unable to determine population density. Therefore, for clarity, we refer to 'abundance' rather than 'density'.

Both herds grew dramatically during the late 20th century, followed by substantial declines (Fig. 1). For La Poile, the herd grew from approximately 500 caribou in 1960 to 10 565 ± 1908 caribou (90% confidence interval) in 1997 before declining to 5400 ± 1075 indi-

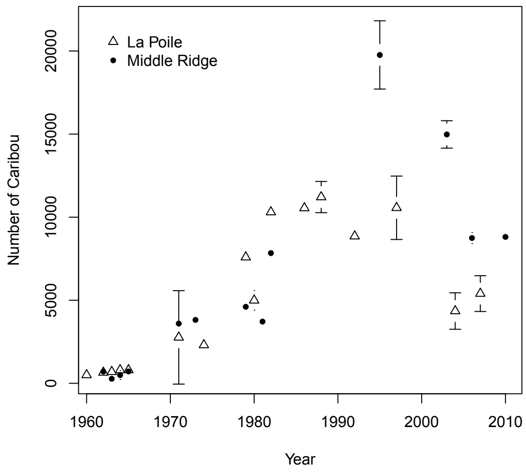

Fig. 1. Estimated population size of the La Poile and Middle Ridge caribou herds, Newfoundland, 1960 to 2010 based on aerial and ground censuses. Bars represent 90% confidence intervals.

viduals by 2007. The Middle Ridge herd grew from 200 animals in 1960 (Bergerud, 1971) to 19 765 ± 2055 caribou in 1995. More recent estimates of Middle Ridge, based on mark-resighting methods, indicated a decline to 14 981 ± 826 caribou in 2003 and 8748 ± 331 caribou in 2006 (Fig. 1).

It is well established that changes in the abundance of migratory caribou tend to be dramatic in their magnitude and that they unfold over the course of decades (Gunn, 2003; Vors & Boyce, 2009). This pattern includes Newfoundland caribou (Bergerud *et al.*, 1983; Mahoney & Schaefer, 2002). Therefore, considering a) the duration of our analysis, b) the consistent trends in growth and decline, and c) the magnitude of this numerical change, we consider the multiple surveys of these two herds (n=13 for Middle Ridge; n=15 for La Poile) to be reasonable representations of annual abundance. To interpolate between census years, we used linear regressions on the $\log_e$-transformed abundance, the standard approach to conveying population growth from successive surveys. Indeed, the r-squared values from these regressions were >0.85, supporting the use of this method for interpolating the abundance during intervening years.

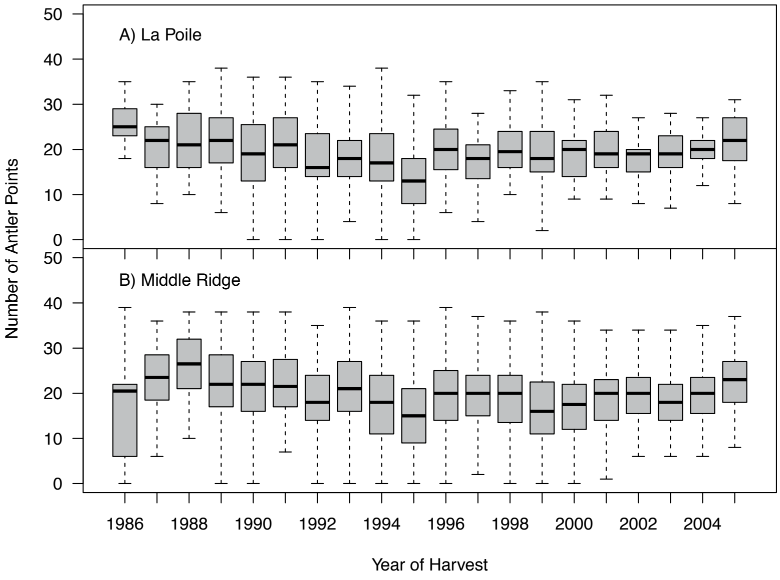

Fig. 2. Annual trends in the number of antler points for prime aged males (≥5 years) in the A) La Poile and B) Middle Ridge herds, 1986 to 2005. The boxes contain the 25th to 75th percentiles of the data and the horizontal line indicates the median. The whiskers extend to 1.5 times the inter-quartile range.

Antler points and jawbone size

We used data from 4462 antlers (n = 1632 antlers for La Poile; n = 2830 for Middle Ridge) from 1986 to 2005 to assess changes in the number of antler points of male caribou (Fig. 2). Herds were analyzed separately. To remove the effect of age, we observed that the number of antler points on male caribou increased from birth until approximately age 5 years and remained relatively constant there-after for both herds. A linear regression of the number of antler points against age confirmed that the number of antler points was independent of age once males were ≥5 years old ($F_{1,1106}$ = 1.49, P = 0.22 for La Poile; $F_{1,1700}$= 0.42, P = 0.52 for Middle Ridge). Thus, we defined prime aged males as those individuals 5 years or older. Filtering for age (≥5 years) and outliers (>39 antler points) left 1108 and 1702 antlers (for La Poile and Middle Ridge, respectively) available for analysis.

We assessed changes in body size for both sexes using jawbones from harvested caribou voluntarily submitted by hunters. For each jawbone, we measured total mandible length and diastema length (Banfield, 1961; Bergerud, 1964). For the La Poile herd, we analyzed jawbones from 2012 males and 386 females, and for Middle Ridge, 2979 males and 677 females. An incisor was extracted from each caribou to estimate age from annuli in the tooth cementum (Matson's Laboratory, Milltown, Montana, USA).

Statistical analyses

To identify trends in antler size, we regressed the mean number of antler points against year of harvest. To assess temporal trends in jawbone size, we statistically removed the effects of age for each sex-herd combination by fitting the sigmoidal Gompertz growth equation (Gompertz, 1825; Winsor, 1932) to each dataset (either total mandible length or diastema length) using the '*nls*' library in the software package *R* (R Development Core Team, 2007). The residuals from this curve-fitting procedure were independent of age and were used to determine trends in jawbone morphology over time by regressing the mean residual value against year of harvest. For out trend analysis, we used the mean value for each harvest year.

Generalized linear models (GLMs; McCullagh & Nelder, 1989) were used to assess the influence of several putative drivers of caribou jawbone size and number of antler points. Potential drivers included age, population abundance, and the mean winter North Atlantic Oscillation (Hurrell, 1995; Hurrell & Dickson, 2004; NOAA, 2008). Conditions during the year of birth are known to influence ungulate life-history characteristics (Forchhammer *et al.*, 2001), and we therefore focused on this period in our selection of putative drivers of jawbone morphology. Antler size may be affected by conditions in either year of birth or current year, and we therefore included conditions for both periods in our models. In addition to considering main effects, the age class of the individual caribou was included as an interaction term for each predictor variable to account for age-class specific responses. Age classes were defined as: yearlings, 2-year-olds, young adults (3-6 years), mid-aged adults (7-10 years), and older adults (11+ years). We also considered an interaction between abundance and winter NAO in year of birth. To eliminate potential problems of multicollinearity, we followed the 'residual and sequential regression' approach (Graham, 2003) where correlations among independent variables was high (i.e., $|r| > 0.6$).

Model selection for antler and jawbone GLM analysis followed an information-theoretic approach using Akaike Information Criterion corrected for small sample sizes (AICc; Akaike, 1973; Burnham & Andersen, 1998). For each analysis, a global model including age, NAO, abundance and two-way interactions among the main predictors was created. Each model was simplified using a step-wise procedure based on AIC_C values (function 'stepAIC' in program R; Venables & Ripley, 1999; R Development Core Team, 2007).

Results

The number of antler points declined between 1986 and 1995 for prime aged males in the La Poile herd and between 1987-1995 in the

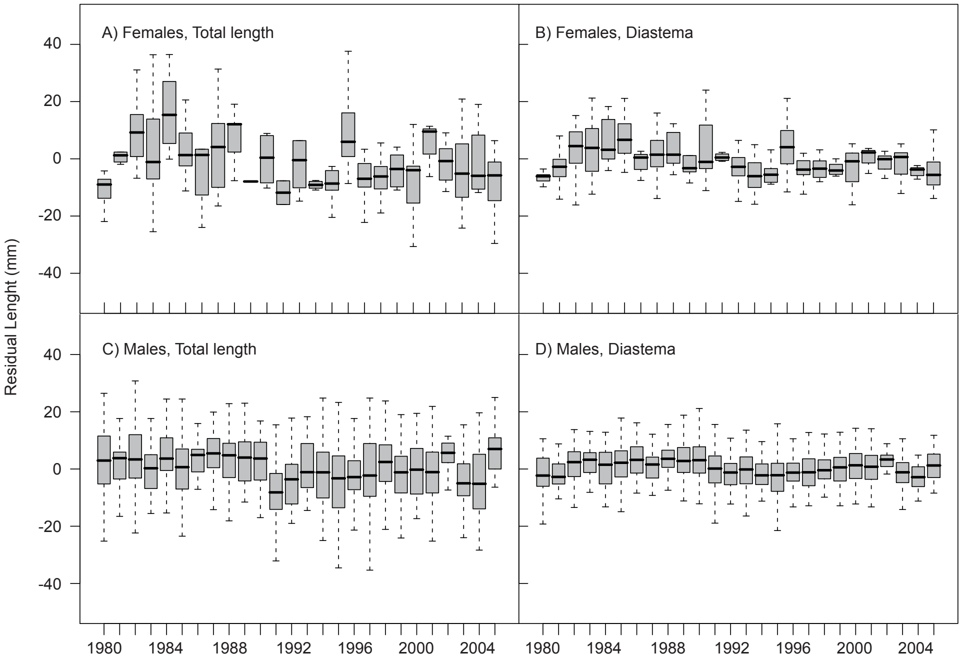

Fig. 3. Trends in jawbone size for males and females in the La Poile herd, 1980-2005, based on residuals from Gompertz growth equations. The boxes contain the 25th to 75th percentiles of the data and the horizontal line indicates the median. The whiskers extend to 1.5 times the inter-quartile range.

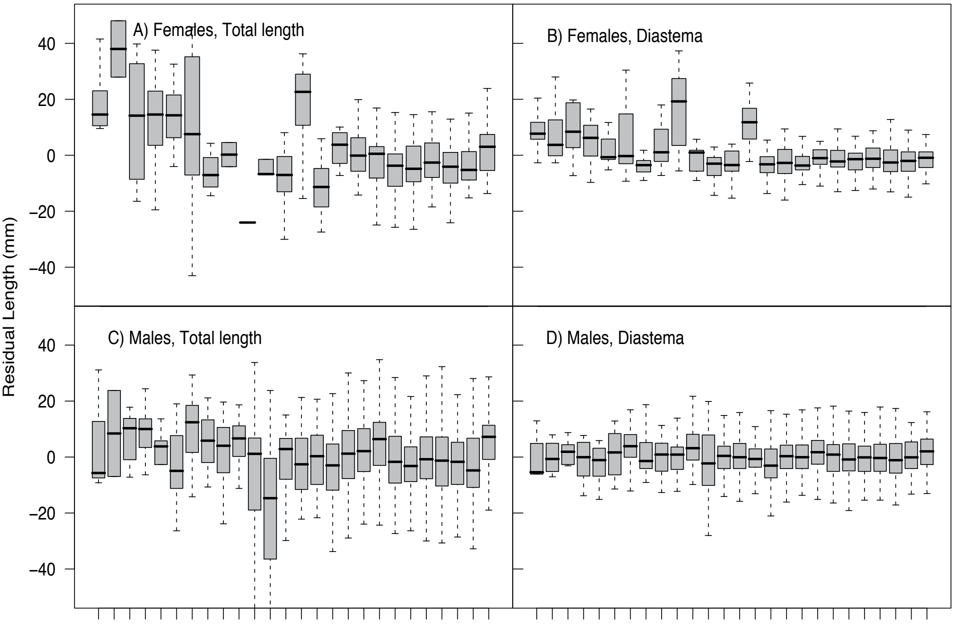

Fig. 4. Trends in jawbone size for males and females in the Middle Ridge herd, 1980-2005, based on residuals from Gompertz growth equations. The boxes contain the 25th to 75th percentiles of the data and the horizontal line indicates the median. The whiskers extend to 1.5 times the inter-quartile range.

Table 1. Average number of antler points, diastema length, and total jawbone length (±1 SE) for prime-aged (>5-year-old) adult male and female caribou from the La Poile and Middle Ridge herds, Newfoundland, across three decades. Antler data were not available for females.

Decade	Sex	Antler Points		Diastema Length (mm)		Total Jawbone Length (mm)	
		La Poile	Middle Ridge	La Poile	Middle Ridge	La Poile	Middle Ridge
1980s	F	---	---	102.6 ± 1.5	105.7 ± 2.3	281.6 ± 3.8	295.7 ± 4.4
1990s	F	---	---	98.4 ± 0.9	99.7 ± 0.7	271.4 ± 1.8	276.1 ± 1.5
2000s	F	---	---	97.3 ± 1.2	97.3 ± 0.5	269.4 ± 3.2	270.7 ± 0.8
1980s	M	21.6 ± 0.7	22.8 ± 0.9	109.1 ± 0.4	114.4 ± 0.8	292.9 ± 1.0	307.5 ± 1.6
1990s	M	17.7 ± 0.3	18.3 ± 0.3	107.8 ± 0.3	113.1 ± 0.2	287.4 ± 0.7	299.5 ± 0.5
2000s	M	19.4 ± 0.4	18.8 ± 0.4	109.1 ± 0.5	112.7 ± 0.4	287.7 ± 0.9	297.0 ± 0.6

Middle Ridge herd ($F_{1,8}$ = 20.18, P = 0.002, R^2 = 0.68; slope -0.84 ± 0.19, R^2 = 0.68 and $F_{1,7}$ = 33.71, P = 0.001, R^2 = 0.80; slope -1.04 ± 0.18, respectively). Between 1995 and 2005, the number of antler points increased in both herds ($F_{1,9}$ = 5.63, P = 0.04, slope +0.38 ± 0.16 and $F_{1,9}$ = 5.71, P = 0.04, slope = 0.36 ± 0.15, respectively). Decadal summaries of antler point data are provided in Table 1.

Despite global models indicating a statistical relationship between antler points and the predictors ($F_{4,1103}$= 21.3, P < 0.0001 for La Poile and $F_{8,1693}$=5.61, P <0.001 for Middle Ridge), there was little explanatory power (R^2 <10% for either herd). Thus, we conclude the models indicated no strong, biological associations between the number of antler points for prime-aged males and population abundance or winter NAO. The presence of statistical significance was presumably due to our large sample sizes.

Once the effects of age were removed, jawbone size (both total length and diastema length) of females decreased in both herds from the early 1980s to 2005 (Figs. 3 and 4). Total mandible length of La Poile females was variable and not clearly representative of a linear decline from 1980-2005 ($F_{1,21}$ = 3.41, P = 0.08; Figure 3A), although a significant declining trend was detected when this first year of data (1980) was removed ($F_{1,20}$ = 10.55, P = 0.004, slope = -0.52 ± 0.16). Diastema length also decreased over time ($F_{1,23}$ = 5.18, P = 0.032, slope = -0.22 ± 0.10; Fig. 3B). Females in the Middle Ridge herd also exhibited progressively shorter mandibles in total length ($F_{1,17}$ = 8.46, P = 0.001, slope = -0.75 ± 0.26; Fig. 4A) and diastema length ($F_{1,21}$ = 10.05, P = 0.005, slope = -0.47 ± 0.15; Fig. 4B).

Directional trends in jawbone size were less apparent for males in either herd (Figs. 3 and 4). Total mandible length did not decline significantly between 1980 and 2005 in either La Poile ($F_{1,24}$ = 2.84, P = 0.105; Fig. 3C) or Middle Ridge ($F_{1,24}$ = 3.12, P = 0.09; Fig. 4C). Diastema length did not change for males in the La Poile herd ($F_{1,24}$ = 1.41, P = 0.247; Fig. 3D) from 1980 to 2005, but did decline from 1982 to 2005 ($F_{1,22}$ = 5.79, P = 0.025, slope = -0.13 ± 0.06). Diastema length did not change linearly between 1980 and 2005 for Middle Ridge males ($F_{1,24}$ = 0.105, P = 0.749; Fig. 4D).

Generalized linear model regression analysis revealed negative relationships of jawbone morphology (total length and diastema length) with population abundance in the year of birth and with winter NAO in year of birth (Tables 2 and 3). The GLM analyses also provide evidence in support of interactions between age class and abundance and/or NAO for most sex-herd combinations (that is, the negative effects of abundance or climate were age class–specific). Overall, the most parsimonious model for each herd-sex combination consis-

Table 2. Parameter estimates (± 1 SE) for the top models predicting total jawbone length for male and female caribou in the La Poile and Middle Ridge herds. The top models were selected by an info-theoretical approach.

Parameter	Estimate	SE
La Poile Females		
Intercept	247.56	10.11
2-year-old	0.74	12.55
YoungAdult	20.95	11.48
MidAgedAdult	35.55	12.29
OlderAdult	54.61	15.00
Abundance	-2.43E-03	1.56E-03
NAO	12.33	6.35
2-year-old:Abundance	3.12E-03	1.87E-03
YoungAdult:Abundance	2.50E-03	1.72E-03
MidAgedAdult:Abundance	1.02E-03	1.81E-03
OlderAdult:Abundance	-2.01E-03	2.33E-03
2-year-old:NAO	-15.80	7.90
YoungAdult:NAO	-13.57	6.97
MidAgedAdult:NAO	-14.88	7.64
OlderAdult:NAO	2.07	10.20
La Poile Males		
Intercept	242.26	2.47
2-year-old	22.73	2.47
YoungAdult	45.90	2.22
MidAgedAdult	53.28	2.29
OlderAdult	56.98	4.42
Abundance	-5.56E-04	1.59E-04
Middle Ridge Females		
Intercept	243.79	6.30
2-year-old	36.36	7.67
YoungAdult	47.93	7.04
MidAgedAdult	64.72	7.67
OlderAdult	34.97	9.67
Abundance	-4.19E-04	3.92E-04
2-year-old:Abundance	-9.62E-04	4.89E-04
YoungAdult:Abundance	-8.11E-04	4.31E-04
MidAgedAdult:Abundance	-1.34E-03	4.56E-04
OlderAdult:Abundance	1.22E-04	5.86E-04
Middle Ridge Males		
Intercept	255.22	4.65
2-year-old	23.17	5.76
YoungAdult	31.80	4.97
MidAgedAdult	51.12	5.14
OlderAdult	59.14	6.84
Abundance	-5.97E-04	2.92E-04
2-year-old:Abundance	1.13E-04	3.56E-04
YoungAdult:Abundance	7.74E-04	3.07E-04
MidAgedAdult:Abundance	3.41E-04	3.17E-04
OlderAdult:Abundance	9.09E-05	4.52E-04

tently explained 40.4 to 45.5% of the variation in total jawbone length and 36.1 to 45.5% of the variation in diastema length.

Discussion

A growing body of evidence suggests that some *Rangifer* populations, like other mobile ungulates (Dublin *et al.*, 1990; Mduma *et al.*, 1999), are regulated by food resources (Skogland, 1983, 1985; Messier *et al.*, 1988; Couturier *et al.*, 1990; Skogland, 1990; Mahoney & Schaefer, 2002). The classic density-dependent responses exhibited by both the La Poile and Middle Ridge herds – a rapid increase in abundance followed by a decline, mirrored by reduced body size – also suggest that a forage-abundance relationship has influenced the dynamics of Newfoundland caribou. Furthermore, a reduction in body size coupled with a 2-month decline in time spent on the annual summer grounds by the neighbouring Buchans herd (Mahoney & Schaefer, 2002) implies summer forage as a likely regulator (Messier *et al.*, 1988). The population trends in the La Poile and Middle Ridge herds are representative of trends observed for several other herds across Newfoundland (Mahoney, unpublished data), raising the possibility that similar forage-abundance relationships are operating in those herds, too.

The negative associations between jawbone size and population abundance offer support for our hypothesis that observed changes in jawbone morphology were due to a density-dependent process (Tables 2 and 3). These density-dependent relationships are, in turn, likely influenced by large-scale climate patterns, such as the North Atlantic Oscillation, that play a role in forage growth patterns and availability (Post & Stenseth, 1999; Post *et al.*, 2003; Post *et al.*, 2008).

Positive and negative NAO phases are associated with specific weather patterns in New-

Table 3. Parameter estimates (± 1 SE) for the top models predicting diastema length for male and female caribou in the La Poile and Middle Ridge herds. The top models were selected by an info-theoretical approach.

Parameter	Estimate	SE
La Poile Females		
Intercept	88.22	5.02
2-year-old	-1.36	5.96
YoungAdult	9.31	5.43
MidAgedAdult	15.78	5.66
OlderAdult	30.00	7.25
Abundance	-1.68E-03	7.90E-04
NAO	2.46	3.53
Abundance:NAO	5.58E-04	3.13E-04
2-year-old:Abundance	1.20E-03	8.88E-04
YoungAdult:Abundance	1.31E-03	8.21E-04
MidAgedAdult:Abundance	1.05E-03	8.51E-04
OlderAdult:Abundance	-1.06E-04	1.14E-03
2-year-old:NAO	-5.08	3.71
YoungAdult:NAO	-8.06	3.30
MidAgedAdult:NAO	-10.17	3.47
OlderAdult:NAO	-1.81	4.38
La Poile Males		
Intercept	82.49	2.82
2-year-old	8.21	3.50
YoungAdult	25.00	2.91
MidAgedAdult	28.37	2.98
OlderAdult	22.17	5.96
Abundance	-6.80E-05	3.35E-04
NAO	2.37	1.08
Abundance:NAO	-2.76E-04	1.31E-04
2-year-old:NAO	-5.07E-05	3.94E-04
YoungAdult:NAO	-6.01E-04	3.38 E-04
MidAgedAdult:NAO	-7.91E-05	3.49 E-04
OlderAdult:NAO	1.26E-03	8.10 E-04
Middle Ridge Females		
Intercept	83.51	3.37
2-year-old	13.54	4.20
YoungAdult	20.37	3.66
MidAgedAdult	34.61	3.98
OlderAdult	19.84	4.21
Abundance	-3.13E-05	2.22E-04
2-year-old:Abundance	-5.09E-04	2.79E-04
YoungAdult:Abundance	-4.94E-04	2.38E-04
MidAgedAdult:Abundance	-9.66E-04	2.51E-04
OlderAdult:Abundance	1.56E-04	2.85E-04
Middle Ridge Males		
Intercept	87.52	1.25
2-year-old	7.80	1.40
YoungAdult	19.46	1.25
MidAdult	28.80	1.27
OlderAdult	31.76	1.61
Abundance	5.52E-05	3.25E-05
NAO	3.97	1.55
2-year-old:NAO	-4.47	1.83
YoungAdult:NAO	-4.16	1.58
MidAgedAdult:NAO	-3.38	1.62
OlderAdult:NAO	-1.92	2.16

foundland that likely affect forage conditions, although the strength of the effect can vary geographically (Catto, 2010). In general, the positive phase of the NAO is associated with below average winter temperatures and increased snowfall in Newfoundland (Topliss, 1997; Catto *et al.*, 2003), whereas the negative phase is associated with warmer, drier winters with reduced snow cover (Catto, 2010). Snowpack depth would affect spring vegetation growth and accessibility, thereby affecting caribou nutrition and body growth. Surface air temperature was also strongly correlated to the normalized difference vegetation index (NDVI; a measure of plant growth) in Newfoundland from 1982 to 1999, roughly corresponding to the period during which caribou populations were increasing throughout Newfoundland (Neigh *et al.*, 2007).

In addition to influencing the growing conditions for forage, climate patterns such as the NAO may affect caribou body morphology though other mechanisms such as insect harassment (Helle & Tarvainen, 1984) or icing of winter food resources (Chan *et al.*, 2005). While the possibility exists that climate could interact with population abundance (Post & Stenseth, 1999), we did not find compelling evidence in either La Poile or Middle Ridge herds (Tables 2 and 3).

Overall, trend analysis indicated females declined in jawbone size at a faster rate than males (based on linear regression slopes), suggesting that females may have been more affected than males by high population densities. The mechanism for this sex-specific response is unclear although adult females must differentially allocate energy reserves to either body growth or reproduction, whereas males invest solely in body growth. However, because most jawbone growth occurs prior to reproductive maturity differential allocation of energy to reproduction is unlikely to be a driving influence.

We also detected herd-specific differences in the response of females to population abundance: the negative effects of abundance appear to be stronger in Middle Ridge relative to the La Poile herd. A more pronounced negative effect of abundance in the Middle Ridge herd is consistent with its larger peak population and faster rate of decline relative to the La Poile herd.

Other explanations for the observed decline in body size have been considered. For example, intensive size-selection for trophy harvest by hunting could reduce or eliminate the phenotypes (Skogland, 1990) and perhaps even genotypes (Coltman *et al.*, 2003) of the largest individuals over time. However, we argue this mechanism is unlikely to account for the changes in the La Poile and Middle Ridge herds for the following reasons. First, while males have comprised, by far, the majority of the harvest (1980-89, 88.7% of the total harvest were males; 1990-99, 87.3% were males), the larger reductions in body size were documented for females. Second, Newfoundland residents are primarily meat-hunters and do not purposefully select trophy animals. Size selectivity is therefore less common than with non-resident hunters. Last, while non-resident hunters are more size selective, they accounted for only a fraction of the total annual harvest. (From 1980-89, 26.4% of all animals harvested were by non-residents; 1990-99, this percentage dropped to 16.6%.) Thus, given the absence of intense trophy selection, this hypothesis is unlikely to explain the morphological patterns in these herds. It is also worth noting that overall harvest rates for La Poile and Middle Ridge were modest – an average of 2.8% and 4.3% during 1980-1989 and 1990-1999 (respectively) when most morphological changes occurred.

The inability of the GLM models to account for decreased antler size may reflect the current nutritional conditions for males (i.e., conditions in year of harvest) rather than conditions in the year of birth. In elk, for example, antler mass appears indicative of prevailing foraging conditions while they are growing (Smith, 1998) and in male caribou, antler mass (but not the number of tines) varies in concert with body mass (Markusson & Folstad, 1997; Thomas & Barry, 2005). In addition, overgrazing may have created foraging conditions that are a cumulative result of past foraging activity and not directly related to current population abundance or climate conditions (Henry & Gunn, 1991). Thus, our analysis of antler points may have been limited by the absence of detailed information on foraging conditions in the year of harvest. We also cannot discount the possibility that antler development is more finely related to changes in abundance than our interpolated values could provide.

In sum, our study points to diminished body size, in these and other large insular Newfoundland herds (Mahoney, 2000; Mahoney & Schaefer, 2002; S. Mahoney and J. Schaefer, unpublished data), as a phenotypic consequence of high abundance and large-scale climate patterns, likely mediated by nutrition. Jawbone size and antler or horn quality are highly sensitive to variation in nutrient quality and availability (Suttie & Kay, 1982; Suttie & Mitchell, 1983; Gordon *et al.*, 2004; Høye & Forchhammer, 2006) and are frequently used as proxies of range quality and condition (Nugent & Frampton, 1994; Hewison & Gaillard, 2001; Schmidt *et al.*, 2001; Keyser *et al.*, 2005; Thomas & Barry, 2005; Weladji *et al.*, 2005; Høye & Forchhammer, 2006). Beyond morphology, other ecological features of Newfoundland caribou coincide with their dramatic numerical fluctuations. These include significant increases in juvenile mortality (Norman & Mahoney, 2007; Mahoney & Weir, 2009), delayed spring and accelerated fall migrations (Mahoney & Schaefer, 2002), and the partial disintegration of herd structure and loss of calving site fidelity (Mahoney, 2000; L. Bridges, unpublished data) The decline of *Rangifer* populations is now widespread across the circumpolar North (Vors & Boyce, 2009) and we surmise that similar morphological trends may be uncovered elsewhere.

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