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ARTICLE

Population decline in semi-migratory caribou (*Rangifer tarandus*): intrinsic or extrinsic drivers?

Guillaume Bastille-Rousseau, James A. Schaefer, Shane P. Mahoney, and Dennis L. Murray

Abstract: Many populations of caribou (*Rangifer tarandus* (L., 1758)) across North America, including Newfoundland, are in a state of decline. This phenomenon may reflect continental-scale changes in either the extrinsic or the intrinsic factors affecting caribou abundance. We hypothesized that caribou decline reflected marked resource limitation and predicted that fluctuations should correspond to time-delayed density dependence associated with a decline in range quality and decadal trends in winter severity. By conducting time-series analysis using 12 populations and evaluating correlations between caribou abundance and trends in (*i*) vegetation available at calving (normalized difference vegetation index, NDVI), (*ii*) winter weather severity (index of North Atlantic Oscillation, NAO), and (*iii*) caribou morphometrics, we observed strong evidence of density dependence in population dynamics (i.e., a negative relationship between caribou population size and caribou morphometrics). Caribou population trajectories were time-delayed relative to winter severity, but not relative to calving-ground greenness. These island-wide correlations could not be traced to dispersal between herds, which appears rare at least for adult females. Our results suggest that trends in winter severity may synchronize broad-scale changes in caribou abundance that are driven by time-delayed density dependence, although it remains possible that calving-ground deterioration also may contribute to population limitation in Newfoundland. Our findings provide the basis for additional research into density dependence and caribou population decline.

Key words: density dependence, climate influence, synchrony, predation, caribou, *Rangifer tarandus*.

Résumé : Plusieurs populations de caribou (*Rangifer tarandus* (L., 1758)) en Amérique du Nord, dont celles de Terre-Neuve, sont en déclin. Ce phénomène peut refléter des changements continentaux dans les facteurs extrinsèques ou intrinsèques affectant leur abondance. Nous supposons que le déclin observé reflète un cycle naturel, et prédisons que les fluctuations devraient correspondre à des effets densité-dépendants différés dans le temps, associés à la qualité de l'habitat et à la sévérité des hivers. Afin de mieux comprendre les raisons expliquant les tendances observées à Terre-Neuve, nous avons conduit des analyses temporelles en utilisant 12 populations et nous avons évalué les corrélations entre l'abondance des caribous et (*i*) la végétation disponible durant la mise-bas (l'indice d'activité végétale, NDVI), (*ii*) la sévérité de l'hiver (l'indice de l'oscillation nord atlantique, NAO) et (*iii*) les mesures morphométriques. Nous avons observé une forte corrélation entre la taille des populations et les effets densité-dépendants. La trajectoire des populations de caribou était aussi corrélée, mais différée avec la sévérité des hivers, mais pas avec la qualité des aires de mise-bas. Ces corrélations n'étaient pas liées à la dispersion des individus entre les troupeaux, qui semblait rare, du moins chez les femelles. Nos résultats suggèrent que les tendances dans la sévérité des hivers pourraient synchroniser à grande échelle les changements d'abondance chez le caribou, bien qu'il semble possible que la dégradation de l'habitat puisse contribuer à la limitation des populations.

Mots-clés : densité dépendence, influence du climat, synchronie, prédation, caribou, *Rangifer tarandus*.

Introduction

Fluctuations in animal population density can be driven by a range of factors, including endogenous (i.e., density-dependent) factors linked to predation, competition, and parasitism (Kendall et al. 1999; Turchin 2003*b*), or exogenous factors such as inclement weather patterns (Stenseth et al. 1999). Fluctuations among many spatially isolated populations frequently are highly synchronous (e.g., Sinclair et al. 1993; Ranta et al. 1997), implying that processes governing population dynamics may operate at scales that span beyond local environments. In light of the variability in environmental and ecological conditions facing caribou across Newfoundland, it is notable that population trajectories remain so closely aligned. It follows that such similarity speaks to the stabilizing influence of exogenous and (or) endogenous factors influencing large-scale caribou population dynamics (Ranta et al. 1997; Ims and Andreassen 2000).

Populations of caribou (*Rangifer tarandus* (L., 1758)) offer one remarkable example of largely synchronous fluctuations spanning broad geographical expanses. During the last 20 years, many caribou populations across the circumpolar North have undergone dramatic declines in numbers (Schaefer 2003; Vors and Boyce 2009; Festa-Bianchet et al. 2011), with climate and anthropogenic activity usually being invoked as the most likely ultimate factors causing these declines; the mechanism underlying these dynamics is through direct effects on plant phenology, predation risk, and extreme weather events (Vors and Boyce 2009; Tyler 2010; Joly et al. 2011). Notwithstanding this current broad-scale decline, historically, most caribou populations of the migratory ecotype experienced repeatable fluctuations in abundance (Gunn

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G. Bastille-Rousseau, J.A. Schaefer, and D.L. Murray. Environmental and Life Sciences Graduate Program, Trent University; 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada.
S.P. Mahoney. Newfoundland and Labrador Department of Environment and Conservation, PO Box 8700, St. John's, NL A1B 4J6, Canada.
Corresponding author: Guillaume Bastille-Rousseau (e-mail: gbastillerousseau@hotmail.com).

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Table 1. Four hypotheses and their predictions proposed to explain fluctuations of Newfoundland caribou (*Rangifer tarandus*).

	Prediction			
Hypothesis	1. Delayed density-dependence	2. Correlation between SF and population estimate	3. Correlation between WS and population estimate	4. Between herd synchrony
1. Winter severity (WS)[a]	Yes	No	Delayed	Strong, despite modest dispersal
2. Spring forage (SF)[b,c]	Yes	Delayed	No	Absent, unless dispersal is important
3. Interaction SF decline and WS (INT)	Yes	Delayed	Delayed	Strong, despite modest dispersal
4. Predation (PR)	No	No	No	Strong

[a] Gunn 2003.

[b] Messier et al. 1988.

[c] Mahoney and Schaefer 2002.

2003; Zalatan et al. 2006), with population trajectories often synchronous across broad landscapes (Gunn 2003). Repeatable fluctuations could be driven by large-scale changes owing to climate variability or time-delayed changes in stressors like predation. It follows that synchronized dynamics across broad landscapes may be related to common ecological and environmental factors driving caribou population abundance and change (Ranta et al. 1997; Ims and Andreassen 2000). However, populations also may be synchronized via dispersal, even in the absence of large-scale extrinsic or intrinsic drivers (Ranta et al. 1995). To date, few studies have tackled questions relating to factors driving synchronous and sometimes recurring large-scale caribou population declines (but for examples see Solberg et al. 2001; Tyler et al. 2008).

We investigated population trajectory of caribou herds on Newfoundland and sought to disentangle the influence of factors implicated in the decline. Specifically, we developed four hypotheses and attendant predictions to compare between potential causes of caribou population change (Table 1). The winter severity hypothesis (hypothesis 1; WS) implicates exogenous factors such as decadal trends in winter climate (Gunn 2003) as the driving force behind caribou population decline. Specifically, nutritional status and body condition may be markedly compromised by periodic winter severity and lead to decline in numbers due to lower survival and (or) productivity. Logically, since the effects of a harsh winter may be transferred to newly born calves (maternal effects; Inchausti and Ginzburg 2009), the WS hypothesis predicts that change in adult caribou body condition will relate to change in population size in a time-delayed manner (>1 year). Second, trends in caribou numbers should be lag-correlated with trends in winter severity but not with vegetation available at calving (spring). It follows that the WS hypothesis predicts a strong between-herd synchrony related to a phase-locking mechanism (sensu Sinclair et al. 1993), rather than due to interherd dispersal (hypothesis 1; Table 1).

Alternatively, the spring forage hypothesis (hypothesis 2; SF) invokes time-delayed density dependence that is driven by fluctuations in spring range quality caused by caribou population size (Couturier et al. 2009*a*). The SF hypothesis should be supported by delayed density dependence in addition to a delayed correlation between population size and trend in range quality that is not associated with annual weather impact. It follows that the SF hypothesis is less likely to involve between-herd synchrony if the catalyst for herd decline is related to local forage deterioration (Table 1). However, it is possible that winter severity and forage deterioration act in tandem, such that winter weather affects not only winter foraging but also spring foraging. Next, according to the "interaction" hypothesis (hypothesis 3; INT), caribou should exhibit delayed density dependence in body condition indices, and population trends should be lag-correlated with both winter severity and spring vegetation indices. Under this hypothesis, it is notable that caribou herds should fluctuate synchronously (Table 1). Finally, the next hypothesis (hypothesis 4; PR) invokes the direct effect of predation on caribou decline, which is supported by the lack of density dependence in caribou body indices and no correlation between population abundance and winter severity or spring forage. Predators, mainly through predation-sensitive foraging, can also induce reduction in body indices similar to those induced by density dependence (Sinclair and Arcese 1995). Such an effect on adult caribou body indices would, however, be minimal since gray wolves (*Canis lupus* L., 1758) have been extinct in Newfoundland since 1922 and no other predators efficiently hunt adult caribou. If predation drives fluctuations, it should induce some degree of between-herd synchrony, mainly due to the mobility and dispersal of predators (hypothesis 4; Table 1).

Materials and methods

Study area

Newfoundland is a 108 860 km² island in eastern Canada (47°44′N, 59°28′W to 51°44′N, 52°38′W), with humid–continental climate and ample year-round precipitation (Environment Canada 2013). Natural habitat consists of coniferous and mixed forests of balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), and white birch (*Betula papyrifera* Marshall), as well as bogs, lakes, and barren rock. During the last 50 years, caribou herds on Newfoundland have undergone marked numerical changes in abundance, with numbers being generally low during the 1960s and 1970s, increasing rapidly during the 1980s to mid-1990s, and declining precipitously following the mid-late 1990s (Mahoney and Schaefer 2002; Mahoney et al. 2011). There are about 14 major and a few smaller caribou herds on Newfoundland, their population ranges varying from <100 km² to 11 000 km²; most herds exhibit semi-migratory characteristics involving philopatric movements similar to those of other caribou populations (Schaefer et al. 2000). Philopatry is apparent among females that move to traditional calving grounds during spring and summer. Caribou herds are largely distinct and spatially independent in Newfoundland. Despite some spatial overlap between a minority of herds, we show that interchange of females between herds is uncommon (see below and supplementary methods[1]). Thus, it is appropriate to consider each herd as a distinct unit. Newfoundland caribou overlap with moose (*Alces alces* (L., 1758)), and potential predators on the island include coyote (*Canis latrans* Say, 1823), American black bear (*Ursus americanus* Pallas, 1780), and Canada lynx (*Lynx canadensis* Kerr, 1792).

Caribou population data

During 1960–2008, 12 caribou herds were intermittently surveyed in spring or fall using traditional aerial counting methods

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[1] Supplementary methods, Table S1, and Fig. S1 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0154.

in a systematic strip, random block, stratified–random block, or mark–resight design (Mahoney et al. 1998; Mahoney and Schaefer 2002). Herds were monitored opportunistically and with variable regularity and intensity; for most populations, surveys occurred regularly during the 1960s, sporadically during the 1970s, and somewhat less frequently during the remaining period (Fig. 1). On average, population sizes were estimated 12.2 ± 1.3 times (mean ± SE) (n = 12) for each herd during the 48-year study period. Our analysis presumed changes in population size were indicative of changes in density, an assumption that appears valid for Newfoundland caribou because the area of herd's range tends to change in tandem with population size (Schaefer and Mahoney 2003). We estimated annual population size by fitting orthogonal polynomial regression equations to each time series and, through a stepwise process, evaluating any increase in fit following addition of higher order terms (Venables and Ripley 2002). Orthogonal polynomial regression allows for estimation of the appropriate process order, as each new order is independent; this reduces problems of collinearity and standard error estimation (Crawley 2007). Although the number of missing annual counts varied from 46% to 79% in the original time series (Fig. 1, Table 2), we consider that broad-scale patterns in abundance were captured reasonably well by the fitted models, including periods of low and high population density at various times during the study (Fig. 1); patterns that were also reflected in survival and recruitment trends. To confirm the robustness of polynomial fits, we evaluated mean absolute values of the residuals for every herd. However, it remains noteworthy that smoothed time series underestimate both process variance and observer error, compared with raw population estimates.

To determine spatial overlap between caribou and whether each herd could be considered an independent unit, we examined movement patterns of radio-collared caribou in each of 12 populations. Since 1980, >900 female caribou have been captured and immobilized from a helicopter (Mahoney and Schaefer 2002). From 1980 to 1999, roughly 550 captured females were fitted with VHF collars and monitored, on average, 1–2 times per month. Since 2005, >130 females have been fitted with GPS collars and an additional >230 received ARGOS collars. GPS collars had a fixed schedule ranging from 2 to 5 h, whereas ARGOS collars obtained locations every 2 days. We defined core area of occupation for each herd by developing a kernel density estimator (Worton 1989) from observations collected during calving (15 May – 1 July). We progressively increased the smoothing parameter value (h) from 500 to 3500 m by 500 m increments, and used a kernel probability isopleth with a value of 50% to obtain a contour surface (see supplementary methods[1]). We selected the smoothing parameter that offered the best compromise between over-smoothing vs. under-smoothing the data, as per previously described methods (Wand and Jones 1995; Kie et al. 2010); this constituted a smoothing parameter value with 2500 m and isopleth value with 50%.

Since 1966, caribou morphometric measurements (jawbone length (n = 11 923), diastema (n = 17 888), molar row length (n = 15 249), number of antler points (n = 7628)) were collected on a voluntary basis from hunter-harvested male and female caribou (Mahoney et al. 2011). This extensive data set from across the island provided an index of animal size and status through time and such data have been used previously to assess how density-dependent competition for resources affects animal condition (Stewart et al. 2005; Couturier et al. 2009*a*; Mahoney et al. 2011). Samples from adult caribou were obtained yearly and pooled among herds, and therefore were restricted to providing an island-wide assessment of caribou body condition.

Vegetation availability and winter climate

We used the normalized difference vegetation index (NDVI) to assess forage availability during calving. This remote-sensing index normally characterizes vegetation greenness and has been used to describe vegetation availability (Boelman et al. 2005). We evaluated annual mean NDVI for each herd in June, using 20 random pixels located inside each core area of the calving ground. NDVI images were acquired from the Canadian long-term satellite data record (LTDR). Data were collected by the AVHRR instruments of the National Oceanic and Atmospheric Administration (NOAA) and were used to generate Canada-wide, 1 km resolution, 10-day imageries spanning 1985–2011. The maximum value between mid-May to 1 July for each pixel was used in calculating mean population range level annual values.

Winter weather patterns were determined by the December–March NAO index (http://www.cgd.ucar.edu/cas/jhurrell/naointro.html; Hurrell 1995). High NAO values are usually related to cold and dry winters in northeastern North America (Couturier et al. 2009*b*); however, owing to a number of unique climatic influences, this pattern may differ to some degree in Newfoundland. We also collected spring and early summer weather data from the Meteorological Service of Canada (Environment Canada 2013), 1980–2011, for six stations in Newfoundland. These data served to determine the yearly mean daily maximum temperature and total amount of precipitation during spring (May and June). To remove the potential influence of current spring weather on NDVI, we first performed a linear model between three predictor variables (spring mean temperature and precipitation of the closest weather station, and winter NAO) and NDVI for each herd, as the response variable. We considered the influence of previous NAO, as a warmer winter can lead to faster melting of the snow (Tyler 2010). We then extracted residuals for each herd to evaluate their correlation with caribou population size; after accounting for winter and spring weather influence, these data should better reflect vegetation patterns resulting from the influence of grazing.

Statistical analysis

Evidence of cyclic fluctuations and delayed density dependence (prediction 1)

We used spectral analysis to estimate the duration of any time-delayed density-dependent response in caribou numbers, by determining whether each caribou population time series underwent a numerical cycle with regular period and amplitude (May 1976; Turchin 2003*a*; Inchausti and Ginzburg 2009). We used detrended N_T time series for each herd and fit Lomb–Scargle periodograms to generate Fourier spectra (Lomb 1976). Populations were considered cyclic if P < 0.05, where $P = 1 - (1 - e^{-z})^n$ and z is the corresponding spectral peak and n is the sample size (Horne and Baliunas 1986; Kendall et al. 1998). Cycle period was calculated as the reciprocal of the spectral frequency (Murray et al. 2008). Note that, as a rule of thumb, for populations experiencing cyclicity due to time-delayed density dependence, the time delay in density dependence should approximate the period length divided by 4 (May 1976). We stress, however, that our efforts were not intended specifically to detect cyclicity in caribou populations but rather to evaluate whether cyclicity was a possible mechanism acting on populations.

We further assessed the nature of density dependence in the population time series by conducting nonlinear time-series modeling using NLTSM (Turchin 2003*a*). Time series were analyzed from response surface methodology using polynomial regression with Box–Cox transformation to approximate the general function of lagged population densities and random noise (Box and Draper 1987). Structural parameters were selected iteratively through sequential-blocks cross-validation (Turchin 2003*a*). The process order (PO), polynomial fit (PF), and dominant Lyapunov exponent (LE) for the cross-validated model were calculated to provide an index of higher order interactions, nonlinearities between population growth and lagged densities, and propensity for system instability, respectively. It follows that PO reflects the feedback structure of population dynamics and PO > 1 indicates when time-delayed density dependence is present (Turchin 2003*a*); PF measures the degree of nonlinearity in the

Fig. 1. Population trajectories for 12 caribou (*Rangifer tarandus*) herds on Newfoundland. Points represent actual population estimates and lines represent estimated population size using the best-fit polynomial equation.

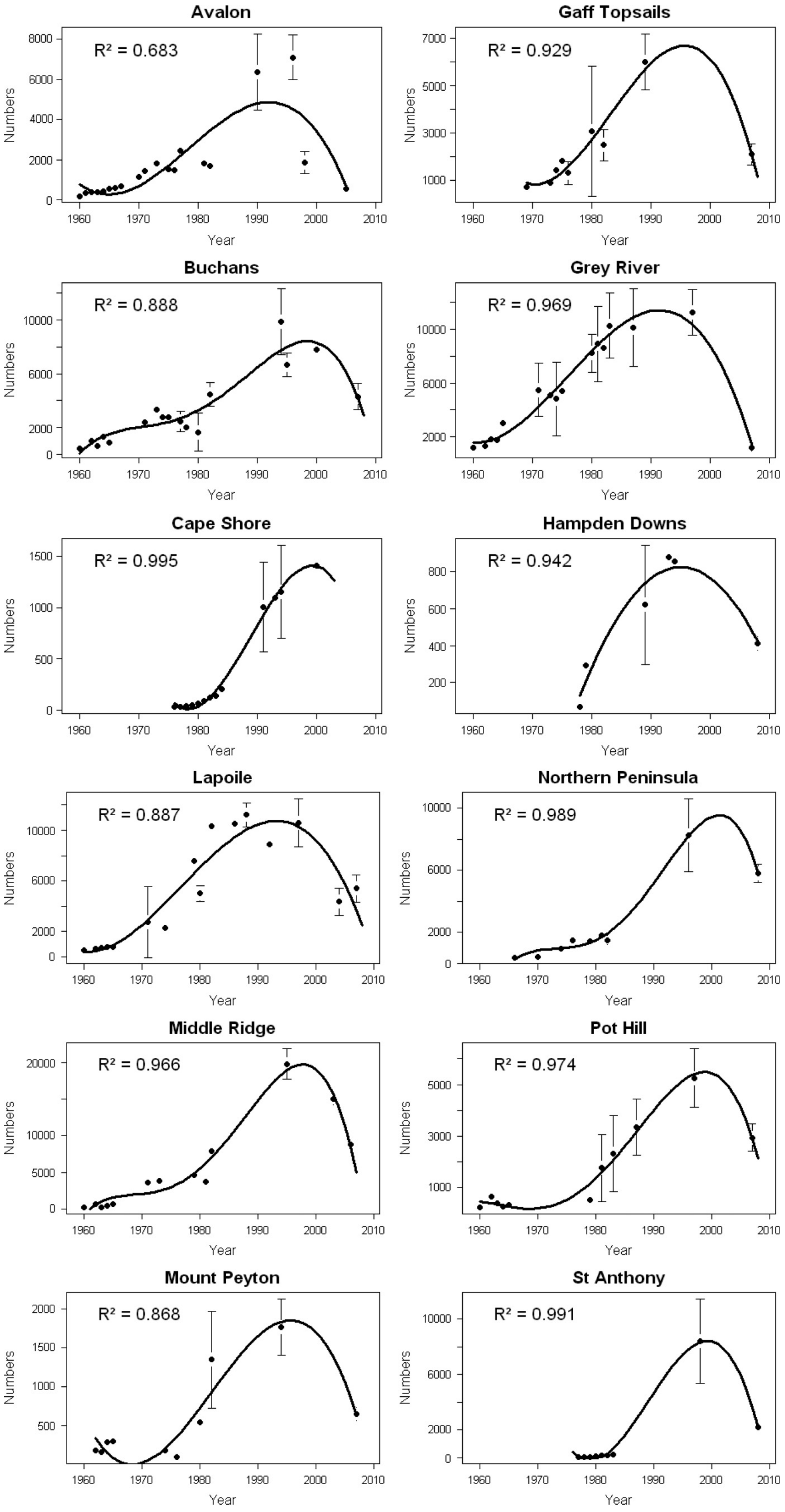


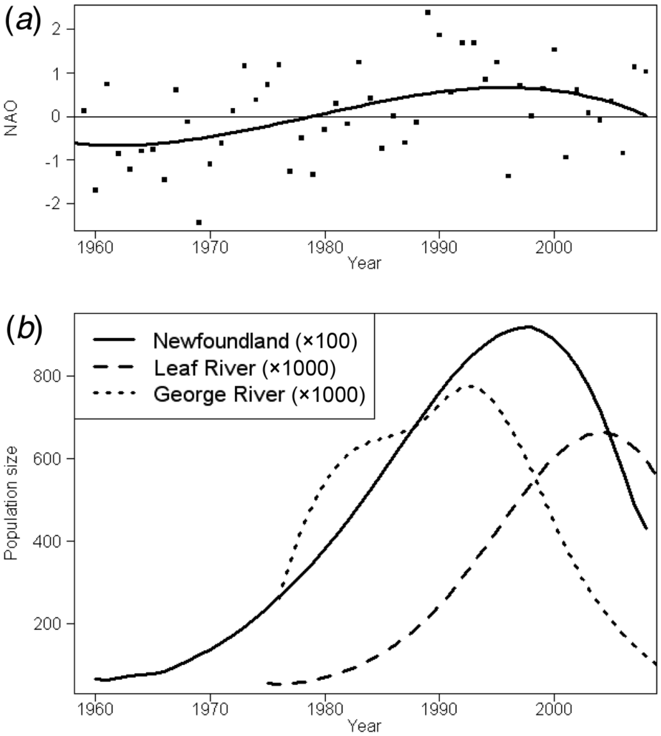
Table 2. Summary of population estimates for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1955–2008).

				Population range				
Herd	Year range	Count	Proportion of year with a count	Minimum	Maximum	Mean	Absolute value of residuals (mean ± SE)	*R*
Avalon	1960–2005	20	0.44	189	7 104	1637.55	701.7±170.5	0.826
Buchans	1960–2007	17	0.36	450	9 834	3229.88	661.1±138.3	0.942
Cape Shore	1976–2000	13	0.54	28	1 410	416.23	28.00±6.25	0.997
Gaff Topsails	1969–2007	9	0.23	720	5 980	2207.33	494.5±91.6	0.964
Grey River	1960–2007	16	0.34	1200	11 225	5526.69	319.9±86.0	0.984
Hampden Downs	1978–2008	6	0.20	69	877	520.83	61.5±15.5	0.971
Lapoile	1960–2007	16	0.34	500	11 210	5145.25	1035.8±220.5	0.942
Middle Ridge	1960–2006	13	0.28	257	19 765	5349.31	896.4±185.1	0.983
Mount Peyton	1962–2007	10	0.22	95	1 762	550.10	155.3±39.0	0.932
Northern Peninsula	1966–2008	9	0.21	400	8 246	2456.33	192.8±51.3	0.994
Pot Hill	1966–2007	11	0.27	250	5 250	1649.64	193.3±51.4	0.987
St. Anthony	1976–2008	10	0.31	21	8 405	1131.40	114.2±45.9	0.995

Note: Equations from the polynomial fit of population time series, as well as absolute residuals (mean ± SE) and associated *R* values, are given.

density-dependent relationship and PF > 1 indicates that the observed dynamics are influenced by nonlinearity; LE is an indicator of trajectory stability with LF > 0 indicating propensity for population instability and nonlinearity (Turchin 2003*a*). Following our predictions, we expected PO > 1, PF > 1, and LE > 0 for all caribou herds.

Fig. 2. Trends in (*a*) the North Atlantic Oscillation (NAO) showing phase of positive and negative values and (*b*) smoothed population estimates of the George River, Leaf River, and Newfoundland herds during 1960–2008.



We assumed that density-dependent competition for resources would be manifest in poorer body condition of caribou and therefore evaluated lagged correlations between caribou morphometrics and population numbers. We produced a multiherd population estimate by pooling estimates for every herd (Fig. 2*b*). The multiherd caribou population estimate served as basis for a comparison with caribou morphometric features. We developed age-specific time series for caribou morphometrics (1978–2005) by averaging annual measurements across each age category (0, 1, 2,…9, ≥10 years). For this analysis, jaw length, diastema length, and antler point counts were segregated by gender, whereas for molar row characteristics, the time series was pooled across gender due to lower sample size and comparable values between males and females (G. Bastille-Rousseau, unpublished data). To assess the correlation between caribou morphometrics and population size, we correlated each morphometric measurement to a population size estimate both in current (N_T) and delayed (N_{T-1}, N_{T-2},…N_{T-5}) time. This approach allowed us to evaluate (*i*) if a negative relationship existed between a given morphometric measurement and population size, as predicted if density dependence is important and (*ii*) whether the measurement was most correlated to the current or time-delayed population density, as would be appropriate if caribou populations are cyclic and regulated by time-delayed density dependence.

To rigorously evaluate if each correlation coefficient for a given morphometric measure and a given time lag was significantly different from zero, we performed a permutation exercise involving a unidirectional *t* test. For each time lag, we generated a set of normally distributed values having a mean of zero and a standard deviation equal to that of the observed set of correlation coefficients from all the different age categories for a specific morphometric. We then evaluated whether the distribution of observed correlation coefficients from the different age groups for a specific morphometric and time-lag combination was significantly different from the generated set of random values. We performed this test 10 000 times for each combination of morphometric and time lag, and reported the mean *t* value and mean significance level across every permutation.

Correlation between population and environmental factors (predictions 2 and 3)

We smoothed NAO time series, while considering cumulative effects of winter severity on population dynamics, by applying a moving mean value using the four previous NAO values with the current value for a given year. A 5-year window was chosen based on previous work evaluating time lags associated with NAO (Hurrell 1995; Hurrell and Van Loon 1997) while also seeking to avoid excessive smoothing. The mean NAO value for a given year was correlated with population estimates for each herd and island-wide estimates. Because each herd was independent and acted as a replicate, we used a Bonferroni correction (α = 0.05 / 12 herds = 0.0042) to assess whether herd sizes were significantly correlated with NAO and to obtain a mean correlation coefficient with confidence interval. We intended to fit each NDVI series for each herd in a similar fashion as NAO, especially since Newton (2012) found a 5-year lag between population size and NDVI, but none of our NDVI series based on actual NDVI values or residuals exhibited

Table 3. Results of spectral analysis for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1960–2008).

Herd	Years	Frequency	*P*	Spectral power	*P*
Avalon	1960–2005	0.0210	<0.001	20.153	<0.001
Buchans	1960–2008	0.0171	<0.001	19.014	<0.001
Cape Shore	1976–2007	0.0261	<0.001	13.415	<0.001
Gaff Topsails	1969–2008	0.0390	0.040	17.681	0.040
Grey River	1960–2007	0.0200	0.028	21.413	<0.028
Hampden Downs	1978–2008	0.0288	0.073	13.129	0.073
Lapoile	1960–2008	0.0185	<0.001	21.366	<0.001
Middle Ridge	1961–2008	0.0190	<0.001	19.065	<0.001
Mount Peyton	1962–2008	0.0205	0.002	20.375	0.002
Northern Peninsula	1966–2008	0.0176	<0.001	17.292	<0.001
Pot Hill	1960–2008	0.0180	<0.001	20.106	<0.001
St. Anthony	1976–2008	0.0278	<0.001	14.209	<0.001

Note: Analysis was conducted on detrended untransformed values and includes estimated spectral frequency and spectral power for Sine component 1 only.

significant trends (all $P > 0.25$). Therefore, we did not assess further the correlations between NDVI and individual population estimates.

Between-herd synchrony (prediction 4)

We tested between-herd synchrony in population size by comparing pairwise correlations between each herd. We also assessed the effect of herd proximity on synchrony by first calculating the interherd distance as the distance from the centre of one calving ground to another, for all herd pairs. We then used a linear model to evaluate if interherd distance influenced the observed correlation (synchrony) between population size estimates. Considering that the Avalon herd was isolated in the southeastern portion of the island and appeared to decline earlier than other herds due to an epizootic disease (Ball et al. 2001), we also conducted the analysis excluding this herd to confirm that results were consistent without the outlier. Statistical analyses were conducted using R version 2.12.2 (R Foundation for Statistical Computing, Vienna, Austria), and we report mean ± SE and Pearson's *R* as a measure of correlation fit, except for polynomial fit where R^2 values are presented.

Results

Multiherd population estimate

All polynomial models fit population trajectories significantly and provided acceptable explanatory power (residual = 404.542 ± 92.857, $R^2 = 0.960 \pm 0.014$; Table 2). Model selection revealed that most herds were structured as third- or fourth-order polynomials, although one population having the lowest estimate (Hampton Downs) had a second-order fit (Table 2). Even among the herds with sparse population estimates or shortened time series, models seemed to capture the broad-scale temporal variability in numbers, including the ubiquitous population peaks during 1990–2000 and the lows before and after this period (Fig. 1). Models fit to Avalon and Buchans populations fell short of their highest numerical estimates, but otherwise models reasonably approximated the amplitude and timing of peak abundance for each herd (Fig. 1).

Prediction 1: delayed density dependence

Table 4. Results of nonlinear time-series analysis for 12 caribou (*Rangifer tarandus*) herds in Newfoundland (1960–2008).

Herd	Years	*n*	Variance	PO	PF	LE
Avalon	1960–2005	46	0.414	3	2	0.178
Buchans	1960–2008	49	0.356	3	2	0.056
Cape Shore	1976–2007	32	0.644	3	2	0.073
Gaff Topsails	1969–2008	40	0.304	3	2	0.309
Grey River	1960–2007	48*	0.288	3	2	0.672
Hampden Downs	1978–2008	41	0.188	2	2	0.210
Lapoile	1960–2008	39	0.427	2	2	0.055
Middle Ridge	1961–2008	48*	0.535	2	2	0.142
Mount Peyton	1962–2008	47	0.743	3	2	0.483
Northern Peninsula	1966–2008	43	0.443	3	2	0.892
Pot Hill	1960–2008	49	0.520	3	2	0.148
St. Anthony	1976–2008	28*	0.572	2	2	0.709

Note: Process order (PO; number of time delays best explaining density dependence), polynomial fit (PF; degree of nonlinearity in the density-dependent relationship), and Lyapunov exponent (LE; index of population stability–instability) are provided.

*Excludes portions of the population time series that are due to fitted population estimates having negative values.

Spectral analysis revealed significant evidence of phases of increase and decrease for all herds (Table 3). All time series had a single significant spectral peak (Sine component 1 only), and the estimated period for the fluctuation (1/frequency) was 47.7 ± 2.4 years ($n = 12$); it was significantly higher, 51.7 ± 1.7 years ($n = 9$; paired $t = 6.989$, $P < 0.001$), when we excluded time series <40 years (Capeshore, Hampden Downs, St. Anthony). Such a period should theoretically correspond to a time delay in density-dependent regulation of roughly 10–14 years if caribou population fluctuations actually reflect periodic fluctuations. Spectral power also was significant among all caribou herds and averaged 18.1 ± 0.9 units ($n = 12$) (Table 3).

Nonlinear time-series analysis suggested that caribou herds had complex structuring. Specifically, all populations had PO ranging between 2 and 3 units (Table 4), implying that their dynamics were governed by long-term time delays in density dependence. The analysis also revealed that all populations had higher order PF, indicating nonlinearities between population growth and lagged densities, as well as non-negative LE, indicating propensity for population instability and nonlinearity (Table 4). Collectively, these findings further supported the importance of delayed density dependence in caribou.

Correlation of caribou morphometrics with current and delayed population size estimates revealed evidence of density-dependent constraints on growth patterns. For female and male antler points, between-age mean correlation coefficients were negative and significant (different from zero) both with current population estimates and when delayed up to 5 years (Table 5). Female diastema length also showed significant or marginally significant mean correlation coefficients with population density for delays from 1 to 5 years. Molar row characteristics also were negatively related to current and 1-year delayed population estimates (Table 5). Correlation coefficients across age groups and morphometric attributes are provided in supplementary Table S1[1].

Predictions 2 and 3: correlations of NDVI and NAO with population size

No temporal trends were observed in the residuals of NDVI values after accounting for the influence of spring and winter weather, thereby negating the ability to test for further correlations with caribou population time series. Correlations between population size and the 5-year mean NAO values were strictly positive and significant for each herd ($R = 0.697 \pm 0.026$, $n = 12$; Table 6), as well as for the island-wide population estimate ($R = 0.792 \pm 0.068$).

Prediction 4: between-herd synchrony

Correlations in population size among herds were high ($R = 0.792 \pm 0.029$, $n = 66$), consistently positive, and almost always statistically significant (supplementary Fig. S1).[1] Moreover, correlation between herds decreased slightly with linear distance between their calving grounds ($R = -0.263$, $t = -2.184$, $P = 0.032$). However, this correlation was strongly influenced by the Avalon herd (the southeasternmost herd), which when removed from the analysis, reduced the statistical significance of distance on herd

Table 5. Correlation coefficients (*R*) between seven body condition indices and island-wide caribou (*Rangifer tarandus*) population size in Newfoundland (1978–2005).

Morphometric	R_t	T	R_{t-1}	T_{t-1}	R_{t-2}	T_{t-2}	R_{t-3}	T_{t-3}	R_{t-4}	T_{t-4}	R_{t-5}	T_{t-5}
Antler points												
Females	–0.72±0.13	**4,15**	–0.734±0.129	**4,12**	–0.735±0.13	**4,08**	–0.734±0.13	**4,07**	–0.732±0.13	**4,06**	–0.73±0.13	**4,06**
Males	–0.48±0.10	**3,37**	–0.472±0.105	**3,25**	–0.445±0.105	**3,03**	–0.42±0.106	**2,86**	–0.401±0.105	**2,75**	–0.386±0.105	**2,64**
Diastema												
Females	–0.24±0.09	2,02	–0.296±0.066	**3,24**	–0.351±0.041	**6,12**	–0.436±0.05	**6,24**	–0.483±0.053	**6,56**	–0.485±0.05	**7,00**
Males	0.17±0.08	–1,59	0.168±0.084	**–1,44**	0.162±0.09	–1,29	0.099±0.096	–0,75	0.015±0.1	–0,11	0.013±0.095	–0,10
Jawbone length												
Females	–0.214±0.143	1,09	–0.263±0.144	1,31	–0.291±0.142	1,47	–0.403±0.153	1,89	–0.438±0.157	2,00	–0.445±0.159	2,01
Males	–0.100±0.05	1,33	–0.077±0.05	1,11	–0.076±0.049	1,13	–0.038±0.059	0,45	0.021±0.072	–0,21	0.051±0.07	–0,52
Molar tooth row (both sexes)	–0.435±0.097	**3,22**	–0.376±0.093	**2,90**	–0.304±0.093	2,36	–0.241±0.095	1,83	–0.189±0.097	1,41	–0.148±0.098	1,09

Note: Age-specific correlation coefficients (mean ± SE) are given for a lag of up to 5 years ($R_T - R_{T-5}$). Probability values refer to *t* values from permutation tests (see Materials and methods) and significant values ($P < 0.05$) are in boldface type. For complete result see supplementary Table S1 and Fig. S1.[1]

Table 6. Correlation coefficients (*R*) for population size of 12 caribou (*Rangifer tarandus*) herds on Newfoundland (1960–2008) and the mean index of the North Atlantic Oscillation (NAO) representing winter severity during the preceding 5 years.

Herd	*R* (mean ± SE)
Avalon	**0.747±0.00031**
Buchans	**0.753±0.000023**
Cape Shore	**0.519±0.0001**
Gaff Topsails	**0.685±0.000033**
Grey River	**0.701±0.000019**
Hampdon Downs	**0.694±0.0003**
Lapoile	**0.753±0.000016**
Middle Ridge	**0.762±0.0000089**
Mount Peyton	**0.782±0.000088**
Northern Peninsula	**0.604±0.000023**
Pot Hill	**0.746±0.00003**
St. Anthony	**0.526±0.000024**
Newfoundland	0.792±0.0000018
Mean	0.689
Upper CI	0.946
Lower CI	0.878

Note: All correlation coefficients are significant (boldface type) when adjusted using a Bonferroni correction. Newfoundland represents island-wide estimate of caribou. CI, confidence interval.

synchrony, while the negative trend was qualitatively upheld ($R = -0.209$, $t = -1.555$, $P = 0.126$).

Discussion

Different hypotheses have been proposed to explain fluctuations in migratory caribou abundance; the prevalent ones being decadal trends in winter severity (Gunn 2003) and density-dependent degradation in range (Crête and Huot 1993; Bergerud 1996; Mahoney and Schaefer 2002). We showed that all herds in Newfoundland fluctuated dramatically over the last 40 years, and that these were synchronized as would be the case if driven by an extrinsic factor (Moran effect; Ranta et al. 1995, 1997). Herd trajectories correlated in a time-delayed manner with NAO values representing winter severity. Because we also found a signature of delayed density dependence between caribou morphometrics, our findings collectively point to winter severity as offering at least a partial explanation for the observed patterns of population change (Table 1). We consider that our results offer new insight into the relative roles of extrinsic and intrinsic drivers affecting population dynamics, and thereby provide a basis for further tests of the natural processes affecting caribou numbers.

All caribou populations on Newfoundland underwent a dramatic increase and decline during the last 40 years; a pattern that was highly synchronous island-wide. Currently, fluctuations among migratory caribou in eastern North America focus on the idea that time-delayed density dependence drives the decline in populations. This process may arise from forage deterioration on calving grounds (hypothesis 2; Table 1), which could be driven by overgrazing and trampling of vegetation (Messier et al. 1988; Bergerud 1996; Mahoney and Schaefer 2002). Our analyses revealed support for density dependence in the absence of evidence of either direct or interactive effects of calving range decline, whereas the strongest support for density dependence was the negative correlation between caribou body condition indices (but mostly antler point counts) and population size. Although time-series analysis should be more sensitive to higher order complexity and structuring in caribou populations, the predicted 2–3 year time lags were considerably shorter than the approximately 10- to 14-year time lags necessary to produce a 50-year numerical cycle, should they exist in caribou. Many ecologists have found difficulty in conceiving of intrinsic factors that could drive such a prolonged time delay in density dependence, and population fluctuations exceeding 10 years should normally be driven by density-independent forces associated with climate (Sinclair et al. 1993). Yet, it is conceivable that the slow rate of growth of lichen, a critical component in caribou diet, could provide such a time delay. Indeed, lichens grow at a rate of 3–5 mm/year and available biomass almost invariably represents an accumulation that spans multiple decades (Messier et al. 1988). Accordingly, recovery of this resource following its over-exploitation by high-density caribou populations could prolong the normal timeline for population recovery and explain the difference in the time lag observed and required for ~50-year cycles. Historical accounts from travel writing and early game management suggest a previous population peak in Newfoundland caribou in the 1890s, followed by a swift decline and long period of stasis that included another, smaller peak in the 1930s (Newfoundland Department of Environment and Conservation, unpublished data). This may suggest an even longer cycle period than that revealed by our data.

Large-scale climatic indices such as the North Atlantic Oscillation (NAO), North Pacific Oscillation (NPO), or the Arctic Oscillation (AO) are correlated with weather severity in different areas and follow decadal trends (Hurrell 1995); variation in these indices also are associated with variation in caribou population demography (Solberg et al. 2001; Couturier et al. 2009*a*; Joly et al. 2011). Associated with the high level of between-herd synchrony, we found that individual herd size correlation with delayed NAO values were relatively high, supporting the contention that winter severity may cause fluctuations in Newfoundland caribou population trajectories and thereby drive synchrony through a Moran effect. Hegel et al. (2012) similarly found partial support for the synchronizing role of winter severity on mountain-dwelling caribou dynamics.

Two others factors may contribute toward synchrony in population dynamics: dispersal and caribou removal by predators or human hunting. Interherd dispersal was uncommon and likely had little influence on population dynamics, which is consistent with the observation that caribou tend to be highly philopatric (Schaefer et al. 2000; Faille et al. 2010; supplementary methods[1]). Similarly, predation seems to be playing a major role in nonmigratory caribou fluctuations (Seip 1991; Wittmer et al. 2005), but most migratory populations can escape predator limitation (Seip 1991) and fluctuations in those herds likely involve multiple causes. Although we did not explicitly test for the role of predation and hunting on population synchrony, we do note that coyotes arrived on Newfoundland in the 1980s and contributed to caribou mortality. Considering the high rate of mortality in neonate caribou mortality owing to predation from other predators like black bears (Mahoney and Weir 2009), the current role of such a force on caribou populations in Newfoundland remains unclear. More importantly, it is notable that caribou population synchrony was quite strong in the increase phases from the 1970s (Fig. 1) and is therefore apparent before the arrival and spread of coyotes across the entire island, leaving coyote predation as an unlikely causative agent in the observed long-term fluctuations in caribou numbers. Hunting has been implicated in the decline of caribou populations under specific circumstances (Payette et al. 2004; Bergerud et al. 2008), but many migratory herds have declined and recovered despite sustained hunting pressure (Zalatan et al. 2006), and over the long term, harvesting of Newfoundland caribou has been regulated through license quotas. Although we cannot entirely discount a lag in management response, which can amplify numerical swings of harvested populations (Fryxell et al. 2010), over-hunting was not a causative factor in the decline, despite gaps in population monitoring resulting in higher than intended harvest rates likely exacerbated the rate of decline (G. Luther, unpublished data).

Even though we argue that polynomial fits were appropriate for capturing broad-scale patterns in caribou population trends, our approach notably did involve interpolation and did compromise to an unknown degree annual variability in numbers. Yet, such variability is an important characteristic of density dependence when evaluating population time series (Clark and Bjørnstad 2004) and should reflect constraints imposed by extrinsic and intrinsic factors acting on the population. However, we believe that complementing analyses of density dependence with time-series analysis of morphometrics clearly illustrate time-delayed density-dependent forces acting on Newfoundland caribou populations. Although our sample of harvested caribou may be biased toward larger individuals, we consider this unlikely. Resident hunters in Newfoundland tend to be less selective and represent a much larger proportion of the harvest than nonresidents (Mahoney et al. 2011). Although other measures of density dependence may be more accurate in documenting density-dependent constraints on growth, trends observed in morphometric sizes should nonetheless be representative of the entire population because any size-related bias would have been consistent. Furthermore, to characterize population density dependence and cyclicity would require more observations and ideally multiple oscillations; the markedly long period of caribou fluctuations (Fig. 1, Fig. 2*b*) currently restricts our analysis to a single oscillation.

The absence of patterns in NDVI time series may reflect low data reliability when assessing yearly variability, particularly because lichens are such a critical resource for caribou (Bergerud 1972) but variation in biomass lead to smaller variation in NDVI than vascular plants (Olthof et al. 2008). Despite our effort in accounting for the influence of winter and spring weather on vegetation growth, NDVI values were still highly variable between consecutive years. However, it is unlikely that Newfoundland caribou do not have any influence on their range quality. For example, at least one herd, the Buchans herd, spent progressively less time on their historical summer range as population density increased over a period of 40 years (Mahoney and Schaefer 2002). Notably, this pattern has since reversed, which is coincident with the population decline in the Buchans herd and, presumably, a concomitant relaxation of food competition (Schaefer and Mahoney 2013). The correlation observed between antler points count and population size for both sexes further corroborates the likely role of range decline in caribou fluctuations. Indeed, because antlers grow mainly during spring and summer, reduction in habitat quality should be reflected more-or-less instantaneously than through the observed time delay. We therefore consider both hypothesis 1 and hypothesis 3 as being nonrefutable given our data.

Considering that decadal trends in winter severity are unlikely to give rise to such long periods in caribou fluctuations, decline in calving ground or summer range also may be implicated in the observed numerical trends. For instance, if NAO was the only factor contributing to caribou population fluctuations, it would be surprising to observe such an early and sharp decline in population size (Fig. 2*b*). This may suggest that trends in winter severity can act as the *zeitgeber* (sensu Sinclair et al. 1993) that would promote synchronized increase in caribou population, whereas spring vegetation ultimately would limit herd abundance. Similar patterns of increase and decrease with respect to NAO also are observed for other migratory woodland caribou in eastern North America (Figs. 2*a*, 2*b*), where deterioration of forage also has been reported (Bergerud 1996; Couturier et al. 2009*a*). However, it is worth reiterating that our current analyses involve correlations meant to test the main factors driving fluctuations in caribou, but that other factors (e.g., parasites, disease, insect harassment, or hunting) also may influence population dynamics. It follows that our observations provide a basis for further study of caribou populations, specifically focusing on long-term trends in forage availability relative to broad-scale climate patterns.

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