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Woodland caribou calf mortality in Newfoundland: insights into the role of climate, predation and population density over three decades of study

Shane P. Mahoney¹ · Keith P. Lewis² · Jackie N. Weir² · Shawn F. Morrison³ · J. Glenn Luther⁴ · James A. Schaefer⁵ · Darren Pouliot⁶ · Rasim Latifovic⁶

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Abstract The rates and causes of juvenile mortality are central features of the dynamics and conservation of large mammals, like woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)), but intrinsic and extrinsic factors may be modified by variations in animal abundance. We tested the influences of population size, climate, calf weight and sex on survival to 6 months of age of 1241 radio-collared caribou calves over three decades, spanning periods of population growth (1979–1997) and decline (2003–2012) in Newfoundland, Canada. Daily survival rates were higher and rose more quickly with calf age during the population growth period compared to the decline. Population size (negatively) and calf weight (positively) affected survival during the decline but neither

had a detectable influence during the growth phase. Sex, climate and plant productivity (the latter two derived from the North Atlantic Oscillation and Normalized Difference Vegetation Index, respectively) exerted minimal influence during either phase. Predation was the dominant source of mortality. The mean percentage of calves killed by predators was 30 % higher during the decline compared to the growth phase. Black bears (*Ursus americanus*) and lynx (*Lynx canadensis*) were the major predators during the population increase but this changed during the decrease to black bears and coyotes (*Canis latrans*). Our findings are consistent with the hypothesis that Newfoundland caribou experienced phase-dependent survival mediated proximally by predation and competition for food.

✉ Jackie N. Weir
jackieweir@gov.nl.ca

Shane P. Mahoney
shane@conservationvisions.com

Keith P. Lewis
keithLewis@gov.nl.ca

Shawn F. Morrison
shawn.morrison@dryasresearch.com

J. Glenn Luther
glennluther@gov.nl.ca

James A. Schaefer
jschaefer@trentu.ca

Darren Pouliot
Darren.Pouliot@NRCan.gc.ca

Rasim Latifovic
Rasim.Latifovic@NRCan.gc.ca

² Sustainable Development and Strategic Science, Department of Environment and Conservation, Government of Newfoundland and Labrador, St. John's, NL A1B 4J6, Canada

³ Dryas Research Ltd., Edmonton, AB T6C 2R6, Canada

⁴ Wildlife Division, Department of Environment and Conservation, Government of Newfoundland and Labrador, Corner Brook, NL A1A 5J7, Canada

⁵ Department of Biology, Trent University, 1600 West Bank Drive, Peterborough, ON K9J 7B8, Canada

⁶ Canada Centre for Remote Sensing, Canada Centre for Mapping and Earth Observation, 560 Rochester Street, Ottawa, ON K1A 0E4, Canada

¹ Conservation Visions Inc., Stn C, 354 Water Street, P.O. Box 5489, St. John's, NL A1C 5W4, Canada

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Introduction

Understanding the factors governing animal abundance is a longstanding theme in ecology (May 1999; Krebs 2002). For large herbivores, variations in juvenile survival and recruitment play dominant roles in driving changes in abundance (Sinclair and Pech 1996; Gaillard et al. 1998, 2000; Owen-Smith 2010); such variations are driven by intrinsic factors (such as reproductive physiology or behaviour), extrinsic factors (such as food, climate and predation) and their interactions (Gaillard et al. 1998).

Juvenile survival is often the most variable vital rate as populations approach carrying capacity (Fowler 1981; Eberhardt 2002; Bonenfant et al. 2009). Adults experiencing density-dependent food competition can be expected to produce smaller calves more vulnerable to predation (Bergerud et al. 2008). Seasonal climate (e.g., severe winters; Hegel et al. 2010) or the interaction between density and climate (Solberg et al. 2001), as well as plant phenology and productivity (Pettorelli et al. 2005a, b; Bergerud et al. 2008), can also create poorer foraging conditions resulting in reduced female body condition and lower calf birth weight, which again, can influence the survival of young herbivores (Jenkins and Barten 2005). Exploiting these vulnerabilities, predators—for example, wolves (*Canis lupus*), lynx (*Lynx canadensis*), coyotes (*C. latrans*), and black bears (*Ursus americanus*) in the case of caribou (*Rangifer tarandus*)—are recognized as the principal mortality agents of juveniles (Bergerud 1971; Wittmer et al. 2005; Bergerud et al. 2008). Further, research on small mammals suggests that the patterns and scale of such density-dependent effects vary as populations increase and decrease (Stenseth et al. 1998). To date such phase-dependent effects have not been examined in large herbivores.

For long-lived species, identifying factors that influence survival across phases of population increase and decline requires long-term studies. Indeed, for migratory caribou, population trajectories typically unfold slowly across multiple decades (Gunn 2003; Bastille-Rousseau et al. 2013) during which population abundance may vary by two orders of magnitude (Gunn 2003; Vors and Boyce 2009). For such populations, phase dependencies created by time lags between population growth and their food supply may also be protracted (Messier et al. 1988; Newton et al. 2014). As the populations grows, caribou may eventually trade-off physical growth and condition in order to reproduce, may forgo reproduction,

and/or switch to less preferred foods thereby buffering the population from decreased availability of preferred forage (Crête and Huot 1993). Meanwhile, for declining populations, recovery of depleted vascular plants and lichens may require several decades, thus hampering population stabilization or recovery (Kumpula et al. 2000; Hansen et al. 2007). Despite these insights, however, sustained studies that investigate the cause-specific mortality of juvenile ungulates against a backdrop of changes in population size and changes in predator guilds remain rare.

Caribou on the island of Newfoundland provide an uncommon opportunity to test these ideas. During 35 years of sustained research into patterns and causes of juvenile mortality, Newfoundland herds have risen and fallen substantially and synchronously (Bastille-Rousseau et al. 2013; Mahoney et al. 2014; Weir et al. 2014). From 1975 to 1996, the island-wide population quadrupled to approximately 94,000 animals, followed by an abrupt decline to approximately 32,000 animals by 2013 (Mahoney et al. 2011; Weir et al. 2014). Coincident with these population size changes, and consistent with population regulation through density-dependent food competition (Crête and Huot 1993), were changes in diet composition, demographic and morphological traits (Mahoney et al. 2011; Weir et al. 2014), as well as changes in geographic distribution and timing of migration (Schaefer and Mahoney 2013). Moreover, coyotes, an important predator of Newfoundland caribou (Lewis and Mahoney 2014; Weir et al. 2014) first became established on the island as the number of caribou was increasing rapidly in the early 1980s; wolves were extirpated nearly a century ago (Moore and Parker 1992).

Here, we report on the patterns and processes underlying calf survival and causes of mortality in Newfoundland caribou, spanning more than 30 years, during contrasting phases of population growth (1979–1997) and decline (2003–2012). During these phases, we monitored the fates and survival of 1241 calves with radio-telemetry. We quantified survival rates, changes in the timing of calf mortality, and identified agents of mortality and changes in the predator guilds. Further, we tested multiple hypotheses regarding the patterns of calf survival, including relationships with population size, calf sex and weight, plant productivity and climate. We anticipated that calf survival would vary directly with calf weight, calf survival would improve with earlier spring, advanced green-up and increased plant productivity, and decrease with winter severity, and that the influence of density on calf survival would be minor during the population increase but inversely related during the decrease phase (Gaillard et al. 1998).

Materials and methods

Study area and population

The island of Newfoundland (106,000 km²) is located on the east coast of Canada (46°N–51°N latitude; Fig. 1). The adjacent Labrador Current and Gulf Stream combine to create a year-round cool, maritime climate. Newfoundland caribou are distributed throughout most of the island (Fig. 1), although there is substantial seasonal variation in their distribution (e.g., calving versus non calving periods). Moose (*Alces alces* (L., 1758)), the only other ungulate on the island, were generally widespread in forested areas. Potential predators of Newfoundland caribou included black bears (*Ursus americanus* (Pallas, 1780)), lynx (*Lynx canadensis* (Kerr, 1792)), bald eagles (*Haliaeetus leucocephalus* (L., 1766)), and coyotes (*Canis latrans* (Say, 1823)) which arrived on the island around the early- to mid-1980s. Wolves (*C. lupus* (Linnaeus, 1778)) were extirpated from

Newfoundland in approximately 1922 (Moore and Parker 1992).

Data collection and preparation

Neonatal calves (<5 days old) were located from helicopters and captured on foot during late May and early June each year, 1979–1997 and 2003–2012. Calves were fitted with expandable VHF radio-collars equipped with mortality sensors and weighed <5 % of body mass (Sikes et al. 2011). Collars were fitted securely to preclude slippage. Calves also were ear-tagged (coloured and coded with a unique ID number), sexed, and weighed. To minimize capture-related stress and abandonment by dams, capture handling times were held to <5 min in most instances. Calves were visually relocated within 24 h of capture to confirm re-bonding with their dams and were monitored daily by radio-telemetry from helicopter or fixed-wing aircraft during the first week post-capture. For the next 4–5 weeks, aerial radio-telemetry surveys

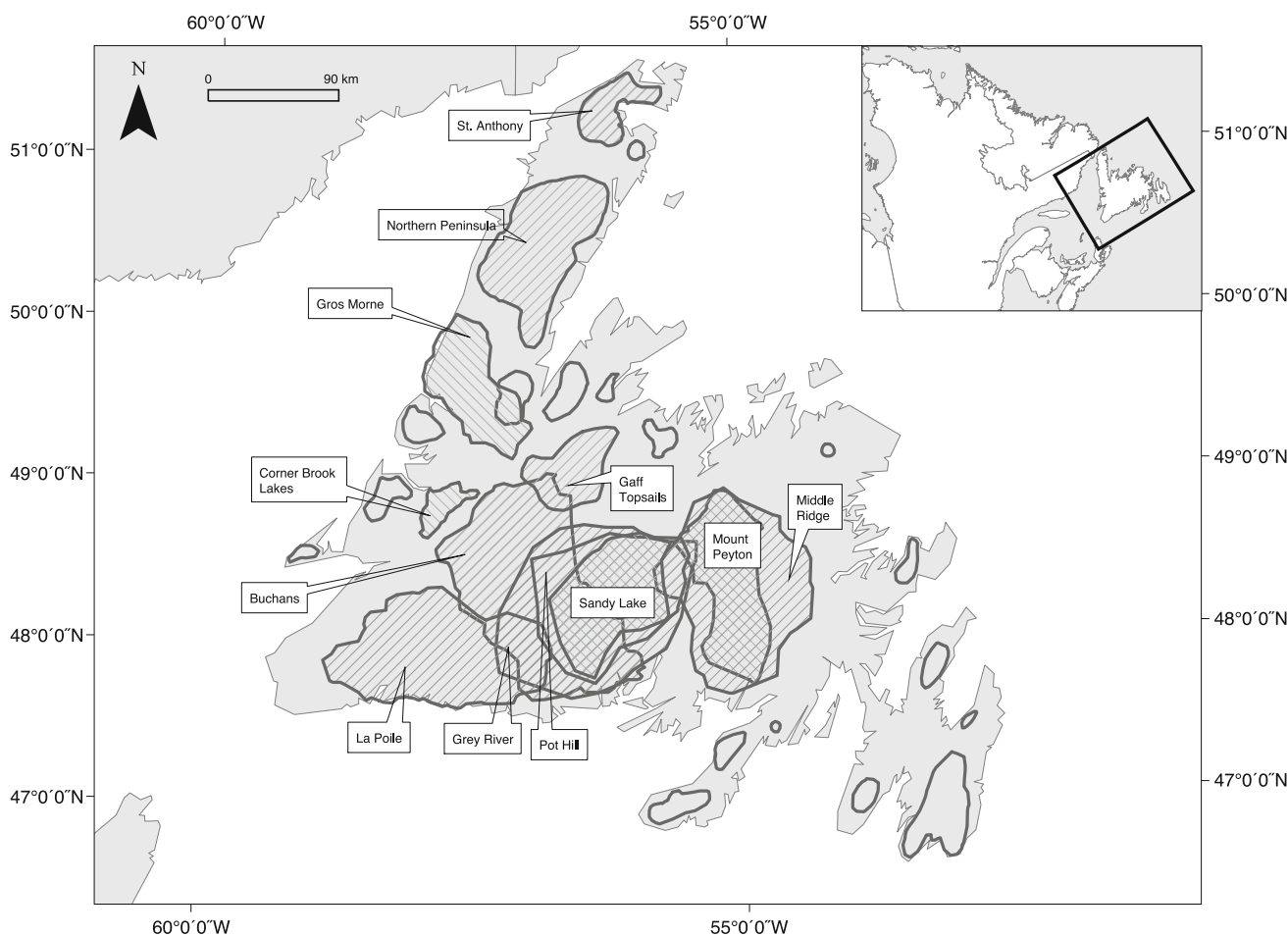


Fig. 1 Ranges of woodland caribou herds in Newfoundland, Canada. *Hatched and labelled polygons* represent herds from which calf survival data were collected

occurred every 2–4 days, and following this, every 5–10 days until August. After August, monitoring typically continued fortnightly or monthly.

We continued these field investigations during the calves' first year of life to determine the timing and causes of mortalities, and survival rates. Mortality signals were identified from aircraft; ground crews retrieved the collars and examined any remains. Systematic examinations of each carcass and vicinity were conducted to determine the cause of death based on overall carcass condition, presence or absence of the dam, predator-inflicted wounds, signs of disease or infection, habitat type, and topography (Mahoney et al. 1990; Trindade et al. 2011). When predation was suspected, a detailed examination of the carcass and surrounding area was carried out—i.e., the location and type of wounds, predator handling (skinning of hides, crushing of large limb bones and skull, viscera removal, burial of partial remains), the presence and condition of the radio-collar (whether blood-stained or damaged), the presence or absence of blood-stained vegetation, predator tracks, scats or hair, resting places (matted vegetation), and evidence of the carcass having been dragged (Mahoney et al. 1990). The area within 30 m of the carcass was searched for additional remains and evidence of predators. Intact collars with little damage and with no nearby remains were assumed to be indicative of a collar slip. When carcass remains were sufficient, they were removed for necropsy by veterinarians. During 2010–2012, predation-related remains were also swabbed for DNA to assist in predator species identification (Mumma et al. 2014).

Our data represent the amalgamation of telemetry studies from various Newfoundland herds. Despite variation in the timing and the contribution of individual herds to the data, we surmise that any bias is likely small. Indeed, across Newfoundland, herds displayed remarkable synchrony in population trends and in demographic and morphological changes throughout the study (Mahoney et al. 2011, 2014; Bastille-Rousseau et al. 2013).

Some calves ($n = 76$) were omitted from analysis. Forty-two were either abandoned by the dam, died during capture, or were never relocated post-capture. Eighteen weighed >12 kg and were likely >5 days old at capture. In 2010, a further 16 calves from the Northern Peninsula herd were censored due to the large number of collar slips early post-capture. In sum, our analysis was based on 1241 calves: 511 from 1979 to 1997 (275 males, 254 females) and 730 from 2003 to 2012 (383 males, 341 females, 6 unknown).

Survival

We focused on calf survival to 6 months of age and considered older calves to be successfully recruited to the

population. While only a small proportion of calves during the population decline phase survived beyond 6 months, we determined through a separate collaring program that the survival rates of 6–12-month-old individuals were comparable to adults (Mahoney and Weir 2009; Trindade et al. 2011).

We estimated survival using nest survival models using Program MARK (White and Burnham 1999; Dinsmore et al. 2002; Rotella et al. 2004). Such models are appropriate for radio-telemetry studies where monitoring intervals are uneven and the fate of the animal at each interval cannot be ascertained with near-certainty. The models required four types of information: the day of radio-transmitter deployment, the last day that an individual was known to be alive, the last day that a live individual was detected or that a mortality event was discovered, and the fate of the individual (whether alive or dead).

Daily nest survival models assume (Rotella et al. 2004): (a) correct classification of individual fates; (b) no influence of collaring and subsequent checks on survival; (c) independence of individual fates; (d) a record of all checks of each individual; and (e) the homogeneity of daily survival rates (DSR). To the extent that our data and methods are demonstrative, we believe that the first four of these assumptions were met (for further details, see Lewis and Mahoney 2014). However, survival through the first 6 months is typically not constant for ungulates and generally increases as calves mature (Larsen et al. 1989; Adams et al. 1995). Therefore, to satisfy the fifth assumption (homogeneity of DSR), we allowed the DSR to increase linearly within the 6-month post-birth period and included this 'TREND' term in our candidate model sets.

We first estimated calf survival to 6 months each year for which radio-telemetry data were available (1979–1997 and 2003–2012), with the DSR term (TREND) applied separately to each year (Dinsmore et al. 2002). To assess temporal changes in the timing of mortality, we compared trends in DSR between the population growth and decline phases. Following this, we tested the influence of several putative factors (i.e., population size, birth weight, and climate) on calf survival. Data for putative factors were not available for all years for which radio-telemetry data existed (see below). Therefore, we limited our analysis to 1987–1997 ($n = 313$) and 2003–2012 ($n = 730$).

Putative factors affecting survival

Population size

The number of caribou across Newfoundland was estimated intermittently, 1960–2012, using a combination of standard strip and stratified random block surveys from fixed-wing aircraft and helicopters, and in later years,

employing mark-recapture methods using helicopters exclusively (Mahoney et al. 1998; Weir et al. 2014). The population growth rates derived from these surveys were highly comparable among herds (Bastille-Rousseau et al. 2013) and were consistent with survival-recruitment schedules (Mahoney and Schaefer 2002). Precise estimates of density (i.e., number of caribou per area) were unavailable because survey estimates did not always control for the occupied area (Mahoney et al. 2011). We based estimates of the size of the island-wide population on pooled data from individual herds. Annual abundance estimates were not available for all herds; in such cases, estimates were interpolated (Mahoney et al. 2011).

Climate

The North Atlantic Oscillation (NAO) is an index of sea-level atmospheric pressure differences across the Atlantic Ocean. In Newfoundland, positive winter NAO values typically are associated with greater snowfall and lower winter temperatures (Catto et al. 2003; Topliss 1997), whereas negative NAO values reflect reduced snow cover and warmer, drier winters (Catto 2010). Monthly NAO values were downloaded from the National Oceanic and Atmospheric Administration (NOAA; <http://www.cpc.ncep.noaa.gov>). We defined the winter NAO as the mean value from December to April, prior to calving.

Vegetation greenness

The Normalized Difference Vegetation Index (NDVI) is based on the absorption of visible (or red) light by plant pigments such as chlorophyll and the reflectance of near-infrared light related to leaf cellular structure. NDVI can be used to measure plant growth, vegetation cover, or biomass production (Pettorelli et al. 2005b, c; Newton et al. 2014). We used time series of NDVI observations to extract proxies for the rate of spring green-up, the start of spring, and peak season productivity.

For NDVI, 10-day composites, 1985–2012, at 1-km spatial resolution were processed by the Canadian Centre for Remote Sensing (following Latifovic et al. 2005). A correction for systematic bias between AVHRR-2 and AVHRR-3 sensors was applied (Latifovic et al. 2012) to improve radiometric consistency between sensors covering the period. The average cloud- and shadow-free NDVI value for each 10-day composite was extracted for all of Newfoundland. The time series of average NDVI values was temporally smoothed to remove outliers using a robust Lowess filter where, at each iteration, data falling below the fit line were removed for the next iteration (Fernandes et al. 2005). Three iterations were used. We extracted several time series metrics for each year: (1) the maximum

difference between 10-day composites from May to July as a measure of the rate of spring green-up (SPRING_RATE); (2) the beginning of the growing season taken as the point where 50 % of the maximum NDVI was observed (SPRING_START); and (3) the maximum seasonal NDVI for each year (MAXNDVI) as a measure of peak season productivity (Jönsson and Eklundh 2002; Pettorelli et al. 2005c). The peak season productivity for the year of birth and the preceding year was used in the modeling analysis.

Calf weight

Body weight was recorded for each neonate at capture and used as a proxy for calf condition. During 1979–1997, however, birth weight records were not cross-referenced with individual calves. Therefore, it was not possible to include birth weight as an individual covariate for this phase; we used mean annual birth weight. During 2003–2012, birth weight was generally available for each individual and was included as a covariate in modeling survival. Some calves ($n = 13$) were released before weighing to ensure re-bonding with the dam. In those cases we substituted the average birth weight in that year for the individual covariate.

Model selection

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and AIC weights (Burnham and Anderson 2002) to evaluate multiple models of survival involving population size (POP), birth weight (WEIGHT), and climate. It is common practice in most mark-recapture analyses to first calculate a variance inflation factor to adjust for any lack of fit of the global model (i.e., a model with all of the relevant explanatory variables) to the data (i.e., encounter histories). However, the global model is saturated for the nest survival model and the variance inflation factor is not identifiable. Therefore, this adjustment is not possible for the nest survival model (Dinsmore et al. 2002), and therefore, we did not compute the global model for these analysis.

The effect of climate conditions was assessed using the winter NAO, peak productivity in the year the calf was born (MAXNDVI_T) and 1 year prior to birth (MAXNDVI_{T-1}), start of spring (SPRING_START), and rate of vegetative green-up (SPRING_RATE). We also tested additive combinations of these models (Burnham and Anderson 2002) and the interaction between POP and NAO. Similar to Dinsmore et al. (2002), the linear increase in DSR (TREND) was applied uniformly across years. We also fit 'INTERCEPT-only' and 'INTERCEPT+TREND' models to the data. The former tested whether non-trended survival was constant among years, the latter whether differences among years were due to

differences in *TREND*. We also fit models with and without *TREND*, but models without *TREND* had low support relative to models with *TREND* (results not presented). To determine if there was a difference in survival between males and females, a variable (*SEX*) was added post hoc to the most supported model in the candidate set. All variables were screened for outliers, multicollinearity, and model redundancy (Burnham and Anderson 2002). Unless otherwise stated, results are expressed as mean \pm SE.

Results

Survival rates and model selection

During the phase of population increase (1979–1997), mean calf survival to 6 months of age was relatively high and constant (66.5 ± 2.4 %) but following the population peak in 1996, declined dramatically (Fig. 2). Indeed, once monitoring resumed in 2003, survival had diminished to just 7.5 ± 3.7 %. Subsequently, survival improved (35.0 ± 4.0 %, 2003–2012), albeit far below pre-peak levels. Despite the upward trend in calf survival after 2003, the caribou population continued to fall (Fig. 2).

The factors governing calf survival varied according to the population phase. When the population was increasing (1987–1997), the most supported model included only *TREND*, reflecting a gradually increasing daily survival rate as summer progressed. Other models (albeit less supported by the data) included the influence of winter (i.e., *NAO*) and the start of spring (Table 1; Fig. 2). However, during the population decline phase, the factors influencing survival were substantially different (Table 1). The most supported model during the decline phase included abundance (*POP*), *NAO*, and their interaction (Table 1; Fig. 2). Survival was negatively related to abundance but *NAO* and interaction term were not significant (Table 2). Similarly, when sex was added to this model, it received less support; the coefficient for this term was not significant (Table 2). The second ranked model included only abundance. A lower-ranked but still well supported model showed survival rates positively related to calf weight (Table 2). Less supported models during that period included forage conditions in spring and summer (as reflected by *NDVI* values).

Timing of mortality

The pattern of calf mortality differed between the phases of population growth and decline (Fig. 3). In addition to annual differences in overall survival, *DSR* was substantially higher during the increase phase than the decline. Prospects for calf survival were not constant within the first

6 months, but tended to rise more quickly as the calf aged during the phase of population increase.

Cause-specific mortality

Predation was the dominant source of mortality during the entire study period (Fig. 4), accounting for 73.7 % (± 4.9 %) of all deaths (range 20.0–100.0 % per year); other sources of mortality such as accidents, disease, or hunting were comparatively minor. Predation as a source of mortality was more than 20 % higher during the decline phase (84.6 ± 0.9 %, range 74.6–94.7 %) relative to the increase phase (62.7 ± 7.1 %, range 20.0–100.0 %; $\chi^2 = 115.1$, $df = 1$, $P < 0.001$).

The suite of predators implicated in calf deaths included black bears, coyotes, lynx, and bald eagles, although the percentage of mortalities ascribed to each species varied annually (Fig. 4). Black bears were responsible for more deaths (52.2 ± 6.7 %) than any other predator species. Expressed as a percentage of all predator-caused deaths, the relative influence of black bears was higher during the growth (64.9 ± 9.8 %) than decline (34.5 ± 4.4 %) phase. Similarly, the contribution of lynx was more than double during the growth (14.6 ± 4.8 %) compared to the decline (6.2 ± 1.6 %) phase. In contrast, coyotes—established about a decade prior to the end of the growth phase—caused few mortalities during that interval but were responsible for 25.8 % (± 4.6 %) of predation events during the decline. Bald eagle predation was minor but increased from 1 to 4 % of all predation mortalities between the growth and decline phases.

Discussion

Drawing on one of the largest and longest-term radio-telemetry data sets on caribou, we assessed factors affecting calf survival across a broad range of population abundance. Our results demonstrate that caribou survival to 6 months of age mirrored the direction of population change during the decline but not during the increase (Fig. 2). During the population decline phase, 50 % of the calves died within the first 6 weeks of life while it took almost 7 months to reach the same mortality proportion during the period of population increase. Population size and calf weight were insignificant influences on calf mortality during the increase phase but emerged as salient influences during the decline (Tables 1, 2).

High variation in juvenile survival is common in large herbivores (Gaillard et al. 1998) and long-lived vertebrates in general (Eberhardt 2002); for caribou, predation on juveniles and low recruitment are regularly cited as significant factors influencing population declines (Boertje

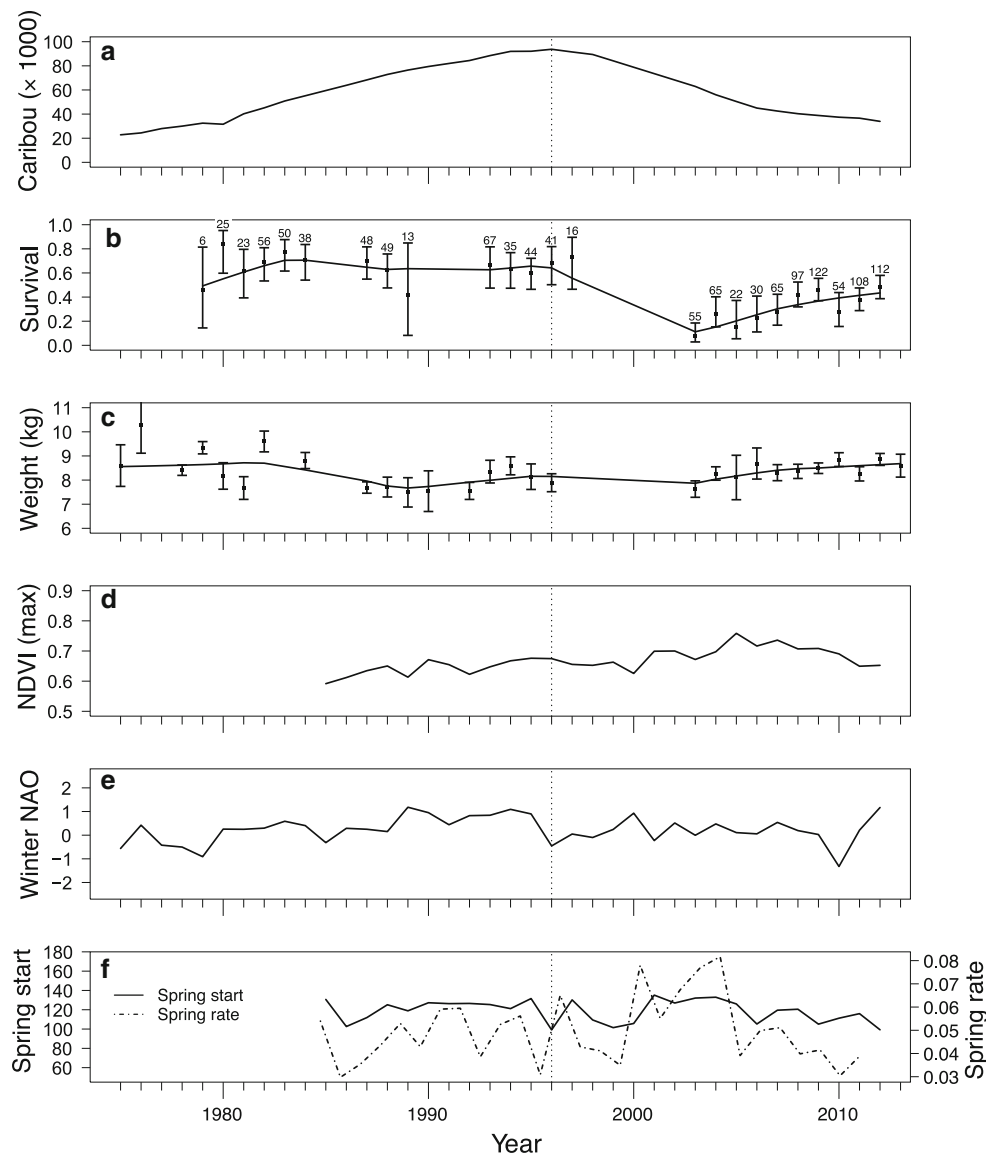


Fig. 2 Variation in the caribou calf survival and its putative predictors in Newfoundland, 1975–2012: **a** caribou abundance, **b** survival to 6 months of age, where *numbers* represent annual sample sizes, **c** neonatal body mass, **d** the maximum normalized

difference vegetation index (NDVI), **e** North Atlantic Oscillation (NAO) during winter, and **f** spring start and rate of green-up. The *vertical dashed line* represents the year of peak population size

et al. 1996; Wittmer et al. 2005; Latham et al. 2013). In our study, black bears, lynx, and coyotes (following their establishment) were the dominant sources of calf mortality (Fig. 4); their relative effects varied through time and increased substantially during the population decline phase. These findings correspond well with the predictable sequence—juvenile survival being the first in a series of changing vital rates that govern population growth for large mammals (Eberhardt 2002). In our study, meteorological conditions and sex of the calf exerted minimal influence (Table 1) during either population phase.

Our estimates of daily survival rates (DSR; Fig. 3) support the idea that neonates are especially vulnerable

to predation (Bergerud 1971; Mahoney et al. 1990; Stuart-Smith et al. 1997; Jenkins and Barten 2005; Pinard et al. 2012); DSR steadily increased through the summer during both population phases. However, the rate of change in DSR differed notably between phases of population increase and decline. Calves born during the increase phase became less susceptible to predation more quickly than those born during the decline (see also Bastille-Rousseau 2014). The protracted vulnerability of calves during population decline was likely due to the lower birth weights of calves born in this period, as conjectured by Jenkins and Barten (2005) for caribou populations elsewhere.

Table 1 Model selection results for caribou calf survival in Newfoundland during population growth (1987–1997) and decline (2003–2012) phase

Period	Candidate model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>	Evidence ratio
1987–1997	TREND	2	895.302	0.000	0.196	1.000
	TREND+SEX	3	896.283	0.981	0.120	1.633
	TREND+NAO	3	896.774	1.472	0.094	2.087
	TREND+WEIGHT _{AVG}	3	896.831	1.529	0.091	2.147
	TREND+SPRING_START	3	896.890	1.588	0.089	2.213
	TREND+POP	3	897.123	1.821	0.079	2.486
	TREND+MAXNDVI	3	897.159	1.857	0.077	2.530
	TREND+SPRING_RATE	3	897.259	1.957	0.074	2.661
	TREND+MAXNDVI_LAG	3	897.268	1.966	0.073	2.672
	TREND+NAO+MAXNDVI	4	898.584	3.282	0.038	5.161
	TREND+NAO+MAXNDVI_LAG	4	898.770	3.468	0.035	5.663
	TREND+MAXNDVI+SPRING_START	4	898.773	3.471	0.035	5.670
2003–2012	TREND+POP+NAO+POP×NAO	5	3151.027	0.000	0.490	1.000
	TREND+POP	3	3152.397	1.371	0.247	1.984
	TREND+POP+NAO+POP×NAO+SEX	6	3152.899	1.873	0.192	2.551
	TREND+WEIGHT _{IND}	3	3155.313	4.286	0.057	8.527
	TREND+SPRING_START	3	3159.208	8.181	0.008	59.779
	TREND+MAXNDVI+SPRING_START	4	3161.002	9.975	0.003	146.570

The number of model parameters (*K*), AIC_c, change in AIC_c from most supported model (ΔAIC_c), Akaike weights (*w_i*), and the evidence ratio for each model are provided. Only models with evidence ratios <6 are presented for 1987–1997 and ΔAIC_c < 10 for 2003–2012. Calf weight was averaged during 1987–1997 (WEIGHT_{AVG}) but was an individual covariate from 2003 to 2012 (WEIGHT_{IND})

Table 2 Estimated coefficients, standard errors (SE), and upper (UCL) and lower (LCL) 95 % confidence limits of the most supported models of caribou calf survival in Newfoundland during population growth (1987–1997) and decline (2003–2012)

Variable	1987–1997				2003–2012			
	Coefficient	SE	LCL	UCL	Coefficient	SE	LCL	UCL
Intercept	4.715 ^a	0.167	4.388	5.042	4.927 ^b	0.261	4.415	5.438
TREND	0.020 ^a	0.003	0.014	0.026	0.024 ^b	0.002	0.020	0.027
POP					−0.028 ^b	0.005	−0.038	−0.018
NAO					−0.0003 ^b	0.0001	−0.0006	0.0002
POP × NAO					0.148 ^b	0.090	−0.028	0.324
SEX					−0.0003 ^c	0.0001	−0.0005	0.000003
WEIGHT					0.175 ^d	0.038	0.102	0.249
SPRING_START					−0.01947 ^e	0.004599	−0.02848	−0.01046

Coefficients are not presented, i.e., blank cells, for poorly supported models (i.e., where ΔAIC_c > 10 or confidence intervals include zero). If coefficients are in two models, the results from the more supported model are presented

^a Model: TREND

^b Model: TREND+POP+NAO+POP×NAO

^c Model: TREND+POP+NAO+POP×NAO+SEX

^d Model: WEIGHT_{IND}

^e Model: SPRING_START

A potential caveat is that collar weight can influence survival (Rasiulis et al. 2014). Indeed, in the latter stages of our study, collars became lighter with improvements in technology. However, we believe this potential bias was minimal across years because collars were heavier during the increase phase—the time when calf survival was

highest. Further, calf survival rates were broadly consistent with estimates derived from routinely conducted herd composition surveys which clearly indicated high calf survival during the population increase phase and drastic declines in survival during the population decline phase (Weir et al. 2014).

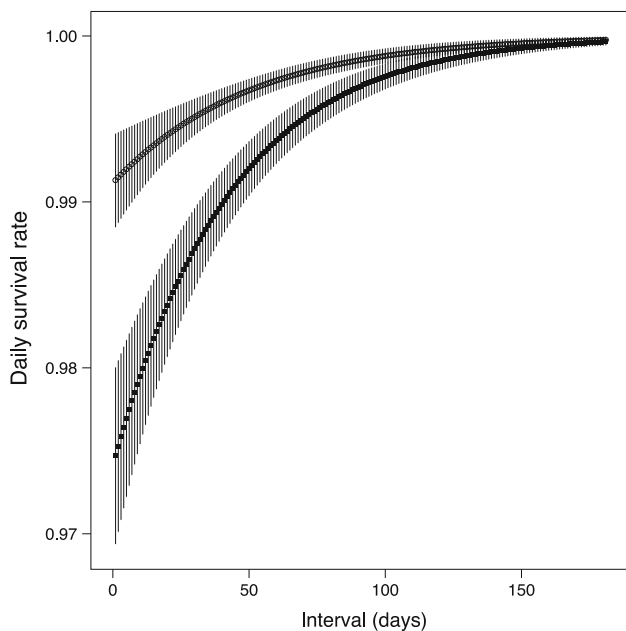


Fig. 3 Daily survival rates of caribou calves in Newfoundland during periods of population growth (1987–1997; *open circles*) and decline (2003–2012; *closed squares*). Lines represent 95 % confidence intervals

We concur with Couturier et al. (2009) that calf weight might serve as a sensitive and practical indicator of population change for migratory caribou. Clearly, there are thresholds of size and vigour that influence susceptibility to predation. Beyond 6 months of age, calves in Newfoundland appear largely to be recruited (Lewis and Mahoney 2014), regardless of the population's growth phase. The daily survival rate increased after 6 months of age, presumably due to (a) black bears entering winter dens and (b) the calves' larger body size and improved mobility, resulting in lower risk from coyotes and lynx (Lewis and Mahoney 2014). Under this scenario, weak cohorts experience significantly elevated predation rates from birth to 6 months of age, sufficient to reduce recruitment to levels that lead to population decline.

Predation by lynx was less common than expected based on studies in Newfoundland during the 1960s and 1970s (Bergerud 1971, 1983). If real, this shift away from lynx as a key caribou predator represents a significant change to the ecology of both species, and our results may, in this sense, be an important window into the dynamic nature of predator guilds (Fig. 4). There are several possible explanations for this shift including changes in (a) lynx abundance as a function of the lynx-hare cycle, (b) changes in caribou habitat selection (Schaefer et al. 2015), (c) abundance of and/or competition with other predators, and (d) the effectiveness of lynx as calf predators at varying levels of caribou abundance (i.e., depensatory predation).

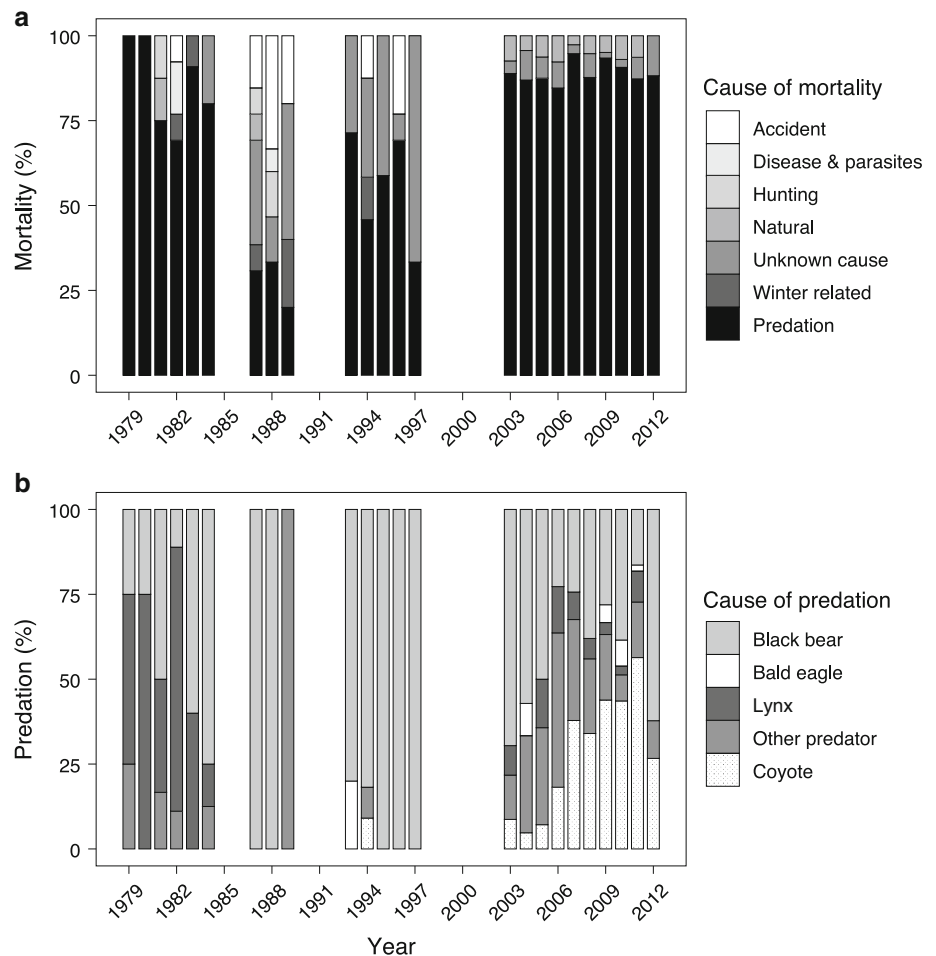
Finally, we have little information on the birth weights of calves in the late 1950s and early 1960s when Bergerud (1971, 1983) conducted his work. Our evidence suggests that cohorts with lower mean birth weights are more vulnerable to predators and perhaps, in the absence of coyotes, lower-weight calves were preferred prey for lynx. However, we also cannot discount the likelihood that black bears may have played a larger role than inferred by Bergerud (1971, 1983) who did not have the advantage of radio-telemetry to examine causes of calf mortality.

We were also surprised by the negligible influence of climate on calf survival (Table 1). Although the interaction of population abundance and the NAO was the most supported model, the coefficient for this term was not significant. Further, the model with only NAO received very little support. These results stand in contrast to studies documenting such effects for climate on ungulate calf birth mass and/or survival (Solberg et al. 2001; Pettorelli et al. 2007; Couturier et al. 2009; Hegel et al. 2010) and our own evidence respecting climate's influence on other morphological traits for caribou (Mahoney et al. 2011). For example, jawbones were smaller for adult female caribou born in Newfoundland following severe winters when population abundance was high (Mahoney et al. 2011), suggesting the potential of at least some maternal effect upon calf birth size. Indeed, the interplay between climate and predators may be subtle. In an analysis of cause-specific mortality of these Newfoundland calves, Bastille-Rousseau (2014) reported that the effect of climate was inconsistent between coyotes and bears; their interactions were further compounded by the phase of population growth.

Nevertheless, our study did confirm a density-dependent relationship with calf survival that expressed itself during the population's declining phase but not during the increasing phase. Such non-linear, density dependent responses are common in large mammals (Fowler 1981; Owen-Smith 2010) and are consistent with theory (Getz 1996).

The year-to-year pattern of Newfoundland caribou calf survival, presented in the form of a clockwise spiral, represents a classic example of delayed density dependence (Fig. 5; Turchin 1990; Sinclair and Pech 1996). Our data also demonstrate that the pattern of survival is dependent on the phase of the population cycle—a phenomenon well documented in microtines (Stenseth 1999), lynx (Stenseth et al. 1998), snowshoe hare [*Lepus americanus* (Erxleben, 1777)]; (Krebs et al. 1995)] and wolves (Post et al. 2002). We documented virtually no change in calf survival as the population tripled and approached peak abundance; it appeared strongly density dependent only after the population peak. Like Isle Royale, Michigan, USA as noted by Post et al. (2002), “prey oscillations may arise from

Fig. 4 a Annual causes of all mortalities of caribou calves in Newfoundland, 1979–2012. **b** Annual causes of predation-related mortalities of caribou calves, by species, in Newfoundland, 1979–2012. *Years without bars* indicate no calves were collared in that particular year



delayed density dependence induced by phase-dependent predation”. Unlike Isle Royale, however, caribou in Newfoundland do not have a specialist predator. The Newfoundland pattern, therefore, may be due to a mismatch between consumers and primary producers—i.e., between caribou and their foods (Bastille-Rousseau et al. 2013; Newton et al. 2014). At the same time, we did see a significant rise in predation during the population decline phase, a moderate phase-dependent predation phenomenon. Somewhat unusual, this relationship involved opportunistic predators not solely dependent on caribou that appear to most actively prey on calves <4 months post-partum.

Unlike survival, Newfoundland caribou morphological and behavioral traits are remarkably consistent with density-dependent effects during the population increase and decrease. Thus, during the caribou population’s increasing phase, we observed diminishment in calf birth weight (Fig. 2), body size of adults (Mahoney and Schaefer 2002; Mahoney et al. 2011; Weir et al. 2014), antler size of males (Mahoney et al. 2011; Weir et al. 2014); weakened affinity to traditional calving grounds (Schaefer and Mahoney 2013), and significantly exacerbated tooth wear (Weir et al.

2014; Schaefer et al. 2015). Providing further corroborative evidence for a density-driven response, all these trends reversed shortly after the caribou population peak and they continue to do so (Schaefer and Mahoney 2013; Weir et al. 2014). These results are consistent with the hypothesis that density dependent forage limitation resulted in decreased vigour of both adult male and female caribou, the latter leading to lower birth weights and perhaps poorer calf condition, in turn resulting in greater and more protracted predation vulnerability and reduced calf survivorship. Expanding upon Eberhardt (2002), we suggest that changes in these morphological indicators may precede changes in vital rates as populations approach maximal levels.

Throughout much of their range, *Rangifer* populations are a conservation concern. Researchers and managers are striving to understand the environmental and demographic processes that underlie the renowned swings in abundance and distribution characteristic of the migratory ecotype (Gunn 2003; Bergerud et al. 2008; Vors and Boyce 2009). This study underscores the importance of shifting factors that influence populations over time—patterns that can be revealed only by long term studies (Leopold et al.

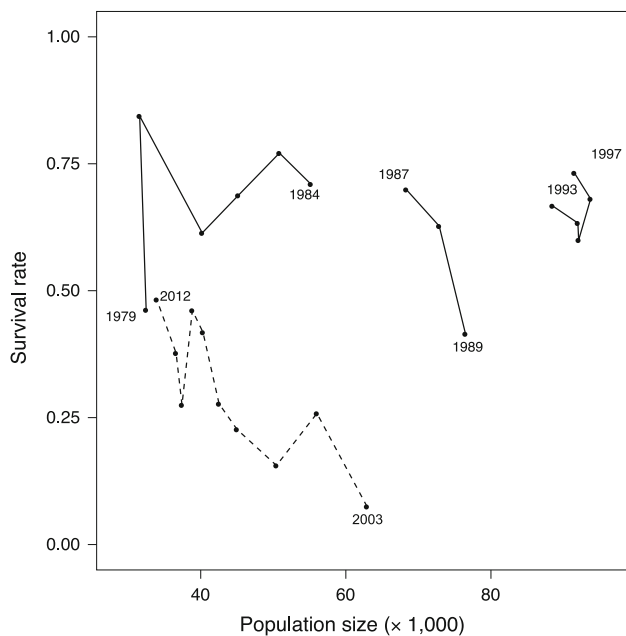


Fig. 5 Calf survival and caribou abundance in Newfoundland depicted in chronological sequence, 1979–2012 (solid lines period of population increase, dashed lines period of population decrease). Breaks in the lines represent years in which no calves were collared

1996). Our study provides evidence that phase dependent, density-dependent processes may ultimately drive these changes. We believe that it adds to the growing predictive power of ecologists regarding the population dynamics of *Rangifer* and other large, herbivorous mammals.

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