Management and Conservation Article

Influence of Density and Climate on Population Dynamics of a Large Herbivore Under Harsh Environmental Conditions

M. ANOUK SIMARD,[1] *Natural Sciences and Engineering Research Council of Canada – Produits forestiers Anticosti Industrial Research Chair, Département de biologie and Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada*

TIM COULSON, *Division of Biology and the Natural Environment Research Council, Centre for Population Biology, Imperial College London, Silwood Park, Ascot, Berkshire, SL5 7PY, United Kingdom*

ANDRÉ GINGRAS, *Direction de l'aménagement de la faune de la Côte-Nord, Ministère des Ressources naturelles et de la Faune, Sept-Îles, QC G4R 1Y8, Canada*

STEEVE D. CÔTÉ, *Natural Sciences and Engineering Research Council of Canada – Produits forestiers Anticosti Industrial Research Chair, Département de biologie and Centre d'études nordiques, Université Laval, Québec, QC G1V 0A6, Canada*

ABSTRACT Dynamics of herbivore populations can be influenced both by density-dependent processes and climate. We used age-at-harvest data for adult female white-tailed deer (*Odocoileus virginianus*) collected over 23 years to estimate survival and reproduction by age class and to identify effects of environmental factors. The study population was located on Anticosti Island (QC, Canada), at the northern limit of the species' range; the population was at high density, and the landscape had scarce forage and abundant snow during winter. Despite severe environmental conditions, population growth apparently increased during the study; adult survival was similar to other populations, although reproduction appeared lower. Winter severity was not related to survival, but density affected adult female survival. Density at estrus was the main factor influencing reproduction of 2- and 3–4-year-olds and also affected reproduction of prime-aged females (5–9-yr-olds), but not of older females. Reproductive rate of younger females was influenced by environmental conditions in autumn, such as high density or snow conditions that limited forage availability. Reproductive success of 5–9- and ≥10-year-old females appeared dependent on spring conditions favoring high-quality forage, probably through effects on neonatal survival. Relative to other studies on northern ungulates, demographic processes in our study appeared to be more affected by autumn and spring climate, in addition to population density, than by winter climate. We thus propose that population density, as well as autumn and spring climate, should be considered in management strategies. Harvest data offered a unique opportunity to study forest ungulates, for which individual monitoring is rarely possible.

KEY WORDS cervids, demography, density-dependence, Normalized Difference Vegetation Index (NDVI), North Atlantic Oscillation index (NAO), population ecology, reproduction, snow, survival, white-tailed deer.

Extrinsic factors, such as climate or vegetation productivity, and intrinsic factors, such as population density or age structure, can affect the demography of large vertebrates (Gaillard et al. 1998, Coulson et al. 2001). Both climate and density operate on reproduction and survival, mainly through effects on individual body condition (Mautz 1978, Jorgenson et al. 1993). The timing and relative importance of density and climate varies among species and along the geographic range of a population (reviewed by Sæther 1997, Mysterud et al. 2003, Sæther et al. 2004).

In seasonal environments, critical periods for individuals are those associated with substantial resource limitation or high energy expenditure, such as periods of snow cover in northern regions (Sæther and Heim 1993, Mysterud and Ostbye 2006) or dry seasons in tropical areas (Owen-Smith et al. 2005). For herbivores, the period of reserves accumulation and vegetation abundance can also have a major impact on individual vital rates (White 1983, Skogland 1985, Ramsey et al. 2002). In northern ungulates, harsh winter weather is likely to mainly affect survival rate (Sæther 1997, Milner et al. 1999, Crampe et al. 2002), whereas climatic conditions influencing forage abundance and quality in summer generally affect fecundity rate

(McCullough 1979, Cook et al. 2004, Stewart et al. 2005). Small differences in timing of vegetation growth in spring, together with the quality and availability of forage, may also have severe effects on adult body mass and neonatal survival (Loison and Langvatn 1998, Pettorelli et al. 2007). In many ungulates, the negative impacts of unfavorable climatic conditions are often more pronounced at high compared to low population density (Coulson et al. 2001, Sæther et al. 2004).

Effects of environmental factors on population dynamics may vary with sex and age, through interactions of population age structure with population density and climate (Coulson et al. 2001). Acquiring information about sex- and age-specific responses to environmental factors is, thus, crucial to understanding population dynamics (Gaillard et al. 1998, Clutton-Brock and Coulson 2002). Juvenile survival, followed by age at first reproduction and prime-age reproductive rate, are usually the first vital rates to be affected by variation in extrinsic and intrinsic factors (Eberhardt 2002). Adult survival is usually less variable but has the highest elasticity (i.e., relative responsiveness of a variable to changes in parameters; Gaillard et al. 1998). Unfortunately, limited sample sizes often restrain the use of age-structured models, especially for adults that are often pooled into one age group (DelGiudice et al. 2006, Heisey

[1] E-mail: marie-anouk.simard.1@ulaval.ca

and Patterson 2006). In ungulates, detailed knowledge of how extrinsic and intrinsic factors affect vital rates of specific sex- and age segments has generally been limited to a few European populations for which longitudinal data on marked individuals were available (e.g., Albon et al. 2000, Coulson et al. 2001, Pettorelli et al. 2003). In North America, long-term longitudinal studies (i.e., following marked individuals through time) on ungulates are even less common; there are a few exceptions for populations living in open range (e.g., Festa-Bianchet et al. 2003, Hamel and Côté 2007), but they are especially limited for forest ungulates (Garrott et al. 2003).

For North American deer (*Odocoileus* spp.), telemetry-based studies documented specific causes of juvenile or adult mortality (Unsworth et al. 1999, DelGiudice et al. 2002, Webb et al. 2007), and others have assessed the effects of resource limitation on life-history traits (McCullough 1979, Ashley et al. 1998). Long-term longitudinal studies on vital rates, however, have been less common and sample sizes have generally been too small to account for age effects (Verme 1969, Fryxell et al. 1991, Post and Stenseth 1998, Sinclair and Parkes 2008). Because most deer populations are harvested through sport hunting, transversal data (i.e., cross-sectional information on different individuals at different time intervals) on individual age-at-harvest exist for many populations. These data have the advantage of being characterized by large sample size and long time series, but they have been rarely used to their full potential (Roseberry and Woolf 1991, Gove et al. 2002). Age-at-harvest data have certain limitations, including possible bias in harvest selectivity or effort, but they can nonetheless contribute to improve our knowledge of population dynamics if used with caution, such as for reconstruction of historical trends in animal abundance (Gove et al. 2002).

Age-at-harvest and reproduction of female white-tailed deer (*O. virginianus*) have been monitored for >20 years on Anticosti Island, Quebec, Canada. This long-term data set offers the possibility to explore effects of environmental factors on survival and reproduction of adult females, especially because predators are absent (DelGiudice et al. 2002, Nelson and Mech 2006). Conditions on Anticosti Island, which include high density (>20 deer/km²), severe winters, and limited forage due to chronic browsing (Simard et al. 2008), offered a unique opportunity to study the demography of an ungulate under harsh environmental conditions.

We first estimated population growth rate, average annual survival, and reproductive rate by age class (2-, 3–4-, 5–9-, and ≥10-yr-olds) of female white-tailed deer. Then, we assessed environmental influences on reproduction and survival of female deer under a set of alternative hypotheses. We hypothesized that female reproduction and survival would be primarily determined by H1) previous year density (Fowler 1981), H2) climate or vegetation productivity during summer and autumn (Boucher et al. 2004), H3) climate during the period of resource deprivation and high energy expenditure (i.e., winter; Mysterud and Ostbye 2006), or H4) interactions of climate and density (Loison and Langvatn 1998). We also hypothesized that H5) female

reproduction, through neonatal survival, would be affected by climate and vegetation productivity in early spring (Pettorelli et al. 2003). We suspected that environmental variation would affect female reproduction age-specifically. For example, density-dependence effects are generally stronger on primiparous females (Festa-Bianchet et al. 1998, Tavecchia et al. 2005). We therefore tested hypotheses on 4 age classes, which was possible due to large sample sizes.

STUDY AREA

Anticosti Island is located in the Gulf of St. Lawrence, Québec, Canada (49°N, 62°W; 7,943 km²). The climate was maritime sub-boreal with cool summers and mild but long winters, with average annual rainfall of about 630 mm and snowfall of about 406 cm (Environment Canada 2006). Over the last 20 years, average snow depth during winter was 80.2 cm, with 96 days with >50 cm of snow on the ground, and average sinking depth for deer was 47 cm (1984–2006 starting mid-Nov; A. Gingras, Ministère des Ressources naturelles et de la Faune, unpublished data). Vegetation was classified as part of the eastern balsam fir–white birch bioclimatic forest region and was dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*). Deer were introduced on Anticosti Island in 1896, and, without predation, deer density rapidly increased to >20 deer/km², which is very high considering that the density of the source population on the mainland was about 1 deer/km² and the highest densities in Québec were about 7–15 deer/km² (Lussier et al. 2008). Due to browsing effects, many species of shrubs and trees are now rare on the island, and others have been almost extirpated (Tremblay et al. 2005). Because deer winter diets are mainly composed of balsam fir (Lefort et al. 2007), balsam fir browse availability declined 70–100%, depending on the site, over the last 25 years (Tremblay et al. 2005). Similarly, there was a 22% decline in protein content of deer autumn diets (Simard et al. 2008). Several factors could explain the high deer density, including stochastic environmental variation (Sæther 1997), supplemental food from litter-fall of lichens and fir twigs (Tremblay et al. 2005), and deer tolerance of long-term forage limitation (Simard et al. 2008). Despite high deer density over time, we observed strong annual variation in density estimated from aerial surveys (e.g., from 18 ± 4 deer/km² in 2001 to 29 ± 6 deer/km² in 2006 in the same area; A. Gingras, unpublished data; correction factor of Potvin and Breton 2005 applied). The number of harvested deer/km² remained stable over the last 20 years, ranging from 1 deer/km² to 1.4 deer/km². About 5–8% of the total population was believed to be harvested each year, 65% of which were males (A. Gringras, unpublished data). Hunter success rate was typically >90%.

METHODS

Vital Rates

We estimated female survival and reproduction based on the age structure and lactation status of deer harvested during
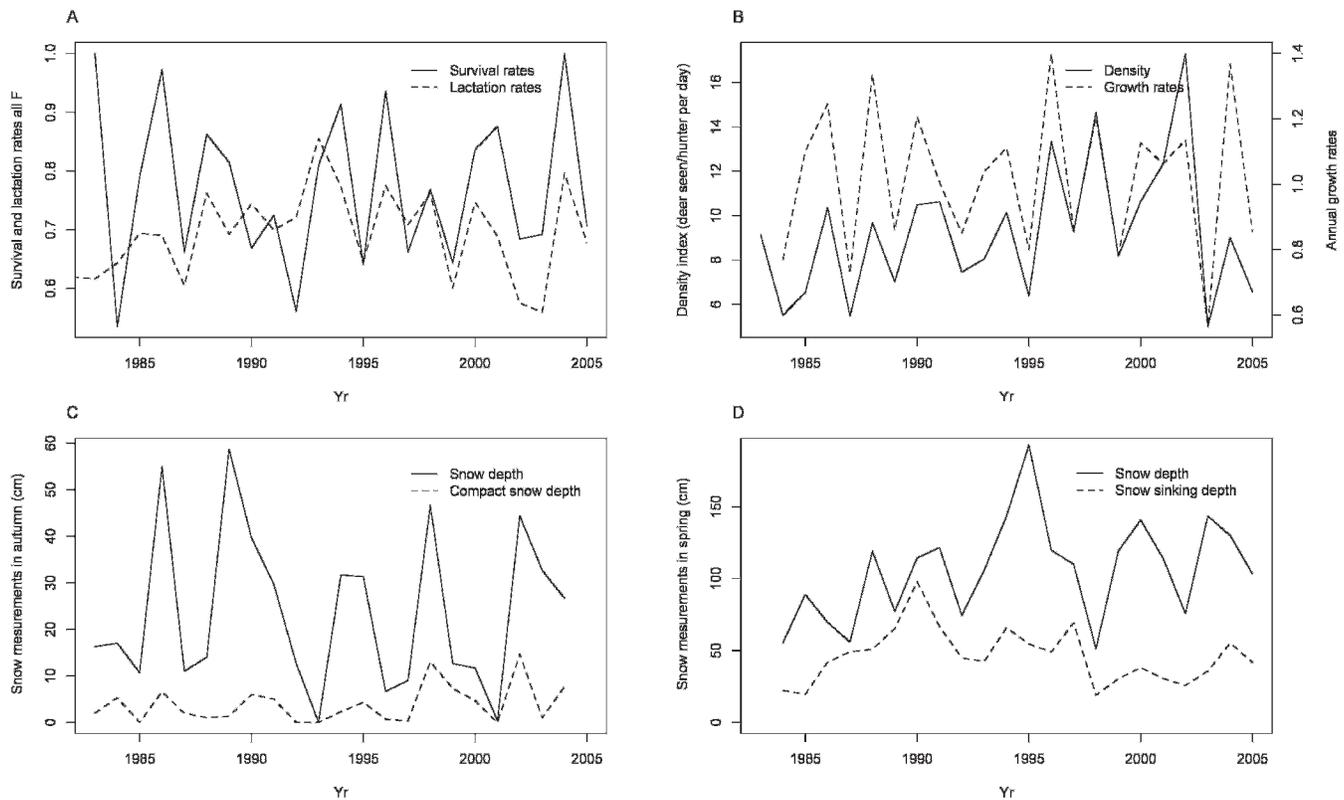
Figure 1. Annual variation, between 1982 and 2005, in (A) survival and lactation rates of female white-tailed deer, (B) deer density index (N_t) and associated growth rate ($\ln N_t / \ln N_{t-1}$), and average snow measurements (snow depth, compact snow depth, and snow sinking depth) in (C) autumn (Nov–Dec) and (D) spring (Mar–May) on Anticosti Island, Québec, Canada.

September to mid-October, 1982–2005 (Fig. 1A). Sample sizes did not reflect changes in density or harvest intensity but were attributed to different sampling effort to obtain incisor teeth from females and data on lactation status.

We sampled on average 326 females/year (range = 194–459), in about equal proportions among 3 sectors of the island (W, center, and E). We estimated deer ages by counting cementum annuli of incisor teeth and used tooth replacement patterns for subadults (Hamlin et al. 2000). Because hunting guides or hunters determined lactation status, it may have induced unquantifiable errors, although presence of milk is easy to observe before mid-October (i.e., the period when we collected most of our data). We assessed errors in lactation estimates on Anticosti Island during 2002–2005 by counting ovulation scars (corpora rubra; see Simard et al. 2008 for details) on collected ovaries and relating the number of ovulation(s) with the lactation status of each individual. Ovulation data revealed that 17% of lactating females produced twins (i.e., ovaries with 2 corpora rubra; A. Simard, Natural Sciences and Engineering Research Council of Canada - Produits forestiers Industrial Research Chair, unpublished data; Table 1). Five percent of females identified as lactating had never ovulated; 14% of nonlactating females had ovulated, and we classified them as nonlactating, assuming pre- or neonatal mortality or error in lactation status (Pekins et al. 1998). We believe that most errors were due to lactation state estimates rather than ovulation estimates, because determination of lactation was made by many observers. We could not account for potential errors in lactation status in the annual estimates of lactation rate, but assumed it was constant across years.

Density

Given infrequent aerial surveys, we used the number of deer seen per hunter per day, available since 1982, as an index of density. On Anticosti Island, this index correlated with regional and annual variation in density estimated from aerial surveys (Pettorelli et al. 2006a; A. Simard, unpublished data). In other ungulate populations, the number of animals seen correlated well with population size based on population reconstruction, using cohort analysis on age-at-harvest data, especially for solitary forest species for which mother–young associations were the largest social group (Solberg et al. 1999, Mysterud et al. 2007), such as white-tailed deer. In one study, deer seen per hunter per day was the hunting metric that was the most independent of hunter selectivity (Mysterud et al. 2007), but a number of other variables such as habitat or weather may affect density estimates (Sylvén 2000, Mysterud et al. 2007, Ranta et al. 2008). We assumed the large sample size of hunters and days of hunting (around 16,000 hunter-days) that we used reduced effects of potentially confounding variables. Unfortunately, a validation of deer seen per hunter per day with marked animals was infeasible; we assumed, despite its limitations, that deer seen per hunter per day (hereafter, density) adequately tracked annual variation in deer density

Table 1. Average life table of female white-tailed deer including rates of survival (s_x), lactation, average ovulation rate of lactating females, and fecundity (m_x; lactation × ovulation), as well as the sample sizes (n) and the proportion of individuals of age x (l_x) from 1982 to 2005, on Anticosti Island, Québec, Canada. We calculated ovulation rate from 2002 to 2005 based on 890 ovary scars.

Age classes	s_x		Lactation		Ovulation		m_x			l_x	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	n	$\bar{x}$	SE
2 yr			0.50	0.05	0.79	0.05	0.40	0.05	1,827	0.24	0.02
3–4 yr	0.77[a]	0.06	0.75	0.05	1.06	0.04	0.79	0.06	2,544	0.32	0.01
5–9 yr	0.82	0.06	0.81	0.04	1.26	0.03	1.02	0.06	2,760	0.35	0.02
≥10 yr	0.68	0.06	0.76	0.04	1.27	0.05	0.97	0.06	707	0.09	0.01
Mean×l_x	0.77	0.04	0.71	0.03	1.07	0.04	0.79	0.04	7,838	1.00	

[a] 2–4-yr-olds for s_x.

and its potential effect on vital rates (H1; Fig. 1B). We transformed density to its natural log in all models to improve normality.

Environmental Variables

We considered environmental variables that could logically affect forage abundance in summer and autumn of the previous year (H2), resource limitation during winter (H3), and green-up date in early spring (H5). We used average monthly temperature as measured at Port-Menier on western Anticosti Island (Environment Canada 2006). We used the North Atlantic Oscillation index (NAO; Osborn 2006) as a global indicator of climate. Biological effects may be more strongly related to global indices than single climatic variables, and global indices are less sensitive to spatial scales (Hurrell 1995). In Canada, positive values of NAO are normally associated with cooler ambient temperatures, northern winds, and dry conditions, whereas negative values are associated with warm and wet conditions (Hurrell et al. 2003). Greater annual variability in NAO is normally seen during winter (Hurrell 1995). Because this index may be less reliable in summer, we did not use it for that season (Forchhammer and Post 2004).

We collected data on snow conditions at 3 stations in balsam fir stands, located at the western end of the island (40 km apart), at 15-day intervals from October to May beginning in 1984. Each station consisted of 3-m graduated rulers ($n = 10$) spaced equidistantly every 5 m on one transect. We measured snow depth (cm) as well as potential sinking depth (cm) of deer using a penetrometer, approximating the foot pressure of deer during locomotion (Verme 1968, Lefort et al. 2007). We subtracted snow sinking depth from snow depth to calculate compact snow depth (cm), which indexed thickness of compacted snow on the ground. We used the NIVA index to assess snow conditions encountered daily by deer (based on data collected every 15 days; expressed in cm × day), which, according to Dumont et al. (2000), indexes winter severity for deer in Québec. NIVA corresponds to the addition of all daily estimates of snow (cumulative snow conditions), or the area under the curve of snow measurements. In models, we divided snow data into 3 periods (autumn, winter, and spring) and used only cumulative snow depth (m × day; in meters to reduce parameter estimates), cumulative snow sinking depth (m × day), and cumulative compact snow depth (m × day). In autumn (Nov–mid-Dec), we used

snow depth and compact snow depth (H2; Fig. 1C). We used cumulative snow depth and sinking depth to model energy expenditures due to locomotion in snow during the entire winter (Nov–May; H3) and late spring (Mar to May; H5; Fig. 1D; Dumont et al. 2000).

To index vegetation productivity, we used corrected Normalized Difference Vegetation Index (NDVI) data acquired by the National Oceanic and Atmospheric Administration–Advanced Very High Resolution Radiometer satellite and processed by Global Inventory Modelling and Mapping Studies. We calculated bimonthly values of NDVI from September 1983 to 2003 with a resolution of 64 km^2 (Pettorelli et al. 2005). At this scale, the study area consisted of 186 pixels. Similar to Pettorelli et al. (2007), we used the sum of NDVI values in May and July–August of each year to distinguish years of low or high vegetation productivity in spring (H5) and summer (H2). We calculated rate of change in plant productivity during green-up as the slope of NDVI between May and late June (H5). However, because this approach smooths the rate of vegetation change during green-up, we also used the maximum slope between every 2 consecutive NDVI values from early May to late June (H5) because rapid vegetation growth in spring can have a negative influence on life-history traits of ungulates by reducing the period of access to high-quality forage (Herfindal and Solberg 2006, Pettorelli et al. 2007).

Statistical Analyses

We calculated average lactation rate (i.e., proportion of lactating F) and age structure with data available from 1982 to 2005. We used the age structure to estimate the proportion of individuals (l_x) and the survival rate (s_x) at age x. Fecundity (m_x) at age x was the product of lactation rate and average ovulation rate of lactating females, 2002–2005, correcting for potential lactation errors and twinning rates (Table 1). We tested the robustness of pooling each age group into larger age classes using linear models for survival or lactation rate as a function of age (factorial). We placed animals of different ages into the same age class when parameters estimated at age x were not significantly different from parameters estimated at age $x + 1$ or $x - 1$. We verified accuracy of new age classes with a log-likelihood deletion test (analysis of variance [ANOVA] procedure; R version 2.10.1, <www.r-project.org/>, accessed 14 Dec 2009). Selected age classes for survival estimates were 2–4-, 5–9-, and ≥10-year-olds, and 2-, 3–4-,

5–9-, and ≥10-year-olds for lactation estimates. We used s_x and m_x per age class to build a population matrix and calculated the population growth rate (λ; eigen procedure; R version 2.10.1). We estimated the standard error of population growth rates using standard errors of adult survival and fecundity estimates. Based on the literature, we assumed an annual survival rate of 0.7 for yearlings (Van Deelen et al. 1997, Xie et al. 1999) and 0.6 for fawns during their first winter (Oct–May; Dumont et al. 2000, Taillon et al. 2006). As a comparison, we also estimated average population growth rate, using annual growth rate calculated from annual variation in the density index [$\ln(N_t) / \ln(N_{t-1})$; Fig. 1B].

To track effects of intrinsic and extrinsic factors on vital rates, we used estimates of lactation rate for each year, 1982–2005, and age class as an estimate of reproductive performance. We calculated survival at time t and for age class $x - y$ as $l_{x-y,t}/l_{(x-1)-(y-1),t-1}$ (e.g., $l_{3-5yr,1983}/l_{2-4yr,1982}$). This method differs from the one discussed in Caughley (1977), because we followed age classes through time and did not assume a stable age distribution each year, an assumption rarely met in ungulate populations (Festa-Bianchet et al. 2003). Our method required large samples, which were unavailable for all age classes in all years; therefore, we averaged the relative survival rate of each age class and used only overall survival per year in the model. Although this reduced precision of the estimates, it allowed us to account for age structure by putting the same weight on each age class and not only on the largest one.

To test effects of density and environmental covariates on vital rates, we first estimated correlations among explanatory variables with Pearson's coefficients and Pearson tests (cor and cor.test procedure; $\alpha = 0.05$; R version 2.10.1). The explanatory variables we tested in the models were density at time $t - 1$ (where $t - 1$ indicates the previous yr) and 15 environmental covariates at time t or $t - 1$. Correlation tests facilitated interpretation of explanatory variables and allowed us to avoid including correlated variables in the same model (i.e., $r > 0.7$). We used data from a longer data set (1964–2005) to verify the correlation of NAO with seasonal temperatures on Anticosti Island and seasonal precipitation from Havre St-Pierre, located 40 km away on the north continental shore.

Because of correlations between some covariates, and to remain conservative relative to degrees of freedom, we did not test for effects of all variables simultaneously in the same model. We used 3 distinct steps, based on Hosmer and Lemeshow (2000), before obtaining final linear models (lm procedure; R version 2.10.1) for each of the 6 response variables (i.e., average survival, average lactation, lactation at 2-, 3–4-, 5–9-, and ≥10-yr-old [arcsin transformed to improve normality]). In the first step, we explored univariate effects of explanatory variables and we selected variables where $\alpha \leq 0.15$ (Hosmer and Lemeshow 2000). This preliminary selection not only allowed us to reduce the number of variables tested in final models to avoid overparameterization and conserve degrees of freedom, but it also allowed us to document the effect of each environmental variable separately before including them together. In the second step, we integrated covariates qualifying under step 1 (unless highly correlated $r > 0.7$) and selected the best model using a deletion test procedure (ANOVA procedure; statistical package R; Crawley 2005). The deletion test (F-test) allowed us to identify, based on residual sums of squares, whether a more complex model was better ($\alpha = 0.05$) or equivalent to a simplified model wherein the parameter(s) had been removed (Crawley 2005). We did not use multimodel inference with Akaike's Information Criterion (AIC) because we could not identify a competitive set of a priori models (Burnham and Anderson 2002). To support our approach, we compared both procedures and confirmed that the deletion test and AIC were generally equivalent. We tested for interactions only in the final step when <4 covariates remained in the model. When >1 covariate was retained in final models, we evaluated each separately, correcting for other variables using the residuals. We tested for normality of the residuals and homogeneity of variance in all models (Crawley 2005).

Model Assumptions

Age-at-harvest data can provide useful information on population dynamics, but such data also have important limitations (Fryxell et al. 1988, Roseberry and Woolf 1991, Solberg et al. 1999, Gove et al. 2002). Survival is especially complex to estimate (Clobert and Lebreton 1991, Murray and Patterson 2006). We made several assumptions to estimate annual vital rates. First, we assumed that age-at-harvest data were not biased by hunter selectivity and, thus, approximated the actual age structure of the population. Because age-structure data obtained through hunting may induce bias in life-history estimates due to hunter selectivity (Martinez et al. 2005) or differences in animal vulnerability (Bunnefeld et al. 2009), we removed yearlings from the sample and limited our analyses to adult females ≥2 years (i.e., those that cannot be differentiated based on size). We did not expect selection bias to be strong for adult females, although some hunters may avoid shooting females with fawns (Nilsen and Solberg 2006). Questionnaires from hunters on Anticosti Island suggested, however, that selective harvesting was rare (A. Simard, unpublished data), and lactation rates of deer harvested by nonresidents (who are usually more selective, 57.9 ± 0.9) versus resident hunters (55.6 ± 0.9) were similar ($t = 0.6$, $P = 0.3$). Average mass of females was similar among females harvested by resident and nonresident hunters, implying no selection for large females (A. Simard, unpublished data). Animal vulnerability to hunting can change depending on age or individual characteristics (Bunnefeld et al. 2009), but this is difficult to verify, as is the case for most sampling schemes involving animal captures. Because hunting pressure on females was low and occurred during a short period on Anticosti Island, we assumed that animals had few chances to learn to avoid being shot; thus, we assumed our hunting-derived samples were representative of the population. Second, we assumed that hunting mortality was low and similar among years, such that variation in total

mortality was mainly caused by variation in natural mortality, not by variation in harvest rate. We based this assumption on the estimate that 2.5–3.6% of all females were harvested annually on Anticosti Island and that hunting pressure was similar across years (A. Gingras, unpublished data). Third, we assumed that the method used to estimate annual survival adequately tracked annual variation in survival without assuming a stable age distribution and static population size. Our method was based on the proportion of one age class that survived from one year (e.g., 2–4-yr-olds) to the next (e.g., 3–5-yr-olds), rather than on the comparison of the same age class across years (Caughley 1977). We did not correct this proportion by population growth rate, as suggested by Caughley (1977), because this would have assumed that all age classes were equally affected by mortality. Despite our precautions, we are aware that using age-at-harvest data to calculate annual survival is not ideal, considering that we cannot validate most assumptions (Roseberry and Woolf 1991, Murray and Patterson 2006); hence, we used average survival and we interpreted our data cautiously.

RESULTS

Population Vital Rates

Annual population growth rate of white-tailed deer on Anticosti Island was 1.06 ± 0.10 ($\lambda \pm$ SE). The growth rate we obtained with the density index (i.e., deer seen per hunter per day) was 1.03 ± 0.06, which was comparable to the matrix-based estimate we obtained from estimated vital rates. Our growth-rate estimates had large confidence intervals. We estimated overall annual survival rate of adult females at 0.77 ± 0.04 (Table 1). We estimated 2-year-olds produced 0.40 ± 0.05 fawns/female. Most females started reproduction at 3 years or 4 years of age, and the highest annual fecundity rate was for prime-aged females (1.02 ± 0.06 fawns/F; Table 1). Females ≥ 10 years old conceived twins at the same rate as did 5–9-year-olds and had similar estimated fecundity (Table 1).

Correlations Among Environmental Factors

Correlations between temperatures in spring and winter as well as among different snow metrics were >0.7; thus, we never included these covariates simultaneously in the same model (Table 2). We observed a correlation between deer density and cumulative snow in autumn ($r = 0.58$), suggesting a positive influence of compact snow depth on the number of deer seen per hunter per day. To ensure that snow cover did not influence the number of deer seen per hunter per day (i.e., meaning a spurious correlation), we confirmed that the correlation was similar to density in September–October ($r = 0.41$), a snow-free period, and that the density index did not correlate with snow depth in autumn ($r = 0.25$). Abundant rain was associated with low values of NAO in autumn ($r = -0.55$) and in spring ($r = -0.40$), whereas high NAO in winter was associated with low temperatures ($r = -0.50$) and high snow sinking depth ($r = 0.46$). Similarly, low temperatures in autumn and spring were associated with high snow measurements in

autumn, winter, and spring (see details Table 2). Snow depth and compact snow depth in autumn were correlated with snow depth ($r = 0.67$) and sink ($r = 0.55$) in winter, but not as much in spring ($r = 0.32$; Fig. 1C, D). We found no significant correlations between weather covariates and NDVI (Table 2).

Annual Variation in Vital Rates

For annual average survival rate, we considered density, cumulative snow depth, and compact snow depth in autumn (all $P \leq 0.15$) as covariates for multivariate modeling (Table 3). We only retained density for the final model ($R^2 = 0.37$, $F_{1,20} = 13.3$, $P < 0.001$); density was negatively related to adult survival (log-transformed; estimate $\pm$ SE = -0.14 ± 0.04; Fig. 2). We dropped cumulative snow as a covariate based on a deletion test of $P = 0.06$ ($F = 3.9$), but we address its potential biological importance in the Discussion section, based on the P-value.

For average lactation rate, we tested 8 covariates based on univariate models (Table 3). We retained 3 of these in the final model ($R^2 = 0.62$, $F_{3,16} = 11.6$, $P < 0.001$): density, NDVI in May, and NAO in spring (Table 3). High lactation rate was associated with low density (estimate $\pm$ SE = -0.15 ± 0.05, $F = 21.1$, $P = 0.01$; Fig. 3A), high vegetation productivity in May (1.08 ± 0.30, $F = 12.5$, $P = 0.002$; Fig. 3B), or low NAO in April–May (-0.05 ± 0.02, $F = 5.9$, $P < 0.03$; Fig. 3C).

For 2-year-old lactation rates, we considered density, cumulative snow depth, and compact snow depth in autumn in multivariate models based on univariate tests ($P \leq 0.15$; Table 3). When we entered these 3 covariates in the same model, however, they were nonsignificant. When we considered density and compact snow depth in separate univariate models, both models were equivalent ($F < 0.001$, $P = 0.99$). Thus, the linear model including a negative effect of density (-0.24 ± 0.09; $R^2 = 0.23$, $F_{1,20} = 7.3$, $P = 0.013$; Fig. 4A) was equivalent to a model including a negative effect of compact snow depth in autumn (-0.13 ± 0.05; $R^2 = 0.22$, $F_{1,20} = 7.1$, $P = 0.015$; Fig. 4B).

For 3–4-year-old lactation rates, we considered 5 covariates as good candidates for multivariate models based on univariate tests (all $P \leq 0.15$; Table 3), but we retained only density in the final model, which indicated a strong negative influence of density on lactation of 3- and 4-year-olds (-0.28 ± 0.05; $R^2 = 0.52$, $F_{1,20} = 23.9$, $P < 0.001$; Fig. 4C). Similar to lactation of 2-year-olds, snow in autumn negatively affected lactation of 3–4-year-olds in a univariate model (-0.12 ± 0.05; $R^2 = 0.31$, $F_{1,20} = 10.4$, $P < 0.004$), but snow in autumn was not significant in a model that also included density as a covariate.

For 5–9-year-old lactation rates, we considered 7 covariates for multivariate models based on univariate tests (all $P \leq 0.15$; Table 3); we retained 3 in the final model ($R^2 = 0.68$, $F_{3,16} = 14.51$, $P < 0.003$), which indicated a negative effect of density (-0.19 ± 0.04, $F = 23.34$, $P < 0.001$; Fig. 5A), a positive effect of NDVI in May (0.58 ± 0.26, $F = 5.05$, $P = 0.04$; Fig. 5B), and a positive effect of snow

Table 2. Pearson correlation coefficients and Pearson tests for correlations between explanatory variables included in different models, testing effects of intrinsic and extrinsic factors on vital rates of white-tailed deer females on Anticosti Island, Québec, Canada. For most variables we used data from 1983 to 2005, except for North Atlantic Oscillation (NAO) index, temperature, and precipitations, for which we used data from 1964 to 2005. t refers to the year the deer was harvested and t − 1 to the previous year.

Variables	Period	Density[a]	Temp	NAO index			Cumulative snow or compact	Cumulative snow or sink		NDVI[b]			
		Sep–Dec t − 1	Apr–May t	Oct–Nov t − 1	Dec–Mar t	Apr–May t	Oct–Dec t − 1	Oct–May t	Mar–May t	Jul–Aug t − 1	May t	Max. increase	Average increase
Density[a]	Sep–Dec t − 1	1.00					0.25/0.58*						
Temp	Jul–Aug t − 1		0.06							0.37			
	Oct–Nov t − 1	−0.27	0.25	−0.25			−0.44*/−0.43*	−0.55*/−0.36					
	Dec–Mar t		0.74*		−0.50*			−0.25/−0.36	−0.32/−0.61*				
	Apr–May t		1.00			−0.14		−0.55*/−0.22	−0.65*/−0.47*		0.13	−0.32	−0.02
NAO index	Jul–Aug t − 1			−0.29				0/−0.03		0.25			
	Oct–Nov t − 1	0.26		1.00	−0.20		0.32/0.27	0.16/0.46*					
	Dec–Mar t				1.00	0.19		0.05/0.22	0.03/0.39				
	Apr–May t					1.00		0.39/0.62[c],*	−0.20/0.13				
Cumulative snow/compact	Oct–Dec t − 1							0.44*/0.12[c],*	0.01/0.31[c]				
Cumulative snow/sink	Oct–May t						0.67[d],*	0.55[b],*	0.28/−0.16[e]		0.27	0.15	−0.05
NDVI	Mar–May t								0.86*/0.22[c]		−0.13/0.13	0.36/−0.04	0.03/0.13
	Jul–Aug t − 1								0.41*/0.82[e],*	1.00		−0.20	−0.32
	May t								0.32[d]		1.00		
	Max. increase											1.00	0.49*
	Mean increase												1.00
Precipitation	Jul–Aug t − 1	−0.12					0.04/−0.02	0.21/0.15		0.22			
	Oct–Nov t − 1 (rain only)			−0.49* (−0.55*)				0.01/−0.25					
	Dec–Mar t				−0.18				0.20/−0.08				
	Apr–May t (rain only)		0.20			−0.34 (−0.40*)		0.27/−0.02	0.14/−0.18		0.37	−0.12	−0.35

[a] Natural–log transformation of deer seen per hunter per day.
[b] Normalized Difference Vegetation Index.
[c] Correlation of snow depth with (sink/snow) at different periods.
[d] Correlation of snow depth with snow sink at the same period.
[e] Correlation of sink with (sink/snow) at different periods.
* Significant correlation at $\alpha = 0.05$.

Table 3. Parameter estimates (Est.) and *P*-values of single-effect models testing the effect of intrinsic and extrinsic factors on average survival, average lactation, and lactation of different age classes for female white-tailed deer measured from 1982 to 2005 on Anticosti Island, Québec, Canada. When $P < 0.15$, we tested variables in final models. The column with Hs refers to the hypothesis number tested. *t* refers to the year the deer was harvested and $t − 1$ to the previous year.

Variables		H	Survival (all) Est.	SE	P	Lactation All Est.	SE	P	2-yr-olds Est.	SE	P	3–4-yr-olds Est.	SE	P	5–9-yr-olds Est.	SE	P	≥10-yr-olds Est.	SE	P
Density[a]	Sep–Dec $t − 1$	H1	−0.14[b]	0.04	***	−0.22[b]	0.05	***	−0.24[b,c]	0.09	*	−0.28[b]	0.06	***	−0.22[b]	0.06	**	−0.2	0.1	○
Temp	Apr–May t	H5				−0.007	0.02		−0.02	0.02		0.02	0.02		−0.01	0.02		0	0.03	
North Atlantic	Oct–Nov $t − 1$	H2	−0.02	0.01		−0.04	0.02	*	−0.01	0.03		−0.04	0.02	○	−0.06	0.02	*	−0.07[b]	0.03	*
Oscillation	Dec–Mar t	H3	−0.02	0.01		−0.005	0.02		−0.007	0.03		−0.01	0.02		0	0.02		−0.01	0.03	
Index	Apr–May t	H5				−0.04[b]	0.03	○	−0.05	0.04		−0.02	0.03		−0.02	0.03		−0.07[b]	0.04	○
Cumulative snow	Nov–Dec $t − 1$	H2	−0.012	0.006	*	−0.015	0.009	○	−0.02	0.01	○	−0.01	0.01		−0.01	0.01		−0.02	0.01	○
Cumulative compact snow	Nov–Dec $t − 1$	H2	−0.045	0.02	●	−0.1	0.03	**	−0.13[b,c]	0.05	*	−0.12	0.04	**	−0.09	0.04	*	−0.08	0.06	
Cumulative snow	Nov–May t	H3	<0.001	<0.001		<0.001	<0.001		<0.001	<0.001		<−0.001	0.001		<0.001	0.001		0	0.001	
Cumulative sink	Nov–May t	H3	−0.001	0.001		0	0.002		0	0.002		0.001	0.002		0.002	0.002		−0.002	0.002	
Cumulative snow	Mar–May t	H5	<0.001	0.001		0.001	0.001	●	0.001	0.001		−0.001	0.001		<0.001	0.001		0	0.001	
Cumulative sink	Mar–May t	H5	0	0.001		−0.003	0.003	*	0.002	0.004		0.004	0.003	●	0.006[b]	0.003	*	0	0.005	**
Normalized	Jul–Aug $t − 1$	H2	−0.26	0.62		1.7	0.8	●	0.9	1.2		0.7	1.1		1.8	0.9	●	3.8	1.2	*
Difference	May t	H5				0.9[b]	0.4		0.5	0.6		0.9	0.5		1.0[b]	0.4	*	1.3[b]	0.6	
Vegetation	Max. inc.[d] t	H5				−1.1	0.5		−0.1	0.8		−1.7	0.6	*	−1.3	0.6	*	−1.6	0.9	○
Index	Mean inc.[d] t	H5				−0.6	0.4		−0.1	0.6		−0.8	0.6		−0.5	0.5		−1.3	0.7	●

[a] Natural-log transformation of deer seen per hunter per day.
[b] Variables selected in the final models.
[c] Lactation at 2 yr of age has 2 equivalent models with one variable in each.
[d] Increase of vegetation green-up in spring.
○ $P < 0.15$, ● $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
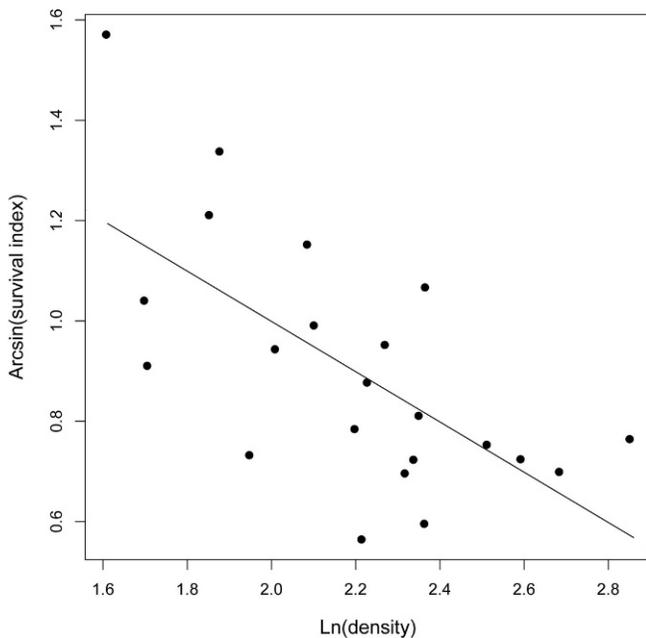
Figure 2. Linear model between density (ln-transformed deer seen per hunter per day) and survival rate (arcsin-transformed) of adult female white-tailed deer on Anticosti Island, Québec, Canada (1982–2005).

sinking depth in spring (0.006 ± 0.002, $F = 15.14$, $P = 0.001$; Fig. 5C).

For lactation rates of $\geq$10-year-olds, we considered 8 covariates for multivariate models based on univariate tests (all $P \leq 0.15$; Table 3); we retained 3 in the final model ($R^2 = 0.45$, $F_{3,18} = 6.76$, $P < 0.003$). Lactation rate of old females was positively associated with NDVI in May (1.52 ± 0.52, $F = 8.45$, $P = 0.009$; Fig. 5D) but negatively related to NAO in spring (-0.09 ± 0.04, $F = 4.99$, $P < 0.04$; Fig. 5E) and NAO in previous autumn (-0.06 ± 0.03, $F = 6.84$, $P = 0.02$; Fig. 5F). We did not detect a density effect on lactation rate by older females. Univariate tests (Table 3) suggested a decrease in the importance of density and compact snow depth in autumn as females aged, and conversely, an increase in the importance of NDVI and NAO. No final models included significant interaction terms (all $P > 0.05$).

DISCUSSION

Long-term monitoring of the white-tailed deer population on Anticosti Island allowed us to estimate demographic parameters and to better understand sources of variation among vital rates. We found that adult survival was principally affected by density (H1) and also by snow conditions in autumn (H2). Average lactation was affected by density (H1) and also by spring conditions (H5), including vegetation productivity and weather. Density in the previous year (H1) and snow conditions in autumn (H2) had stronger effects on reproduction of young adults than older adults, whereas spring conditions (H5) only affected lactation rates of older females. Our results suggested that conception for young females depended on environmental conditions in autumn. Conception rates were high for older females, but their offspring were susceptible to neonatal mortality under unfavorable spring conditions. Our results also suggested the importance of forage availability in autumn during snow-free periods (H2). Surprisingly, we found no effect of winter conditions on vital rates (H3) and no interactions among extrinsic and intrinsic factors (H4).

Population Vital Rates

Abundance of winter browse and diet quality during early autumn declined over the last 25 years on Anticosti Island (Tremblay et al. 2005, Simard et al. 2008), but the demographic vigor of the population did not appear to be affected. Population growth during the last 2 decades was surprising, given similar hunting statistics during 1977–1979 and 2002–2004 (Simard et al. 2008). Although it is possible that our estimates of fawn or yearling survival were too high and were responsible for such an increase, we found similar results when calculating the average population growth rate from the density index. Both estimates of population growth rate were, however, imprecise (i.e., with a CI that included 1), which may have resulted from high annual variability in vital rate estimates, especially reproductive rates (or the density index; see Fig. 1A, B). It might be inappropriate to make inference based on the average population growth rate over 25 years when annual variation was high. Nevertheless, a possible explanation for a population increase could be the senescence of balsam fir forests, which could have increased the number of fallen trees during winter over the last decade (Tremblay et al. 2005). Such winter forage enhancement unrelated to deer-density feedbacks could promote population growth.

Similar to other northern forest deer populations (Heard et al. 1997, Hewison and Gaillard 2001, DelGiudice et al. 2007), fawns did not conceive on Anticosti Island. We estimated lower fecundity rates of 0.40 ± 0.12 for 2-year-olds and 0.92 ± 0.07 for $\geq$3-year-olds (i.e., age at ovulation of 1.5-yr- and $\geq$2.5-yr-olds) compared to other white-tailed deer populations (e.g., 1.3 for 1.5-yr-olds and 1.6 for $\geq$2.5-yr-olds in northern MN; DelGiudice et al. 2007), even considering our estimates included neonatal mortality. We obtained results similar to females kept experimentally under severe food restrictions (0.62 for 1.5-yr-olds and 0.95 for $\geq$2.5-yr-olds; Verme 1965, 1969). Our estimated adult ($\geq$2.5-yr-olds) female survival of 77% was slightly lower than the 82% survival estimate obtained from 82 radiocollared adult females, also on Anticosti Island, during 1986–1990 (Potvin et al. 1997). Our estimate was similar to other white-tailed deer populations under severe winter conditions with predation (on mainland QC 79.3% for $\geq$1.5-yr-olds [Dumont et al. 2000]; in northern MN 76% for $\geq$1.5-yr-olds [DelGiudice et al. 2002]) or black-tailed deer (*O. hemionus columbianus*) populations under limited food resources (in Western Cascades 75% for $\geq$1.5-yr-olds [Gilbert et al. 2007]; on Vancouver Island 74% for $\geq$1.5-yr-olds [McNay and Voller 1995]).

Density Effects

Density has been reported to be an important regulating factor in animal populations in many studies (Fowler 1981,
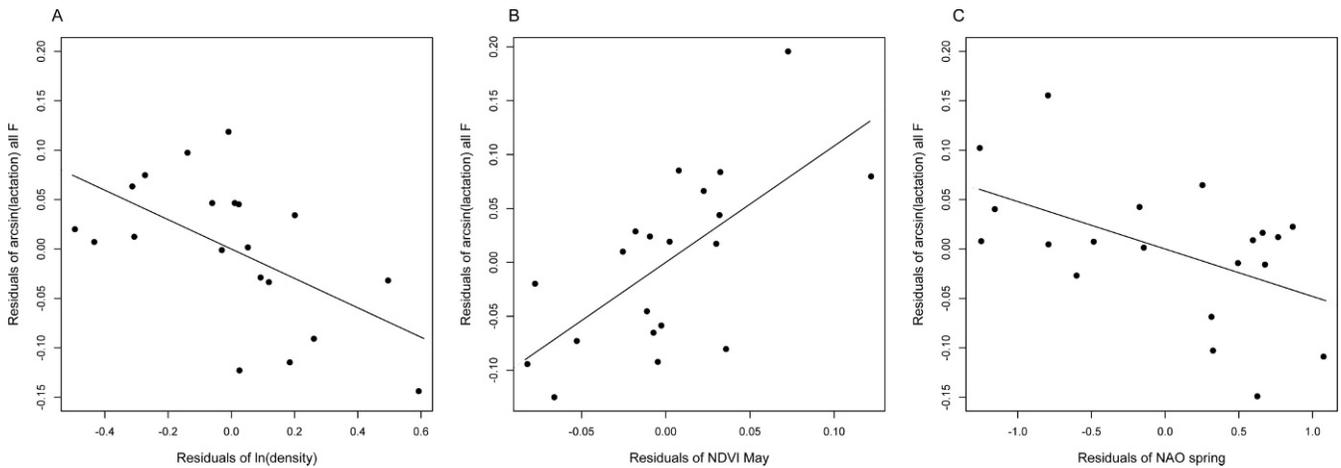
Figure 3. Linear models explaining average lactation rate (arcsin-transformed) of all adult female white-tailed deer on Anticosti Island, Québec, Canada (1982–2005). Lactation was affected by (A) density (ln-transformed deer seen per hunter per day), (B) Normalized Difference Vegetation Index (NDVI) in May, and (C) North Atlantic Oscillation (NAO) index in spring. We present results as the residuals of the dependent and independent variables once corrected for other variables included in the model.

McCullough 1999). High density induces competition for food and is likely to have a strong negative feedback on vital rates, especially for young individuals (Singer et al. 1997, Coulson et al. 2001), but exceptions have been documented (Mysterud and Ostbye 2006). We demonstrated that even at northern latitudes, where we intuitively expected climate to be the main liming factor, density-dependence processes were the main determinants of both female reproduction and adult survival. We found that a negative feedback of density with a 1-year lag was particularly important in explaining annual variation in average adult survival and lactation, with the exception of ≥10-year-old females. Density-dependence in survival has been more commonly documented in juvenile than adult ungulates (Festa-Bianchet et al. 2003). We used average adult survival in our models, but with equal weight for each age group, so we are confident we documented real rather than apparent density-dependence, which is often not the case when age-structure is ignored (Festa-Bianchet et al. 2003). We propose that density-

dependence increased forage competition in summer–autumn and reduced individual body condition at the onset of winter, which could be especially important on Anticosti Island, where we found a reduction in forage abundance in autumn and winter over the last 25 years (Tremblay et al. 2005, Simard et al. 2008). Anticosti deer accumulate less fat reserves in autumn when population density is high (A. Simard, unpublished data), which could consequently reduce winter survival or autumn conceptions. It would have been interesting to estimate age-specific survival, including fawns and yearlings, as their sensitivity to population density is expected to be stronger than for adults (Gaillard et al. 2000), but this was not possible.

The influence of density on female reproduction has been previously demonstrated but often included effects on neonate survival (Gaillard et al. 1998). We estimated the density index during the autumn preceding fawn birth and so the index was, therefore, more likely to represent density effects at conception or during early pregnancy. Density
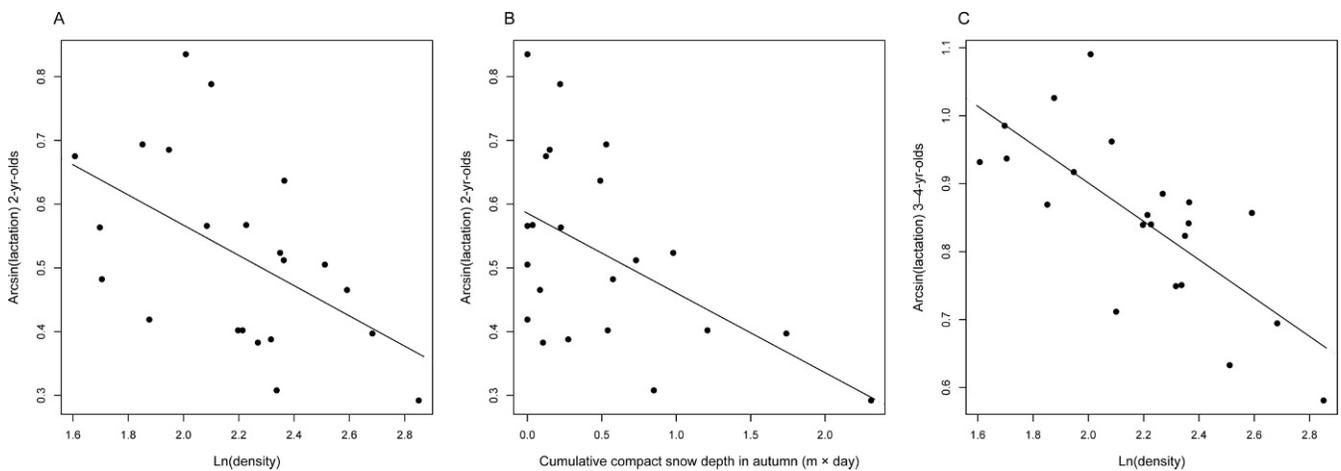

Figure 4. Linear models explaining lactation rate (arcsin-transformed) of young adult female white-tailed deer on Anticosti Island, Québec, Canada (1982–2005). Equivalent models for lactation of 2-year-olds show the effect of (A) density (ln-transformed deer seen per hunter per day) or (B) cumulative compact snow depth in autumn, and (C) the model for 3–4-year-olds shows the effect of density.
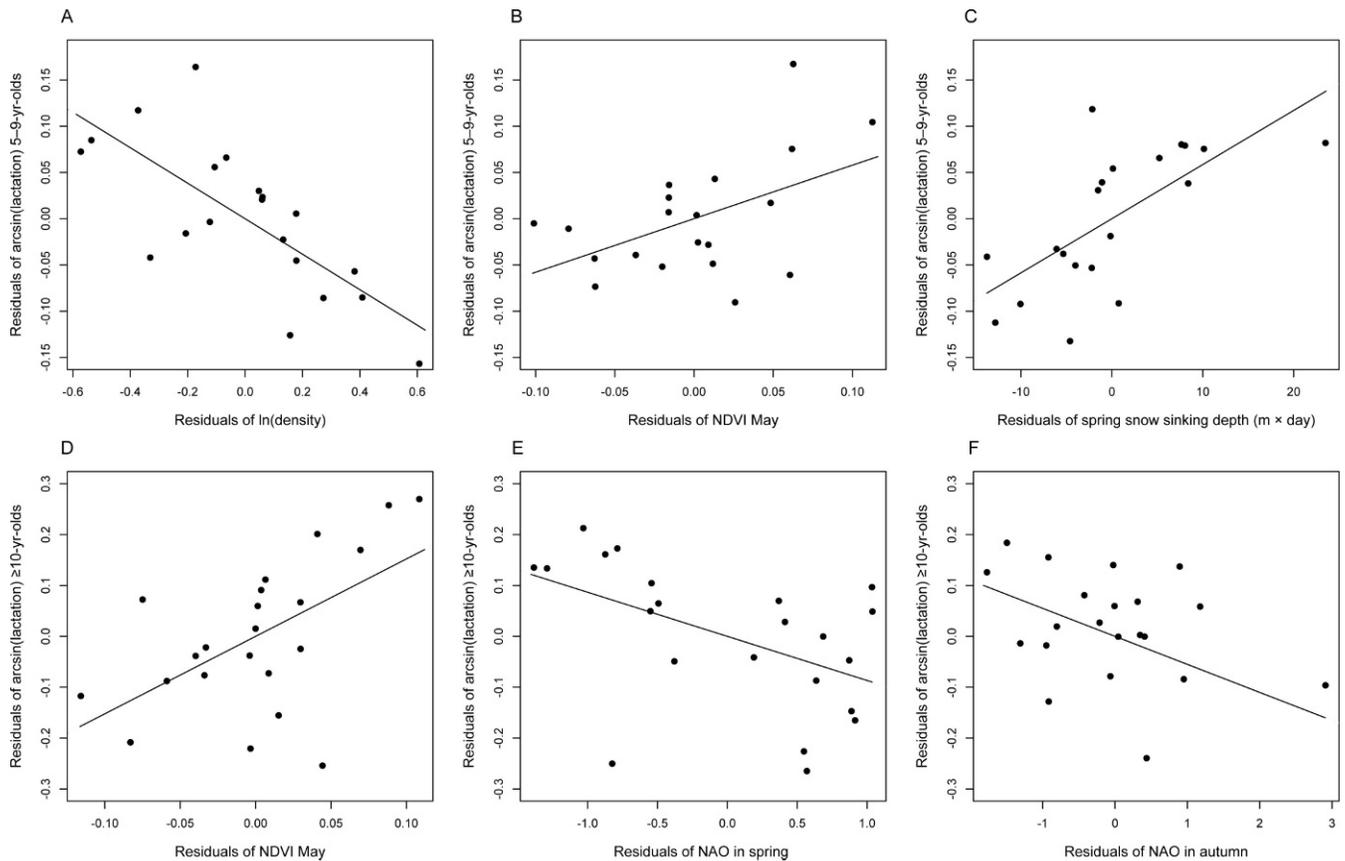
Figure 5. Linear models explaining lactation rate (arcsin-transformed) of prime-age and older adult female white-tailed deer on Anticosti Island, Québec, Canada (1982–2005). Models for lactation of 5–9-year-olds show the effect of (A) density (ln-transformed deer seen per hunter per day), (B) Normalized Difference Vegetation Index (NDVI) in May, and (C) cumulative snow sinking depth in spring. Models for ≥10-year-olds show the effect of (D) NDVI in May, (E) North Atlantic Oscillation (NAO) index in spring, and (F) NAO index in autumn. We present results as the residuals of the dependent and independent variables once corrected for other variables included in each model.

more commonly affects age at first reproduction than adult fertility (Sæther 1997), but our results were similar to those for red deer (*Cervus elaphus*) on Rhum and Soay sheep (*Ovis aries*) on St-Kilda, where both age at first reproduction and fertility of adult females were affected by density (Coulson et al. 2000). The study on red deer suggested that in years when competition for forage was high, adult females had difficulty replenishing their fat reserves before estrus after weaning their previous calf (Clutton-Brock et al. 1997, Clutton-Brock and Coulson 2002), and we suspect a similar mechanism on Anticosti Island. We also suggest that young adult females in our study were not as efficient at replenishing their fat reserves as experienced females; density effects were stronger on 3–4-year-old females than on 5–9-year-olds, whereas more experienced or dominant females (≥10-yr-olds) were not affected by density (see also Hamel et al. 2010). It is possible that 2-year-old females were affected by conditions at birth or other factors that we did not account for, which could explain why the model for this specific age class had the lowest coefficient of determination.

Environmental Effects

Environmental covariates are expected to have strong effects on population vital rates (Sæther 1997), especially for species that are relatively small and have high costs of thermoregulation and locomotion in adverse weather (Holand et al. 1998, Coulson et al. 2000, Mysterud and Ostbye 2006). Considering the small size of white-tailed deer and their distribution in North America, winter severity is normally a strong limiting factor in northern populations facing heavy natural predation (Post and Stenseth 1998, DelGiudice et al. 2002). We expected the same for deer of Anticosti Island, although there were no predators on the island. Surprisingly, we did not find negative effects of winter NAO or snow sinking depth on female survival or lactation. Winter weather or snow commonly has a stronger effect than density on ungulate body weight (red deer [Loison and Langvatn 1998]; roe deer [*Capreolus capreolus*; Mysterud and Ostbye 2006]), first-year survival (red deer [Loison and Langvatn 1998]; Soay sheep [Forchhammer et al. 2001]), adult survival (Soay sheep [Milner et al. 1999]; white-tailed deer [DelGiudice et al. 2002]), and overall recruitment (elk [*Cervus canadensis*; Garrott et al. 2003]; white-tailed deer [Garroway and Broders 2007]). As suggested by Portier et al. (1998), it is possible that only exceptionally long, cold, and snowy winters affected white-tailed deer on Anticosti Island and that with the variables we used in our models we could not detect such an effect. We had no data accounting for winter duration. The

challenge is to properly interpret timing and mechanisms by which weather variables influence vital rates (Hallett et al. 2004). Winter effects were also possibly more important for fawns (Taillon et al. 2006) or adult males (Mysterud et al. 2004), which we did not model in our study. Another explanation is that winter severity may be more detrimental where deer are subject to predation, because this would increase energy expenditure due to vigilance and escape behavior. For white-tailed deer, mortality due to wolf (*Canis lupus*) predation was directly related to snow depth (Nelson and Mech 1986, DelGiudice 1998). In elk, negative effects of snow depth were only detected where wolves were present; otherwise, elk density was the main regulating factor (Hebblewhite et al. 2002).

Early spring vegetation and spring climate had a strong influence on lactation rates. Spring conditions are crucial for ungulates, because early vegetation onset allows females to replenish fat and protein reserves following winter restriction and to allocate resources to late gestation and lactation, thereby increasing offspring survival (Portier et al. 1998, Sims et al. 2007, Therrien et al. 2007). Positive effects of wet weather in spring have been reported on birth weight and neonatal survival (Portier et al. 1998, Clutton-Brock and Coulson 2002). On Anticosti Island, NAO and NDVI in spring were associated with effects on female lactation: negative NAO was correlated with abundant spring precipitation, thereby possibly increasing plant biomass, with probable positive effects on recruitment (Lenart et al. 2002). We did not observe negative effects of maximum or average increases in NDVI or a significant effect of temperature in spring, which are normally associated with reduced access to high-quality forage (Lenart et al. 2002, Pettorelli et al. 2007). However, we found a positive influence of snow sinking depth (but not snow depth) on the lactation rate of prime-aged females. Presumably, increasing snow sinking depth should increase energy expenditures in late winter, a period of high mortality (Taillon et al. 2006). Positive effects of snow depth on recruitment rate have been previously observed in moose (*Alces alces*; Solberg et al. 1999) and red deer (Forchhammer et al. 2001). It is possible that if snow is slow to melt in spring and covers the ground longer, then subsequent forage production may increase and availability of high-quality forage may extend later into lactation (Langvatn et al. 1996, Mysterud et al. 2001). We observed effects of spring conditions only for lactation rates of prime-aged and older females.

Winter severity has been the focus of many studies on population dynamics of northern ungulates (Mech et al. 1987, DelGiudice et al. 2002), but recently the importance of forage abundance or quality during the short vegetative growing season has been increasingly recognized as a crucial limiting factor (Cook et al. 2004, Langvatn et al. 2004, Herfindal and Solberg 2006). Forage abundance in summer and autumn affects body growth and lipid reserves of ungulates (Hjeljord and Histøl 1999). Body condition at the onset of the rut and winter could then affect age at first reproduction, conception rate, and winter survival (Sæther et al. 1996, Cook et al. 2004). On Anticosti Island, autumn appeared to be important for body reserves accumulation, but a decline in diet quality over the last 25 years has reduced mass gain in autumn and lowered female mass at estrus (Simard et al. 2008). We expected periods of resource accumulation to be important for deer, but we found no effect of summer vegetation productivity on vital rates. Weather in autumn appeared to have important effects on vital rates: lactation rates of ≥10-year-old females were positively affected by abundant rainfall (negative NAO); cumulative compact snow depth had a negative effect on the lactation of most age-classes, especially younger adults (see Table 3); and cumulative snow depth negatively affected survival. Snow in late autumn likely reduced access to forage at a critical time, before estrus and winter, when deer were still restoring body reserves. Interestingly, compact snow had a generally stronger effect on lactation rates than snow depth (although these metrics are strongly correlated). Periods of freezing and cold rains during autumn may contribute to form crusted snow, impacting deer foraging. For a given snow depth, crusted versus fluffy snow may have very different effects on access to forage (see Fig. 1C).

Study Limitations

Our study was based on the assumption that ages-at-harvest data were not biased by hunter selectivity and were representative of the annual natural age structure of the population. Although hunter selectivity for adult females was weak, we cannot exclude that vulnerability to hunting can vary with age, experience, or reproductive status of females (Bunnefeld et al. 2009). Unfortunately, we could not address uncertainty associated with hunter selectivity; however, because we examined relative changes in demographic parameters, we expected that as long as possible biases were similar through time, they would not have a strong impact on our results, especially as we accounted for age classes. Finally, transversal data have the advantage of providing large sample sizes over wide geographic areas (Herfindal and Solberg 2006).

An additional limitation of our study is that we accounted for environmental variations using large-scale indices, for which accuracy and precision at smaller scales are difficult to estimate (Ranta et al. 2008). Indeed, global climatic indices are not always representative of local weather conditions (Stenseth and Mysterud 2005). Likewise, density indices are often imprecise and may be biased (Krebs 1991), and NDVI indices have rarely been validated with data on plant quality and abundance (Hamel et al. 2009). Nevertheless, assessing variation in climate, density, and vegetation using indices such as NAO (Stenseth and Mysterud 2005), hunting statistics (Mysterud et al. 2007), and NDVI (Pettorelli et al. 2006*b*) is generally appropriate to identify relative changes in environmental parameters on a temporal basis. Large-scale indices, despite certain limitations, have largely contributed to expand our comprehension of animal population ecology (Herfindal and Solberg 2006, Martinez-Jauregui et al. 2009).

MANAGEMENT IMPLICATIONS

Our results suggest caution in assuming that winter severity is the principal factor regulating northern deer populations and we propose that population density, as well as autumn and spring climate, should also be considered in management strategies. Similarly, management actions undertaken to promote population maintenance or growth, such as supplemental winter feeding, may not be the most effective strategy to achieve the population objective. Our results are also relevant for issues of deer overabundance because they suggest that management attempts to reduce population densities can be rapidly compensated by increases in survival or reproductive rates if harvest rates are not high enough or environmental factors are mild (McCullough 1999, Côté et al. 2004, Giles and Findlay 2004). Finally, our results suggest that climate change may favor population growth in northern regions or the northern expansion of deer range, because warm and wet weather in spring–autumn and late snow in autumn had a positive effect on deer recruitment and survival.

ACKNOWLEDGMENTS

LITERATURE CITED

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. Journal of Animal Ecology 69:1099–1110.

Ashley, E. P., G. B. McCullough, and J. T. Robinson. 1998. Morphological responses of white-tailed deer to a severe population reduction. Canadian Journal of Zoology 76:1–5.

Boucher, S., M. Crête, J.-P. Ouellet, C. Daigle, and L. Lesage. 2004. Large-scale trophic interactions: white-tailed deer growth and forest understory. Ecoscience 11:286–295.

Bunnefeld, N., D. Baines, D. Newborn, and E. Milner-Gulland. 2009. Factors affecting unintentional harvesting selectivity in a monomorphic species. Journal of Animal Ecology 78:485–492.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference. A practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London, United Kingdom.

Clobert, J., and J. D. Lebreton. 1991. Estimation of demographic parameters in bird populations. Pages 75–103 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population study: relevance to conservation and management. Oxford University Press, New York, New York, USA.

Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society B 357:1285–1298.

Clutton-Brock, T. H., A. W. Illius, K. Wilson, B. T. Grenfell, A. D. C. MacColl, and S. D. Albon. 1997. Stability and instability in ungulate populations: an empirical analysis. American Naturalist 149:195–219.

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155.

Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113–147.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:528–531.

Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society B 267:1771–1779.

Crampe, J. P., J. M. Gaillard, and A. Loison. 2002. Winter snowfall: a variable factor in recruitment by isard populations (Rupicapra pyrenaica pyrenaica). Canadian Journal of Zoology 80:1306–1312. [In French with English abstract.]

Crawley, M. J. 2005. Statistical computing. An introduction to data analysis using S-Plus. John Wiley and Sons, Chichester, United Kingdom.

DelGiudice, G. D. 1998. Surplus killing of white-tailed deer by wolves in north-central Minnesota. Journal of Mammalogy 79:227–235.

DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. C. Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. Journal of Wildlife Management 70:1556–1568.

DelGiudice, G. D., M. S. Lenarz, and M. C. Powell. 2007. Age-specific fertility in northern free-ranging white-tailed deer: evidence for reproductive senescence? Journal of Mammalogy 88:427–435.

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.

Dumont, A., M. Crête, J.-P. Ouellet, J. Huot, and J. Lamoureux. 2000. Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. Canadian Journal of Zoology 78:764–776.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Environment Canada. 2006. Climate normals and averages, daily data reports of Port-Menier's station from 1995 to 2005. Canada's National Climate Archive. <http://climate.weatheroffice.gc.ca>. Accessed 5 Dec 2006.

Festa-Bianchet, M., J.-M. Gaillard, and S. D. Côté. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. Journal of Animal Ecology 72:640–649.

Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367–379.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindström, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721–729.

Forchhammer, M. C., and E. Post. 2004. Using large-scale climate indices in climate change ecology studies. Population Ecology 46:1–12.

Fowler, C. W. 1981. Density dependence as related to life history strategies. Ecology 62:602–610.

Fryxell, J. M., D. J. Hussell, A. B. Lambert, and P. C. Smith. 1991. Time lags and population fluctuations in white-tailed deer. Journal of Wildlife Management 55:377–385.

Fryxell, J. M., W. E. Mercer, and R. B. Gellately. 1988. Population dynamics of Newfoundland moose using cohort analysis. Journal of Wildlife Management 52:14–21.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–62.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology, Evolution, and Systematics 31:367–393.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology 81:33–45.

Garroway, C. J., and H. G. Broders. 2007. Adjustment of reproductive investment and offspring sex ratio in white-tailed deer (Odocoileus virginianus) in relation to winter severity. Journal of Mammalogy 88:1305–1311.

Gilbert, B. A., K. J. Raedeke, and J. R. Skalski. 2007. Modeling black-tailed deer population dynamics using structured and unstructured approaches. Journal of Wildlife Management 71:144–154.

Giles, B., and C. Findlay. 2004. Effectiveness of a selective harvest system in regulating deer populations in Ontario. Journal of Wildlife Management 68:266–277.

Gove, N. E., J. R. Skalski, P. Zager, and R. L. Townsend. 2002. Statistical models for population reconstruction using age-at-harvest data. Journal of Wildlife Management 66:310–320.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75.

Hamel, S., and S. D. Côté. 2007. Trade-off in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. Animal Behaviour 75:217–227.

Hamel, S., S. D. Côté, and M. Festa-Bianchet. 2010. Maternal characteristics and environment affect the costs of reproduction in female mountain goats. Ecology 91:2034–2043.

Hamel, S., M. Garel, M. Festa-Bianchet, J. M. Gaillard, and S. D. Coté. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46:582–589.

Hamlin, K. L., D. F. Pac, C. A. Sime, R. M. DeSimone, and G. L. Dusek. 2000. Evaluating the accuracy of ages obtained by two methods for Montana ungulates. Journal of Wildlife Management 64:441–449.

Heard, D., S. Barry, G. Watts, and K. Child. 1997. Fertility of female moose (Alces alces) in relation to age and body composition. Alces 33:165–176.

Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:789–799.

Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. Journal of Wildlife Management 70:1544–1555.

Herfindal, I., and E. J. Solberg. 2006. Environmental phenology and geographical gradients in moose body mass. Oecologia 150:213–224.

Hewison, A. J. M., and J. M. Gaillard. 2001. Phenotypic quality and senescence affect different components of reproductive output in roe deer. Journal of Animal Ecology 70:600–608.

Hjeljord, O., and T. Histøl. 1999. Range-body mass interactions of a northern ungulate—a test of hypothesis. Oecologia 119:326–339.

Holand, O., A. Mysterud, A. Wannag, and J. D. C. Linnell. 1998. Roe deer in northern environments: physiology and behaviour. Pages 117–137 in R. Andersen, P. Duncan, and J. D. C. Linnell, editors. The European roe deer: the biology of success. Scandinavian University Press, Oslo, Norway.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley and Sons, New York, New York, USA.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. Science 269:676–679.

Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. The North Atlantic Oscillation: climatic significance and environmental impact. Geophysical Monograph Series. American Geophysical Union, Washington, D.C., USA.

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. Canadian Journal of Zoology 71:2509–2517.

Krebs, C. J. 1991. The experimental paradigm and long term population studies. Ibis 133 Supplement:3–8.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Langvatn, R., A. Mysterud, N. Stenseth, and N. Yoccoz. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. American Naturalist 163:763–772.

Lefort, S., J.-P. Tremblay, F. Fournier, F. Potvin, and J. Huot. 2007. Importance of balsam fir as winter forage for white-tailed deer at the northeastern limit of its distribution range. Ecoscience 14:109–116.

Lenart, E. A., R. T. Bowyer, J. V. Hoef, and R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. Canadian Journal of Zoology 80:664–678.

Loison, A., and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489–500.

Lussier, A., C. Sirois, and A. Dicaire. 2008. Inventaire aérien de population de cerf de Virginie. Décembre 2007. Minitère des Ressources naturelles et de la Faune, Direction de l'aménagement de la faune Estrie-Montréal-Montérégie, Québec, Canada. [In French.]

Martinez, M., C. Rodriguez-Vigal, O. Jones, T. Coulson, and M. A. San Miguel. 2005. Different hunting strategies select for different weights in red deer. Biology Letters 1:353–356.

Martinez-Jauregui, M., A. San Miguel-Ayanz, A. Mysterud, C. Rodriguez-Vigal, T. Clutton-Brock, R. Langvatn, and T. Coulson. 2009. Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? Global Change Biology 15:1727–1738.

Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88–90.

McCullough, D. R. 1979. The George Reserve deer herd. University of Michigan Press, Ann Arbor, USA.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy 80:1130–1146.

McNay, R. S., and J. M. Voller. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. Journal of Wildlife Management 59:138–146.

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winter snow. Journal of Animal Ecology 56:615–627.

Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. Journal of Animal Ecology 68:1235–1247.

Murray, D. L., and B. R. Patterson. 2006. Wildlife survival estimation: recent advances and future directions. Journal of Wildlife Management 70:1499–1503.

Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. Journal of Zoology 264:209–215.

Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915–923.

Mysterud, A., E. L. Meisingset, V. Veiberg, R. Langvatn, E. J. Solberg, L. E. Loe, and N. C. Stenseth. 2007. Monitoring population size of red deer Cervus elaphus: an evaluation of two types of census data from Norway. Wildlife Biology 13:285–298.

Mysterud, A., and E. Ostbye. 2006. Effect of climate and density on individual and population growth of roe deer Capreolus capreolus at northern latitudes: the Lier valley, Norway. Wildlife Biology 12:321–329.

Mysterud, A., N. C. Stenseth, N. G. Yoccoz, G. Ottersen, and R. Langvatn. 2003. The response of terrestrial ecosystem to climate variability associated with the North Atlantic Oscillation. Pages 235–

263 *in* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, editors. The North Atlantic Oscillation: climatic significance and environmental impact. American Geophysical Union, Washington, D.C., USA.

Nelson, M., and L. D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 50:691–698.

Nelson, M., and L. D. Mech. 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. American Midland Naturalist 155:373–382.

Nilsen, E. R., and E. J. Solberg. 2006. Patterns of hunting mortality in Norwegian moose (*Alces alces*) populations. European Journal of Wildlife Research 52:153–163.

Osborn, T. 2006. North Atlantic Oscillation index. Climatic Research Unit, University of East Anglia, Norwich, United Kingdom. <http://www.cru.uea.ac.uk/cru/data/nao.htm>. Accessed 20 Sep 2006.

Owen-Smith, N., D. Mason, and J. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology 74:774–788.

Pekins, P. J., K. S. Smith, and W. W. Mautz. 1998. The energy cost of gestation in white-tailed deer. Canadian Journal of Zoology 76:1091–1097.

Pettorelli, N., S. D. Côté, A. Gingras, F. Potvin, and J. Huot. 2006*a*. Aerial surveys versus hunting statistics to monitor deer density: the example of Anticosti Island (Québec, Canada). Wildlife Biology 13:321–327.

Pettorelli, N., S. Dray, J.-M. Gaillard, D. Chessel, P. Duncan, A. Illius, N. Guillon, F. Klein, and G. V. Laere. 2003. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. Oecologia 137:363–369.

Pettorelli, N., J.-M. Gaillard, A. Mysterud, P. Ducan, N. C. Stenseth, D. Delorme, G. Van Laere, C. Toïgo, and F. Klein. 2006*b*. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112:565–572.

Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Côté. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20:503–510.

Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J. T. Jorgenson, and N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology 245:271–278.

Post, E., and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology 67:537–543.

Potvin, F., and L. Breton. 2005. Testing 2 aerial survey techniques on deer in fenced enclosures—visual double-counts and thermal infrared sensing. Wildlife Society Bulletin 33:317–325.

Potvin, F., L. Breton, and A. Gingras. 1997. Déplacements et survie hivernale des biches d'Anticosti de 1986 à 1990: une étude télémétrique. Direction de la faune et des habitats. Ministère de l'Environnement et de la Faune, Québec, Canada. [In French.]

Ramsey, D., M. Efford, P. Cowan, and J. Coleman. 2002. Factors influencing annual variation in breeding by common brushtail possums (*Trichosurus vulpecula*) in New Zealand. Wildlife Research 29:39–50.

Ranta, E., Å. Lindström, H. Lindén, and P. Helle. 2008. How reliable are harvesting data for analyses of spatio-temporal population dynamics? Oikos 117:1461–1468.

Roseberry, J. L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143–149.

Sæther, B.-E., R. Andersen, O. Hjeljord, and M. Heim. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. Ecology 77:1493–1500.

Sæther, B.-E., and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. Journal of Animal Ecology 62:482–489.

Sæther, B.-E., W. J. Sutherland, and S. Engen. 2004. Climate influences on avian population dynamics. Advances in Ecological Research 35:185–209.

Simard, M. A., S. D. Côté, R. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on the life history traits of a large herbivore. Journal of Animal Ecology 77:678–686.

Sims, M., D. A. Elston, A. Larkham, D. H. Nussey, and S. Albon. 2007. Identifying when weather influences life-history traits of grazing herbivores. Journal of Animal Ecology 76:761–770.

Sinclair, A. R. E., and J. P. Parkes. 2008. On being the right size: food-limited feedback on optimal body size. Journal of Animal Ecology 77:635–637.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61:12–25.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54:359–374.

Solberg, E. J., B.-E. Sæther, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. Journal of Animal Ecology 68:186–204.

Stenseth, N., and A. Mysterud. 2005. Weather packages: finding the right scale and composition of climate in ecology. Journal of Animal Ecology 74:1195–1198.

Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia 143:85–93.

Sylvén, S. 2000. Effects of scale on hunter moose *Alces alces* observation rate. Wildlife Biology 6:157–165.

Taillon, J., D. G. Sauvé, and S. D. Côté. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. Journal of Wildlife Management 70:1445–1454.

Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. C. Pilkington, F. M. D. Gulland, and T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. Ecology 74:201–213.

Therrien, J.-F., S. D. Côté, and M. Festa-Bianchet. 2007. Conservative maternal care in an iteroparous mammal: a resource allocation experiment. Behavioral Ecology and Sociobiology 62:193–199.

Tremblay, J.-P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks? Canadian Journal of Zoology 83:1087–1096.

Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.

Van Deelen, T. R., H. Campa, J. B. Haufler, and P. D. Thompson. 1997. Mortality patterns of white-tailed deer in Michigan's upper peninsula. Journal of Wildlife Management 61:903–910.

Verme, L. J. 1965. Reproduction studies on penned white-tailed deer. Journal of Wildlife Management 29:74–79.

Verme, L. J. 1968. An index of weather severity for northern deer. Journal of Wildlife Management 32:566–574.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. Journal of Wildlife Management 33:881–887.

Webb, S. L., D. G. Hewitt, and M. W. Hellickson. 2007. Survival and cause-specific mortality of mature male white-tailed deer. Journal of Wildlife Management 71:555–558.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40:377–384.

Xie, J., H. R. Hill, S. R. Winterstein, H. Campa, R. V. Doepker, T. R. Van Deelen, and J. Liu. 1999. White-tailed deer management options model (DeerMOM): design, quantification, and application. Ecological Modelling 124:121–130.

Associate Editor: McCorquodale.