

# The quantitative effects of population density and winter weather on the body condition of white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada

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**Abstract:** Understanding the underlying mechanisms that cause variation in survival and the reproductive success of animals is essential for predicting variation in population parameters. To gain an understanding of the effects of density and winter weather severity on white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), we examined the effects of current-year deer density and cumulative weekly average values for snow depth, rainfall, and the number of degrees below  $-15^{\circ}\text{C}$  until the time of death, as well as cumulative effects of density and snow depth over the previous one and two winters, on the body condition of adult females, adult males, and fawns. Model selection using Akaike's Information Criterion and multi-model inference suggested that snow depth was the best predictor of body condition for all three age/sex groups. Winter rainfall was the next most influential predictor for adult females and adult males but was not important in determining fawn body condition. Temperature had the least influence on the body condition of all three age/sex groups. Deer density during the winter of death had minimal effects for all groups and we found no evidence that cumulative multiyear variables influenced body condition. We hypothesize that cohort variation may better explain previous findings showing effects of multiyear variables. A model for estimating the proportion of animals in poor body condition for each age/sex group is presented.

**Résumé :** Si l'on veut pouvoir prédire la variation des paramètres démographiques chez les animaux, il est essentiel de comprendre les mécanismes sous-jacents responsables de la variation de la survie et du succès reproductif. Afin de déterminer les conséquences de la densité et de la rigueur du climat hivernal sur le cerf de Virginie, *Odocoileus virginianus* (Zimmermann, 1780), nous avons examiné les effets sur la condition corporelle des femelles adultes, des mâles adultes et des faons de la densité des cerfs pendant l'année courante, ainsi que des valeurs hebdomadaires cumulées de l'épaisseur de la neige, des précipitations et du nombre de degrés sous  $-15^{\circ}\text{C}$  jusqu'au moment de la mort; nous avons aussi étudié les effets cumulés de la densité et de l'épaisseur de la neige au cours de l'hiver précédent et des deux hivers antérieurs. La sélection des modèles d'après le critère d'information d'Akaike et l'inférence multi-modèles indique que l'épaisseur de la neige est la meilleure variable prédictive pour tous les trois groupes d'âge/sexe. Les pluies d'hiver sont la variable suivante en importance pour prédire la condition corporelle des adultes femelles et mâles, mais pas celle des faons. La température est la variable qui a le moins d'influence pour les trois groupes d'âge/sexe. La densité durant l'hiver du décès a peu d'importance pour tous les groupes et il n'y a pas d'indication que les variables cumulées sur plusieurs années influencent la condition corporelle. Notre hypothèse veut que la variation de la cohorte explique mieux les résultats antérieurs qui montrent les effets de variables mesurées sur plusieurs années. Nous présentons un modèle pour estimer la proportion des animaux en mauvaise condition corporelle dans chaque groupe d'âge/sexe.

[Traduit par la Rédaction]

## Introduction

Identifying the underlying mechanisms that cause variation in survival and reproductive success can improve understanding of what regulates and limits wild animal populations (Morrison 2001). Demographic variability occurs as a result of the additive physiological and behavioral responses of individuals to their environment. The annual life histories

of temperate-zone animals are characterized by (i) periods of low resource availability, leading to decreases in somatic and gametic growth and population declines, and (ii) periods of high resource availability, when somatic growth and reproduction occur (Boyce 1979). Many recent studies have shown that both density-independent (e.g., climate) and density-dependent (e.g., forage competition) factors can influence the dynamics of animal populations (Sæther 1997;

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Forchhammer et al. 1998; Gaillard et al. 1998; Post and Stenseth 1998, 1999; Kruuk et al. 1999a, 1999b; Lesage et al. 2001; Patterson and Power 2002; Hallet et al. 2004). Quantification of the effects of these different factors requires long-term data sets including a full range of weather conditions and population densities (Hallet et al. 2004).

For example, ungulates respond both behaviorally and physiologically to weather- and density-related factors, with responses manifested in population dynamics (Gaillard et al. 1997, 1998; Sæther 1997; Post and Stenseth 1998, 1999; Kruuk et al. 1999a, 1999b; Forchhammer et al. 2001; Lesage et al. 2001; Patterson and Power 2002). The depth and persistence of snow cover affect the costs of locomotion (Parker et al. 1984) and availability of browse (Post and Stenseth 1999). Winter rainfall and (or) low temperatures may increase the metabolic costs of thermoregulation and reduce forage availability by forming an icy crust on snow, making it difficult for animals to gain access to forage (Clutton-Brock and Albon 1982; Aanes et al. 2000; Solberg et al. 2001). High densities can negatively affect ungulate populations through increased forage competition (Post and Stenseth 1999).

Determining and quantifying the effects of winter weather and density-dependent factors may be complicated by temporally lagged effects, whereby the density or weather conditions of a previous winter influence animals more than those of the current winter (Clutton-Brock et al. 1997; Forchhammer et al. 1998; Post and Stenseth 1998, 1999; Loison et al. 1999a). Cumulative multiyear effects of winter weather and density have also been reported (Mech et al. 1987; Post and Stenseth 1998; Patterson and Power 2002). Nonetheless, measurable effects may be manifested on adult body condition or body mass (Post et al. 1997; Loison et al. 1999b; Post and Stenseth 1999; Myrsterud et al. 2000, 2001), offspring sex ratio (Kruuk et al. 1999b; Post et al. 1999; Stenseth 1999; Myrsterud et al. 2000), early growth rates or body mass of offspring (Adams and Dale 1998; Hjeljord and Hystol 1999; Loison et al. 1999a; Post and Stenseth 1999; Forchhammer et al. 2001; Weladji and Holand 2003), adult survival (Potvin et al. 1981; Loison and Langvatn 1998; Loison et al. 1999b; Post and Stenseth 1999), and offspring survival (Adams and Dale 1998; Loison and Langvatn 1998; Post and Stenseth 1999; Lee et al. 2000).

In this paper we examine and quantify the effects of winter weather and population density on the body condition of white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780), from a northeastern North American population in Nova Scotia, Canada (Fig. 1), during 1987–2002. Nova Scotia is close to the northern extent of the white-tailed deer's range, where severe winters may create an energetic bottleneck (Potvin et al. 1981; Dumont et al. 2000). To minimize the energetic costs of severe winter weather, white-tailed deer may migrate to traditional wintering areas (Verme 1973; Huot 1974; Drolet 1976; Nelson 1995; MacDonald 1996; Lock 1997; Patterson et al. 1998; Morrison et al. 2002). Such migration is stimulated by decreasing temperature (Kearney and Gilbert 1976) and increasing snow depth (Ozoga and Gysel 1972; Verme 1973; Drolet 1976; Tierson et al. 1985; Sabine et al. 2002). Deer movement becomes significantly restricted and more energetically costly at snow

depths greater than 40 cm (Drolet 1976; Parker et al. 1984), and the rate and timing of migration to wintering areas closely correspond with snow depths of 40 cm (Sabine et al. 2002).

Energetic costs may be lower in traditional wintering areas because such areas typically consist of mature coniferous trees that intercept snowfall, reducing snow depth and moderating wind and temperature (Weber et al. 1983), and communal trails reduce the costs of locomotion. However, extended periods of confinement in traditional wintering areas may lead to the depletion of browse and increased forage competition. When and where winter weather is less severe, white-tailed deer overwinter on their summer range, where browse availability is generally higher (Mautz et al. 1976; Lock 1997; Morrison et al. 2002; Sabine et al. 2002).

Winter conditions affect the nutritional states of age and sex groups differentially. Fawns are more susceptible to winter starvation than adults because of their limited fat reserves, resulting from the need to direct energy toward both growth and fat deposition prior to winter, and their small body size (i.e., increased cost of thermoregulation; Vreeland et al. 2004). Consequently, we expect fawns to be more susceptible to adverse winter conditions and to have a higher probability of entering winter in poor body condition than adult males and females. Fat reserves of adult males are more depleted during the autumn rut than those of adult females, leaving males more vulnerable to starvation during severe winters (Mautz et al. 1976; Moen 1976), so we expect adult males to have a lower probability of entering winter in poor body condition than fawns and a higher probability than adult females. The autumn breeding season does not cause depletion of body fat reserves in female cervids (Crête and Huot 1993), but nutritional demands on pregnant females increase throughout gestation into lactation (Mauget et al. 1997). Gestation begins in November and parturition occurs from mid-May to early June in Nova Scotia. Over 90% of the total costs of gestation occur during the third trimester (Pekins et al. 1998). Relative to nonpregnant deer, this represents costs for pregnant deer that are 45% greater in the third trimester and 16% greater over the whole pregnancy (Pekins et al. 1998). Pregnant adult females starting winter in poor or marginal body condition have reduced survival probability (Moen 1976; Mautz 1978) and an increased likelihood of abortion or producing a small fawn (Verme 1965). The main difference between adult males and adult females is that adult females may divert energy away from reproduction and toward self-maintenance if winter conditions become severe, whereas males have already depleted energy reserves during the rut.

The objectives of this paper were to (i) identify the most important density and winter weather variables influencing white-tailed deer body condition and quantify their effects; (ii) determine whether cumulative multiyear effects of these variables occur; and (iii) develop a predictive model that could estimate the proportion of the population in poor body condition. We expected that body condition at the start of winter would depend upon both the ability to accumulate fat reserves prior to winter and the relative costs of the fall rut, and that the energetic costs during winter would vary among age/sex groups (e.g., gestation in females), resulting in sex- and age-specific variation in body condition.

## Materials and methods

Our study animals were primarily road-killed and were sampled within 3 days of death. Collisions between white-tailed deer and vehicles typically occur in the early evening and early morning (Allen and McCullough 1976; Haikonen and Summala 2001); however, information pertaining to annual variation in deer–vehicle collisions is lacking. O’Gara and Harris (1988) cautioned that road-killed animals may not be useful as a representative sample of a population, suggesting that malnourished animals may travel on highways that have been cleared of snow in an attempt to reduce energy expenditure. Others have suggested that roadkills are reliable for estimating population age and sex structure and have found that variation in the number of roadkills is most closely related to traffic flow, population density, and sex- and season-specific behaviors (Allen and McCullough 1976; Groot Bruinderink and Hazebroek 1996; McCaffery 1973; Mysterud 2004). In our data set, 14% of animals had femur marrow fat levels below 25%, 18% had levels between 25% and 50%, 28% had levels between 50% and 85%, and 40% had levels above 85%. Because this sampling method yielded a wide range of values, we feel this data set is appropriate for this analysis and representative of the population at large, if not entirely random.

We divided our sample into three age/sex groups: fawns (males and females <12 months old;  $n = 794$ ), adult females (18 months – 8 years old;  $n = 848$ ), and adult males (18 months – 8 years old;  $n = 524$ ). Fawns were distinguished from adults by examining tooth wear and development (Severinghaus 1949). Staff of the Nova Scotia Department of Natural Resources (NSDNR) georeferenced road-killed animals and visually assessed femur marrow fat content as an indicator of body condition (Cheatum 1949; Neiland 1970; Cook et al. 2001). Fat stores in ungulates are used sequentially: subcutaneous fat reserves are used first, followed by mesentery, kidney, and bone marrow reserves (Ransom 1965; Chan-McLeod et al. 1995). Because femur marrow fat is among the final fat deposits used, any femur marrow fat depletion is indicative of poor body condition (Mech and DelGiudice 1985; Takatsuki 2000; Yokoyama et al. 2000; Cook et al. 2001); the most that one can conclude from high femur marrow fat content is that there is no evidence of malnutrition (Mech and DelGiudice 1985). Cook et al. (2001) found that Rocky Mountain elk (*Cervus elaphus* L., 1758) with >6% body fat had an average femur marrow fat content of 91.8%. Similarly, Torbit et al. (1985) found that mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) with 6%–12% body fat maintained femur marrow fat content above 80%. Thus, femur marrow fat content below 80%–90% likely indicates poor body condition (below 5%–6% body fat): fat reserves either have not been deposited or substantial amounts have been used. We categorized animals with femur marrow fat content below 85% as being in poor condition and those with femur marrow fat content above 85% as showing no evidence of poor body condition.

To assess which factors most influence the body condition of white-tailed deer, we used a logistic regression framework whereby animals in poor body condition (femur marrow fat content <85%) were coded as 1 and animals showing no evidence of poor body condition (femur marrow fat content >85%) were coded as 0. Before analysis, we randomly parti-

**Table 1.** Set of 19 a priori candidate logistic regression models for predicting the probability of being in poor body condition for white-tailed deer (*Odocoileus virginianus*) in Nova Scotia, Canada, 1987–2002.

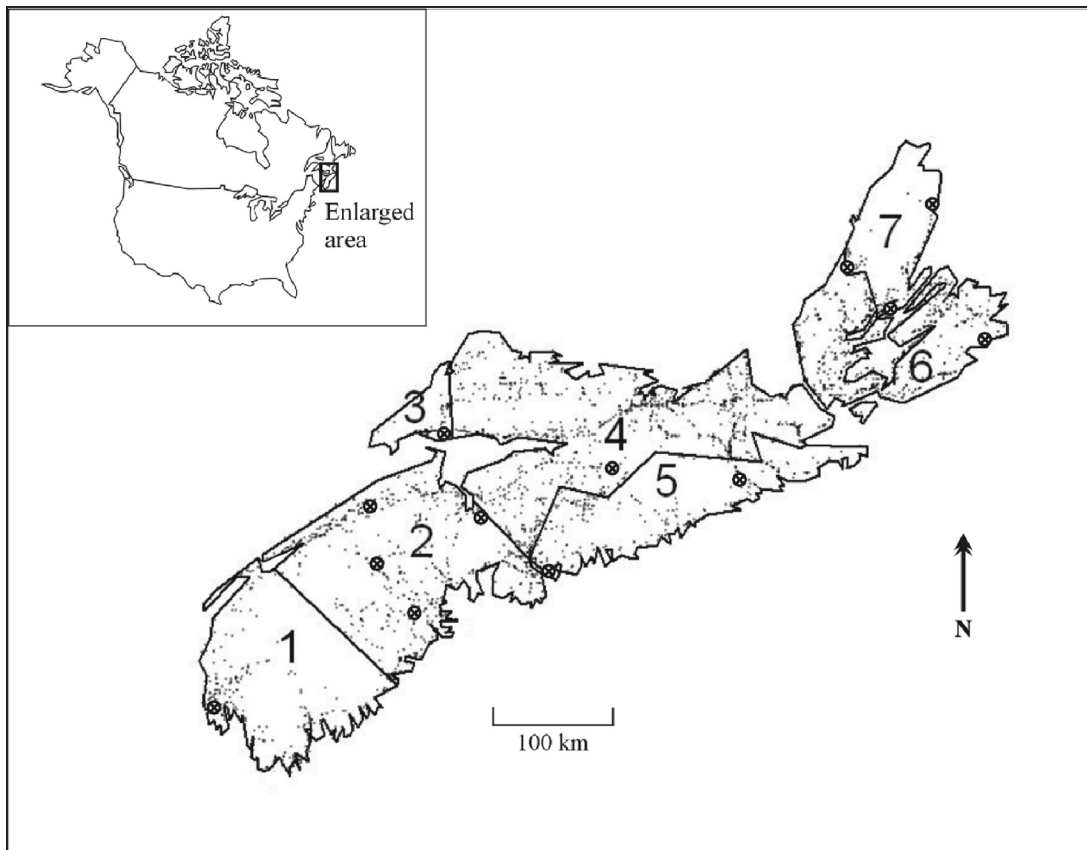
Model	Variables
1	Density
2	Density1
3	Density2
4	Snow depth
5	Snow depth1
6	Snow depth2
7	Snow depth, temperature
8	Snow depth1, temperature
9	Snow depth2, temperature
10	Snow depth, rainfall
11	Density, snow depth
12	Density1, snow depth1
13	Density2, snow depth2
14	Density1, snow depth2
15	Density2, snow depth1
16	Density, snow depth, temperature
17	Snow depth, temperature, rainfall
18	Density, rainfall, temperature
19	Density, snow depth, rainfall, temperature

tioned our data for each age/sex group into a model-fitting data set (70% of data) and a model-validation data set (30% of data). The model-validation data set was used only to detect major spurious results from the selection of the best models and effect sizes of variables and was not used for testing predictions or inference.

Following a review of more than 20 papers discussing the effects of winter weather on ungulates, we constructed a set of 19 a priori candidate models (Table 1) representing multiple working hypotheses that were subsequently ranked using Akaike’s Information Criterion (AIC; Burnham and Anderson 2002) for each age/sex group. We used binomial family generalized linear models with a logit link in S-PLUS® 2000 (MathSoft Engineering and Education, Inc. 1999; Hosmer and Lemeshow 2000). We then calculated Akaike weights ( $w_i$ ), the probability that the  $i$ th model is the best approximating model among all candidate models (Burnham and Anderson 2002). For the models constituting the 95% confidence set, based upon Akaike weights, we calculated the difference between the AIC of each model and that of the best approximating model ( $\Delta_i$ ) and the sum of the Akaike weights of the  $i$ th model and all higher ranking models ( $\Sigma w_i$ ).

In some cases a multivariate model may perform well even though not all variables contained within it are important (Hosmer and Lemeshow 2000), so we calculated normalized Akaike weights ( $Nw_i$ ) for the variables occurring in the 95% confidence set (Burnham and Anderson 2002). If a variable had a normalized Akaike weight greater than 0.60 (arbitrarily chosen a priori), we considered it to be important. For all important variables, we present the model-averaged parameter estimates ( $\beta$ ) with estimated unconditional standard errors (SE; Burnham and Anderson 2002) and odds ratios (antilogarithm of  $\beta$ ) with associated 95% confidence intervals (CI; Hosmer and Lemeshow 2000).

**Fig. 1.** Map of Nova Scotia, Canada, in relation to North America (inset), showing the locations of seven deer management zones, 13 weather stations (⊗), and road-killed white-tailed deer (*Odocoileus virginianus*) used to determine the effects of winter weather and population density on body condition, 1987–2002.



Model-averaged parameter estimates often have less bias and more precision than the parameter estimate of only the best model and so are desirable when the goal is prediction (Burnham and Anderson 2002).

The NSDNR has divided Nova Scotia into seven deer management zones (Fig. 1), and density was calculated for each zone based upon pellet group surveys conducted during April and May of each year (see Patterson and Power 2002 for methodology). We assigned a year and zone density value for each sample (i.e., deer). Weather data were obtained from 13 weather stations (Meteorological Service of Canada – Atlantic Region, Environment Canada) so that regional weather variations could be accounted for (Fig. 1). Deer were assigned to the closest weather station based upon their kill site using a geographic information system (ArcGIS®, Environmental Systems Research Institute, Inc. 2003). The average distance to the closest weather station was 33.6 km ( $\pm 19$  km SD). All weather data analysed are from 1 November to 15 May (earliest snowfall to latest snowmelt) from 1987 to 2002.

Winter weather variables used were snow depth, rainfall, and temperature. Snow depth and rainfall values were calculated as the sum of weekly averages of each variable during the winter of death until the week of death. The temperature variable was calculated as the sum of degrees below  $-15^{\circ}\text{C}$  of weekly average minimum temperatures.

Jensen et al. (1999) found that decreasing temperature did not increase the metabolic rate of white-tailed deer fawns

until it dropped below  $-11.2^{\circ}\text{C}$ , and Moen (1985) suggested that thermoregulatory costs for non-fasting adults are minimal until temperatures are below  $-20^{\circ}\text{C}$ . In the winter severity index used by DelGiudice et al. (2002) for Minnesota,  $-17.7^{\circ}\text{C}$  was used as the point at which temperature affects female white-tailed deer. We chose  $-15^{\circ}\text{C}$  as an approximate threshold where thermoregulatory costs begin for each of the age/sex groups.

To test for cumulative effects of snow depth and population density over consecutive winters, we also constructed variables that contained the value from the winter of death plus the value from the entire previous winter (snow depth1 and density1) and variables that contained the value from the winter of death plus the value from the previous two winters (snow depth2 and density2).

We expected that adult females would enter winter in better body condition than adult males, which in turn would enter winter in better body condition than fawns. Therefore, we predicted that (i) the y-intercepts of the logistic curves would be greatest for fawns, followed by adult males and then adult females; (ii) logistic curves for the important variables for fawns and adult males would have similar slopes; and (iii) adult males and fawns would have a higher probability of being in poor body condition than adult females over the same range of values for given independent variables. Standard errors for the y-intercepts of the final model were estimated via bootstrap methods (Sokal and Rohlf 1995). The model-fitting and validation data sets were com-



**Table 2.** Difference in Akaike's Information Criterion between the  $i$ th and the top-ranked model ( $\Delta i$ ), Akaike weights ( $w_i$ ), and the sum of Akaike weights ( $\Sigma w_i$ ) for all models up to the  $i$ th model for models comprising  $\geq 95\%$  of Akaike weights explaining the probability of white-tailed deer in Nova Scotia, Canada, being in poor body condition.

Model	$\Delta i$	$w_i$	$\Sigma w_i$
<b>Adult females</b>			
Snow depth, temperature, rainfall (2)	0.000	0.645	0.645
Snow depth, temperature, rainfall, density (5)	1.245	0.346	0.991
<b>Adult males</b>			
Snow depth, temperature, rainfall, density (3)	0.000	0.374	0.374
Snow depth, temperature, rainfall (11)	0.300	0.322	0.695
Snow depth (4)	2.347	0.116	0.811
Snow depth, density (1)	2.984	0.084	0.895
Snow depth, temperature (5)	3.604	0.062	0.957
<b>Fawns (male and female)</b>			
Snow depth, temperature (3)	0.000	0.427	0.427
Snow depth, temperature, density (4)	1.102	0.246	0.673
Snow depth, temperature, rainfall (1)	1.937	0.162	0.835
Snow depth, temperature, rainfall, density (2)	2.940	0.098	0.933
Snow depth (5)	4.704	0.041	0.974

**Note:** Numbers contained in brackets are model rankings from the model-validation data sets.

bined for each age/sex group and random samples (with replacement) of 70% were generated for each data set. This procedure was repeated for 1000 iterations.

## Results

For adult females, the 95% confidence sets consisted of two and six models for the model-fitting and model-validation data sets, respectively (Table 2). The top-ranked model from the adult female model-fitting data set included the variables snow depth, temperature, and rainfall. The adult male 95% confidence sets consisted of five and seven models for the model-fitting and model-validation data sets, respectively (Table 2). The top-ranked model from the model-fitting data set contained the variables density, snow depth, rainfall, and temperature. The 95% confidence sets for fawns comprised five models for the model-fitting data set and three models for the model-validation set (Table 2). The top model from the fawn model-fitting data set contained snow depth and temperature. The overlap of models and variables within the models from the 95% confidence sets of the model-fitting and model-validation data sets suggests that the model rankings are not spurious; hereafter, we present results from the 95% confidence sets from the model-fitting data sets.

The models consisting of "snow depth, temperature, rainfall" and "snow depth, temperature, rainfall, density" were included in the 95% confidence sets for all age/sex groups. Despite the inclusion of density during the year of death in some models for each age/sex group (Table 2), this variable was considered to be of minimal importance, as normalized Akaike weights for this variable for each age/sex group were less than 0.60 (Table 3). Similarly, there was minimal evidence that rainfall affected body condition in fawns (normalized Akaike weights  $< 0.60$ ), although it was included in two models from the 95% confidence set (Tables 2, 3). There

**Table 3.** Normalized Akaike weights ( $Nw_i$ ) for the variables occurring in the models constituting the 95% confidence sets (see Table 2).

Age/sex group	Snow depth	Temperature	Rainfall	Population density
Adult females	1.00	1.00	1.00	0.35
Adult males	1.00	0.79	0.73	0.48
Fawns (male and female)	1.00	0.96	0.27	0.35

**Note:** Variables with  $Nw_i < 0.60$  (chosen a priori) were not considered to have an important effect on the body condition of white-tailed deer.

was no evidence for cumulative effects of previous winters on body condition and no model from any of the 95% confidence sets included multiyear variables (snow depth1, snow depth2, density1, density2; see Table 2).

Snow depth (adult females,  $\beta_{\text{snow depth}} = 0.0029$ , SE = 0.0004; adult males,  $\beta_{\text{snow depth}} = 0.0034$ , SE = 0.0008; fawns,  $\beta_{\text{snow depth}} = 0.0029$ , SE = 0.0006) was included in all models constituting the 95% confidence set for adult females, adult males, and fawns (Table 2) and had a normalized Akaike weight of 1.00 (Table 3). The odds of being in poor body condition when snow depth increases from 0 to 500 cm increase by 4.21 times ( $\exp(0.0029 \times 500)$ ; 95% CI: 2.79–6.34) for adult females, 5.57 times (95% CI: 2.67–11.64) for adult males, and 4.18 times (95% CI: 2.30–7.59) for fawns (see Table 4).

Rainfall (adult females,  $\beta_{\text{rainfall}} = 0.0135$ , SE = 0.0039; adult males,  $\beta_{\text{rainfall}} = 0.0142$ , SE = 0.0070) was included in each of the two best models forming the 95% confidence sets for adult females and adult males (Table 2) and had normalized Akaike weights of 1.00 and 0.73, respectively (Table 3). For every increase in rainfall from 0 to 90 mm, the odds of being in poor body condition increase by 3.37 times

**Table 4.** Model-averaged parameter estimate ( $\beta$ ) with standard error (SE) and the odds ratio with 95% confidence interval (CI) for variables with  $Nw_i > 0.60$  (see Table 3).

Variable	$\beta$ (SE)	Odds ratio (CI)
<b>Adult females</b>		
Snow depth	0.0029 (0.0004)	4.21 (2.79–6.34)
Temperature	–0.0260 (0.0142)	0.77 (0.58–1.02)
Rainfall	0.0135 (0.0039)	3.37 (1.69–6.74)
<b>Adult males</b>		
Snow depth	0.0034 (0.0008)	5.57 (2.67–11.64)
Temperature	0.0234 (0.0019)	1.26 (1.22–1.31)
Rainfall	0.0142 (0.0061)	3.58 (1.21–10.48)
<b>Fawns (males and females)</b>		
Snow depth	0.0029 (0.0006)	4.18 (2.30–7.59)
Temperature	0.0495 (0.0202)	1.64 (1.10–2.44)

**Note:** Odds ratios for snow depth are for an increase of 500 cm; odds ratios for temperature represent a decrease in temperature of 10 °C below –15 °C; and odds ratios for rainfall represent an increase of 90 mm.

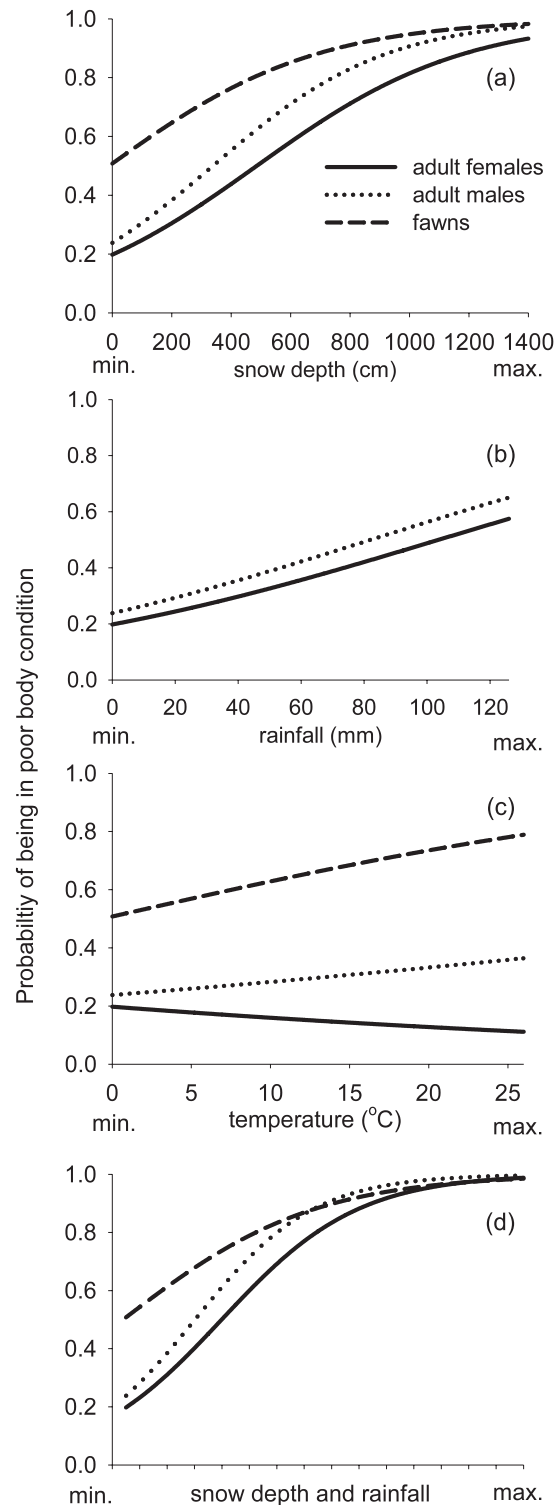
(95% CI: 1.6877–6.7370) for adult females and by 3.58 times (95% CI: 1.2284–10.4280) for adult males (see Table 4).

The variable temperature (adult females,  $\beta_{\text{temperature}} = -0.0260$ , SE = 0.0142; adult males,  $\beta_{\text{temperature}} = 0.0234$ , SE = 0.0019; fawns,  $\beta_{\text{temperature}} = 0.0495$ , SE = 0.0202) had high normalized Akaike weights for each age/sex group and was included in all or most of the models in the 95% confidence sets (Tables 2, 3). For an increase in the temperature variable of 10 °C (i.e., a drop of 10 °C below –15 °C), the odds of being in poor body condition are 0.7710 (95% CI: 0.58–1.02) for adult females, 1.2632 (95% CI: 1.22–1.31) for adult males, and 1.6408 (95% CI: 1.10–2.44) for fawns (see Table 4).

Fawns entered winter with the highest probability of being in poor body condition (logistic curve y-intercept of 0.51, SE = 0.07), followed by adult males (y-intercept of 0.24, SE = 0.08) and adult females (y-intercept of 0.20, SE = 0.08; Fig. 2). Although adult males have a higher probability of being in poor body condition than adult females, overlapping standard errors suggest that differences may be small. Based upon the slope in Fig. 2d, adult male body condition appears to decline most rapidly as winter severity increases, although fawns have a higher probability of being in poor body condition for each given important variable earlier than adult males as a result of differences in body condition at the beginning of winter.

The effect of snow depth is greatest on fawns and least on adult females (Fig. 2a). The effect of rainfall is quite similar between adult females and adult males (Fig. 2b). The effect of temperature on each age/sex group varies considerably: fawns are most affected, followed by adult males, and adult females apparently become more likely to be in good body condition as the temperature variable increases (i.e., as it becomes colder for longer; Fig. 2c). The similarity between the logistic curves for snow depth only and for the combined effects of snow depth and rainfall illustrate that over the range of weather conditions, snow depth is the primary influence on body condition (Fig. 2d).

**Fig. 2.** Logistic curves ( $P(Y_i) = \exp(\beta_0 + \beta_1 + \beta_2)/1 + \exp(\beta_0 + \beta_1 + \beta_2)$ ) showing the probability of being in poor body condition for white-tailed deer (fawns, adult males, and adult females) in Nova Scotia, Canada, 1987–2002, as (a) snow depth (0–1446 cm), (b) rainfall (0–126 mm), and (c) temperature (degrees below –15 °C) increase between 1 November and 15 May. (d) Combined (snow depth and temperature only) logistic curve for the probability of being in poor body condition for the minimum to maximum values for each variable.



## Discussion

Our results suggest that within the normal range of conditions experienced in Nova Scotia, winter weather conditions (primarily snow depth and rainfall) can adversely affect the body condition of all age/sex groups of white-tailed deer in a predictable manner. In eastern Canada, white-tailed deer losses to malnutrition are thought to play a minor role in population dynamics (Whitlaw et al. 1998; Patterson et al. 2002). Particularly harsh winters may cause females to divert resources away from reproduction so that the energy expenditures required for developing a foetus to full term and for lactation can be avoided, leading to a better chance of surviving the winter and recovering to reproduce again in future years (Clutton-Brock et al. 1989). The period of worst body condition coincides with winters' end and the most energetically expensive trimester of gestation, so it seems likely that winter weather influences population change in this region through low recruitment rates and the effects of low birth weight and slow development on lifetime reproductive success rather than through direct losses due to overwinter starvation.

We considered the variable for cumulative average weekly snow depth during the winter of death to have the greatest overall effect on the body condition of all sex/age classes of deer. This variable occurred in all models in each of the 95% confidence sets and had the greatest effect on body condition for the range of conditions occurring during the study period. Cumulative average weekly rainfall had the second greatest influence on the body condition of adult males and adult females. Cumulative average weekly temperature below  $-15^{\circ}\text{C}$  had the least influence among variables that showed evidence of affecting body condition. Similarly, DelGiudice et al. (2002) found that snow depth had a much greater influence on the chance of survival of female white-tailed deer than did number of days below  $-17.7^{\circ}\text{C}$ , and Hobbs (1989) found that nutritional restriction resulting from snow cover had a much greater influence on deer body condition than ambient temperature.

We suggest that the evidence for effects of temperature found in our analysis may be a spurious result because (i) in each age/sex group, >50% of the values for the temperature variable were zero, (ii) the difference between the extreme values of temperature in our data set ( $0$ – $25^{\circ}\text{C}$ ) may not represent a biologically meaningful change, and (iii) the model-averaged parameter estimate for adult females was  $-0.0260$ , suggesting that as temperature decreases, the chances of being in good body condition increase. An alternative explanation could be that, on average, high values for the temperature variable (i.e., lower temperatures for longer periods) correspond to lower amounts of rainfall. We have shown that as the amount of rainfall decreases, so too does the likelihood of adult females being in poor body condition. If this relationship holds true, it seems possible, considering the range of relatively moderate overwinter temperatures occurring in Nova Scotia and the fact that adult females enter winter with the highest body fat reserves, that "colder" may in fact be better for adult female white-tailed deer in Nova Scotia. We acknowledge that if this were true, one would expect no effect of temperature rather than the negative relationship found here, and also that this relationship would not be found if the temperature variable included much lower

temperatures for longer periods. Because the effects of temperature on adult males and fawns were as expected and the parameter estimates were consistent among models within all three age/sex groups, the results could imply that there are indeed intraspecific differences in the response of age/sex groups to temperature.

We found very little evidence for density-dependent effects on body condition during the winter of death. Although density was included in some models, its normalized Akaike weight was never greater than 0.60. This was surprising, as Patterson and Power (2002) found that the proportion of fawns, yearlings, and adults suffering from severe malnutrition (<25% femur marrow fat content) within the same population was correlated to deer density during the winter of death. This may be explained by the differences in peak population sizes included in the respective analyses. The deer population during our study period peaked at 106 301 deer in 1987–1988. Data analysed for the same population by Patterson and Power (2002) included population highs ranging between 119 237 and 144 987 from 1984 to 1987 that were not available for our study. Both theoretical (Fowler 1981) and field studies (Sæther et al. 1996; Andersen and Linnell 2000) indicate that density-dependent suppression of population growth in large herbivores is not likely to occur until densities approach carrying capacity. Browse surveys indicate that the winter carrying capacity for deer in Nova Scotia is lower than that in other areas of northeastern North America (Potvin and Huot 1983; Lock 1997; Dumont et al. 2000), which suggests that density-dependent forage competition may become an important factor affecting body condition at higher densities, although it may not have been a factor at the population densities observed during our study.

Adult females entered winter with the lowest probability of being in poor body condition, followed by adult males and then fawns (Fig. 2d). This is likely explained by the small body size of fawns, the high energetic costs of the autumn rut to adult males (Moen 1976; Mautz 1978), and the low initial costs of gestation to adult females (Pekins et al. 1998). Differences in the probability of entering winter in poor body condition between adult males and adult females, although trending toward our prediction (adult males > adult females), appear to be minimal (overlapping standard errors of y-intercepts). A possible explanation for this may be age-related variation in participation in the autumn rut. In Norway, Yoccoz et al. (2002) found that weight loss among prime-aged male red deer (genus *Cervus* L.) was much greater than that of young and senescent male red deer. They suggested that this was related to the inability of the latter to defend a harem and thus, they do not incur costs associated with the autumn rut. If a similar pattern occurs in white-tailed deer, then variation in reproduction among males may account for the apparent similarity in the probability of entering winter in poor body condition between adult males and adult females.

The smaller effect sizes for adult females (Figs. 2a–2c) may be a result of females aborting foetuses or diverting energy toward self-maintenance rather than gestation and lactation (Ricca et al. 2002). Clutton-Brock et al. (1989) found that the costs of gestation for female red deer were minimal compared with the costs of lactation. They also found that the chances of an adult female surviving the subsequent win-



ter decreased with increasing current winter rainfall for females that reared a calf until weaning, but not for females that lost a calf shortly after birth or were barren. Similarly, the chances of producing a calf the following summer decreased with increasing current winter rainfall for females that had raised a calf to at least 6 months of age, but not for barren females or those that had lost their calf soon after birth. This suggests that fitness increases for prime-aged females if they divert energy away from current reproduction during severe winters. Because the costs of gestation for white-tailed deer occur primarily during the third trimester (Pekins et al. 1998), and in some places fawn abandonment has been shown to be a significant factor contributing to fawn mortality (Ricca et al. 2002), it appears that the reproductive costs and benefits to white-tailed deer of raising fawns until weaning and delaying reproduction may be similar to those suggested by Clutton-Brock et al. (1989) for red deer.

Mech et al. (1987) and McRoberts et al. (1995) found that in Minnesota, snow depth (sum of monthly maximum snow depths) affected white-tailed deer demography cumulatively, with changes in fawn:doe ratios becoming measurable only after 3 years. Patterson and Power (2002) suggested that white-tailed deer in Nova Scotia may respond to the effects of winter weather (snowfall) and population density from the previous 2 years, resulting in changes in population growth rates. They proposed that the cumulative effects of these variables were due to the inability of white-tailed deer to fully recover from the effects of severe winters during previous years. If this were the case, we would expect to find evidence for cumulative effects of snow depth or density on body condition. As we found no evidence for any of the multiyear variables, we suggest that variation among cohorts may explain the apparent cumulative life-history effects reported to be induced by environmental conditions and (or) density dependence. Cohort variations occur when individuals within a certain cohort experience common environmental conditions (density-dependent or density-independent) that generate differences in future reproductive performance, which then make that cohort distinguishable from others (Beckerman et al. 2002). Beckerman et al. (2002) suggested that mature females that experience unfavourable environmental conditions causing poor nutrition can pass on the effects of that malnutrition to the next generation. As we found no evidence of a carryover, the observed cumulative effects of environmental conditions on deer population dynamics may be better explained by inheritance of the effects of the maternal environment, perhaps exacerbated by further adverse conditions, than by the inability of animals to recover from the detrimental effects of previous winters.

Because northern white-tailed deer usually do not reproduce until their second year (Smith 1991), the 2- to 3-year cumulative effects of winter weather found by Mech et al. (1987) and Patterson and Power (2002) may be explained if a cohort is in utero during a severe winter and is born smaller: the cohort would have reduced initial and lifetime reproductive success that would become measurable when it reproduced two winters thereafter. This effect would be particularly pronounced if the age structure of the population in question was young, as is the case with most harvested ungulate populations (e.g., Langvatn and Loison 1999; Festa-

Bianchet et al. 2003). Messier (1991, 1995) reanalysed the data set of Mech et al. (1987) under the premise that nutrition is not dichotomous but continuous, so that the effects of the most recent winter should be most influential and the effects of previous winters increasingly less influential (Mech et al. (1987) found measurable effects only after 3 years). Messier (1991, 1995) suggested that density dependence and wolf (*Canis lupus* L., 1758) predation limited the white-tailed deer in this population and found no effect of the previous winters' snow. However, Post and Stenseth (1998) examined the effect of the North Atlantic Oscillation (large-scale climate index) on the same population and found a lag of 3 years before its demographic effects became measurable in population growth; they suggested that this supported the hypothesis of Mech et al. (1987) regarding the cumulative effects of winter weather. As the above papers do not address the fundamental biological factor thought to lead to demographic variation (i.e., body condition), we believe our study illustrates that the putative cumulative effects of winter weather may in fact be the result of the detection of lagged cohort effects within variables constructed to measure the multiyear cumulative effects of winter weather. We concur with Patterson and Power (2002) that the findings of Post and Stenseth (1998) may in fact be a better illustration of lagged effects than of cumulative effects, providing further support that previous demonstrations of cumulative effects may in fact represent cohort variation. Fat deposition is key to the overwinter survival of white-tailed deer and so it seems logical that prime-aged adult females would direct energy first toward survival and then toward reproduction. This would increase lifetime reproductive success, especially if reproductive success in the following year is enhanced by the animal being in better body condition.

Trade-offs between survival and fecundity in ungulates and their dependence on current and previous environmental conditions have been documented (Gaillard et al. 1997, 2003; Kruuk et al. 1999a). Gaillard et al. (2003) highlighted two paths through which cohort variation could affect population dynamics. The first is the immediate effect that poor maternal condition and unfavourable environmental conditions can have on first-year survival of a cohort, resulting in reduced recruitment. The second is a long-term path whereby conditions before and (or) immediately after birth affect the subsequent reproductive quality of the animal.

We have demonstrated that in Nova Scotia the body condition of white-tailed deer during winter is most negatively affected by increasing snow depth and exposure to rainfall. Previous studies have illustrated that overwinter mortality due to malnutrition in this area is minimal (Whitlaw et al. 1998; Patterson et al. 2002) and that poor maternal body condition may lead to variation in recruitment and lifetime reproductive success (e.g., Clutton-Brock et al. 1989). We suggest that the primary pathway through which winter weather influences demographic variation in this population is through its influence on maternal body condition and subsequent reproductive success.

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## References

- Aanes, R., Sæther, B.-E., and Øritsland, N. 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. *Ecography*, **23**: 437–443.
- Adams, L., and Dale, B. 1998. Reproductive performance of female Alaskan caribou. *J. Wildl. Manag.* **62**: 1184–1195.
- Allen, R., and McCullough, D. 1976. Deer–car accidents in southern Michigan. *J. Wildl. Manag.* **40**: 317–325.
- Andersen, R., and Linnell, J. 2000. Irruptive potential in roe deer: density-dependent effects on body mass and fertility. *J. Wildl. Manag.* **64**: 698–706.
- Beckerman, A., Benton, T., Ranta, E., Kaitala, V., and Lundberg, P. 2002. Population dynamic consequences of delayed life-history effects. *Trends Ecol. Evol.* **17**: 263–269.
- Boyce, M. 1979. Seasonality and patterns of natural selection for life histories. *Am. Nat.* **114**: 569–583.
- Burnham, K., and Anderson, D. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Chan-McLeod, A., White, R., and Russell, D. 1995. Body mass and composition indices for female barren ground caribou. *J. Wildl. Manag.* **59**: 278–291.
- Cheatum, F. 1949. Bone marrow as an index of malnutrition in deer. *N.Y. State Conserv.* **3**: 19–22.
- Clutton-Brock, T.H., and Albon, S.D. 1982. Winter mortality in Red deer (*Cervus elaphus*). *J. Zool. (Lond.)*, **198**: 515–519.
- Clutton-Brock, T.H., Albon, S.D., and Guinness, F.E. 1989. Fitness costs of gestation and lactation in wild mammals. *Nature (Lond.)*, **337**: 260–262.
- Clutton-Brock, T.H., Illius, A.W., Wilson, K., Grenfell, B.T., MacColl, A.D.C., and Albon, S.D. 1997. Stability and instability in ungulate populations: an empirical analysis. *Am. Nat.* **149**: 195–199.
- Cook, R., Cook, J., Murray, D., Zager, P., Johnson, B., and Gratson, M. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. *J. Wildl. Manag.* **65**: 973–987.
- Crête, M., and Huot, J. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Can. J. Zool.* **71**: 2291–2296.
- DelGiudice, G.D., Riggs, M.R., Joly, P., and Pan, W. 2002. Winter severity, survival and cause-specific mortality of female white-tailed deer in north central Minnesota. *J. Wildl. Manag.* **66**: 698–711.
- Drolet, C. 1976. Distribution and movements of white-tailed deer in southern New Brunswick in relation to environmental factors. *Can. Field-Nat.* **90**: 123–136.
- Dumont, A., Crête, M., Puellet, J.-P., Huot, J., and Lamoureux, J. 2000. Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. *Can. J. Zool.* **78**: 764–776.
- Environmental Systems Research Institute, Inc. 2003. ArcGIS®. Version 8.3 [computer program]. Environmental Systems Research Institute, Inc., Redlands, Calif.
- Festa-Bianchet, M., Gaillard, J.-M., and Côté, S.D. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *J. Anim. Ecol.* **72**: 640–649.
- Forchhammer, M.C., Post, E., and Stenseth, N.C. 1998. Breeding phenology and climate. *Nature (Lond.)*, **391**: 29–30.
- Forchhammer, M.C., Clutton-Brock, T.H., Lindström, J., and Albon, S.D. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *J. Anim. Ecol.* **70**: 721–729.
- Gaillard, J.-M., Boutin, J.-M., Delmore, D., Van Laere, G., Duncan, P., and Lebreton, P.-D. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**: 502–513.
- Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**: 58–63.
- Gaillard, J.-M., Loison, A., Toigo, C., Delmore, D., and Van Laere, G. 2003. Cohort effects and deer population dynamics. *Ecoscience*, **10**: 412–420.
- Groot Bruinderink, G., and Hazebroek, E. 1996. Ungulate traffic collisions in Europe. *Conserv. Biol.* **10**: 1059–1067.
- Haikonen, H., and Summala, H. 2001. Deer–vehicle crashes. Extensive peek at 1 hour after sunset. *Am. J. Prev. Med.* **21**: 209–213.
- Hallet, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M., and Grenfell, B.T. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature (Lond.)*, **430**: 71–75.
- Hjeljord, O., and Histol, T. 1999. Range–body mass interactions of a northern ungulate — a test of hypothesis. *Oecologia*, **119**: 326–339.
- Hobbs, N. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildl. Monogr.* No. 101.
- Hosmer, D., and Lemeshow, S. 2000. Applied logistic regression. Wiley, New York.
- Huot, J. 1974. Winter habitat of white-tailed deer at Thirty-one Mile Lake, Quebec. *Can. Field-Nat.* **88**: 293–301.
- Jensen, P.G., Pekins, P.J., and Holter, J.B. 1999. Compensatory effect of the heat increment of feeding on thermoregulation costs of white-tailed deer fawns in winter. *Can. J. Zool.* **77**: 1474–1485.
- Kearney, S., and Gilbert, F. 1976. Habitat use by white-tailed deer and moose on sympatric range. *J. Wildl. Manag.* **40**: 645–657.
- Kruuk, L.E., Clutton-Brock, T.H., Rose, K.E., and Guinness, F.E. 1999a. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proc. R. Soc. Lond. B Biol. Sci.* **266**: 1655–1661.
- Kruuk, L.E., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M., and Guinness, F.E. 1999b. Population density affects sex ratio variation in red deer. *Nature (Lond.)*, **399**: 459–461.
- Langvatn, R., and Loison, A. 1999. Consequences of harvesting on age structure, sex ratio and population dynamics of red deer *Cervus elaphus* in central Norway. *Wildl. Biol.* **5**: 213–223.
- Lee, S., Press, M., Lee, J., Ingold, T., and Kurttila, T. 2000. Regional effects of climate change on reindeer: a case study of the Muotkatunturi region in Finnish Lapland. *Polar Res.* **19**: 99–105.
- Lesage, L., Crête, M., Huot, J., and Ouellet, J.-P. 2001. Evidence for a trade-off between growth and body reserves in northern white-tailed deer. *Oecologia*, **126**: 30–41.
- Lock, B.A. 1997. Deer wintering habitat models for two regions of Nova Scotia, M.Sc. thesis, Acadia University, Wolfville, N.S.
- Loison, A., and Langvatn, R. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia*, **116**: 489–500.
- Loison, A., Langvatn, R., and Solberg, E. 1999a. Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography*, **22**: 20–30.

- Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J., and Jullien, J.-M. 1999b. Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, **80**: 2539–2554.
- MacDonald, B. 1996. Spatial distribution, survivorship and effects of forest harvesting on over wintering white-tailed deer in Nova Scotia. M.Sc. thesis, Acadia University, Wolfville, N.S.
- MathSoft Engineering and Education, Inc. 1999. S-PLUS® 2000 for Windows [computer program]. MathSoft Engineering and Education, Inc., Cambridge, Mass.
- Mauget, C., Mauget, R., and Sempéré, A. 1997. Metabolic rate in female European roe deer (*Capreolus capreolus*): incidence of reproduction. *Can. J. Zool.* **75**: 731–739.
- Mautz, W. 1978. Sledding on a bushy hillside: the fat cycle in deer. *Wildl. Soc. Bull.* **6**: 88–90.
- Mautz, W., Silver, H., Holter, J., Hayes, H., and Urban, W., Jr. 1976. Digestibility and related nutritional data for seven northern deer browse species. *J. Wildl. Manag.* **40**: 630–638.
- McCaffery, K.R. 1973. Road-kills show trends in Wisconsin deer populations. *J. Wildl. Manag.* **37**: 212–216.
- McRoberts, R.E., Mech, L.D., and Peterson, R.O. 1995. The cumulative effect of consecutive winters' snow depth on moose and deer populations: a defence. *J. Anim. Ecol.* **64**: 131–135.
- Mech, L.D., and DelGiudice, G.D. 1985. Limitations of the marrow-fat technique as an indicator of body condition. *Wildl. Soc. Bull.* **13**: 204–206.
- Mech, L.D., McRoberts, R.E., Peterson, R.O., and Page, R.E. 1987. Relationship of deer and moose populations to previous winters' snow. *J. Anim. Ecol.* **56**: 615–627.
- Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *J. Anim. Ecol.* **60**: 377–393.
- Messier, F. 1995. Is there evidence for a cumulative effect of snow on moose and deer populations? *J. Anim. Ecol.* **64**: 136–140.
- Moen, A. 1976. Energy conservation by white-tailed deer in the winter. *Ecology*, **56**: 192–198.
- Moen, A. 1985. The biology and management of wild ruminants. Part 5. Meteorology and thermal relationships of wild ruminants. Corner Brook Press, Lansing, N.Y.
- Morrison, M.L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *J. Wildl. Manag.* **65**: 613–623.
- Morrison, S., Forbes, G., and Young, S. 2002. Browse occurrence, biomass, and use by white-tailed deer in a northern New Brunswick deer yard. *Can. J. For. Res.* **32**: 1518–1524.
- Mysterud, A. 2004. Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildl. Biol.* **10**: 203–211.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C., and Langvatn, R. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**: 959–974.
- Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Langvatn, R., and Steinheim, G. 2001. Nonlinear effects of large-scale climate variability on wild and domestic herbivores. *Nature (Lond.)*, **410**: 1096–1099.
- Neiland, K. 1970. Weight of dried marrow as an indicator of fat in caribou femurs. *J. Wildl. Manag.* **34**: 904–907.
- Nelson, M. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. *Can. J. Zool.* **73**: 1069–1076.
- O'Gara, B., and Harris, R. 1988. Age and condition of deer killed by predators and automobiles. *J. Wildl. Manag.* **52**: 316–320.
- Ozoga, J., and Gysel, L. 1972. Response of white-tailed deer to winter weather. *J. Wildl. Manag.* **36**: 892–896.
- Parker, K.L., Robbins, C.T., and Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manag.* **48**(2): 474–488.
- Patterson, B., and Power, V. 2002. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia*, **130**: 62–71.
- Patterson, B.R., Benjamin, L.K., and Messier, F. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. *Can. J. Zool.* **76**: 1885–1897.
- Patterson, B.R., MacDonald, B.A., Lock, B.A., Anderson, D.A., and Benjamin, L.K. 2002. Proximate factors limiting population growth of white-tailed deer in Nova Scotia. *J. Wildl. Manag.* **66**: 511–521.
- Pekins, P.J., Smith, K.S., and Mautz, W.W. 1998. The energy cost of gestation in white-tailed deer. *Can. J. Zool.* **76**: 1091–1097.
- Post, E., and Stenseth, N.C. 1998. Large-scale climate fluctuation and population dynamics of moose and white-tailed deer. *J. Anim. Ecol.* **67**: 537–543.
- Post, E., and Stenseth, N.C. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**: 1322–1339.
- Post, E., Stenseth, N.C., Langvatn, R., and Fromentin, J. 1997. Global climate change and phenotypic variation among red deer cohorts. *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 1317–1324.
- Post, E., Forchhammer, M.C., Stenseth, N.C., and Langvatn, R. 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. *Am. Nat.* **154**: 194–204.
- Potvin, F., and Huot, J. 1983. Estimating carrying capacity of a white-tailed deer wintering area in Québec. *J. Wildl. Manag.* **42**: 463–475.
- Potvin, F., Huot, J., and Duchesneau, F. 1981. Deer mortality in the Pôhénégamook wintering area, Québec. *Can. Field-Nat.* **95**: 80–84.
- Ransom, A. 1965. Kidney and marrow fat as indicators of white-tailed deer condition. *J. Wildl. Manag.* **29**: 397–398.
- Ricca, M., Anthony, R., Jackson, D., and Wolfe, S. 2002. Survival of Columbian white-tailed deer in western Oregon. *J. Wildl. Manag.* **66**: 1255–1266.
- Sabine, D., Morrison, S., Whitlaw, H., Ballard, W., Forbes, G., and Bowman, J. 2002. Migration of white-tailed deer under varying winter climate regimes in New Brunswick. *J. Wildl. Manag.* **66**: 718–728.
- Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* **12**: 143–149.
- Sæther, B.-E., Andersen, R., Hjeljord, O., and Heim, M. 1996. Ecological correlates of regional variation in life history of the moose *Alces alces*. *Ecology*, **77**: 1493–1500.
- Severinghaus, C. 1949. Tooth development and wear as criteria of age in white-tailed deer. *J. Wildl. Manag.* **13**: 195–216.
- Smith, W. 1991. *Odocoileus virginianus*. *Mamm. Species. No.* **388**: 1–13.
- Solberg, E., Jordhoy, P., Strand, O., Aanes, R., Loison, A., Sæther, B.-E., and Linnell, J. 2001. Effects of density dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography*, **24**: 441–451.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Co, New York.
- Takatsuki, S. 2000. Kidney fat and marrow fat indices of the sika deer population at Mount Goyo, northern Japan. *Ecol. Res.* **15**: 453–457.
- Tierson, W., Mattfeld, G., Sage, R., and Behrend, D. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. *J. Wildl. Manag.* **49**: 760–769.

- Torbit, S., Carpenter, L., Swift, D., and Alldredge, A. 1985. Differential loss of fat and protein by mule deer during winter. *J. Wildl. Manag.* **49**: 80–85.
- Verme, L. 1965. Reproduction studies on penned white-tailed deer. *J. Wildl. Manag.* **29**: 74–79.
- Verme, L. 1973. Movements of white-tailed deer in upper Michigan. *J. Wildl. Manag.* **37**: 545–552.
- Vreelend, J., Diefenbach, D., and Wallingford, B. 2004. Survival rates, mortality causes, and habitats of Pennsylvania white-tailed deer fawns. *Wildl. Soc. Bull.* **32**: 542–553.
- Weber, S., Mautz, W., Lanier, J., and Wiley, J. 1983. Predictive equations for deeryards in northern New Hampshire. *Wildl. Soc. Bull.* **11**: 331–338.
- Weladji, R., and Holand, O. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. *Oecologia*, **136**: 317–323.
- Whitlaw, H., Ballard, W., Sabine, D., Yound, S., Jenkins, R., and Forbes, G. 1998. Survival and cause-specific mortality rates of adult white-tailed deer in New Brunswick. *J. Wildl. Manag.* **62**: 1335–1341.
- Yoccoz, N.G., Mysterud, A., Langvatn, R., Stenseth, N.C. 2002. Age- and density-dependent reproductive effort in male red deer. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 1523–1528.
- Yokoyama, M., Uni, H., Suzuki, M., Kaji, K., and Ohtaishi, N. 2000. Indices for nutritional condition and thresholds for winter survival in sika deer in Hokkaido, Japan. *Jpn. J. Vet. Res.* **48**: 119–127.