CHAPITRE 1

Synergistic effects of population density and environmental factors on the body condition of female white-tailed deer in autumn

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RÉSUMÉ

La capacité à prédire l'allocation d'énergie aux différents paramètres de la condition corporelle, en fonction des contraintes environnementales, est une composante clé dans la compréhension des processus gouvernant la dynamique des populations. Grâce à un suivi à long terme (2002–2013), nous avons évalué l'influence de la densité de population et des facteurs environnementaux sur les paramètres individuels de la condition corporelle des femelles du cerf de Virginie récoltées pendant la chasse à l'automne sur l'île d'Anticosti, Québec, Canada. Nous avons utilisé la masse corporelle, la masse du muscle péronier et l'épaisseur du gras sous-cutané de la fesse pour évaluer le statut nutritionnel de 3 123 femelles. Nous avons observé que la demande énergétique induite par la lactation affectait négativement tous les paramètres de la condition corporelle à l'automne. Une densité de population élevée réduisait les gains automnaux sous forme de réserves en gras et en protéines. L'effet négatif des précipitations hivernales sur les réserves automnales en gras était seulement détecté à faible densité de population. Une faible valeur de l'indice différentiel normalisé de la végétation (NDVI, pour l'acronyme de *Normalized Difference Vegetation Index* en anglais) au printemps contribuait à de plus grandes réserves en protéines à l'automne. Inversement, une valeur élevée de NDVI au printemps réduisait la masse corporelle, et cette influence était plus marquée à densité de population élevée. Notre étude de 12 ans a permis de détecter les effets synergiques entre la densité de population et les facteurs environnementaux sur les indicateurs physiologiques de la condition des femelles adultes du cerf de Virginie, tels que la masse corporelle et les réserves en gras et en protéines. Notre étude apporte de nouvelles connaissances pour mieux anticiper la façon dont les populations d'ongulés nordiques, limitées en ressources, peuvent répondre aux changements environnementaux futurs.

ABSTRACT

The ability to predict energy allocation for different body condition parameters, according to environmental constraints, is a key component in understanding the processes underlying population dynamics. We investigated the influence of population density and environmental factors on individual body condition parameters for female white-tailed deer based on long-term monitoring (2002–2013) of autumn harvest on Anticosti Island, Québec, Canada. We used dressed body mass, peroneus muscle mass, and rump fat thickness to evaluate the nutritional status of 3 123 adult females. We found that the energetic demands of lactation negatively affected all body condition parameters in autumn. High population density reduced autumn gains in body fat and body protein contents. The negative effect of winter precipitations on fat reserves in autumn only occurred at low population density. Low Normalized Difference Vegetation Index (NDVI) in spring favoured higher protein reserves in autumn. Conversely, high NDVI in spring reduced dressed body mass, and this influence was more pronounced under high population density. Our 12-year study allowed us to detect synergistic effects of population density and environmental factors on physiological indicators of the body condition of adult female white-tailed deer, including body mass, fat and protein reserves. Our study provides additional insights on how northern ungulates that are driven by food limitation may respond to future environmental changes.

KEY WORDS *Odocoileus virginianus,* resource allocation, body condition indices, environmental variation, population density.

INTRODUCTION

The body condition of an animal represents the balance between its energetic intake and nutritional requirements and expenditures (Parker *et al.* 1996, 2009), which generally vary with environmental conditions. In seasonal environments, ungulates experience energetic constraints because of the large seasonal contrasts in climate and food availability. For example, the rate of food intake for caribou and reindeer (*Rangifer tarandus*) increases during summer when resources are most abundant (Chan-McLeod *et al.* 1994), allowing them to maximize body reserves (Cook *et al.* 2004a). These reserves are then depleted during prolonged winters, when resources become scarce (Mautz 1978). Individuals also differ in physiological demands according to their reproductive status (Mysterud *et al.* 2004). Unlike males, whose body condition highly decreases during the rut (Barboza *et al.* 2004), the body condition of females in temperate regions peaks in early winter when nutritional demands are low (Parker *et al.* 2009). It then declines to its lowest point during spring-early summer, due to the low quality and availability of forage and the nutritional requirements of gestation, and the particularly pronounced demands associated with lactation (Moen 1978, Mauget *et al.* 1997). Replenishment of endogenous reserves in summer and autumn is therefore critical to restore body condition, and ultimately ensure over-winter survival and subsequent reproduction. In addition to these intrinsic factors, body condition of ungulates may also be influenced by extrinsic factors such as population density and climate.

Population density may influence body condition through its impact on the availability of high forage quality (Bonenfant *et al.* 2009). During spring and summer, ungulates select plant species that maximize energy acquisition (Pettorelli *et al.* 2003), but intraspecific competition for forage may restrict individuals to poor vegetation patches (Freeland & Choquenot 1990). This density-induced nutritional limitation is known to affect less competitive individuals, leading to a deterioration of body condition over time (Bonenfant *et al.* 2009). Density-dependent processes may have an immediate impact on body condition (Gaillard *et al.* 2000) or may be delayed in time (Messier *et al.* 1988). Solberg *et al.* (2004), for example, reported that poor condition during the year of birth had long-lasting negative effects on the body mass of adult moose (*Alces alces*), resulting in the expression of cohort effects.

Climate may influence directly body condition because variations in individual energy requirements may be induced by intra- and inter-annual fluctuations in climatic conditions and weather (Gaillard *et al.* 2000). At northern latitudes, ungulates are often exposed to extreme winter conditions. Snow depth may influence energy expenditure during locomotion (Parker *et al.* 1984, 1999) and limit food acquisition (White *et al.* 2009). Winter is often critical because low temperatures, rain events and strong winds may increase metabolic costs

associated with thermoregulation (Parker & Robbins 1985). Moreover, rain-on-snow events may reduce access to vegetation (Stien *et al.* 2010). Climate also acts indirectly on body condition through its influence on vegetation. The variability of climate patterns alters the onset of vegetation growth (Pettorelli *et al.* 2007b) and the chemical composition of plants (Lenart *et al.* 2002), which are crucial determinants of ungulate diet quality. In northern ungulates, the timing of snowmelt determines the timing of vegetation emergence (Kudo 1991). Early onset of vegetation after the snowmelt may have a positive influence on ungulate body condition because it is usually associated with slow plant development and extended periods of high quality forage (Pettorelli *et al.* 2005b, 2007b), leading to high nutrient intake and high digestibility for deer (Parker *et al.* 1999).

Population density and environmental stochasticity are known to have synergistic effects on life-history traits in ungulates (Sæther 1997, Coulson *et al.* 2000, Mason *et al.* 2014), although their combined influence on physiological indicators, such as body fat and body protein contents, are less documented. The assessment of body condition through morphological measurements is a key tool to evaluate the nutritional status of individuals (Parker *et al.* 2009). It is an informative way to investigate energy allocation in response to environmental variability and has been used in several ungulate species [e.g., roe deer *Capreolus capreolus* (Hewison *et al.* 1996), caribou (Chan-McLeod *et al.* 1999, Barboza *et al.* 2004), moose (Herfindal *et al.* 2006a), impala *Aepyceros melampus* (Marshal *et al.* 2012)]. Body fat and body protein contents are good predictors of body condition because they fulfill two distinct physiological functions (Parker *et al.* 2009): body fat is the main energy reserve in mammals and is efficiently catabolized when required under environmental or physiological stress (Barboza *et al.* 2009), whereas body proteins are available primarily to satisfy biomechanical functions, tissue repair, and milk production (Barboza *et al.* 2009). Reserves in the form of proteins are less efficiently converted into energy but can be catabolized when all fat reserves have been used (Mautz 1978). Finally, body mass is another morphological measurement which is an integrative index of body condition (Taillon *et al.* 2011) widely used to assess variability in body condition (Parker *et al.* 2009).

Here we investigated the factors that influence body mass, body fat, and body protein contents of female white-tailed deer during autumn on Anticosti Island (Québec, Canada). A prior study by Simard *et al.* (2014) based on a 5-year monitoring program was unable to detect temporal variations in body condition parameters. Our long-term monitoring (2002–2013) thus provided an opportunity to better understand the variability in body condition parameters from an individual perspective, while accounting for spatiotemporal variability. In addition, data from different geographical areas of the island allowed us to consider a broad range of population densities and environmental conditions. Access to harvested carcasses in autumn allowed us to measure body condition in a critical period of individual energy storage (Parker *et al.* 2009). Finally, Anticosti Island provided

an interesting case study because of the absence of predators, the harsh and variable environmental conditions, and the severe chronic browsing by overabundant white-tailed deer that has occurred over the last decades (Tremblay *et al.* 2005).

We hypothesized that body condition of females in autumn would be determined by intrinsic characteristics. We predicted that lactation would induce reproductive costs (Mauget *et al.* 1997) that would be reflected by a decrease in body mass, body fat, and body protein content. We also hypothesized that variation in extrinsic factors would affect body condition parameters directly through energy expenditure, as well as indirectly through the alteration of resource availability and quality. We predicted that high population density (i.e., higher competition for resources) during the year of harvest, the previous year, and the year of birth as well as harsher climate (e.g., high snow accumulation) during the previous winter would negatively affect body mass, body fat, and body protein contents in autumn. Finally, we predicted that high forage quality during the previous spring, as estimated by the normalized difference vegetation index (NDVI; Pettorelli *et al.* 2005a), would increase all body condition parameters in autumn. We expected that the combined effects of population density and environmental conditions would have stronger consequences than their respective single effects on body condition; we thus considered interactions in our models (see Table 1.1 for a summary of our predictions).

Table 1.1. Direction of the predicted responses of body condition parameters to individual characteristics and environmental conditions for adult female white-tailed deer on Anticosti Island (Québec, Canada) between 2002 and 2013. Parameters of body condition include dressed body mass, peroneus muscle mass, and rump fat thickness. Peroneus muscle mass was used as an index of body protein reserves, whereas rump fat thickness was used as a proxy of body fat reserves.

Parameters of body condition	Individuals			Environmental conditions					Interaction
	Age	Date	Lactation status (yes)	Density at harvest	Density the previous year	Density the year of birth	Climate	Forage quality	Density * Climate
Dressed body mass	↗	↗	↗	↗	↗	↗	↗	↖	↗↗
Peroneus muscle mass	↗	↖	↗	↗	↗	↗	↗	↖	↗↗
Rump fat thickness	∅	↖	↗	↗	↗	↗	↗	↖	↗↗

∅, no effect; ↖, increase; ↗, decrease; ↗↗, strong decrease.

METHODS

Study area and population

White-tailed deer were introduced on Anticosti Island (49.5°N, 63°W; 7 943 km^2; Québec, Canada) in 1896. The population rapidly increased from *ca.* 220 to >150 000 deer, which represents a current density of >20 deer/km^2 with certain areas exceeding 50 deer/km^2 (Tremblay *et al.* 2006). Located in the Gulf of St. Lawrence, the island is at the northern limit of the range of white-tailed deer in North America. Climatic conditions are maritime sub-boreal, characterized by cool summers and long winters. Total annual precipitations were 917 ± 130 mm (mean ± SD), with about the third falling as snow (Environment Canada 2006). The intensive browsing of white-tailed deer on Anticosti Island had altered the composition of the native plant community, strongly reducing the abundance of white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam fir (*Abies balsamea*), which is being gradually replaced by less palatable species like white spruce (*Picea glauca;* Barrette *et al.* 2014).

Body condition

White-tailed deer were harvested by hunters each year from September to early December. Between 169 and 353 females were measured every year from 2002 to 2013 in the five study zones (West end, West, Central, North-East, and South-East; Figure 1.1), for a total of 3 123 measured individuals. We estimated age using examination of cementum annuli on incisors (Hamlin *et al.* 2000). We estimated body condition of deer within 48 h after harvest, by measuring dressed body mass (i.e., total body mass after removing viscera and blood), peroneus muscle mass, and rump fat thickness. We measured dressed body mass of adult females (i.e., ≥2.5 years old) using a spring scale (± 0.25 kg).

We indexed protein reserves by extracting peroneus muscles (i.e., *peroneus tertius* with extensor *digitorum longus* and extensor digit III) from the right hind leg and weighing (± 0.5 g) using a Pesola scale (Pesola AG, Baar, Switzerland). It provides a useful measurement of body protein reserves in autumn (Huot 1988, Chan-McLeod *et al.* 1995) and has been validated as a predictor of total protein mass in cervids using caribou (Crête *et al.* 1993, Taillon *et al.* 2011).

We estimated fat reserves by measuring rump fat thickness (± 0.2 cm) through the insertion of a ruler into the fat layer at 5 and 10 cm from the base of the tail at an angle of 45˚ from the backbone (Leader-Williams & Ricketts 1982). We then averaged both measurements. This index was a good proxy of fat reserves in Rocky Mountain elk (*Cervus elaphus nelsonii*; Cook *et al.* 2001) and has been validated with white-tailed deer

(Simard *et al*. 2014).

The lactation status of females was assessed by looking for the presence of milk in the udder. When milk could be extracted from the udder, the female was classified as lactating and otherwise not (Noble & Hurley 1999).
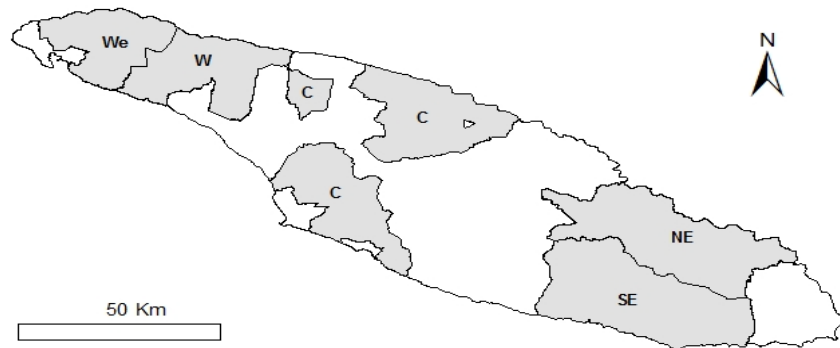
Figure 1.1. Location of the 5 study zones from which deer were harvested from 2002 to 2013 on Anticosti Island (Québec, Canada): West end (We), West (W), Central (C), North-East (NE), and South-East (SE).

Population density

Given the infrequent aerial surveys on the island, we used an index of density based on the number of deer seen per hunter per day, which has been validated with aerial survey data (Pettorelli *et al.* 2007a, Simard *et al.* 2012). In our study, hunter observations were used to determine the spatiotemporal variation in population density for the five study zones (Appendix 1). Population density estimates varied from a minimum of 3.4 ± 0.2 deer (mean ± SE) in 2003 in the North-East zone to a maximum of 35.0 ± 1.2 deer seen per hunter per day in 2002 in the South-East zone. With the collaboration of hunters and hunting guides, each harvested deer was located using landmarks (e.g., roads, trails, etc.) on a map distinct for each study zone.

Climatic conditions

We collected monthly values of total precipitation and temperature (i.e., minimum and maximum) over the period 1984–2013 to consider the environmental conditions of the years in which studied deer were born. We used interpolated data (McKenney *et al.* 2006) from the Meteorological Service of Canada because temperature and precipitation data were not available for the whole island. The interpolated grid data were produced using thin plate smoothing splines as implemented in the ANUSPLIN software package (Hutchinson

2004). The variables included in ANUSPLIN model specifications were the latitude, longitude, and elevation of each harvested deer. We estimated the average values of winter temperatures and the cumulative values of winter precipitations in January, February, and March.

We estimated the influence of snow on deer body condition using snow depth and sinking depth measured at two stations on the western end of the island. These two measures were gathered at 15-day intervals from October to May beginning in 1984. Snow depth (cm) was recorded using 10 graduated 3-m rulers spaced equidistantly every 5 m on a permanent transect. Sinking depth (cm) of deer was measured using a penetrometer imitating the foot pressure of deer during locomotion (Verme 1968). Cumulative snow sinking depth, corresponding to the sum of the products of weekly or biweekly sinking depths and the number of days between consecutive readings (NIVA value; transformed from cm*day to m*day in models), was used as an index of winter severity (Potvin & Breton 1992).

Vegetation

Vegetation phenology dynamics is well captured by variations in the NDVI (Justice *et al.* 1985). We used NDVI from satellite imagery as a proxy of vegetation productivity to assess the impact of plant phenology on deer body condition (Pettorelli *et al.* 2005a). We used images from the Advanced Very High Resolution Radiometer (AVHRR) provided by the Canadian long-term satellite data record (Canada Center for Remote Sensing 2016). Images had a resolution of 1 km in composites of 10 days and minimized artifacts caused by cloud cover. The pixels associated with water were removed. NDVI values ranging from 0 to 1 were produced, where green vegetation results in high values. Using ArcGIS 10.3.3 (ESRI, Redland, USA), we georeferenced the locations of harvest sites and created a circular buffer zone of 5 km radius around each site to characterize the home range of harvested deer and obtain a representative value of the NDVI. In each buffer zone, we extracted the average NDVI values from May to June for the period 1985–2013, because this temporal window corresponds to the period when vegetation starts growing and reaches a plateau. We calculated the average NDVI in May and the slope between average NDVI in early May and late June for each individual buffer zone, which we used as indices of vegetation productivity and rate of change in productivity, respectively (Pettorelli *et al.* 2007b). Rapid changes in NDVI during the green-up period usually have a negative influence on ungulates because they shorten the period of accessibility of high-quality forage (Pettorelli *et al.* 2007b).

Statistical analyses

We used linear mixed-effects models (lme4 package, Bates *et al.* 2015; R 3.2.3. v.10.X, R Development Core Team 2015) to investigate the variance observed in body condition parameters (i.e., dressed body mass,

peroneus muscle mass, and rump fat thickness) according to 11 explanatory variables (i.e., age, date of harvest, lactation status, density during the year of harvest, density during the previous year, density during the year of birth, winter temperature, winter precipitation, cumulative snow sinking depth, NDVI in spring, and rate of spring green-up; see Appendix 2 for a list of descriptive statistics of quantitative variables). We plotted residuals against the explanatory variables to detect non-linear relationships. The interaction between year and study zone was expressed as a random effect in all models. We identified this list of explanatory variables based on our biological knowledge of ungulates in general, and of white-tailed deer on Anticosti Island in particular (Simard *et al.* 2014). We assessed multicollinearity between explanatory variables using the variance inflation factor (VIF). Considering that multicollinearity may affect parameter estimates when VIF ≥3 (Zuur *et al.* 2010), variables were weakly correlated (VIF <2.2), except for spring NDVI and the rate of spring green-up (r = |0.8|). These variables were thus never included together in the same model. We standardized the rate of spring green-up by using a z-transformation (Schielzeth 2010).

We used Akaike's Information Criterion (AIC; Burnham & Anderson 2002) to select the most parsimonious model [lowest delta AIC (ΔAIC)]. For each response variable (i.e., dressed body mass, peroneus muscle mass, and rump fat thickness), we built a set of 23 candidate models using the tiered procedure of Hosmer & Lemeshow (2000; see Appendix 3 for the full list of candidate models; Simard *et al.* 2014). For all models, we grouped winter temperature and precipitation variables together. Our first step was to compare the AIC values of a null model (i.e., Model 0; model that included only the intercept) and of a reference model (i.e., Model 1; model that included age, date and lactation status) to reject the null hypothesis in all analyses. In a second step, we added explanatory variables related to density (i.e., Density^t, Density^{t-1} or Density^{birth}; see Appendix 2) to the reference model to build Models 2–8. If any model within the density candidate models had a ΔAIC value <2 compared to the reference model, the most parsimonious density model was selected for the final hierarchical selection step. Models 9–19 tested the improvement of model fit by adding environmental variables (i.e., Winter_T°, Winter_prec, Snow_depth, NDVI and Green-up; see Appendix 2) to the reference model. If an environmental model had a ΔAIC <2 compared to the reference model, we kept the most parsimonious environmental model for the final hierarchical selection step. Based on the results of models 2–19, all the variables retained (i.e., density + environmental variables) in the second and third steps of the hierarchical selection were added to the original reference model (i.e., Model 1) to build Model 20. This model corresponded to the best single-effects model and was used as the new reference model. For the final step, we assessed whether the interaction terms (i.e., two or three-way interactions) explained additional variance in response variables compared to the new reference model. For each response variable, the most parsimonious model was selected among models 20–23 (Table 1.2).

RESULTS

The hierarchical model selection procedure led to the selection of different models for each response variable (Table 1.2). Winter minimum temperature, cumulative snow sinking depth, and deer density during the previous year were retained in the final models, but the 95% confidence intervals (CI) estimated for these effects all included 0 (Table 1.3).

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Table 1.2. Most parsimonious models explaining the variation of body condition parameters (dressed body mass, $n = 2718$; peroneus muscle mass, $n = 2721$; rump fat thickness, $n = 2715$) of adult female white-tailed deer harvested on Anticosti Island (Québec, Canada) between 2002 and 2013. All models included the random term year × zone. The number of parameters (k) and Akaike's Information Criterion (AIC) values are presented. See details of hierarchical selection of all models tested in Appendix 3.

Response variable and model	k	AIC
Dressed body mass		
Age + Date + Lact + Density^t + Density^{birth} + NDVI + Density^t × NDVI	11	15,976.03
Peroneus muscle mass		
Age + Date + Lact + Density^t + Density^{birth} + Snow_depth + NDVI + Density^{birth} × NDVI + Density^{birth} × Snow_depth	13	21,293.32
Rump fat thickness		
Age + Date + Lact + Density$t$ + Density$t$-1 + Winter_T° + Winter_prec + Snow_depth + Green-up + Density$t$ × Winter_T° + Density^t × Winter_prec + Density^t × Green-up + Density^t × Snow_depth	17	6,491.71

Lact = lactation status, Density^t = density during the year of harvest, Density^{t-1} = density during the previous year, Density^{birth} = density during the year of birth, Winter_T° = winter temperature, Winter_prec = winter precipitation, Snow_depth = cumulative snow sinking depth, and Green-up = rate of spring green-up.

Dressed body mass

The dressed body mass of female white-tailed deer harvested in autumn averaged 47.9 ± 0.1 kg (mean ± SE; range: 23.0–60.0 kg). Age, date of harvest, lactation status, deer density during the year of birth, and the interaction between deer density during the year of harvest and spring NDVI influenced the dressed body mass of female white-tailed deer (Table 1.3). Dressed body mass was on average 1.8 ± 0.2 kg lower for lactating females than non-lactating females. For both lactating and non-lactating females, dressed body mass increased with age (Table 1.3), but raw data showed a decline after 11.5 years of age, indicating a potential effect of senescence (Figure 1.2). Dressed body mass increased throughout the hunting season and was positively related to deer density during the year of birth (Table 1.3). The NDVI in spring negatively affected dressed body mass, and this influence was stronger at high density than at low density (Table 1.3 and Figure 1.3).

Peroneus muscle mass

Peroneus muscle mass of harvested deer averaged 89.2 ± 0.3 g (range: 10.2–180.0 g). Age, lactation status, and deer density during the year of harvest influenced peroneus muscle mass (Table 1.3). Peroneus muscle mass was on average 1.2 ± 0.6 g lower for lactating females than non-lactating females. Peroneus muscle mass increased with age, but did not increase throughout the hunting season (Table 1.3). Deer density during the year of harvest had a negative effect on muscle mass (Table 1.3). At low density, the peroneus muscle mass of harvested deer was 2.0 ± 0.7 g higher than at high density.

Rump fat thickness

Rump fat thickness in autumn averaged 1.50 ± 0.02 cm (range: 0.00–5.15 cm). Date of harvest, lactation status, and the interaction between density during the year of harvest and winter precipitation influenced rump fat thickness in autumn (Table 1.3). Rump fat accumulated during autumn (from September 1st to December 5th) for all females (Table 1.3), but did not change significantly with age (Table 1.3). Rump fat thickness was lower for lactating females than non-lactating females (Table 1.3). The rate of the spring green-up had a positive influence on rump fat thickness (Table 1.3). At low density, increased winter precipitations reduced rump fat thickness, whereas no effect was observed at high density (Table 1.3 and Figure 1.4).

Table 1.3. Parameter estimates (Estim.) ± SE (with *t* and 95% CI) from the best-supported linear mixed-effects model describing dressed body mass (*n* = 2718), peroneus muscle mass (*n* = 2721) and rump fat thickness (*n* = 2715) for adult female white-tailed deer harvested on Anticosti Island (Québec, Canada) between 2002 and 2013. The variables with 95% CI that did not include 0 are indicated in bold.

Explanatory variable	Dressed body mass (kg)				Peroneus muscle mass (g)				Rump fat thickness (cm)			
	Estim.	SE	t	95% CI	Estim.	SE	t	95% CI	Estim.	SE	t	95% CI
Intercept	**39.0**	**1.5**	**25.4**	**[35.94; 42.11]**	**96.8**	**5.5**	**17.7**	**[85.94; 107.55]**	**2.7**	**0.6**	**4.8**	**[1.59; 3.89]**
Age	**0.3**	**0.03**	**10.0**	**[0.24; 0.36]**	**0.6**	**0.1**	**8.0**	**[0.48; 0.80]**	-0.002	0.005	-0.3	[-0.01; 8.67]
Date at harvest	**0.056**	**0.004**	**13.8**	**[0.05; 0.06]**	-0.01	0.01	-0.7	[-0.03; 0.01]	**0.016**	**0.001**	**22.9**	**[0.01; 1.77]**
Lactation status	**- 1.9**	**0.19**	**- 9.6**	**[- 2.25; - 1.49]**	**- 2.0**	**0.5**	**- 3.8**	**[- 2.96; - 0.94]**	**- 0.52**	**0.03**	**- 15.3**	**[- 0.59; - 4.56]**
Density the year of harvest	0.03	0.11	0.3	[- 0.19; 0.26]	**- 0.3**	**0.1**	**- 3.5**	**[- 0.52; - 0.13]**	**- 0.15**	**0.03**	**- 4.8**	**[- 0.21; - 8.36]**
Density during the previous year									0.001	0.006	0.1	[-0.01; 1.33]
Density during the year of birth	**0.04**	**0.02**	**2.03**	**[0.001; 0.087]**	0.1	0.3	0.4	[- 0.51; 0.79]				
Winter minimum temperature									-0.001	0.054	- 0.02	[- 0.11; 0.11]
Winter precipitation									**- 0.01**	**0.002**	**- 4.4**	**[- 0.01; - 5.08]**
Cumulative snow sinking depth					0.01	0.07	0.1	[- 0.13; 0.14]	0.01	0.01	1.3	[- 0.006; 0.032]
NDVI in spring	- 4.6	4.2	- 1.1	[- 12.91; 3.73]	- 19.8	10.9	- 1.8	[- 41.21; 1.64]				
Rate of the spring green-up									0.1	0.1	2.0	**[1.31; 104.67]**
Interactions (*)												
Density^t*Winter_T°									- 0.003	0.004	- 0.6	[- 0.01; 5.40]
Density^t*Winter_prec									**0.001**	**≤0.001**	**4.2**	**[0.0003; 8.6777]**
Density^t*Snow_depth									- 0.001	0.001	- 1.3	[- 0.0019; 0.0004]
Density^t*NDVI	**- 0.8**	**0.4**	**- 2.2**	**[- 1.47; - 0.06]**								
Density^t*Green-up									- 0.004	0.005	- 0.1	[- 5.6; 1.9]
Density^birth*Snow_depth					0.005	0.004	1.3	[- 0.003; 0.012]				
Density^birth*NDVI					- 0.9	0.7	- 1.2	[- 2.33; 0.61]				

Density^t = density during the year of harvest, Density^{t-1} = density during the previous year, Density^{birth} = density during the year of birth, Winter_T° = winter temperature, Winter_prec = winter precipitation, Snow_depth = cumulative snow sinking depth, and Green-up = rate of spring green-up.
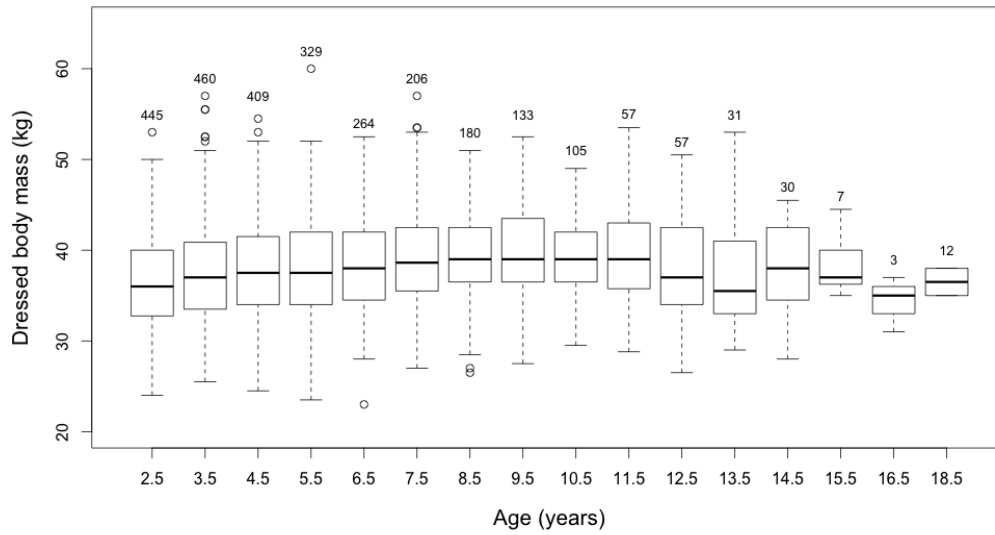
Figure 1.2. Variation of dressed body mass according to age of adult females (both lactating and non-lactating) harvested on Anticosti Island (Québec, Canada) between 2002 and 2013. Middle horizontal bars indicate medians. Sample sizes for each age class are indicated above bar.
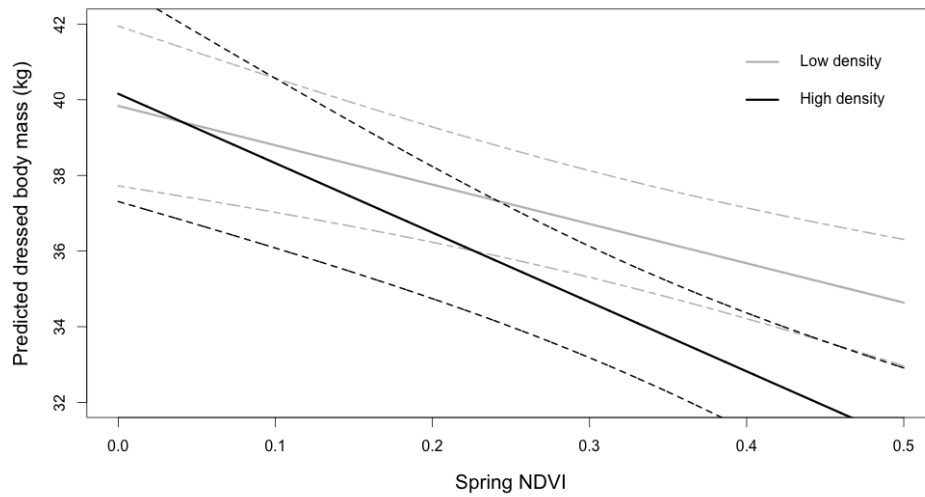
Figure 1.3. Variation (± SE in dotted lines) in predicted values of dressed body mass for adult female white-tailed deer relative to population density and spring NDVI values on Anticosti Island (Québec, Canada) between 2002 and 2013. Low density was set at 7.5 deer seen per hunter per day, whereas high density was set at 18.0 deer seen per hunter per day. A zero value of NDVI indicates no vegetation whereas values close to 1 indicate the highest abundance of vegetation.
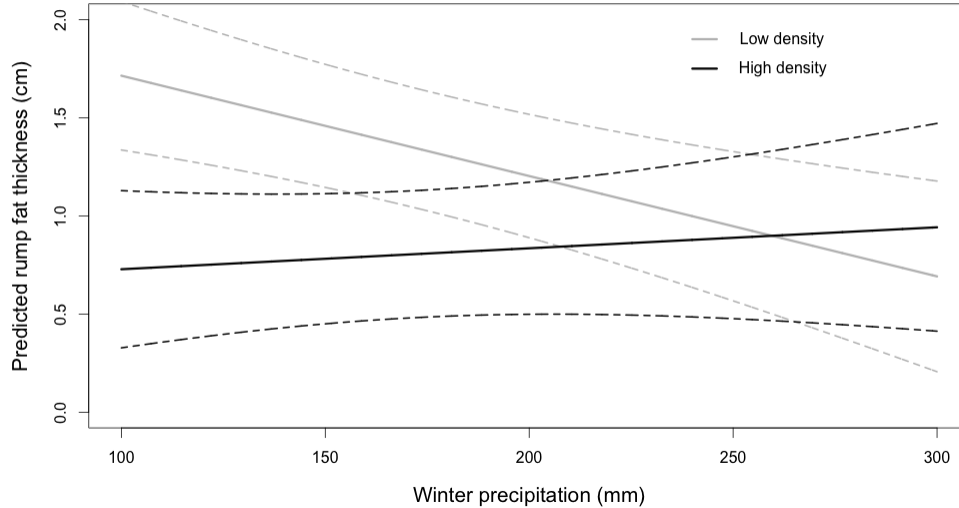
Figure 1.4. Variation (± SE in dotted lines) in predicted values of rump fat thickness for adult female white-tailed deer relative to population density and winter precipitation on Anticosti Island (Québec, Canada) between 2002 and 2013. Low density was set at 7.5 deer seen per hunter per day, whereas high density was set at 18.0 deer seen per hunter per day.

DISCUSSION

Using 12 years of data, we investigated the factors that determine body condition parameters of adult female white-tailed deer during the hunting season. We demonstrated that variability in body condition parameters was linked to intrinsic characteristics, population density, and environmental factors. We confirmed most of the single effects of population density and environmental conditions on female body condition found by Simard *et al.* (2014); additionally, our long-term monitoring allowed us to unravel their combined effects. Globally, most indices of body condition were influenced by age, lactation status, and date of harvest. Deer density during the year of harvest, winter precipitation, NDVI in spring, and rate of spring green-up were also retained in most models.

In ungulates, reproductive females face high nutritional demands during lactation (Mauget *et al.* 1997). In accordance with Simard *et al.* (2014), energetic demands of lactation affected all parameters of body condition of females on Anticosti Island. However, after reproductive investment in summer, differences between rump fat thickness of lactating and non-lactating females decreased as the autumn progressed, resulting in similar body fat levels in late autumn (Appendix 4). These results suggest that compensatory mechanisms allow lactating females to limit the energetic costs associated with lactation. For example, obligatory lipogenesis

(Verme & Ozoga 1980) or hyperphagia (Wairimu & Hudson 1993) could help lactating females to rapidly accumulate fat reserves to replenish their body condition before winter (Barboza & Parker 2008). Reproductive females are subject to lipogenesis because it is a process under endocrine control that is triggered by the decline in prolactin which usually occurs during late lactation (Meier 1977). In adult females, lipogenesis deposits parts of ingested energy as subcutaneous fat reserves. Likewise, hyperphagia can compensate for expenditures or low forage supplies by increasing both feeding time and feeding rates (Wairimu & Hudson 1993, Hamel & Côté 2009). It should allow deer to build up fat reserves to withstand the severity of winter. Despite heightened reserve depletion, summer recovery seems to be rapid in white-tailed deer on Anticosti Island, as has also been observed in Svalbard reindeer (Reimers et al. 1982).

Density-dependent processes such as competition among the individuals in a population may lead to a deterioration of animal body condition (Bonenfant et al. 2009). As expected, our results unveiled that density during the year of harvest had a negative influence on protein and fat reserves (see also Simard et al. 2014). This result may be due to intra-specific competition for forage, which increases at high density and reduces the intake rate per capita (Skogland 1983). High densities of deer on Anticosti Island have reduced forage abundance in autumn and winter by chronic overgrazing (Tremblay et al. 2005, Simard et al. 2008), which has led to a degradation of their habitat (Barrette et al. 2014). For females living at high population density and accumulating low fat reserves in summer and autumn, over-winter survival and reproduction could be compromised (Cook et al. 2004b). We also expected that high postnatal densities would have long-lasting negative effects on adult body condition (Solberg et al. 2004). Surprisingly, females born in high-density years had a larger dressed body mass comparatively to females born in low-density years. We suggest that high densities were the result of previous favorable habitat conditions. Consequently, females born in these high densities benefited from appropriate habitat condition early, and therefore were able to reach higher body mass later than individuals born at low density. It could also means that individuals born in the largest cohorts likely underwent strong natural selection for best condition, such as higher body mass, and individuals of higher biomass had higher survival.

In addition, our results demonstrated that density-dependent patterns varied between years likely due to annual variation in winter conditions. Harsher conditions in winter may induce higher costs of thermoregulation (Parker & Robbins 1985) and locomotion in snow (Parker et al. 1984), resulting in a loss of nutritional status. Our study highlighted that the effect of winter conditions on fat reserves could be mediated by population density. At low density, we detected a negative influence associated with heavy winter precipitation on body condition of individuals. Deer appeared unable either to reduce the rate of decline in fat reserves metabolised during severe winters (i.e., energy costs exceeded energy intake) or to compensate for this nutritional stress

with reserves accumulated from summer forage (Mautz 1978), a critical period for deposition of body reserves (Parker *et al.* 2009). In this case, previous winter forage and winter precipitation seemed to be the main bottom-up factors that influenced major energy reserves in autumn. This trend has also been observed for Coats Island caribou (*R. t. groenlandicus*), for which winter resources limited the population because of the hard-packed snow cover that restricted animals from accessing poor quality vegetation (Adamczewski & Hudson 1993). Adamczewski & Hudson (1993) reported that body fat in animals decreased by *ca*. 13 kg between November and June. However, at high population density, individuals in our study were probably in such bad condition that winter precipitations did not seem to affect fat reserves any further. Body fat was $23.5 \pm 0.1\%$ (mean ± SE) lower at high density comparatively to low density. At the peak population size for the Rivière-George caribou herd, animals accumulated only limited fat reserves in summer likely because of inadequate nutrition during this period (Huot 1989). Thus, it is possible that fat accumulation in our study was insufficient to encounter the severity of the winter at high density even though deer body condition was enhanced in late autumn.

At high latitudes, changes in environmental conditions also induce seasonality in plant growth. This variation in the timing of vegetation emergence influences ungulate forage quality (Johnstone *et al.* 2002). We expected that high spring NDVI and low rates of spring green-up would favour body condition, because early and gradual start of plant growth should provide high nutritional value for a prolonged period (Pettorelli *et al.* 2005b, 2007b). In our study, a higher plant quality in spring led to a lower body condition in autumn, a result that was also observed by Simard *et al.* (2014). Early onset of green-up was associated with a depletion of protein reserves in autumn, while a rapid spring green-up was associated with an accumulation of fat reserves in autumn. We also found synergetic effects of population density and environmental factors along these lines. High spring NDVI values reduced dressed body mass, but this influence was strongest in areas where population density was high. In our study, however, spring NDVI was inversely proportional to the rate of spring green-up (Appendix 5). Thus, rapid plant development was associated with a late spring onset because vegetation grows faster when spring is delayed (Hamel *et al.* 2009). We suggest that vegetation patterns on Anticosti Island are more related to the ones observed at higher latitudes, where plant development during spring is rapid and the growing season is short. In this way, our results are consistent with those of Herfindal *et al.* (2006b), who found that moose had a greater body mass in areas associated with late spring onset and a rapid rate of green-up. On Anticosti Island, a rapid green-up can benefit individuals even if the vegetation is of lower quality overall (Van der Wal *et al.* 2000), because of the low forage abundance after the long winter. This suggests that during spring and summer, variation in forage productivity is more important than forage quality for white-tailed deer body mass in autumn. Coulombe *et al.* (2008) reported a positive effect of forage abundance on autumn body mass likely due to a shift in activity budgets when forage abundance increased.

Deer on Anticosti Island reduced the proportion of daily time spent active when forage abundance increased since they could fill their rumen faster (Coulombe *et al.* 2008). However, it is possible that the impact of environmental conditions on body mass is larger under high population density because individuals are less likely to be buffered against environmental fluctuations when resources are scarce (Herfindal *et al.* 2006a). Finally, our results indicate no direct effect of density on dressed body mass. This is consistent with the food hypothesis (Sinclair *et al.* 1985), which outlines density-dependent effects on life-history traits through variation in resource availability as opposed to density per se (Fryxell *et al.* 1991).

In conclusion, our 12-year study, based on the use of abundant hunting data from several areas, allowed detecting spatiotemporal variation in deer body condition according to environmental constraints. Our simultaneous measures of dressed body mass, peroneus muscle mass, and rump fat thickness provided complementary information on body condition of female white-tailed deer, because they represented responses of different physiological functions. The annual monitoring of nutritional indices in ungulates could serve as an indicator of ecological changes, and may thus provide a quantitative basis helping setting harvest objectives or supporting adaptive management (Morellet *et al.* 2007).

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