CHAPITRE 2

Reproductive plasticity of female white-tailed deer at high density and under harsh climatic conditions

PASCALE AYOTTE[1][§], M. ANOUK SIMARD[2] & STEEVE D. CÔTÉ[1]

[1]Chaire de recherche industrielle CRSNG en aménagement intégré des ressources de l'île d'Anticosti; Département de biologie and Centre d'études nordiques; Université Laval; Québec, QC, Canada G1V 0A6.

[2]Ministère des Forêts, de la Faune et des Parcs; Direction de la biodiversité et des maladies de la Faune; Québec, QC, Canada G1S 4X4.

[§]Corresponding author; Tel: 418 656-2131 #8152; E-mail: pascale.ayotte.1@ulaval.ca

RÉSUMÉ

Les stratégies biodémographiques des femelles ongulés dépendent des processus dépendants et indépendants de la densité qui affectent la condition corporelle. En utilisant un suivi à long terme des traits biodémographiques des femelles du cerf de Virginie (2002–2014), nous avons évalué l'influence de la densité de population et des facteurs environnementaux sur l'effort reproducteur des femelles. Nous avons également évalué les conséquences post-reproductives sur la condition corporelle en utilisant la masse corporelle et les réserves de gras et de protéines à l'automne suivant la conception. Nos résultats montrent qu'à densité de population élevée, les femelles réduisent leur investissement dans la reproduction, ce qui correspond à une stratégie de reproduction conservatrice. En revanche, les femelles nées à densité de population élevée étaient plus enclines à se reproduire et concevoir de grandes tailles de portée, comparativement aux femelles nées à faible densité de population. Il s'agit possiblement d'une conséquence de la forte pression de sélection connue en début de vie. À faible densité de population, les femelles nées durant un printemps avec un débourrement de la végétation lent tendaient à retarder l'âge à la première conception. La condition corporelle était affectée par la reproduction; la lactation avait un grand impact négatif sur la masse corporelle et les réserves corporelles, alors que la conception avait un impact négatif seulement sur les réserves de gras. Notre étude à long terme démontre que pour les femelles vivant à densité de population élevée et sous des conditions climatiques rigoureuses, la plasticité des stratégies biodémographiques est un déterminant majeur du potentiel reproducteur.

ABSTRACT

Life-history strategies of female ungulates usually depend on density-dependent and –independent processes affecting body condition. Using a long-term data set on life-history traits of female white-tailed deer (2002–2014), we investigated the influence of population density and environmental factors on the reproductive effort of females. We also evaluated post-reproductive consequences on body condition using body mass, body fat, and body protein contents in the autumn following conception. We found that under high densities females had a lower reproductive rate, which corresponds to a conservative reproduction strategy. However, females born at high density were more likely to reproduce and conceive larger litter size than females born at low density, a possible consequence of strong selective pressure in early-life. At low density, females born during a spring with a slow green-up tended to delay age at first conception. Body condition was affected by reproduction; lactation had a large negative impact on body mass and body reserves, and conception had a negative impact on body fat. Our long-term study demonstrates that plasticity in life-history strategies is a major determinant of reproductive potential for females living at high density and under harsh climates.

KEY WORDS Anticosti Island, life-history strategies, conception, body condition, environmental variation, *Odocoileus virginianus*, white-tailed deer.

INTRODUCTION

In temperate regions, female ungulates encounter large contrasts in climate and resource availability over the seasons, affecting energy intake and how they cope with changing physiological demands (Parker *et al.* 2009). In response to these contrasts, northern ungulates generally tend to store body reserves during summer to improve body condition, ensure over-winter survival, and improve future reproductive success (Chan-McLeod *et al.* 1994, Cook *et al.* 2004, Festa-Bianchet & Côté 2008). Other environmental factors, such as high level of intraspecific competition (Stewart *et al.* 2005, Tavecchia *et al.* 2005) or severe climate conditions (Monteith *et al.* 2013), may interfere with the ability of individuals to store body reserves, creating a trade-off between growth, survival, and subsequent reproduction (Bonenfant *et al.* 2009).

In response to these trades-offs, different life-history strategies may be used, leading to variation in reproductive success. In most ungulate species, as population density increases, females favour their body maintenance and survival by reducing reproductive effort (Bonenfant *et al.* 2009). This reduction may be achieved, for example, by reducing litter size (e.g., roe deer; *Capreolus capreolus*, Andersen & Linnell 2000, moose; *Alces alces*, Gingras *et al.* 2014) or delaying age at primiparity (e.g., roe deer, Gaillard *et al.* 1992, red deer; *Cervus elaphus*, Bonenfant *et al.* 2002, elk; *Cervus canadensis*, Stewart *et al.* 2005). Because females should take longer to regain body condition following reproduction at high density (Clutton-Brock & Coulson 2002), the energy allocated to current reproductive effort may reduce the probability of subsequent reproduction (Hamel *et al.* 2011).

Independently of density-dependent processes, environmental conditions may affect reproduction directly by affecting offspring survival or indirectly through their effects on body condition of females. For example, high snow accumulation increases the cost of locomotion for ungulates during winter (Parker *et al.* 1984, 1999) while limiting food acquisition (White *et al.* 2009). Spring weather also induces variability in the onset of vegetation growth, which determines foraging conditions available to replenish body condition (Pettorelli *et al.* 2005). Climate-induced food limitation in late winter was reported to reduce fecundity of female reindeer (*Rangifer tarandus*) during the subsequent autumn (Tveraa *et al.* 2003).

The influences of population density and environmental conditions on life history strategies may also be delayed. Unfavourable environmental conditions at birth, such as high population density, may have long-lasting negative impacts on reproductive performance (Gaillard *et al.* 1992, Panagakis *et al.* 2017) because of their influence on individual growth and development, which may ultimately affect the quality of adults (Hamel *et al.* 2009). In Soay sheep (*Ovis aries* L.), lasting effects of harsh conditions in the first year of life had

negative influence on body mass, which may delay age at maturity and at first reproduction, and reduce litter size (Forchhammer *et al.* 2001). Harsh conditions can also lead to the selection of certain individuals within a population. For example, restricted forage conditions in the year of birth favoured the survival in the population of female white-tailed deer that had fewer reproductive pauses and higher weaning success (Simard *et al.* 2014b).

Differences in life-history strategies among individuals are expressed through age-related variations in body condition and in the probability of reproduction, with body mass being generally positively correlated with female age (McNamara & Houston 1996). In reindeer and moose, for example, larger females had a greater probability of reproduction than smaller ones (Sand 1996, Tveraa *et al.* 2003, respectively). At old age, the deterioration of physiological capabilities reduces reproductive effort, a process known as reproductive senescence (Medawar 1946, Williams 1957, Hamilton 1966, Kirkwood & Austad 2000). This age-related decline in reproductive effort may be influenced by early-reproductive investment, considering that females producing more offspring in early life tend to reach senescence at a younger age (Ericsson *et al.* 2001, Nussey *et al.* 2006).

Despite age-related strategies, females face the continuous challenge of maintaining energy balance during reproduction. Reproduction is energetically expensive partly because of the fetus development, but mostly because of the high nutritional requirements associated with lactation (Moen 1978, Mauget *et al.* 1997). When energy intake cannot completely meet the energetic demand of lactation, it requires an extensive mobilization of the remaining body reserves following winter (Tollefson *et al.* 2010). If females cannot compensate for reproductive costs and replenish body reserves during summer and autumn, they may be forced into a trade-off between survival and subsequent reproduction (Bårdsen & Tveraa 2012). The body condition reached before the next reproductive event is therefore critical and depends on previous reproduction and resource availability. Female ungulates may adopt a risk-sensitive reproductive allocation strategy to be more resilient to the unpredictable availability of food resources (Bårdsen *et al.* 2010). By storing energy as body reserves, these females reduce their short-term reproductive allocation to ensure future reproduction (Bårdsen *et al.* 2008, Hamel *et al.* 2010).

White-tailed deer (*Odocoileus virginianus*) on Anticosti Island provides a good model to study the effects of density and environmental factors on life-history strategies. This is an overabundant population, free of predators and living under harsh and variable environmental conditions. Based on the results of a previous 5-year study (Simard *et al.* 2014b), our main objective was to investigate the factors affecting life-history

strategies of females using a time series with much greater variability in density and environmental conditions. The use of 13 years of monitoring of individual body condition and conception should provide insights into the mechanisms affecting life-history strategies in a resources-limited population. We aimed to 1) determine the influence of density-dependent and -independent factors on the reproductive effort of female white-tailed deer, and 2) assess post-reproductive consequences on body condition. We hypothesized that variations in population density and environmental conditions would determine reproductive effort, which consequently determine post-reproductive body condition. We predicted that high population density, winter with abundant snow, and low quality forage in spring would decrease litter size at conception and delay age at first reproduction. Moreover, we predicted a synergistic effect of density and unfavorable environmental conditions (i.e., snowy winter or low quality forage) on reproductive effort. We expected that post-reproductive consequences on body condition would be determined by the combined effect of litter size and lactation status.

METHODS

Study area and deer population

Anticosti Island (49°N, 62°W; 7,943 km^2) is located in the Gulf of St. Lawrence (Québec, Canada), and corresponds to the northern limit of the range of white-tailed deer in North America. Cool and rainy summers, and long and snowy winters characterize the maritime sub-boreal climate of the island. Temperature averages 16°C in July and -11°C in January (Environment Canada 2006). Annual precipitations average 63 cm of rain and 406 cm of snow (Environment Canada 2006). Following the introduction of ca. 220 deer on the Island in 1896, the population increased rapidly (>20 deer/km^2; Potvin & Breton 2005). In the past decades, deer browsing has modified the composition of the native plant communities by suppressing the regeneration of white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), and balsam fir (*Abies balsamea*; Tremblay *et al.* 2005), which have been replaced by less palatable species such as white spruce (*Picea glauca*). Nevertheless, the reduction in the availability of high quality forage has not led to a decline in the deer population, and density on the island has remained high (Simard *et al.* 2008). Deer survival and their ability to sustain harsh forage conditions have been linked to the availability of alternative food sources such as winter litterfall of lichen and fir twigs (Tremblay *et al.* 2005, Lefort *et al.* 2007), deer long-term tolerance to forage limitations (Simard *et al.* 2008), and their digestive plasticity for a low quality diet (Bonin *et al.* 2016).

Female reproductive status

During the hunting seasons (September–December) of 2002–2014, we evaluated the body condition of harvested females, and collected their teeth and ovaries (see Appendix 6 for details of sample sizes per year). We estimated age at harvest by counting cementum annuli of incisor teeth (Hamlin *et al.* 2000), from which we

calculated age at conception for the previous autumn (i.e., age at harvest - 1). We only considered adult female ovaries (i.e., 2.5 to 18.5 years old at harvest) because fawns (≤1.5 years old at harvest) do not reproduce on Anticosti Island (Simard *et al.* 2014b).

We assessed reproductive status using regressing luteal structures in ovaries, assuming that most females conceived at the first ovulation of the season (Guinness *et al.* 1971). We processed ovaries as Goudreault (1980) to obtain thin sections (10-µm) of tissues fixed on microscope slides that were examined with an optical microscope (10X or 4X depending on the observer, $n = 2$). We identified the past reproductive status of females based on the presence of scars in ovaries. The *corpus luteum* (CL) of pregnancy, a structure formed after ovulation (1, 2 or 3 depending on litter size), regresses immediately after parturition into *corpus rubrum* (CR, <1 year old), and then into smaller scars called *corpus albicans* (CA, >1 year old; Langvatn *et al.* 1994). We used CR occurrence as an index to confirm parturition during the preceding summer as validated in red deer (*Cervus elaphus*; Langvatn *et al.* 1994). CA do not provide a reliable quantification of the past reproductive events because this degenerative structure may underestimate previous parturitions (Langvatn *et al.* 1994), however they allow the differentiation of nulliparous (i.e., no CA observed) and multiparous females (CA observed together with CR; Simard *et al.* 2014b). We confirmed the concordance among the two observers by comparing the observed number of CR ($R^2 = 1.0$, $n = 30$, $P < 0.001$), CA ($R^2 = 0.9$, $n = 30$, $P < 0.001$), as well as the total number of scars (i.e., CR + CA; $R^2 = 0.9$, $n = 30$, $P < 0.001$).

The lactation status of females was assessed by hunting guides or hunters during field dressing according to the presence or absence of milk in the udder (Noble & Hurley 1999). We assumed that the effectiveness of hunters to estimate lactation status did not change throughout autumn, because the proportion of lactating females was similar in early and late autumn (73 ± 2% before 15 October versus 74 ± 2% after 15 October; $\chi^2 = 0.1$, df = 1, $P = 0.8$). Overall, 13% of females had conceived (CR_1, CR_2 or CR_3) but were identified as non-lactating. We assumed fawn mortality rather than incorrect identification of lactation status (Simard *et al.* 2014b). In contrast, misidentification of reproductive status occurred, because 5% of females identified as lactating did not show signs of ovulation for the preceding year (i.e., absence of CR in ovaries; Simard *et al.* 2014b). We removed these observations from our database because we could not confirm whether these females were misidentified as lactating or were indeed still nursing a yearling.

Post-reproductive body condition

We measured dressed body mass (i.e., total body mass after removing viscera) using a spring scale (± 0.25 kg). We estimated body protein reserves by weighting (± 0.5 g) the peroneus muscles using a Pesola

scale (Pesola AG, Baar, Switzerland) because this muscle group has been previously validated as a reliable predictor of protein reserves in ungulates (Crête *et al.* 1993, Taillon *et al.* 2011). Finally, we estimated body fat by inserting a ruler into the rump fat layer (maximum thickness ± 0.2 cm) at 5 and 10 cm from the base of the tail at a 45° angle from the backbone (Leader-Williams & Ricketts 1982). We then averaged both measurements to obtain an index of fat reserves, which has been validated in white-tailed deer (Simard *et al.* 2014a).

Influence of environmental factors on female reproduction

Population density

We used the number of deer seen per hunter per day as an index of population density at conception (i.e., the year preceding the harvest). Estimated population density varied from 3.4 ± 0.2 to 35.0 ± 1.2 deer (mean ± SE) seen per hunter per day. This index was available for all study zones-year combinations (Figure 2.1), and has been validated in earlier studies on Anticosti Island (Pettorelli *et al.* 2007a, Simard *et al.* 2012).
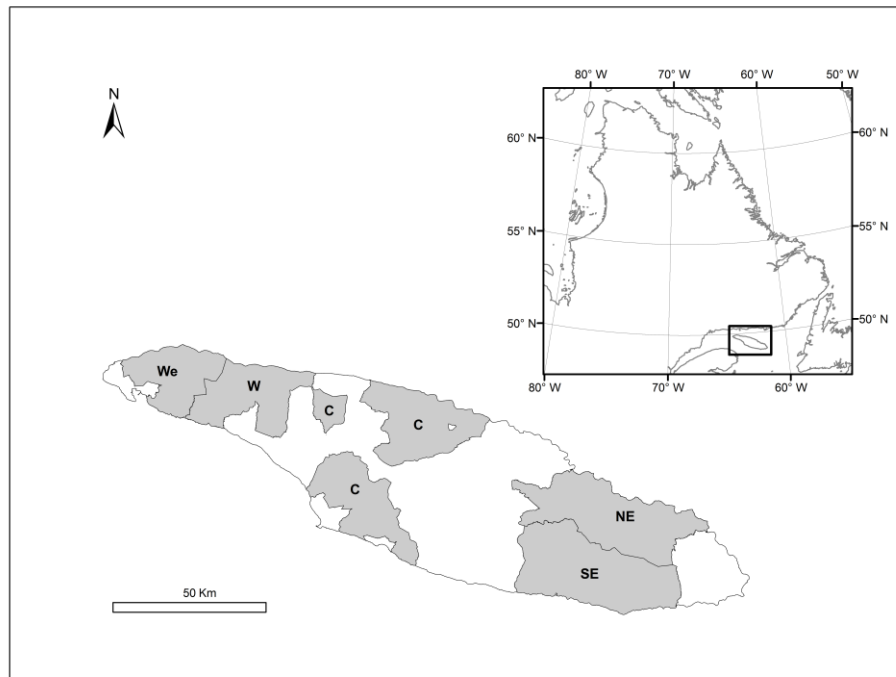

Figure 2.1. Location of the 5 study zones from which deer were harvested from 2002 to 2014 on Anticosti Island (Québec, Canada): West end (We), West (W), Central (C), North-East (NE), and South-East (SE).

Snow

We assessed the influence of snow on reproductive effort of females using snow depth and snow sinking depth. We collected snow measurements at 15-day intervals (October to May beginning in 1984) from 2 stations on the western end of the Island. We measured snow depth (cm) using 10 graduated 3-m rulers and snow sinking depth (cm) using a penetrometer imitating the foot pressure exerted by deer during locomotion (Verme 1968). We used cumulative snow sinking depth in winter (November-May) and spring (March-May) before conception as indices to estimate energy expenditure for locomotion in snow (Simard *et al.* 2014b). We calculated these indices of winter severity (Potvin & Breton 1992) by adding the product of weekly or biweekly sinking depths and the number of days between consecutive readings (NIVA value; m×day). We used cumulative compact snow depth in autumn (November-December) of conception to estimate the hard layer that limits food acquisition (White *et al.* 2009). We calculated this index of thickness of compacted snow on the ground as Simard *et al.* (2014b), by subtracting cumulative sinking depth from cumulative snow depth.

Vegetation

We used the normalized difference vegetation index (NDVI) from satellite imagery to assess the effect of vegetation productivity on reproduction. We used images (1 km resolution, 10 days composite images eliminating most cloud cover) collected from the Advanced Very High Resolution Radiometer (AVHRR; Canada Center for Remote Sensing 2016). We excluded pixels of water, and extracted NDVI values ranging from 0 to 1, where green vegetation resulted in higher values. We georeferenced the locations of harvest sites using ArcGIS 10.3.3 (ESRI, Redland, USA). We then created a buffer zone of 5 km radius around each harvest site to characterize the home range of the harvested deer and obtain a representative value of the NDVI. We extracted the average NDVI values associated with those buffer zones from 1 May to 30 June (1985–2014) because this temporal window corresponds to the period when vegetation starts growing and reaches a plateau. We calculated the average NDVI in May and used this value as an index of vegetation productivity (Pettorelli *et al.* 2007b). We also calculated the slope between average NDVI in early May and late June to assess the rate of change in productivity (i.e., the speed of spring vegetation onset; Pettorelli *et al.* 2007b). On Anticosti Island, rapid onset of vegetation associated with delayed spring appears to be advantageous for body condition in white-tailed deer (Ayotte *et al.*; unpublished data, Simard *et al.* 2014a).

Statistical analyses

Female reproduction

We used generalized linear mixed-effects models with the Poisson family (lme4 package, Bates *et al.* 2015; R 3.2.3. v.10.X, R Development Core Team 2015) to assess the influence of density and environmental factors on reproduction. All models included the interaction between year and study zone as a random effect. We investigated the variance observed in reproductive effort parameters (i.e., litter size at conception and age at first conception) according to the following set of explanatory variables: deer density during the year of birth, deer density at conception, cumulative snow sinking depth during the spring preceding conception, cumulative compact snow during the autumn of conception, NDVI during the spring preceding conception, NDVI during the spring the year of birth, the rate of spring green-up preceding conception, and the rate of spring green-up the year of birth (see Appendix 7 for a list of descriptive statistics of quantitative variables). The model that estimated the influence of environmental conditions on litter size at conception included age and age^2 as covariables. We used the variance inflation factor (VIF) to assess multicollinearity among potential explanatory variables. The highest VIF value was 2.2, thus lower than the value of 3 above which multicollinearity may affect parameter estimates (Zuur *et al.* 2010). Spring NDVI and the rate of spring green-up the year of birth (r = |0.7|) were never included together in the same model. We standardized explanatory variables by using a z-transformation (Schielzeth 2010).

We used Akaike Information Criterion (AIC) to select the best models (Burnham & Anderson 2002) explaining variability in litter size at conception [LS] and age at first reproduction [AF]. We based model selection on the hierarchical procedure of Simard *et al.* (2014a; see Appendix 8 for the full list of candidate models). To estimate the influence of environmental conditions on litter size, we first compared the AIC values of the null model (i.e., Model 0; including the intercept) and two reference models (i.e., Model 1; including age as a covariate, and Model 2; including age and age^2). To estimate the influence of environmental conditions on age at first reproduction, we used the null model as the reference model (Model 1; model that included only the intercept). In a following step, we added explanatory variables related to density (i.e., Density^{t-1} or Density^{birth}; see Appendix 7) to the reference model to build Models 2–5 (LS) and 2–4 (AF). If any model within the density candidate models had a ∆AIC value <2 compared to the reference model, the most parsimonious density model was selected for the next step of hierarchical selection. Models 6-24 (LS) and 5-23 (AF) tested the improvement of model fit by adding environmental variables (i.e., Snow^{spring}, Snow^{autumn}, NDVI^{birth}, Green-up^{t-1}, and Green-up^{birth}; see Appendix 7) to the reference model. If an environmental model had a ∆AIC <2 compared to the reference model, we kept the most parsimonious environmental model for the next step. Based on the results of models 3–24 (LS) and 2–23 (AF), all the variables retained (i.e., density +

environmental variables) in the preceding steps of the hierarchical selection were added to the original reference model (i.e, Model 2 for LS, and Model 1 for AF) to build a new reference model. Those Models 24 (LS) and 23 (AF) corresponded to the best single-effect models. 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 25–28 (LS) and 24–27 (AF).

We used generalized additive mixed models (gamm; *mgcv* package, Wood 2006; R 3.2.3. v.10.X, R Development Core Team 2015) with smoothing spline to analyse variation in litter size in relation to the age of females, as this relationship was expected to be nonlinear. These models combine the utilities of linear mixed-effects models (lme; Pinheiro & Bates 2000) and generalized additive models (gam; Hastie & Tibshirani 1990) so that random factors, fixed factors and nonlinear predictor variables can all be estimated in the same model. We used the quasipoisson family because the data were overdispersed. We included year nested within study zone as a random effect.

Body condition and reproductive effort

To evaluate how body condition related to past reproductive effort, we performed linear mixed-effects models within the *lme4* package (Bates *et al.* 2015; R 3.2.3. v.10.X, R Development Core Team 2015). We plotted residuals against the explanatory variables to detect non-linear relationships. We investigated the variance observed in the body condition parameters (i.e., dressed body mass, peroneus muscle mass and rump fat thickness) according to age at conception, date at harvest, litter size at conception, lactation status, and the interaction of these last two variables. All models included the interaction between year and study zone as a random effect (see Appendix 9 for the full list of models). We used Pearson correlation to assess correlation between explanatory variables and confirmed that variables were uncorrelated (*r's* <|0.5|).

RESULTS

Influence of environmental factors on female reproduction

In 2002–2014, we observed 86% conception rate in harvested female white-tailed deer on Anticosti Island (*n* = 1089). Among these females, 60% conceived a single fawn, 25% conceived twins, and 1% conceived triplets. High population density at conception negatively influenced litter size, i.e. conceiving more than one fetus was more frequent under low densities (35%) compared to high densities (25%; Table 2.1 and Figure 2.2). Litter size at conception decreased by 38 ± 14% when population density increased from 5 to 35

deer seen per hunter per day (Table 2.1 and Figure 2.2). On average, females conceived less than one fetus when population density was >18 ± 4 deer seen per hunter per day (Table 2.1 and Figure 2.2). High population density in the 1st year of life tended to contribute to larger litter size (Table 2.1 and Figure 2.2). Twenty nine percent of females born at low density conceived more than one fetus compared to 36% for those born at high density (Table 1 and Figure 2). Litter size at conception increased by 47 ± 30% when population density at birth increased from 5 to 35 deer seen per hunter per day (Table 2.1 and Figure 2.2).

Age at conception of females ranged from 1.5 to 17.5 years (median=4.5 years) and positively influenced litter size (Table 2.1). We observed a peak in the number of fetuses conceived around 9.5 years of age, but no apparent senescence (Figure 2.3 and Appendix 10; edf = 4.438, F = 29.028, P <0.001). First reproduction occurred at 1.5 years old for 37% of the females, 31% at 2.5 years old, 15% at 3.5 years old, 13% at 4.5 years old, 3% at 5.5 years old, and 3% between 6.5 and 9.5 years old. High density at conception tended to negatively affect age at first conception and reversed the positive effect of a rapid rate of the spring green-up during the year of birth on age at first conception (Table 2.1 and Figure 2.4).

Table 2.1. Parameter estimates (Estim.) ± SE (with Z and 95% CI) from the best-supported generalized linear mixed-effects models describing litter size at conception ($n = 1089$) and age at first reproduction ($n = 248$) for adult female white-tailed deer harvested on Anticosti Island (Québec, Canada; 2002–2014). The variables with 95% CI that did not include 0 are indicated in bold.

Explanatory variable	Litter size at conception				Age at first reproduction			
	Estim.	SE	Z	95% CI	Estim.	SE	Z	95% CI
Intercept	**0.17**	**0.04**	**3.6**	**[0.08; 0.27]**	**1.00**	**0.04**	**25.5**	**[0.93; 1.08]**
Age at conception	**0.24**	**0.04**	**6.3**	**[0.17; 0.32]**				
Age^2	**- 0.07**	**0.02**	**- 3.1**	**[-0.12; -0.03]**				
Density at conception	**- 0.09**	**0.04**	**- 2.1**	**[-0.177; -0.006]**	- 0.05	0.06	- 0.9	[-0.16; 0.06]
Density during the year of birth	0.06	0.03	1.9	[-0.001; 0.121]				
Cumulative snow sinking depth in spring before conception	0.03	0.04	0.8	[-0.04; 0.11]				
Cumulative compact snow in autumn at conception					0.07	0.05	1.3	[-0.03; 0.17]
Rate of spring green-up during the year of birth					- 0.02	0.04	- 0.6	[-0.10; 0.05]
Interaction (×) Density^{t-1} × Green-up^{birth}					0.07	0.04	1.9	[-0.003; 0.149]

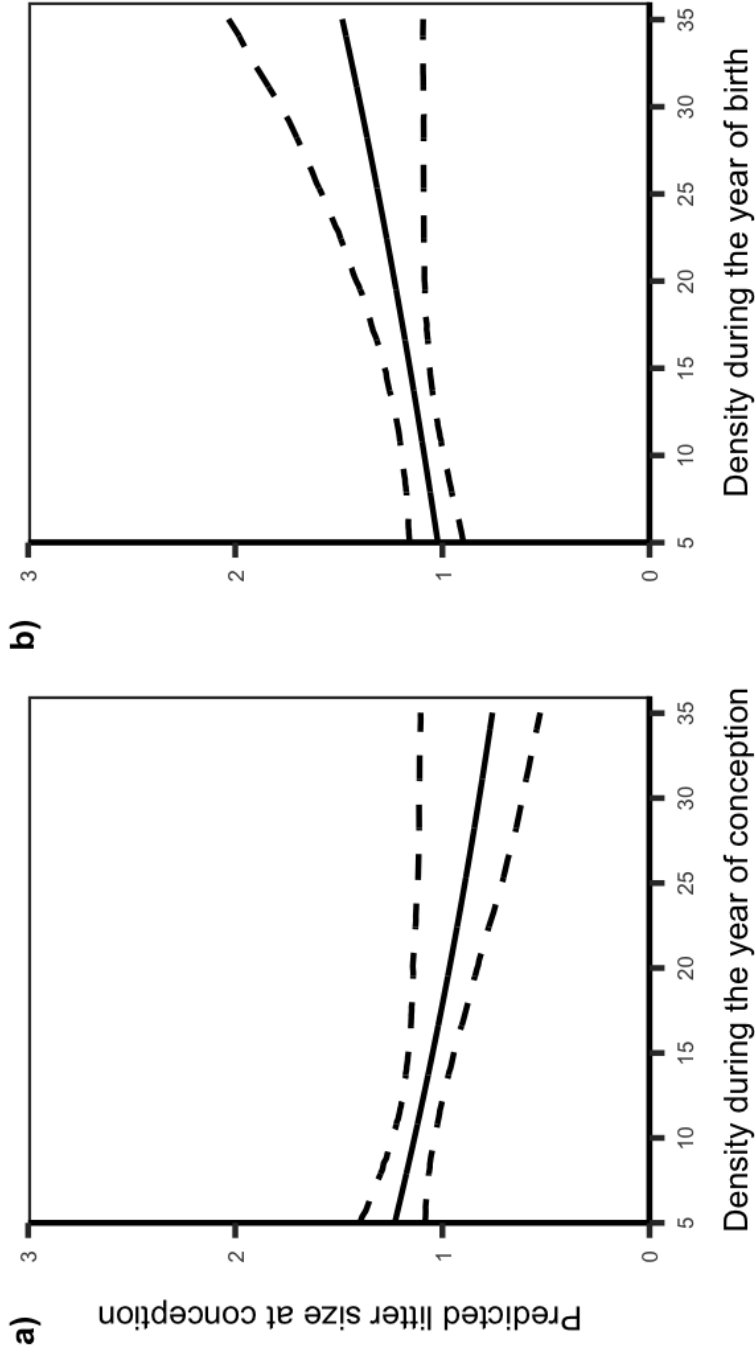Density^{t-1} = density at conception, Green-up^{birth} = rate of spring green-up during the year of birth

Figure 2.2. Influence of a) population density and b) population density during the year of birth on litter size for white-tailed deer females harvested on Anticosti Island (Québec, Canada; 2002–2014). Predicted line (± SE in dotted lines) is drawn from parameters estimated with generalized linear mixed-effects models.

54
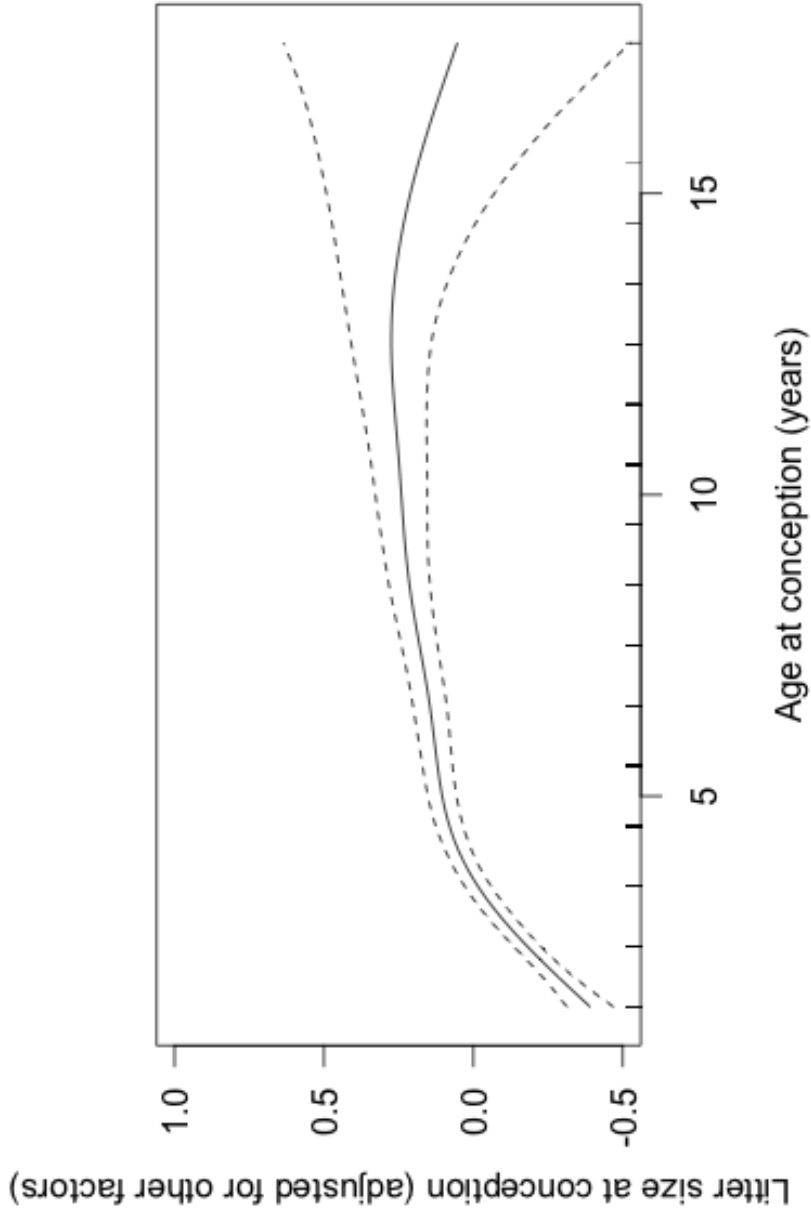
Figure 2.3. The relationship between litter size at conception and age at conception for female white-tailed deer on Anticosti Island (Québec, Canada; 2002–2014). The curve shown is the result of fitting a generalized additive mixed model with a smoothing spline. The solid line is the predicted value of litter size at conception as a function of age. The dashed lines are approximate 95% pointwise confidence intervals. The short inside tick marks on the abscissa represent the proportion of observations.
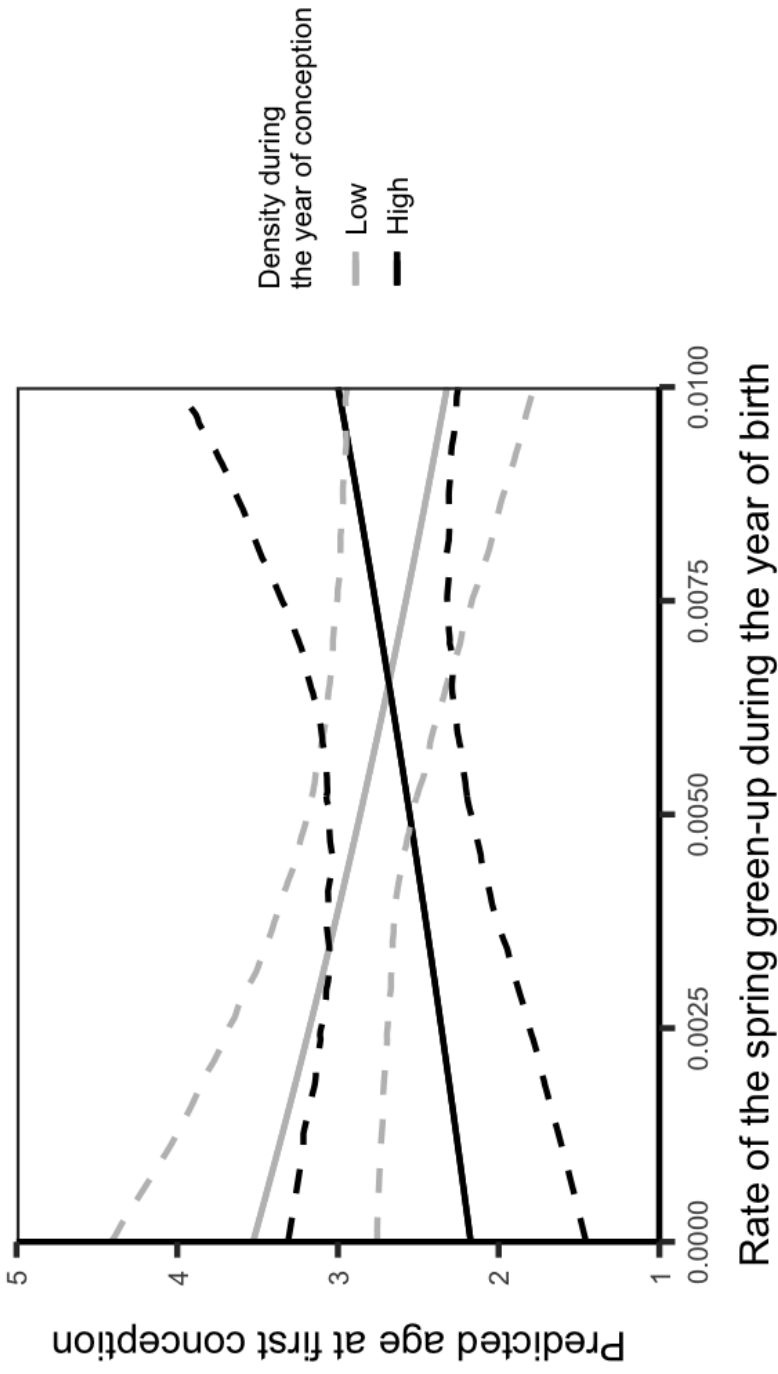
Figure 2.4. Variation (± SE in dotted lines) in predicted values of age at first reproduction for adult female white-tailed deer relative to population density and the rate of the spring green-up during the year of birth on Anticosti Island (Québec, Canada; 2002–2014). Low density was set at 7 deer seen per hunter per day, whereas high density was set at 19 deer seen per hunter per day.

Post-reproductive body condition

Age had a positive influence on all three parameters of body condition (Table 2.2). Lactation status and litter size at conception did not have a combined effect on body condition, but they both had single effects (Table 2.2). The main difference in body condition in autumn was between non-lactating and lactating females, independently of litter size (Table 2.2 and Figure 2.5). Dressed body mass was on average 5.2% lower for lactating females than non-lactating females, peroneus muscle mass 1.4% lower, and rump fat thickness 33.3% lower. Litter size at conception did not influence significantly dressed body mass and peroneus muscle mass, but reduced rump fat thickness (Table 2.2 and Figure 2.6). Overall, the average rump fat thickness was 2.31 ± 0.09 cm for females that had not conceived, 1.88 ± 0.09 cm for females that had conceived (1, 2 or 3 fetuses) but were not lactating, and 1.41 ± 0.03 cm for females that had conceived and were lactating.

Table 2.2. Parameter estimates (Estim.) ± SE (with *t* and 95% CI) from linear mixed-effects models describing dressed body mass (*n* = 1061), peroneus muscle mass (*n* = 1073) and rump fat thickness (*n* = 1071) for adult female white-tailed deer harvested on Anticosti Island (Québec, Canada; 2002–2014) according to reproduction parameters. 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	35.97	1.00	35.85	[34.01; 37.94]	89.63	2.01	44.63	[85.69; 93.57]	1.30	0.17	7.58	[0.96; 1.63]
Age at conception	**0.31**	**0.05**	**6.22**	**[0.21; 0.41]**	**0.47**	**0.14**	**3.34**	**[0.19; 0.75]**	0.02	0.01	1.92	[-0.0004; 0.0351]
Date at harvest	**0.07**	**0.01**	**10.18**	**[0.06; 0.08]**	-0.01	0.02	-0.36	[-0.04; 0.03]	**0.02**	**0.001**	**14.62**	**[0.015; 0.020]**
Litter size at conception	-0.43	0.38	-1.12	[-1.17; 0.32]	-0.61	1.07	-0.57	[-2.70; 1.48]	**-0.23**	**0.07**	**-3.37**	**[-0.365; -0.097]**
Lactation status	**-3.02**	**0.58**	**-5.17**	**[-4.17; -1.88]**	**-3.79**	**1.63**	**-2.33**	**[-6.99; -0.60]**	**-0.59**	**0.10**	**-5.67**	**[-0.80; -0.39]**
Interaction (×)												
Litter size at conception × Lactation status	0.79	0.50	1.57	[-0.20; 1.77]	2.35	1.40	1.67	[-0.40; 5.09]	0.09	0.09	1.03	[-0.08; 0.27]

58
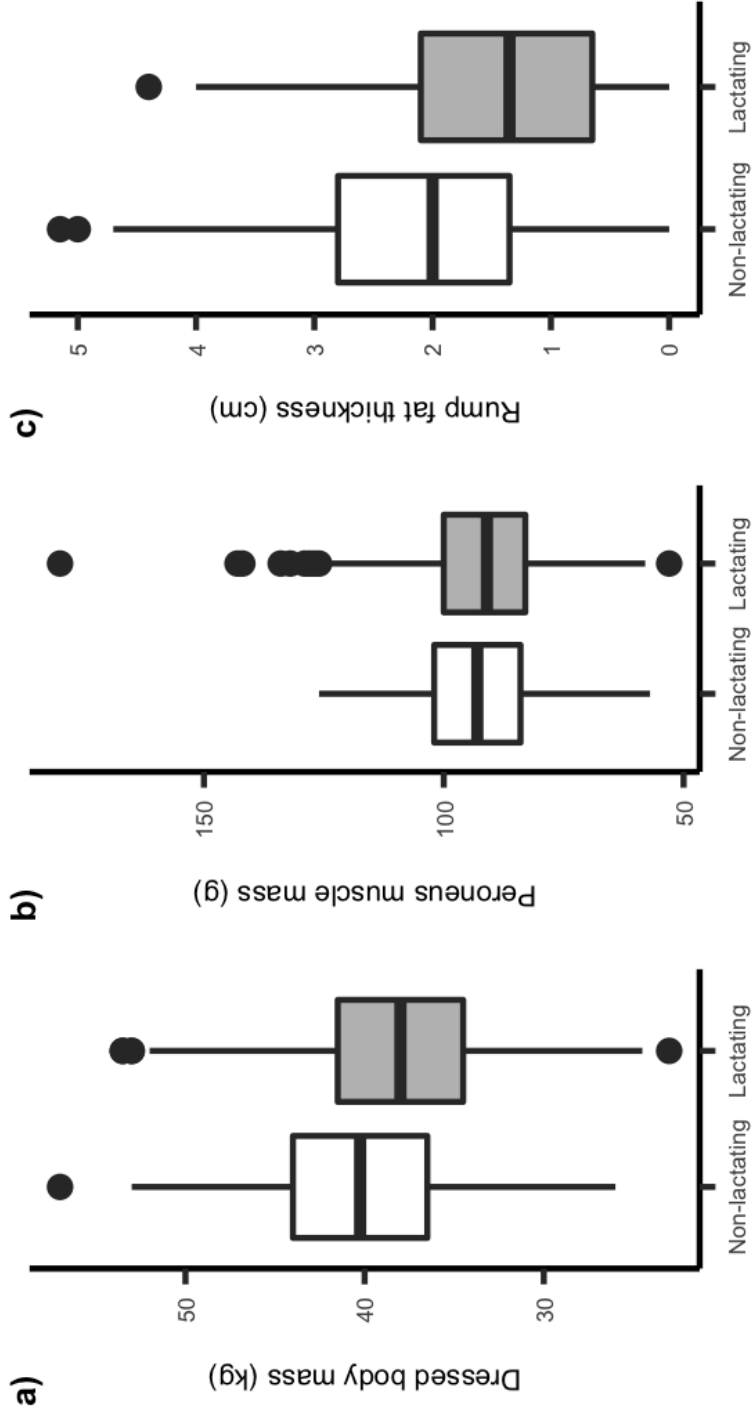
Figure 2.5. Influence of lactation status on a) dressed body mass, b) peroneus muscle mass and c) rump fat thickness in autumn for female white-tailed deer harvested on Anticosti Island (Québec, Canada; 2002–2014). Middle horizontal bars indicate medians; boxes represent the range between first and third quartiles; vertical bars represent the range between the 5th and 95th percentiles, and black dots are outliers.
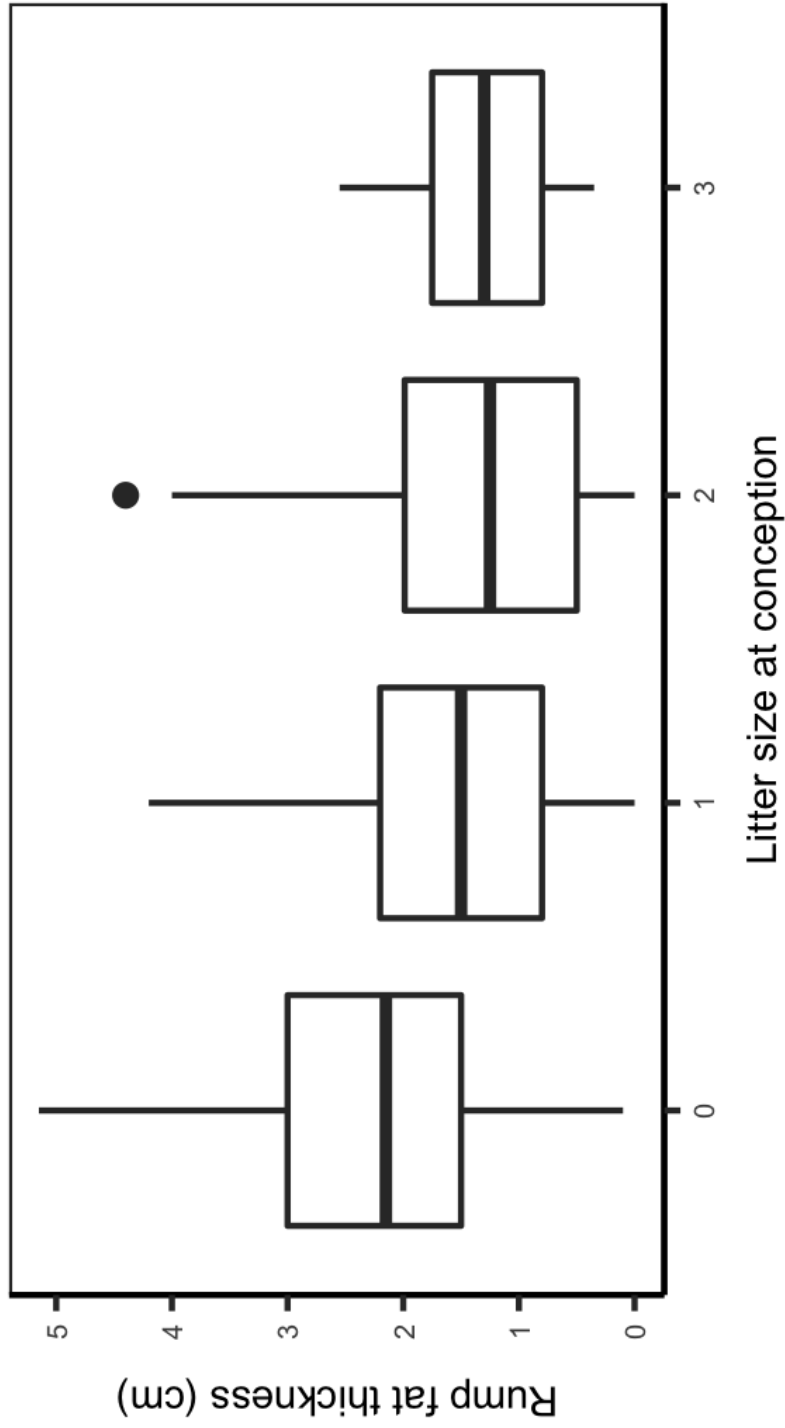
Figure 2.6. Influence of litter size at conception on body condition in the following autumn for female white-tailed deer harvested on Anticosti Island (Québec, Canada; 2002–2014). Middle horizontal bars indicate medians; boxes represent the range between first and third quartiles; vertical bars represent the range between the 5th and 95th percentiles, and black dots are outliers.

DISCUSSION

Using long-term monitoring (2002–2014), we confirmed that female white-tailed deer allocate energy to reproductive effort according to annual variations in environmental conditions, likely to minimize reproductive costs, as previously observed by Simard *et al.* (2014b). Additionally, we determined a threshold in population density at *ca.* 18 deer seen per hunter per day above which females seemed to adopt a conservative reproductive strategy. We also observed that females born under high densities tended to conceive larger litter sizes. Surprisingly, we found that females facing harsh conditions at birth and during the year of conception tended to reproduce early. In accordance with Simard *et al.* (2014b), our research revealed that female post-reproductive body condition was determined by the reproductive outcome. We confirmed that lactation had a strong negative impact on body condition in autumn. However, we found that body condition was not linked to the number of fetuses conceived, but rather to conceiving or not.

Density and environmental influences on female reproduction

Our results revealed that variations in population density modified the life-history tactics of females. When density at conception was >18 ± 4 deer seen per hunter per day, female deer on Anticosti Island appeared to use a conservative reproductive strategy. They did not reproduce or had a small litter size more likely to survive the winter, while not decreasing the potential for future reproduction. This reproductive plasticity was also observed in moose (Gingras *et al.* 2014) and corresponds to the risk-sensitive regulation of reproductive allocation, in which individuals anticipate resource scarcity for the following winter (Bårdsen *et al.* 2010). High density increases intra-specific competition for forage, and it is expected to reduce intake *per capita*, hence also reducing body reserves in a critical period (Parker *et al.* 2009). Thus, female deer at high population density accumulated less fat reserves in autumn than females at low density, prior to conception, and entered winter in poor body condition (Simard *et al.* 2014a). Accordingly, due to the large energy costs of reproduction that females face, adjustments in life-history tactics can be decisive under harsh conditions at high population density.

Conversely to deer density at conception, deer density at birth tended to increase the probability for females to conceive twins or triplets. Because of the high demographic vigor of deer, high density at birth may imply that environmental conditions of the previous year were favourable, allowing females to grow rapidly (Ayotte *et al*.; unpublished results). This could have allowed them to produce larger litter sizes (i.e., 2-3 fetuses). An alternative explanation is that individuals born in the larger cohorts likely underwent strong selective pressure for the best body condition (e.g., higher biomass), which ultimately resulted in higher survival and reproductive outcomes (Simard *et al.* 2014b, Plard *et al.* 2015).

Surprisingly, few factors explained the age at first conception of female deer on Anticosti Island. Age at first conception tended to be driven by the interaction between habitat conditions early in life and density at conception. Indeed, under low density, females born during a spring with a slow green-up tended to delay primiparity (3.3 ± 0.2 versus 2.8 ± 0.2 years-old, for slow and fast spring green-up, respectively). Early and gradual vegetation emergence in spring (i.e., slow spring green-up) is thought to provide a prolonged period of high quality forage (Pettorelli *et al.* 2005, 2007b). However, on Anticosti Island, slow spring green-up had a negative effect on fat reserves in autumn in female white-tailed deer (Ayotte *et al.*; unpublished results, Simard *et al.* 2014a). We thus hypothesise that a slow spring green-up is unlikely to allow females to reach the biomass required to come into oestrus and reproduce at a young age (Hamilton & Blaxter 1980). However, at high densities, the effect was opposite: females born during a spring with a slow rate of vegetation green-up conceived earlier. Usually, young females experiencing a limitation in food resources are expected to delay the onset of reproduction (Eberhardt 2002). In our study, under severe early-life conditions (referring to a bad start in life; Solberg *et al.* 2004) and high density at conception, females seemed to prioritize reproduction over survival. It is possible that under difficult environmental conditions affecting long-term survival, it could be more profitable to reproduce early instead of delaying reproduction in an uncertain future, which resembles more the fast strategy of short-lived species (Promislow & Harvey 1990).

Assuming that body condition is related to age, the probability to conceive larger litter sizes should also increase with age (McNamara & Houston 1996), mostly because the energetic demand for milk production associated with twins or triplets is high (Moen 1978, Mauget *et al.* 1997). Our results are in accordance with these predictions: young females tended to have smaller litter sizes than older females. This is likely due to the trade-off among growth, survival and reproduction (Stearns 1992), because older females, while also being more experienced, may allocate to reproduction the resources that younger females need for growth and to reach maturity (Flajšman *et al.* 2017). This could explain why older females may accumulate more energy as subcutaneous fat reserves to allocate to reproduction. This is consistent with Monteith *et al.* (2013) who reported that the regulation of energy balance in female mule deer (*Odocoileus hemionus*) was state-dependent and related to individual experience.

Conception rate increased with age for female white-tailed deer on Anticosti Island (Simard *et al.* 2014b). However, we could not identify reproductive senescence, possibly due to low sample size (*n* = 26) for females older than 11.5 years, which did not allow us to adequately estimate variability in litter size at conception. Borowik *et al.* (2016) reported no reproductive senescence in a low-density population of red deer, where yearling and old females were in good body condition to reproduce, mainly due to excellent forage conditions. In our high-density population, where competition is strong and resources are scarce (Tremblay *et al.* 2005),

we expected to detect reproductive senescence in females because they appear to show senescence in body condition (Ayotte *et al*.; unpublished results). Reproductive effort of females over their lifetime on Anticosti Island should have been represented by a bell-shaped curve, as observed in other ungulates (Mysterud *et al.* 2002) and many placental mammals (Nussey *et al.* 2013). However, more studies with larger samples of old females are needed to investigate female reproductive senescence on Anticosti Island. In addition, using longitudinal data could be useful to better test evolutionary predictions of aging (Nussey *et al.* 2013). Long-term individual-based field studies allow, for example, detecting an increased allocation of resources to early life reproduction, which is usually associated with a rapid decline in reproductive performance in later life (Nussey *et al.* 2009).

Post-reproductive body condition

The impact of current reproductive effort on body condition in autumn was mainly attributed to lactation. Body mass, body fat, and body protein contents were lower for lactating females than for non-lactating females in autumn, independently of litter size at conception. This difference in body condition suggests proximal costs of reproduction that lactating females cannot completely compensate with summer foraging. Proximal costs of reproduction have also been observed in other ungulates, such as female elk, which lost 50% of their body fat after reproduction, due to reproductive effort (Cook *et al.* 2004).

Our results highlight that to investigate the costs of reproduction on body condition in autumn it is useful to assess different body condition parameters (i.e, body mass, body fat, and body protein contents; Simard *et al.* 2014b) representing distinct physiological functions (Parker *et al.* 2009). Because body proteins are generally catabolized when all fat reserves have been used (Mautz 1978), the diminution of body proteins observed in lactating females indicates a more stressful situation than the sole diminution of fat reserves. This suggests that the energy allocated to lactation is high (Chan-McLeod *et al.* 1994, Parker *et al.* 2009), and may eventually compromise subsequent reproduction. In addition, the impact could be greater if females face harsh environmental conditions, high population densities (Clutton-Brock *et al.* 1983, Stearns 1989) or both, and ultimately induce feedback effects on lifetime reproductive performance.

As Simard *et al.* (2014b), we did not observe a cost gradient dependent on the interaction between litter size (CR_{0-3}) and lactation status (NL or L), i.e. CR_0-NL<CR_1-NL<CR_2-NL<CR_3-NL<CR_1-L<CR_2-L<CR_3-L. In contrast, we found a cost gradient dependent on conception and lactation status, i.e. CR_0-NL<$CR_{1,2,3}$-NL<$CR_{C1,2,3}$-L. The main differences in fat reserves in autumn were linked to these three classes. i.e. no conception, conceiving with reproductive interruption or carrying a young to term (including lactation). In our

study, we only had data on female body condition in autumn after conception, so that for females that conceived but were non-lactating, we only had signs of conception without any information on the date of fawn loss. Thus, we cannot associate the decrease in fat reserves of these females only to the costs of gestation.

Our results do not support the results of Simard *et al.* (2014b) that fat reserves were lower for females that conceived twins compared to singletons. As mentioned above, the cost gradient was only linked to conceiving or not. Additionally, we did not confirm that non-lactating females had a similar body condition whether they conceived or not. Consequently, our results indicated larger costs of gestation compared to what we expected based on Simard *et al.* (2014b), although the energy costs of gestation remained lower than those of lactation. In white-tailed deer, mass loss for females in gestation corresponded to an increase of 16% of the energy costs, compared to non-gestating females (Pekins *et al.* 1998). Mass recovery, however, could partially be achieved by compensatory mechanisms in summer, such as hyperphagia (Wairimu & Hudson 1993). Females would then need to increase feeding time and/or feeding rates to rapidly build up body reserves before the winter.

Further considerations

Our 13-year study highlights the occurrence of reproductive plasticity in female white-tailed deer. We demonstrated the relevance of considering density-dependent mechanisms and inter-annual variability in environmental conditions to better understand life-history strategies, since both trigger plasticity in reproductive effort. A good understanding of how these factors affect life-history strategies is particularly important for harvested populations because their adaptive management requires information on future reproductive performance at the population level. In this regard, identifying threshold densities where females modify life-history strategies is particularly relevant. Additionally, our long-term study shows that while the main costs of reproduction were attributed to lactation, the costs of gestation were also significant.

ACKNOWLEDGEMENTS

REFERENCES

Andersen, R. & J. D. C. Linnell. 2000. Irruptive potential in roe deer: density-dependent effects on body mass and fertility. *The Journal of Wildlife Management*, 64: 698-706.

Bårdsen, B.-J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz & R. A. Ims. 2008. Experimental evidence of a risk-sensitive reproductive allocation in a long-lived mammal. *Ecology*, 89: 829-837.

Bårdsen, B.-J. & T. Tveraa. 2012. Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. *Journal of Animal Ecology*, 81: 364-376.

Bårdsen, B.-J., T. Tveraa, P. Fauchald & K. Langeland. 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia*, 162: 627-639.

Bates, D., M. Mächler, B. M. Bolker & S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67: 1-48.

Bonenfant, C., J.-M. Gaillard, T. Coulson, M. Festa-Bianchet, A. Loison, M. Garel, L. E. Loe, P. Blanchard, N. Pettorelli, N. Owen-Smith, J. Du Toit & P. Duncan. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research*, 41: 313-357.

Bonenfant, C., J.-M. Gaillard, F. Klein & A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography*, 25: 446-458.

Bonin, M., J.-P. Tremblay & S. D. Côté. 2016. Contributions of digestive plasticity to the ability of white-tailed deer to cope with a low-quality diet. *Journal of Mammalogy*, 97: 1406-1413.

Borowik, T., P. Wawrzyniak & B. Jędrzejewska. 2016. Red deer (*Cervus elaphus*) fertility and survival of young in a low-density population subject to predation and hunting. *Journal of Mammalogy*, 97: 1671-1681.

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

Canada Center for Remote Sensing, Natural Ressources Canada**.** 2016. <http://www.nrcan.gc.ca/earth-sciences/geomatics/satellite-imagery-air-photos/long-term-satellite-data-records/10935%3E. Accessed 22 Jan. 2016.

Chan-McLeod, A. C. A., R. G. White & D. F. Holleman. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. *Canadian Journal of Zoology*, 72: 938-947.

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

Clutton-Brock, T. H., F. E. Guinness & S. D. Albon. 1983. The costs of reproduction to red deer hinds. *Journal of Animal Ecology*, 52: 367-383.

Cook, R. C., J. G. Cook & L. D. Mech. 2004. Nutritional condition of northern yellowstone elk. *Journal of Mammalogy*, 85: 714-722.

Crête, M., J. Huot, R. Nault & R. Patenaude. 1993. Reproduction, growth and body composition of Rivière George caribou in captivity. *Arctic*, 46: 189-196.

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

Environment Canada. 2006. Climate normals and averages, daily data reports of Port-Menier's station from 1995 to 2005. Atmospheric Environment Service, Ontario, Canada.

Ericsson, G., K. Wallin, J. P. Ball & M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology*, 82: 1613-1620.

Festa-Bianchet, M. & S. D. Côté. 2008. Mountain goats: ecology, behavior, and conservation of an alpine ungulate. Island Press, Washington, USA.

Flajšman, K., K. Jerina & B. Pokorny. 2017. Age-related effects of body mass on fertility and litter size in roe deer. *PloS one*, 12: e0175579

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

Gaillard, J.-M., A. J. Sempéré, J.-M. Boutin, G. Van Laere & B. Boisaubert. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Canadian Journal of Zoology*, 70: 1541-1545.

Gingras, J., S. Couturier, S. D. Côté & J.-P. Tremblay. 2014. Opposite responses of body condition and fertility in adjacent moose populations. *The Journal of Wildlife Management*, 78: 830-839.

Goudreault, F. 1980. Reproduction and population dynamics of white-tailed deer on Anticosti Island. *MSc Thesis.* Université Laval, Québec, Canada.

Guinness, F. E., G. A. Lincoln & R. V. Short. 1971. The reproductive cycle of the female red deer, *Cervus elaphus* L*. Journal of Reproduction and Fertility*, 27: 427-438.

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

Hamel, S., S. D. Côté & M. Festa-Bianchet. 2011. Tradeoff between offspring mass and subsequent reproduction in a highly iteroparous mammal. *Oikos*, 120: 690-695.

Hamel, S., J.-M. Gaillard, M. Festa-Bianchet & S. D. Côté. 2009. Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, 90: 1981-1995.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology*, 12: 12-45.

Hamilton, W. J. & K. L. Blaxter. 1980. Reproduction in farmed red deer 1. Hind and stag fertility. *Journal of Agricultural Science*, 95: 261-273.

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

Hastie, T. J. & R. J. Tibshirani. 1990. Generalized Additive Models. Chapman & Hall, London, UK.

Kirkwood, T. B. L. & S. N. Austad. 2000. Why do we age? *Nature*, 408: 233-238.

Langvatn, R., Ø. Bakke & S. Engen. 1994. Retrospective studies of red deer reproduction using regressing luteal structures. *The Journal of Wildlife Management*, 58: 654-663.

Leader-Williams, N. & C. Ricketts. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. *Oikos*, 38: 27-39.

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

Mauget, C., R. Mauget & A. Sempéré. 1997. Metabolic rate in female European roe deer (*Capreolus capreolus*): incidence of reproduction. *Canadian Journal of Zoology*, 75: 731-739.

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

McNamara, J. M. & A. I. Houston. 1996. State-dependent life histories. *Nature*, 380: 215-221.

Medawar, P. B. 1946. Old age and natural death. *Modern Quarterly*, 1: 30-56.

Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *The Journal of Wildlife Management*, 42: 715-738.

Monteith, K. L., T. R. Stephenson, V. C. Bleich, M. M. Conner, B. M. Pierce & R. T. Bowyer. 2013. Risk-sensitive allocation in seasonal dynamics of fat and protein reserves in a long-lived mammal. *Journal of Animal Ecology*, 82: 377-388.

Mysterud, A., G. Steinheim, N. G. Yoccoz, Ø. Holand & N. C. Stenseth. 2002. Early onset of reproductive senescence in domestic sheep, *Ovis aries*. *Oikos*, 97: 177-183.

Noble, M. S. & W. L. Hurley. 1999. Effects of secretion removal on bovine mammary gland function following an extended milk stasis. *Journal of Dairy Science*, 82: 1723-1730.

Nussey, D. H., H. Froy, J.-F. Lemaître, J.-M. Gaillard & S. N. Austad. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, 12: 214-225.

Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie & T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecology Letters*, 9: 1342-1350.

Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton & T. H. Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. *The American Naturalist*, 174: 342-357.

Panagakis, A., S. Hamel & S. D. Côté. 2017. Influence of early reproductive success on longevity and late reproductive success in an alpine ungulate. *The American Naturalist*, 189: 667-683.

Parker, K. L., P. S. Barboza & M. P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. *Functional Ecology*, 23: 57-69.

Parker, K. L., M. P. Gillingham, T. A. Hanley & C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildlife Monographs*, 143: 1-48.

Parker, K. L., C. T. Robbins & T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *The Journal of Wildlife Management*, 48: 474-488.

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

Pettorelli, N., S. D. Côté, A. Gingras, F. Potvin & J. Huot. 2007a. Aerial surveys vs hunting statistics to monitor deer density: the example of Anticosti Island, Québec, Canada. *Wildlife Biology*, 13: 321-327.

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

Pettorelli, N., R. B. Weladji, Ø. Holand, A. Mysterud, H. Breie & N. C. Stenseth. 2005. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biology Letters*, 1: 24-26.

Pinheiro, J. C. & D. M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York, USA.

Plard, F., N. G. Yoccoz, C. Bonenfant, F. Klein, C. Warnant & J.-M. Gaillard. 2015. Disentangling direct and growth-mediated influences on early survival: a mechanistic approach. *Journal of Animal Ecology*, 84: 1363-1372.

Potvin, F. & L. Breton. 1992. Rigueur de l'hiver pour le cerf au Québec : description de l'indicateur prévisionnel NIVA et présentation d'un logiciel approprié. *Ministère du Loisir, de la Chasse et de la Pêche, Québec. Rep. SP 1936.*

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

Promislow, D. E. L. & P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology*, 220: 417-437.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia*, 106: 212-220.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1: 103-113.

Simard, M. A., S. D. Côté, A. Gingras & T. Coulson. 2012. Tests of density dependence using indices of relative abundance in a deer population. *Oikos*, 121: 1351-1363.

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

Simard, M. A., J. Huot, S. de Bellefeuille & S. D. Côté. 2014a. Influences of habitat composition, plant phenology, and population density on autumn indices of body condition in a northern white-tailed deer population. *Wildlife Monographs*, 187: 1-28.

Simard, M. A., J. Huot, S. de Bellefeuille & S. D. Côté. 2014b. Linking conception and weaning success with environmental variation and female body condition in a northern ungulate. *Journal of Mammalogy*, 95: 311-327.

Solberg, E. J., A. Loison, J.-M. Gaillard & M. Heim. 2004. Lasting effects of conditions at birth on moose body mass. *Ecography*, 27: 677-687.

Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology*, 3: 259-268.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

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

Taillon, J., V. Brodeur, M. Festa-Bianchet & S. D. Côté. 2011. Variation in body condition of migratory caribou at calving and weaning: which measures should we use? *Ecoscience*, 18: 295-303.

Tavecchia, G., T. Coulson, B. J. T. Morgan, J. M. Pemberton, J. G. Pilkington, F. M. D. Gulland & T. H. Clutton-Brock. 2005. Predictors of reproductive cost in female soay sheep. *Journal of Animal Ecology*, 74: 201-213.

Tollefson, T. N., L. A. Shipley, W. L. Myers, D. H. Keisler & N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *The Journal of Wildlife Management*, 74: 974-986.

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

Tveraa, T., P. Fauchald, C. Henaug & N. G. Yoccoz. 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. *Oecologia*, 137: 370-376.

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

Wairimu, S. & R. J. Hudson. 1993. Foraging dynamics of wapiti stags (*Cervus elaphus*) during compensatory growth. *Applied Animal Behaviour Science*, 36: 65-79.

White, K. S., G. W. Pendleton & E. Hood. 2009. Effects of snow on sitka black-tailed deer browse availability and nutritional carrying capacity in Southeastern Alaska. *The Journal of Wildlife Management*, 73: 481-487.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11: 398-411.

Wood, S. N. 2006. Generalized additive models: an introduction with R. CRC press, Florida, USA.

Zuur, A. F., E. N. Ieno & C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1: 3-14.