Opposite Responses of Body Condition and Fertility in Adjacent Moose Populations

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ABSTRACT Moose (Alces alces) populations exceed 3 individuals/km² in some wildlife reserves and parks of northeastern Canada. Heavy browsing pressure at such densities is potentially altering the ecological integrity of forests with eventual negative consequences for moose. We hypothesized that regulation by resources would be limited by the capacity of female moose to modulate their reproductive strategies to maintain high fertility despite a decline in body condition. We observed a 20–33% decline in rump fat thickness in males and females, respectively, from the high density Matane Wildlife Reserve in Eastern Québec in October compared to an adjacent population. We also observed a lower mass of the peroneus group of muscles for males (−3%) and prime-aged females (−8%) in the Matane Wildlife Reserve than in the adjacent population. Females from the Matane Wildlife Reserve population had a lower twinning ovulation rate (1 out of 20 vs. 7 out of 21 ovulating females in the adjacent population) but >15% higher overall ovulation rate. Our results suggest that female moose can maintain high fertility despite a decline in body condition, by reducing their litter size at ovulation and conserving energy to increase the probability of annual reproduction. The adjustment of female reproductive strategies illustrates the plasticity of moose in response to decreasing habitat quality. We conclude that in the absence of specialist predators, equilibrium with forage is unlikely for large herbivores in the short or mid-term. Active management of moose populations is likely required to maintain the ecological integrity of boreal forests. © 2014 The Wildlife Society.

KEYWORDS body condition, boreal forest, density dependence, eastern Québec, fertility, forest regeneration, Moose Alces alces, overabundance, reproductive strategies.

Two alternative hypotheses are commonly proposed to explain the population limitation of large herbivores (Crête and Courtois 1997). Under the predator-regulation hypothesis, predation stabilizes herbivores at low density, releasing vegetation from top-down control by consumers and reducing competition for forage (Sinclair and Arcese 1995). Messier and Crête (1985) showed that the combined predation of wolves (Canis lupus) and black bears (Ursus americanus) could regulate moose numbers at low density. The food-limitation hypothesis proposes that an herbivore population increases until it reaches a dynamic equilibrium with food resources (bottom-up control; Caughley 1970). Many studies have implicated a density-dependent equilibrium between forage and ungulate abundance (McCullough 1979, Sinclair et al. 1985, McLaren and Peterson 1994) or limitation from resources (Crête and Courtois 1997). However, several large herbivore populations increased considerably in abundance worldwide in recent decades (Côté et al. 2004), and dramatic shifts in forest composition toward resistant plant species were observed (Coomes et al. 2003, Martin et al. 2010, Gosse et al. 2011). These cases raise questions about the equilibrium between herbivores and their food resources, especially in changing environment with low predation (Crête and Courtois 1997, Sæther 1997, Peterson 1999).

The selective browsing of large herbivores has direct effects on vegetation by reducing seedling growth or killing seedlings of preferred plant species (McInnes et al. 1992, Tremblay et al. 2007, Hidding et al. 2012), and indirect effects by favoring species that are tolerant or resistant to browsing (Pastor et al. 1993, Mathisen et al. 2010). Consequently, abundant large herbivores can force forests toward alternative successional pathways and reduce the quantity and quality of their food resources (McLaren et al. 2004, Tremblay et al. 2007, Hidding et al. 2014). For instance, in Newfoundland, densities of moose (Alces alces) up to 3/km² negatively affected the capacity of balsam fir (Abies balsamea [L.] Mill.) to regenerate following canopy disturbance (Gosse et al. 2011).
A decline in diet quality can eventually affect body condition of ungulates by reducing growth, fat reserves, and muscle mass (Stewart et al. 2005, Toigo et al. 2006, Simard et al. 2008, Cook et al. 2013). Relationships between nutritional condition of the range and body mass have been observed in several large herbivores (Severinghaus 1979, Simard et al. 2008, Couturier et al. 2009a, Rodriguez-Hidalgo et al. 2010, Cook et al. 2013). Body condition can also affect survival, particularly for juveniles in winter (Loison et al. 1999).

As nutritional condition decline, the fertility of large herbivore females may decrease through a resource-dependent reduction in body condition, especially in body fat reserves (Ferguson et al. 2000, Stewart et al. 2005, Cook et al. 2013). Reproduction involves high metabolic costs for females, mostly during lactation (Clutton-Brock et al. 1989). The probability of ovulation can be influenced by body condition during oestrus (Sand 1996, Testa and Adams 1998). For instance, in Sweden, a 25% decrease in the body mass of yearling moose females in autumn resulted in a 42% decline in the probability of ovulation (Sand 1996). At high density, a trade-off between growth and reproduction often results in delayed maturity among young females (Jorgenson et al. 1993, Forchhammer et al. 2001, Bonenfant et al. 2009). Litter size can also decrease with declining body condition (Franzmann and Schwartz 1985, Kech et al. 2000). For example, in a low-density region (0.2 moose/km²) to a high-density region (>4.0 moose/km²), the moose twinning rate varied from 49% to 1% (Ferguson et al. 2000). However, some studies suggested that the high productivity rate in abundant large herbivore populations could be maintained despite chronic herbivory (Skogland 1990, Sæther et al. 1996, Simard et al. 2008). With a decline in browse availability, females can modify their reproductive strategy to maintain a high fertility rate (Clutton-Brock et al. 1996). Simard et al. (2008) observed that white-tailed deer (Odocoileus virginianus) females on Anticosti Island, Quebec, conserved energy by reducing their litter size at ovulation to increase the probability of reproducing during most years.

Overabundance has been recently described in some wildlife reserves and parks of eastern Canada where moose density has increased exponentially since the 1990s, exceeding 4 individuals/km² (Lamoureux et al. 2007, Goss et al. 2011). The extinction of the wolf (Canis lupus), conservative hunting regulations, and productive early successional habitat types generated by forest harvesting, may have favored the increase of populations (Côté et al. 2004). A shortage in deciduous stems and an increase in the balsam fir browsing rate suggested that moose populations exceeded carrying capacity (M. Fleury, Faune-Experts, unpublished report showing that 83% of available twigs from deciduous species and 51% from balsam fir have been browsed) estimated at approximately 2 moose/km² (Crète 1989). The heavy browsing pressure at such densities may be altering the ecological integrity of balsam fir-paper birch (Betula papyrifera Marshall) forests of eastern Quebec with implications for moose populations (Gosse et al. 2011).

We investigated the relationships among moose body condition and fertility in 2 adjacent moose populations. We hypothesized that regulation by resources would be limited by the capacity of female moose to modulate their reproductive strategies to maintain high fertility despite a decline in body condition. We predicted that a decline in body condition would lead to a reduction in the number of double ovulations and an increase in the overall ovulation rate.

**STUDY AREA**

We compared fall body condition and female fertility in moose between 2 wildlife reserves located 20 km apart in the Gaspé Peninsula in eastern Québec with contrasting environmental conditions, especially regarding moose abundance. These populations had experienced different hunter harvest regimes and appeared to differ relative to moose density. The moose population in the Matane Wildlife Reserve (66.45°–67.30°N, 48.53°–48.92°W) was estimated at 4.8 ± 0.7/km² in 2007 (Lamoureux et al. 2007) and 3.3 ± 0.3/km² in 2012 (Lamoureux et al. 2012). To derive these estimates, the wildlife agency used helicopter surveys following a 2-phase sampling plan described in Rivest et al. (1990); in the first phase, observers mapped all moose yards within 66% of the 1,282-km² study area (n = 355) and they counted moose in 22.8% (n = 81) of the yards in the second phase. A multiplication factor of 1.52 was applied to correct for visibility bias following Crète et al. (1986). Similarly, the population from the Chic-Chocs Wildlife Reserve (48.75°–49.13°N, 65.50°–66.17°W) was estimated at 1.11 moose/km² from an aerial coverage of 96.3% of the 1,129-km² study area with counts of all moose in all yards (n = 267; Dorais and Lavergne 2010). Consistent with the results of the aerial surveys, the mandatory reports of the total number of moose seen by hunter groups (4 persons for up to 4 consecutive days) in autumn 2011 were 20.7 ± 2.6 in Matane and 4.6 ± 0.4 in Chic-Chocs Wildlife Reserve (D. Gagnon and B. Drouin, Société des établissements de plein air du Québec, personal communication).

This region has a perhumid sub-boreal climate with cool summers, cold winters and abundant rainfall and snowfall. The average temperature annually, in July, and in January are respectively 1.5°C, 16.2°C, and −14.6°C near the Matane Wildlife Reserve and 1.7°C, 16.4°C, and −13.9°C near the Chic-Chocs Wildlife Reserve (Environment Canada 2012). The average annual precipitation of rain and snow are 728.5 mm and 405.7 cm near Matane Wildlife Reserve (Environment Canada 2012). The topography is rugged, with some mountains reaching over 850 m above sea level (average elevation [x ± SD] of 440 ± 170 m in Matane Wildlife Reserve and 560 ± 140 m in Chic-Chocs Wildlife Reserve). The forest is part of the boreal zone and mostly part of the eastern balsam fir-paper birch bioclimatic subregion (Saucier et al. 2009). Mature forests were dominated by balsam fir, white spruce (Picea glauca [Moench] Voss), black spruce (P. mariana [Mill.] Britton, Sterns & Poggenb), paper birch, and quaking aspen
(Populus tremuloides Michx.; Sauzier et al. 2009). Dominant understorey forage species included balsam fir, mountain maple (Acer spicatum Lam.), paper birch, pin cherry (Prunus pensylvanica L. f.), quaking aspen, redosier dogwood (Cornus sericea ssp. sericea L.), red elderberry (Sambucus racemosa var. racemosa L.), and American mountain-ash (Sorbus americana Marshall). Wolves were extirpated from the region about a century ago (Boisjoly et al. 2010); black bears and coyotes (Canis latrans) were the only natural predators of moose calves. Other mammalian herbivores included white-tailed deer (<0.66/km²; Huot and Lebel 2012) and snowshoe hare (Lepus americanus).

METHODS

Fall Body Condition

We derived body condition indices from 572 moose killed by sport hunters between 8 September and 29 October 2009 (nMatane = 137, nChic-Chocs = 126) and 2010 (nMatane = 143, nChic-Chocs = 166). We recorded harvest date, sex, and the reproductive state of females inferred from the presence of white milk in the udder. We estimated the age of moose via microhistological analysis of cementum layers from incisor teeth (Rolandsen et al. 2008), and we indexed skeletal growth by measuring hind foot length from the calcaneum to the tip of the hoof (Zannèse et al. 2006). We estimated subcutaneous fat reserves from the average rump fat thickness at 5 cm and 10 cm along an incision at 45° cranial from the base of the tail (±0.05 cm; Huot 1988) and intraperitoneal fat reserves from kidney fat mass (±0.05 g, ACBplus 3000, Adam Equipment, Danbury, CT, USA; Anderson et al. 1990). Stephenson et al. (1998) provided predictive equations to estimate overall lipid reserves at multiple deposition sites from maximum rump fat thickness or kidney fat mass. We could not use the equation for rump fat because the measurements had not been taken at the same location and with the same tools. We used the mass of a group of indicator muscles as a proxy of muscular mass; we dissected the muscle peroneus tertius with extensor digitorum longus and extensor digit III attached from the lower part of the leg and weighed them soon after collection (hereafter, peroneus; ±0.05 g, ACBplus 3000; Couturier et al. 2009a). Peroneus data were not available in 2010. We also obtained dressed body mass (live mass minus viscera and bleedable blood; ±0.5 kg, CS2000 scale, Salter Brecknell, Pointe-Claire, Québec, Canada).

Female Fertility

We evaluated female fertility from the count of ovulation scars in 93 ovary pairs collected from female moose killed by hunters (nMatane = 18 and 25, nChic-Chocs = 11 and 39 in 2009 and 2010, respectively). We preserved and prepared ovaries for microscopic examination (10×) following the method described in Simard et al. (2008) with the exception of coloring 1 10-μm slice out of 50. We counted the number of corpus luteum (CL) originating from recent ovulation (<1 year) and corpus albicans (CA) referring to an ovulation that occurred the previous year (Langvatn et al. 1994). For ovulation of the current year, we restricted the count of CL to ovaries of adult females killed after 5 October (nMatane = 26, nChic-Chocs = 36) because the period of peak conception in this area occurs from 23 September to 8 October. Therefore, most females should have ovulated by that time (Sigouin et al. 1997). We derived 3 indices of female fertility: adult ovulation rate, corresponding to the percentage of adults that had at least 1 ovulation (CL ≥ 1 or CA ≥ 1); yearling ovulation rate (CL ≥ 1); and adult double ovulation rate, corresponding to the percentage of ovulating adult females that had 2 ovulations within a single year (CL = 2 or CA = 2). We cannot exclude that luteinized, non-ruptured follicle not directly associated with previous pregnancies and parturitions such as corpus luteum accessorium (CLA) or corpus albicans accessorium (CAA) were misidentified as CA. CAA are more frequent in young individuals (Langvatn et al. 1994). We think the error rate for both sites is unbiased because the ovaries in our dataset come from female samples with a similar age distribution (x ± SD = 5.9-yr-old ± 4.4 in 2009 and 5.9-yr-old ± 2.8 in 2010 for the Chic-Chocs Wildlife Reserve compared to 5.5-yr-old ± 2.8 in 2009 and 4.5-yr-old ± 2.7 in 2010 for the Matane Wildlife Reserve).

Statistical Analyses

For all body condition parameters, we performed sex-specific analyses (n = 316 males and 256 females) because of differences in life histories. We excluded combinations of age and site (wildlife reserve) for which n < 4 (i.e., calves, males ≥8.5 years old, and females ≥11.5 years old). We compared body condition parameters between the 2 sites using general linear models (function lm, package stats, R version 2.14.0, www.r-project.org; Crawley 2007), and used age, age² (non-linear effect), year, and reproductive state for females as potential predictor variables. We included the harvest date as a covariate for all analyses involving body mass. We added kidney mass as a covariate to models of kidney fat mass to correct for the effect of organ size on fat mass (Serrano et al. 2008) and the hind foot length to models of peroneus mass to correct for the effect of body size.

We compared variability in adult ovulation and adult double ovulation rates for moose from the 2 sites using a generalized linear mixed model with a binomial error distribution and a logit link (function glmer, package lme4, R version 2.14.0; Crawley 2007), and used age, age² (non-linear effect), year, and reproductive state for females as potential predictor variables. We included the harvest date as a covariate for all analyses involving body mass. We added kidney mass as a covariate to models of kidney fat mass to correct for the effect of organ size on fat mass (Serrano et al. 2008) and the hind foot length to models of peroneus mass to correct for the effect of body size.

We transformed variables to ensure normality requirements using the box-cox procedure (package MASS, R version 2.14.0; Crawley 2007). We log-transformed kidney fat and square-root transformed rump fat thickness. We compared only models that were linked to our hypotheses, including simple effects, their 2-way and 3-way interactions, and the explanatory variable site. We found no strong correlation among independent variables according to the variation inflation factor (VIF < 10; Chatterjee and Price 1977). We
compared hierarchical models using the Akaike’s Information Criterion with a correction for finite sample sizes (AICc) and selected the model with the lowest AICc (Burnham and Anderson 2002). We also tested factors included in models within ΔAICc ≤ 2 of the best model (Stephens et al. 2005). We used least square means (package lsmeans, R version 2.14.0; Crawley 2007) to conduct a posteriori comparisons. Results are presented as means or lsmeans ±95% confidence intervals. The threshold for statistical significance was fixed at α = 0.05.

RESULTS

Fall Body Condition

The best model, and all alternative models for the variation in the rump fat thickness of males, included the 3-way interaction among site, age, and harvest date (Table 1). During the period of peak conception (mid-Sep to mid-Oct), rump fat thickness of males 4.5–7.5 years old decreased faster than for males ≤ 3.5 years old (Fig. 1a). The rump fat thickness of males 4.5–7.5 years old was similar at both sites in mid-September (15 Sep: F1,231 < 1.4, P > 0.2 for all models) and was 20% lower at the Matane Wildlife Reserve than at the Chic-Chocs Wildlife Reserve at the beginning of October (1 Oct: F1,231 > 4.3, P < 0.04 for all models; Fig. 1a), which was a trend that could still be observed by mid-October (15 Oct: F1,231 < 4, P > 0.07 for all models; Fig. 1a). We found no differences in rump fat throughout autumn in younger males (F1,231 < 0.9, P > 0.2 for all models). For females, the 2-way interaction between site and harvest date was included in the best model and in all alternative models (Table 1). The accumulation of rump fat was similar in females at both sites in September (F1,181 < 2.7, P > 0.1 for all models; Fig. 1b). Rump fat was relatively stable for females at the Chic-Chocs Wildlife Reserve but decreased progressively from 5.3 cm at the beginning of the period of peak conception to 3.2 cm by mid-October at the Matane Wildlife Reserve, which was a 33% difference with females from the Chic-Chocs Wildlife Reserve (15 Oct.: F1,181 = 10.4, P = 0.01; Fig. 1b). For females, age, age², and reproductive state were also included in all competing models (Table 1). The rump fat thickness of females increased non-linearly with age (age: F1,180 > 18.6, P ≤ 0.001; age²: F1,180 > 15.4, P ≤ 0.001 for all models). Lactating females had less rump fat than non-lactating females (2.7 cm ± 0.5 vs. 4.2 cm ± 0.5; F1,180 > 0.5, P ≤ 0.001 for all models). The 2-way interactions site × age and site × reproductive state were included in 1 of the 2 best models, but the parameters were not significant (F1,180 < 0.7, P = 0.4 for all models; F1,180 = 0.4, P = 0.5, respectively; Table 1).

Variation in the mass of kidney fat in males was best explained by models including age² and harvest date (Table 2). The mass of kidney fat increased with age until males were 4.5 years old and decreased thereafter (1.5-yr-old = 535 g ± 62, 4.5-yr-old = 642 g ± 58, 7.5-yr-old = 548 g ± 56; age²: F1,153 = 7.1, P = 0.008). The mass of kidney fat decreased during the period of peak conception (F1,153 > 255.7, P ≤ 0.001 for all models). Site was included in 1 of the 2 models with ΔAICc < 2, but the parameter was not significant (F1,153 = 0.3, P = 0.6; Table 2). For females, all competing models included age, age², harvest date, and reproductive state (Table 2). The mass of kidney fat increased with age until females were 6.5 years old and decreased thereafter (1.5-yr-old = 590 g ± 98, 6.5-yr-old = 811 g ± 100, 10.5-yr-old = 706 g ± 164; age: F1,141 > 4.5, P < 0.04; age²: F1,141 > 5.1, P < 0.03 for all models). It also decreased with harvest date (F1,141 > 6.3, P < 0.01 for all models) and was lower for lactating females than for non-lactating females (515 g ± 74 vs. 720 g ± 77; F1,141 < 15.1, P < 0.002 for all models). Site was included in 1 of the 4 best models, but the effect did not differ from 0 (F1,141 = 0.2, P = 0.6; Table 2).

The best model and all alternative models of the variation in the mass of the peroneus for males, included age, age², and harvest date (Table 3). The peroneus mass increased non-linearly with age (age: F1,82 > 34.9, P ≤ 0.001; age²: F1,84 > 10.1, P < 0.002 for all models; Fig. 2) and decreased with harvest date (F1,84 > 3.9, P < 0.05 for all models). Site was included in the best model and in 1 of the 2 best alternative models. The peroneus mass was 3% lower at the Matane Wildlife Reserve than at the Chic-Chocs Wildlife Reserve for all ages (F1,83 = 4.0, P = 0.05; Fig. 2). The 2-way interaction site × age appeared in the second alternative model, but the parameter was not significant (F1,82 = 0.5, P = 0.5; Table 3). For females, all competing models included age, reproductive state, and the 2-way interaction between site and age² (Table 3). The peroneus mass increased with age (F1,67 > 47.0, P ≤ 0.001 for all models; Fig. 2) and was lower

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**Table 1.** Factors contributing to the variation in the rump fat thickness of moose (males: n = 240; females: n = 188) in 2 adjacent wildlife reserves from eastern Quebec, Canada in 2009–2010. We compared alternative general linear models, denoted by Mx for males and Fx for females, using the Akaike’s Information Criterion with a correction for finite sample sizes (AICc); we present only models with ΔAICc ≤ 2 for concision. We included, age, age², harvest date, year, and reproductive state as covariates. Parameter estimates with an asterisk (*) are statistically different from 0 (α = 0.05).

<table>
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<th>Age²</th>
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<th>Year</th>
<th>Reproductive state</th>
<th>Site × age</th>
<th>Site × harvest date</th>
<th>Site × reproductive state</th>
<th>Site × age × harvest date</th>
<th>AICc</th>
<th>ΔAICc</th>
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<td></td>
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<td>–0.04</td>
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Figure 1. Variation in the rump fat thickness of moose, a proxy of subcutaneous fat reserves, in relation with harvest date and age in 2 adjacent wildlife reserves from eastern Quebec, Canada, in 2009–2010 for (a) males \( (n = 240) \), and (b) females \( (n = 188) \). Subcutaneous fat reserves of prime-aged males and females were lower at the Matane Wildlife Reserve during the energy demanding rut period. The moose population was estimated at 3.3 ± 0.3/km² at the Matane Wildlife Reserve and 1.1 moose/km² at the Chic-Chocs Wildlife Reserve. Symbols represent the mean rump fat thickness ±95% confidence intervals estimated from best general linear models. Significant differences between sites are indicated by an asterisk (*). A small offset was added to values on the x-axes to improve readability.

Table 2. Factors contributing to the variation in the mass of kidney fat in moose (males: \( n = 157 \); females: \( n = 147 \)) in 2 adjacent wildlife reserves from eastern Quebec, Canada in 2009–2010. We compared alternative general linear models, denoted by Mx for males and Fx for females, using the Akaike's Information Criterion with a correction for finite sample sizes (AIC\(_c\)); we present only models with ΔAIC\(_c\) ≤ 2 for concision. We included age, age\(^2\), harvest date, year, reproductive state, and average mass of kidneys as covariates. Parameter estimates with an asterisk (*) are statistically different from 0 \( (\alpha = 0.05) \).

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<th>Reproductive state</th>
<th>AIC(_c)</th>
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Table 3. Factors contributing to the variation in the peroneus mass of moose (males: \( n = 89 \); females: \( n = 74 \)) in 2 adjacent wildlife reserves from Eastern Quebec, Canada in 2009. We compared alternative general linear models, denoted by Mx for males and Fx for females, using the Akaike's Information Criterion with a correction for finite sample sizes (AIC\(_c\)); we present only models with ΔAIC\(_c\) ≤ 2 for concision. We included age, age\(^2\), harvest date, year, and reproductive state as covariates. Parameter estimates with an asterisk (*) are statistically different from 0 \( (\alpha = 0.05) \).

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<th>Age</th>
<th>Age(^2)</th>
<th>Harvest date</th>
<th>Reproductive state</th>
<th>Site × age</th>
<th>Site × age(^2)</th>
<th>AIC(_c)</th>
<th>ΔAIC(_c)</th>
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DISCUSSION

The comparison of body condition from moose killed by sport hunters in 2 adjacent wildlife reserves with contrasted habitat conditions, revealed lower subcutaneous fat reserves, and muscular mass in the high density Matane Wildlife Reserve. Females from this population had fewer double oovulations, but a higher overall ovulation rate, compared to females from the close Chic-Chocs Wildlife Reserve. Females from the Matane Reserve apparently conserve energy by reducing litter size at ovulation to increase the probability of reproducing in most years (Simard et al. 2008). Our results support Sæther et al. (1996) and Simard et al. (2008), suggesting that in the absence of predation, an equilibrium with forage is unlikely for moose.

We cannot exclude potential differences in the productivity of the habitat between the 2 wildlife reserves. The Chic-Chocs Wildlife Reserve is on average 100 m higher in

![Figure 2. Peroneus mass of moose, a proxy of the muscular mass, in relation with age and sex (males: n = 89; females: n = 74) in 2 adjacent wildlife reserves from eastern Québec, Canada, in 2009. The moose population was estimated at 3.3 ± 0.3 km² at the Matane Wildlife Reserve and 1.1 moose/ km² at the Chic-Chocs Wildlife Reserve. Symbols represent the mean peroneus mass ±95% confidence intervals estimated from the best general linear models. Significant differences between sites are indicated with an asterisk (*). A small offset was added to values on the x-axis to improve readability.](image)

for lactating females than for non-lactating ones ($F_{1,66} > 9.3, P < 0.003$). The mass of the peroneus for females aged 1.5 years old and ≥ 5.5 years old was similar at both sites ($F_{1,67} < 1.5, P > 0.2$ for all models) but was 8% lower at the Matane Wildlife Reserve for females aged 2.5–7.5 years old than at the Chic-Chocs Wildlife Reserve ($F_{1,67} > 7.9, P < 0.006$ for all models; Fig. 2).

Variation in the dressed body mass of males was best explained by models including age, age², and harvest date (Table 4). The male dressed body mass increased non-linearly with age (1.5-yr-old = 230 kg ± 14, 4.5-yr-old = 339 kg ± 8, 7.5-yr-old = 389 kg ± 12; age: $F_{1,114} > 129.2, P < 0.001$; age²: $F_{1,115} > 17.5, P < 0.001$ for all models) and decreased with harvest date ($F_{1,115} > 6.9, P < 0.01$ for all models). Site and the 2-way interaction site × age occurred, respectively, in 4 and 2 of the 5 best alternative models, but their parameters were not significant (site: $F_{1,115} < 1.4, P > 0.2$; site × age: $F_{1,115} < 1.8, P > 0.2$ for all models). For females, the best model and all alternative models of the variation in dressed body mass included age, age², and reproductive state (Table 4). The female dressed body mass increased with age until females were 7.5 years old and decreased thereafter (1.5-yr-old = 206 kg ± 10, 7.5-yr-old = 297 kg ± 13, 10.5-yr-old = 241 ± 43; age: $F_{1,153} > 172.6, P < 0.001$; age²: $F_{1,154} > 37.5, P < 0.001$ for all models). Lactating females had lower dressed body mass than did non-lactating females (247.0 kg ± 9.0 vs. 268.0 kg ± 6.8; $F_{3,154} > 16.0, P < 0.001$ for all models).

**Female Fertility**

The single best model ($\text{AIC}_c = 101.3$) of the variation in adult ovulation rate included site ($Z_{1,17} = -2.0, P = 0.05$), as well as the linear and quadratic effects of age (age: $Z_{1,17} = 2.1, P = 0.04$; age²: $Z_{1,17} = -2.9, P = 0.004$). The ovulation rate of adult females was 15% higher at the Matane Wildlife Reserve ($n = 36$) than at the Chic-Chocs Wildlife Reserve ($n = 44$; Fig. 3). At the former site, only 1 out of 20 ovulating adult females had 2 ovulations (5%), whereas double ovulations reached 33% at the Chic-Chocs Wildlife Reserve ($n = 21$).

**Table 4. Factors contributing to the variation in the body mass of moose (males = 235; females = 158) in 2 adjacent wildlife reserves from eastern Québec, Canada in 2009–2010. We compared alternative general linear models, denoted by Mx for males and Fx for females, using the Akaike’s Information Criterion with a correction for finite sample sizes (AICc); we present only models with ΔAICc ≤ 2 for concision. We included age, age², harvest date, year, and reproductive state as covariates. Parameter estimates with an asterisk (*) are statistically different from 0 ($z = 0.05$).**

<table>
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<tr>
<th>Site</th>
<th>Age</th>
<th>Age²</th>
<th>Harvest date</th>
<th>Year</th>
<th>Reproductive state</th>
<th>Site x age</th>
<th>AICc</th>
<th>ΔAICc</th>
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altitude than the Matane Wildlife Reserve, and the stocking of deciduous trees tends to be less in Chic-Chocs than in Matane (Berger and Blouin 2006). However, we think that the difference in moose density indicated both by aerial surveys, the standard for the estimation of populations of large herbivores (Boyce et al. 2012), and independent data on the number of moose seen by hunters while hunting remains the most striking difference between the 2 adjacent populations. Differences in habitat productivity related to temperature and edaphic conditions and past hunting regimes likely have both contributed to shape the moose populations in these 2 areas.

Fall Body Condition

Moose in the Matane Wildlife Reserve had lower subcutaneous fat reserves estimated from rump fat thickness than moose from the Chic-Chocs Wildlife Reserve. The subcutaneous fat reserves of females in the Matane Wildlife Reserve decreased by 40% during the period of peak conception, leading to a difference in rump fat thickness of 33% compared to females from the Chic-Chocs Wildlife Reserve by mid-October. Studies on the annual fat cycle of northern large herbivores reported that fat stored in fall is crucial for winter survival and reproduction (Parker et al. 2009, Cook et al. 2013). In the Pacific Northwest, USA, Bender et al. (2008) reported that the odds of dying on annual basis increased approximately 1.4 times for each percent less body fat for elk (Cervus elaphus). Poor nutrition in summer may reduce the accumulation of subcutaneous fat reserves (Simard et al. 2010, Tollefson et al. 2010, Cook et al. 2013), but because rump fat thickness was similar in both populations before the period of peak conception, our results might be better explained by increased social interactions (Vander Wal et al. 2012). Yet, the influence of smaller fat reserve can exert carry-over effects through winter on parturition, calf size at birth and growth, juvenile growth, and age at first breeding (Cook et al. 2013). The subcutaneous fat reserves of males decreased rapidly during early fall, mostly for prime-aged males. Prime-aged male ungulates are more active and cease (or strongly decrease) eating when the rut occurs, resulting in increased energy expenditure, reduced energy intake, and reduced fat accumulation (Yoccoz et al. 2002). The rump fat thickness in older males was lower in the Matane Wildlife Reserve than in the Chic-Chocs Wildlife Reserve but only at the end of September and the beginning of October. This suggests higher energy demands during the rut at high density because of the increased frequency of interactions (Pélabon et al. 1999, Vander Wal et al. 2012). However, later in the rut, the rump fat thickness of prime-aged males from the Chic-Chocs Wildlife Reserve decreased slightly faster to eventually reach that of prime-aged males from the Matane Wildlife Reserve. The subcutaneous fat reserves are depleted before intraperitoneal fat reserves (Riney 1955, Cook et al. 2001). We did not detect any difference in intraperitoneal fat reserves as indexed by kidney fat mass; this was an expected result as data collection occurred after the summer when the availability and quality of forage were maximal (Parker et al. 2009). Intraperitoneal fat reserves were probably maximal and remained unchanged during our sampling period. Kidney fat mass is also known as an unresponsive index because of its curvilinear relationship to lipid reserves; lipid reserves increase rapidly for small increases in kidney fat mass at low values and level off at higher values (Robbins 1993).

We observed a decrease in the muscle mass of males (3%) and prime-aged females (8%) in the Matane Wildlife Reserve. McArt et al. (2009) observed that moose in regions of Alaska where digestible proteins were more readily available, accumulated 18 kg more lean body mass than moose in regions with poorer nutritional resources during the summer. They also concluded that summer dietary nitrogen availability may act as a nutritional constraint on moose. In elk populations of northeast Oregon, USA, a 10% decline of female loin muscle thickness resulted in a 50% decrease of the probability of winter survival (Cook et al. 2004). Reproduction incurs high protein demand for females, mostly during lactation (Parker et al. 2005, Barboza and Parker 2008). The accumulation of protein stores in females may, therefore, be more affected by food shortages. Unlike many studies that showed relationships between habitat quality and body mass (Severinghaus 1979, Bonenfant et al. 2009, Couturier et al. 2009b), we found no reduction in the dressed body mass of moose in the high density Matane Wildlife Reserve. Dressed body mass integrates many components such as skeletal mass, fur, and antlers (Schulte-Hostedde et al. 2005, Toigo et al. 2006) and may be less sensitive to small changes in body condition (Chan-McLeod et al. 1995).

Figure 3. Ovulation rate of adult female moose (n = 80) as a function of age in 2 adjacent wildlife reserves from eastern Québec, Canada averaged over 2008, 2009, and 2010. The moose population was estimated at 3.3 ± 0.3/ km² at the Matane Wildlife Reserve and 1.1 moose/km² at the Chic-Chocs Wildlife Reserve. Symbols represent the ovulation rate ±95% confidence intervals estimated from the best models. Sample size is indicated over or under error bars. A small offset was added to values on the x-axis to improve readability.
Female Fertility
The pattern of variation in fertility for female moose that we observed is similar to what Simard et al. (2008) reported for an overabundant, white-tailed deer population on Anticosti Island, revealing the plasticity of moose in response to decreasing diet quality. Our results showed that females in the Matane Wildlife Reserve had a much lower twinning rate but a >15% higher ovulation rate overall, compared to females from the Chic-Chocs Wildlife Reserve. Caring for twins represents a substantial energetic investment for females, resulting in important loss of body reserves (Franzmann and Schwartz 1985, Keech et al. 2000). Females may have difficulty replenishing their reserves before estrus after weaning their previous twins and may skip a reproductive year (Clutton-Brock et al. 1997, Clutton-Brock and Coulson 2002, Tollefson et al. 2010). When competition is high, females may adopt a conservative reproductive strategy by reducing their litter size at ovulation and conserving energy to increase the probability of reproducing during most years (Simard et al. 2008). This trade-off between litter size and annual reproduction may allow females to maintain a high fertility rate despite a decline in body condition. However, we only verified female reproduction during the ovulation period. A reduction in body condition may lead to a higher abortion rate, lower size at birth, lower survival of offspring until weaning, and lower recruitment (Testa and Adams 1998). In ungulates with a relatively large sexual dimorphism and a long gestation period, mothers could bias investment towards daughters that are less costly to produce by adjusting the sex ratio at birth and/or by differential provisioning (Sheldon and West 2004). We believe the quadratic effect of age, suggesting a senescence effect or a lower reproductive effort in females living up to 7.5 years old, should be interpreted with caution because of the low number of reproductive tracts available from which to draw inference in females from our study (Fig. 3).

MANAGEMENT IMPLICATIONS
Our study indicates that even though body condition is reduced at densities >3/km² in the Matane Wildlife Reserve, moose population growth rates could be maintained through changes in their reproductive strategy. In this context, a hands-off approach relying on natural regulation from the resources alone could lead to a loss of resilience of the habitat as the moose population grows overabundant. Although hunting has been successfully used to control large herbivore populations (e.g., Hothorn and Muller 2010), it may not replace the ecological role of carnivores (Kuijper 2011). Our study provides compelling evidence supporting active management of moose populations to reach ecological goals. In 2008, a management plan aimed at the female segment of the population was implemented in the Matane Wildlife Reserve to reduce moose abundance. The harvest of females increased from 75 to about 500 in 5 years, reducing the moose population from 4.8/km² in 2007 to 3.3/km² in 2012 (Lamoureux et al. 2012). Hunting can serve as an efficient management tool if managers and stakeholders agree on the ecological consequences of overabundant populations of large herbivores.

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