

Forage-mediated density and climate effects on body mass in a temperate herbivore: a mechanistic approach

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Abstract. The interplay between density and climate in shaping the dynamics of herbivore populations is widely acknowledged, and current research is fueled by the identification of mechanisms underlying their effects on individuals and populations. We assessed whether forage availability mediated the effects of density and winter climate on body mass of white-tailed deer (*Odocoileus virginianus*) yearlings by experimentally reducing deer density to 7.5 and 15 deer/km² during eight growing seasons, and by using causal (graphical) hierarchical models and Bayesian hierarchical modeling to assess relationships. The abundance of preferred forage decreased with deer density and varied quadratically (positive parabola) with winter North Atlantic Oscillation (NAO), whereas the fall mass of yearlings increased with forage abundance and spring mass. Fall mass did not differ between experimentally reduced deer densities, yet experimental yearlings were 30% heavier than yearlings harvested at ambient densities. Hence, forage abundance simultaneously mediated the effects of density and climate on fall body mass, which was also influenced by carry-over effects of spring body mass. Our findings increase our ability to anticipate how temperate large herbivores will respond to ongoing changes in intrinsic (e.g., large-herbivore density) and extrinsic (e.g., climate) factors.

Key words: boreal forest; browsing experiment; density dependence; density independence; life-history traits; North American Oscillation; *Odocoileus virginianus*; path analysis; ungulates; white-tailed deer.

INTRODUCTION

The role of density-dependent processes in shaping the dynamics of populations has intrigued ecologists for decades (Nicholson 1933, Brook and Bradshaw 2006). While the existence of density dependence is now widely recognized, current research is fueled by the identification of mechanisms underlying its effect on populations (Krebs 1995, Bonenfant et al. 2009). Density does not act directly on population abundance; rather, it affects demographic processes (e.g., survival and reproduction) resulting from density-induced responses of life-history traits (Caswell 2000). Hence, one approach adopted to unravel the mechanisms of density dependence has been to search for the effect of density on life-history traits of individuals and on demographic parameters of populations (Lebreton and Clobert 1991). Another complementary approach, the so-called mechanistic paradigm (Krebs 1995), aims to identify the trophic interactions, such as exploitative competition, that convey the effect of density on either individuals or populations.

In addition to intrinsic factors such as density, extrinsic factors such as climate can also shape life-history traits, and hence demographic processes (Birch 1957). In herbivores, climate contributes to drive variations in life-history traits in addition or in interaction with density (Sæther 1997, Coulson et al. 2000), and the effects of both factors can be mediated by the same trophic interactions. For instance, herbivore density or climate can drive the abundance of vegetation, which can, in turn, modulate the degree of food competition between herbivores and affect their life-history traits (e.g., for density, Skogland 1985; for climate, Fryxell 1987, Forchhammer et al. 2001). In recent years, much attention has been devoted to the interplay between density and climate in shaping the life-history traits of herbivores (e.g., Sæther 1997, Coulson et al. 2000, Solberg et al. 2001, Patterson and Power 2002, Creel and Creel 2009, Garel et al. 2011). Fewer studies, however, have investigated simultaneously the influence of forage, density, and climate on life-history traits of large herbivores (e.g., Skogland 1985, Herfindal et al. 2006, Brown 2011, Dou et al. 2013). Among those studies, only a handful assessed the indirect role of foraging conditions in mediating the effects of climate on life-history traits, using analytical methods than can quantify direct and indirect relationships (Myrsetud et

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al. 2008, Nielsen et al. 2012, Texeira et al. 2012). Yet, to our knowledge, the hypothesis that both herbivore density and climate could simultaneously drive foraging conditions, which would in turn affect the life-history traits of herbivores, remains to be tested.

Our objective was to use a mechanistic approach to assess whether life-history traits could be simultaneously shaped by the indirect effects of density and climate mediated by forage availability in a large herbivore in absence of predation. As stipulated by the food hypothesis (Sinclair et al. 1985), density-induced variations in forage abundance is the most likely mechanism through which density can act on life-history traits in large herbivores not subject to predation (Choquenot 1991, Bonenfant et al. 2009). Yet, as climate-induced variations in vegetation abundance are ubiquitous across the temperate biome (Forchhammer et al. 2001, reviewed by Kreyling 2010), the potential dual action of density and climate on vegetation cannot be overlooked. We addressed this objective using a key life-history trait of large temperate herbivores; namely, fall body mass of yearlings. Body mass is indeed considered a pivotal life-history trait through which density and climate can operate on demographic processes (reviewed by Gaillard et al. 2000, Bonenfant et al. 2009), and variations in life-history traits of juveniles or yearlings account for most of the variation in growth rates of large-herbivore populations (Gaillard et al. 2000). As climate during the previous winter can contribute to shape variations in the fall body mass of temperate herbivores (e.g., Loison and Langvatn 1998, Post and Stenseth 1999), determining whether its effect is mediated by summer foraging conditions (Mysterud et al. 2008) or carry-over effects of spring body mass (Harrison et al. 2011) should also contribute to enhance our understanding of climate effects on temperate herbivores.

We examined the causal relationships underlying the effects of density and climate on body mass of yearling white-tailed deer (*Odocoileus virginianus*; hereafter “deer”) by experimentally reducing deer density during the growing season, and by using causal (graphical) hierarchical models (Shipley 2009) and Bayesian hierarchical modeling (Gelman and Hill 2007) to unravel relationships. We hypothesized that: (1) Density would negatively impact summer forage abundance, (2) which, in turn, would negatively affect fall mass; (3) fall mass would also decrease directly with density; and the influence of winter climate on fall mass would be mediated by both (4) summer forage abundance and (5) spring mass.

METHODS

Study area

The experiment was conducted from 2002 to 2009 on Anticosti Island in the Gulf of St. Lawrence, Quebec, Canada (49.06–49.95° N, 61.67–64.52° W; 7943 km²). Mean air temperatures are 16°C in July and –11°C in January (Environment Canada 2006). Snow precipita-

tion averages 328 cm annually, while rainfall averages 61 cm (Environment Canada 1982). The forests of Anticosti Island belong to the boreal zone and are part of the eastern balsam fir–white birch bioclimatic region. At the end of the 19th century, a founding population of ~220 deer was introduced on the island. In the absence of natural predators, the population peaked in the 1930s, has remained high thereafter (averaging ~20 deer/km²; Potvin et al. 2003) and has been exerting dramatic negative impacts on plant communities (Tremblay et al. 2005).

Experimental design

The randomized experimental design consisted of three replicated blocks. Each block was composed of two adjacent experimental units receiving one level of the density treatment: 7.5 deer/km² and 15 deer/km² (three deer in 40 ha and 20 ha enclosures, respectively; for a complete description of the experiment, see Tremblay et al. 2006). From 2002 to 2009, we captured deer on Anticosti Island, relocated them in the experimental enclosures each spring (28 April to 12 June) and euthanized them in late fall (14 November to 13 December). We distributed mainly yearlings (11–12 months old at the time of capture; hereafter “experimental yearlings”) and adults among the experimental units (yearlings averaged 73% of deer introduced in the units). Enclosures were located in balsam fir-dominated forests partially cut (about 70%) in the early summer of 2001.

Forage abundance

We estimated forage abundance in 40 permanent sampling stations randomly established in each experimental unit in 2002. From 2002 to 2004, in 2007, and in 2009, we estimated percent of ground cover and height of preferred field layer plant species (*Chamerion angustifolium*, *Cornus canadensis*, *Maianthemum canadense*, *Rubus idaeus*, *Rubus pubescens*) in two 1-m² plots per station randomly located in a 10 × 10 m quadrat (cluster sampling). We then predicted the aboveground dry biomass (g/m²) per species using regressions between percent plant cover, height, and mass of dried plants (see details in Tremblay et al. 2006). From 2002 to 2004, and from 2007 to 2009, we also counted the number of saplings (>10–200 cm) of preferred browse species (*Betula papyrifera* and *Abies balsamea*) in three 4-m² circular plots established at 5-m intervals north of each sampling station. We obtained an index of forage abundance per experimental unit using the first axis of a principal component analysis (PCA) computed with the summed biomass of field layer plants and the summed number of saplings of browse species. This index of forage abundance (hereafter “forage abundance”) discriminated sampling units (experimental unit per year) with high vs. low abundance of preferred species (Appendix A).

Body mass of experimental and reference yearlings

From 2002 to 2009, we measured total body mass of 75 deer with a spring scale (± 0.25 kg) prior to their introduction in the experimental units (hereafter “spring mass”), and we measured their dressed mass (total mass minus viscera and bleedable blood) when culling them in fall (hereafter “fall mass”). We excluded adults from analyses because of low sample size. We used 651 yearlings harvested in three hunting zones at ambient densities (>20 deer/km² on average; Rochette and Gingras 2007) from 2002 to 2009 as reference yearlings, and we measured their fall mass.

Winter climate

We indexed winter climate using the North Atlantic Oscillation (Osborn 2010) values averaged annually from December to March (hereafter “winter NAO”; Hurrell 1995). In our study area, winter NAO is negatively correlated with winter temperatures (December to March), and positively correlated with snow sinking depth (Simard et al. 2010).

Statistical analyses

First, we tested all hypotheses with experimental yearlings using the two following statistical approaches, as recommended by Clough (2012): (1) causal (graphical) hierarchical models were used to test specific hypotheses (Shipley 2009), including different combinations of our five hypotheses; and (2) Bayesian hierarchical methods based on Markov Chain Monte Carlo (MCMC) simulations were used to estimate posterior distribution of parameters (Gelman and Hill 2007). In a second step, we performed an additional test of the third hypothesis (negative effect of density on fall mass) by comparing experimental yearlings with reference yearlings using Bayesian models. We performed this second step because forage abundance and spring mass were not available for reference yearlings.

First step.—We formulated 15 biologically meaningful causal models including different combinations of the hypothesized causal relationships (global model, Fig. 1; all causal models, Appendix B: Fig. B1). We specified a direct effect of density on fall mass in every causal model, as we explicitly manipulated density in our experiment, but we excluded the effect of density mediated by forage abundance from two models. In every model, we included sex as a covariate to take into account its effect on spring mass and fall mass (Simard et al., *in press*). We took into account the blocked experimental design by specifying a random intercept per block for both forage abundance and fall mass, and a random intercept per experimental unit (nested within block intercepts) for fall mass.

We assessed the adequacy of each causal model using the Shipley’s d-sep test (confirmatory path analyses, Appendix B; Shipley 2009). This test consists of assessing simultaneously the independence claims implied by a given causal model. We implemented the d-

sep test using Bayesian numerical methods based on MCMC simulations, and assuming uninformative prior distributions of parameters. For every adequate model, i.e., those respecting the independence criteria of the d-sep test (Appendix B), we used Bayesian hierarchical modeling to estimate the mean of the posterior distribution and the 95% credibility intervals of the parameters (MCMC simulations with uninformative prior distributions). Some values of forage abundance were missing for years 2005, 2006, and 2008, so we imputed them directly in the MCMC simulations (Appendix B). We based our interpretation of those adequate models on credible intervals of parameters that did not overlap zero (credible interval criterion; Li and Lin 2010), except for the direct effect of density on fall mass that was included by default in all models. We used this model selection approach (combining the d-sep test with the credible interval criterion) rather than the deviance information criterion (DIC, a criterion similar to AIC that trades-off model fit and complexity), because models with and without imputed values of forage abundance could not be compared using the deviance information criterion (Daniels et al. 2012). The approach of combining the d-sep test with the credible interval criterion may select more than one equivalent model, and this uncertainty in model selection must be acknowledged while interpreting results by using all selected models for inference. We implemented MCMC simulations using the library rjags (Plummer 2011) in R (R Development Core Team 2012).

Second step.—To determine if fall body mass of deer increased when we experimentally reduced densities, we compared fall body mass of experimental yearlings with reference yearlings. We compared four different Bayesian models including the variable density (ambient densities vs. reduced densities; included in every model), but also the covariates sex and date of harvest or euthanasia (hereafter “date”; Simard et al., *in press*). We aimed to minimize spatial differences between experimental and reference yearlings by attributing all reference yearlings harvested in the west end and west hunting zones to the block A, and those harvested in the central hunting zone to either block B or C (random attribution). We specified an intercept per block. We selected the best-fitting model using the DIC (Spiegelhalter et al. 2002).

In both steps, we initially assessed the linearity and the residuals of the different relationships included in the models using generalized additive mixed models (GAMM; library mgcv; Wood 2006); we specified quadratic effects of winter NAO and year since the start of the experiment on forage abundance (first step), and of winter NAO and date on fall mass (second step). We report the means and credible intervals of posterior distributions estimated with non-transformed variables hereafter to highlight biological effects and those estimated with standardized variables are presented in

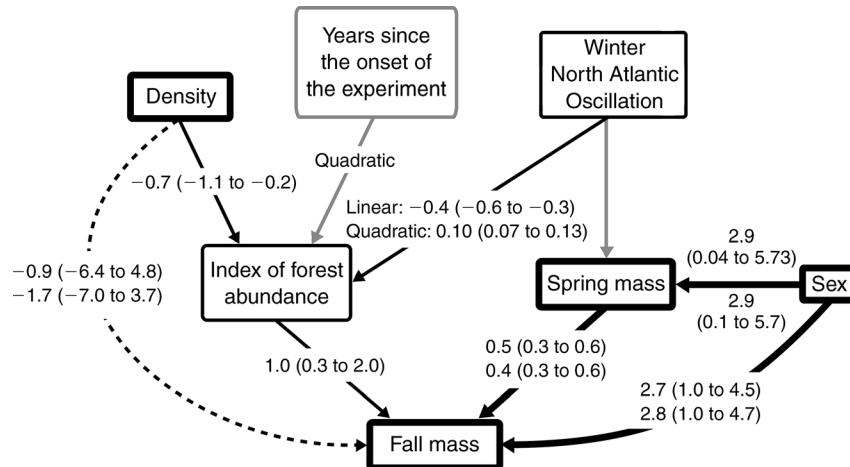


FIG. 1. Causal models showing the causal relationships explaining variations in the fall mass of white-tailed deer (*Odocoileus virginianus*) on Anticosti Island in the Gulf of St. Lawrence, Quebec, Canada. For every effect, we indicated the mean of the posterior distribution and its 95% credible interval (in parentheses) estimated with untransformed continuous variables under a Bayesian hierarchical approach. The effects included in the two models used for inference are shown by black lines (first model), and by thick black lines and thick black boxes (second model). The dashed line indicates the effect included by default in the two models used for inference, but whose 95% credible intervals overlapped 0 (density); gray lines and a gray box show the effects included in the global model, but not in the two models used for inference.

Appendix B (first step) and in Appendix C (second step) to ease comparison of effect sizes.

RESULTS

Experimental yearlings

Fall dressed mass and spring total mass of experimental yearlings ($n = 75$) averaged 42.0 kg (range 27.5–54.5 kg) and 27.5 kg (range 16.5–46.3 kg), respectively. We based our interpretation on the two adequate models that respected both the d-sep and the credible interval criteria (Fig. 1; in Appendix B: Table B1). Both models showed that spring mass positively influenced fall mass, males were heavier than females both in spring and fall, and density did not directly affect fall mass (as in all adequate models; see Appendix B). These effects were the only ones included in the second model, whereas the first model also showed a negative effect of density combined to a quadratic effect (positive parabola) of winter NAO on forage abundance and a positive effect of forage abundance on fall mass (Fig. 2A, B). The influence of winter NAO on spring mass was absent of those two models. All variables included in the second model were also included in the first one (nested models), and using the posterior distributions of one model or the other did not change the interpretation (Fig. 1).

Experimental vs. reference yearlings

Fall dressed mass of reference yearlings harvested at ambient densities averaged 32.8 kg (range 22–56 kg, $n = 651$). The best-fitting model explaining variations in fall mass of experimental and reference yearlings included density, winter NAO, their interaction, sex, and date. Experimental yearlings were 5.5 kg heavier (95% CI 3.6–

7.5) than reference yearlings harvested at ambient densities, males were 3.1 kg (95% CI 2.5–3.8) heavier than females and the date had a quadratic effect on fall mass (date, 0.4 kg/10 days, 95% CI 0.3–0.6; date², -0.10, 95% CI -0.16 to -0.04). Winter NAO had a quadratic (positive parabola) effect on experimental deer (winter NAO, -0.09, 95% CI -0.36 to 0.18; winter NAO², 0.11, 95% CI 0.02–0.20) and a quadratic (negative parabola; Fig. 2C) effect on reference deer (winter NAO, 0.04, 95% CI -0.07 to 0.15; winter NAO², -0.09, 95% CI -0.12 to -0.05; Fig. 2C).

DISCUSSION

Forage abundance simultaneously mediated the effects of density and climate on deer fall body mass, which was also shaped by carry-over effects of spring body mass. As predicted, the abundance of preferred forage decreased with deer density and varied with winter NAO, whereas deer fall mass increased with forage abundance and spring mass. Winter NAO did not influence spring mass, and fall mass did not differ between the two experimentally reduced densities, yet experimental yearlings were 30% heavier than yearlings harvested at ambient densities.

Density dependence in life-history traits: a mechanistic approach

Density dependence in life-history traits is widespread in large herbivores (reviewed by Bonenfant et al. 2009). It is generally recognized that density dependence can be mediated by forage abundance in large herbivores (Sinclair et al. 1985, Langvatn et al. 1996, Bonenfant et al. 2009). There are numerous studies separately showing negative effects of herbivore density on

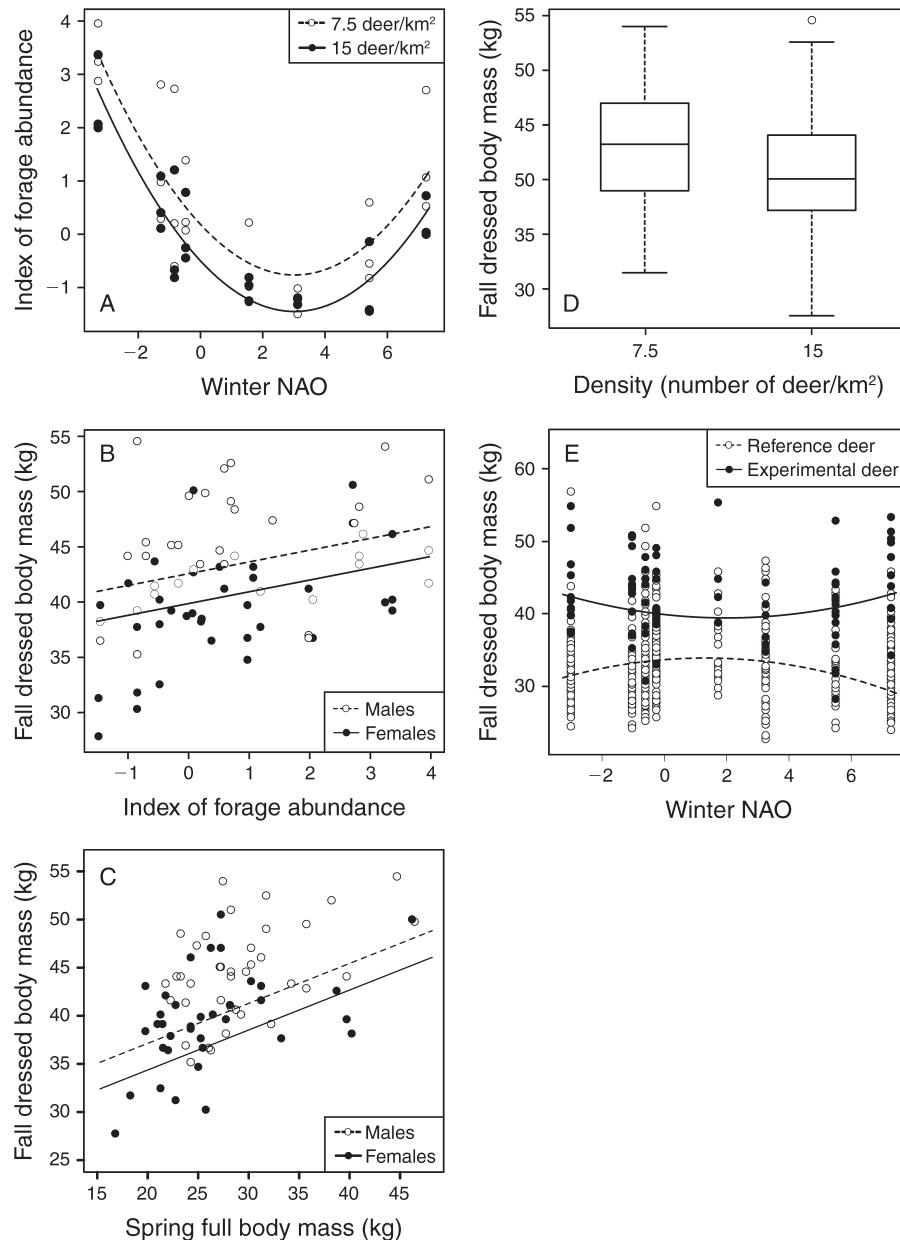


FIG. 2. (A) Influence of white-tailed deer density and winter North Atlantic Oscillation (NAO) on forage abundance; (B) influence of forage abundance and sex on fall dressed body mass of experimental yearlings; (C) influence of spring full body mass on fall dressed body mass of experimental yearlings; (D) fall dressed mass of experimental yearlings against experimental levels of the deer density treatment (the middle lines indicate medians, box limits are the first and third quartiles, whiskers indicate most extreme points ≤ 1.5 times the interquartile range, and dots indicate outliers); (E) influence of winter NAO on fall dressed body mass of experimental and reference yearlings. Symbols indicate raw data and predicted curves are drawn from parameters estimated with Bayesian hierarchical models. A higher winter NAO indicates colder temperatures and higher snow sinking depth, and a higher index of forage abundance indicates higher abundance of preferred forage species.

preferred vegetation (e.g., Hobbs et al. 1996, Horsley et al. 2003, Tremblay et al. 2006, Austrheim et al. 2008), and positive and negative effects of forage abundance (e.g., Skogland 1985, Bårdsen et al. 2008, Brown 2011) and herbivore density (e.g., Clutton-Brock et al. 1991, Coulson et al. 2000, Pettorelli et al. 2001, Møbak et al. 2013), respectively, on herbivores. Yet, to our knowl-

edge, the hypothesis that the effect of density on life-history traits can be mediated by forage abundance remained to be tested using analytical approaches that can quantify the contribution of direct and indirect effects on life-history traits, respectively. Here, we deepened the understanding of mechanisms underlying density dependence in the life-history traits of large

herbivores by quantifying simultaneously, using hierarchical Bayesian models, an indirect effect of density on the mass of yearlings, mediated by the direct effect of density on forage and the direct effect of forage abundance on yearlings' fall mass. Because this result was obtained using experimental data from a randomized and replicated density manipulation conducted over eight years, it provides a robust indication that forage abundance can indeed mediate the effect of density on herbivores. Finally, using hierarchical models allowed us to accurately estimate the uncertainty around parameter estimates; using simpler models (e.g., three separate nonhierarchical models: [1] density→forage abundance, [2] forage abundance→body mass, and [3] density→body mass) may lead to similar parameter estimates, but the uncertainty around those estimates is hard to quantify accurately without using hierarchical models (Gelman and Hill 2007).

In our study system, density dependence in the abundance of preferred forage species resulted from the suppression of growth and reproduction of those species under higher browsing pressure (Tremblay et al. 2006). Negative effects of herbivore density on the abundance/density of preferred species have also been demonstrated experimentally in other study systems (e.g., elk *Cervus elaphus* in sagebrush grassland [Hobbs et al. 1996], white-tailed deer in northern hardwood forest [Horsley et al. 2003], sheep *Ovis aries* in an alpine ecosystem [Austrheim et al. 2008]). The positive effect of forage abundance during the growing season on body mass may partly result from the decrease in the proportion of time spent active by the experimental deer as forage abundance increased (Coulombe et al. 2008). Indeed, Coulombe et al. (2008) suggested that, as forage abundance increased, deer could fill their rumen faster, and hence, had reduced energy requirements.

Density dependence was more easily detected when comparing higher levels of densities in our study. Indeed, we detected a direct negative effect of density on fall mass when comparing experimental with reference deer, yet we did not observe a difference in mass between experimentally reduced levels of densities. This suggests that the strength of density dependence may increase with density in our study system, yet this remains to be formally tested. When taking into account the mechanistic nature of density dependence, however, we did detect indirect density dependence in mass of experimental deer. Although average mass was not different between the two levels of reduced densities, variations in forage abundance partly induced by density, but also by winter NAO, affected mass. Hence, measuring mediating variables (here forage abundance) and taking into account the simultaneous effect of climate on those mediating variables may lead to the identification of weaker density-dependent effects that can be hard to detect if density is tested alone.

Because we did not manipulate density in hunting zones, we cannot exclude that other confounding factors

may partly explain the smaller body mass of reference than experimental deer. For example, the enclosures were established in balsam fir-dominated forests partially cut (about 70%), while hunting zones consisted of a matrix of different types of forest stands (balsam fir-, white spruce-, and black spruce-dominated stands) and open habitats (e.g., cuts, peatlands, windthrows, and so on). Previous work, however, indicates that the negative effect of natural variations in density on fall mass of harvested yearling had the largest effect size, whereas the only habitat-related variable that influenced yearling fall mass was the proportion of balsam fir-dominated stands (Simard et al., *in press*). Yet, the percentage of balsam fir-dominated stands was more or less the same in both experimental enclosures (~30%) and hunting zones (~35%). In addition, we cannot exclude that other factors such as higher vulnerability to hunting of smaller yearlings, or lower access to resources for reference yearlings due to their potential lower social rank than experimental yearlings, may have slightly affected the differences in mass that we observed. Yet, the more likely hypothesis to explain the 30% difference in fall mass between experimental and reference yearlings remains the important difference in the abundance of preferred species between natural densities and experimental densities (Tremblay et al. 2006).

We did not measure the quality of forage in our study, although it may have contributed to a better understanding of the patterns observed in our data. On one hand, the positive effect of the index of abundance of preferred species on fall mass could have resulted from deer being able to feed preferentially on species of higher quality at low density, as shown in domestic sheep (Møbæk et al. 2009). On the other hand, forage quality within species/functional groups could have been higher at intermediate than at low densities (15 vs. 7 deer/km², respectively, in our study), as supported by Stewart et al. (2006), who observed a peak in forage quality at intermediate elk densities. Although this remains to be tested, this could explain why there was no direct effect of density on fall mass, because the effects of quality and quantity could have evened-out each other.

*Climate-induced variations in life-history traits:
a mechanistic approach*

We showed that forage abundance during the growing season also mediated the effect of climate on fall body mass using hierarchical models able to highlight mechanisms involved in the relationships. Causal relationships between climate, forage and mass have also been shown in domestic lambs (Nielsen et al. 2012) and red deer in Norway (Mysterud et al. 2008) using similar hierarchical analytical approaches than in our study. Spring and winter climate influenced fall mass of lambs both directly and indirectly through plant phenology, and warmer spring temperatures induced earlier onset of vegetation available for red deer, and consequently improved their fall mass. Our study

provided a test of the hypothesis that climate can affect life-history traits through its effect on forage conditions. These results contribute to deepen our knowledge about the mechanisms underlying the effect of climate on life-history traits (e.g., Coulson et al. 2000, Solberg et al. 2001, Creel and Creel 2009), and to go further than nonhierarchical models that cannot highlight mechanisms involving more than one level of causality. Our study brings robust empirical support to the hypothesis, still unverified up to now to our knowledge, that both density and climate can operate via the same mechanism; namely, by modulating forage abundance and hence intraspecific competition (Langvatn et al. 1996).

We showed that forage abundance was lower at average values of winter NAO. To interpret the mechanisms underlying this effect, we would need to investigate species-specific responses of vegetation to winter NAO, as mediated by temperature and snow conditions. Indeed, our index of forage abundance encompassed an ensemble of plant species that could respond differently to variations in winter climatic conditions (Kreyling 2010). For instance, growth of temperate shrubs responded in species-specific ways to manipulation in snow depth and timing of snowmelt (Wipf et al. 2009). Hence, understanding the influence of winter climate on summer forage abundance would benefit from further work addressing questions beyond the scope of this study.

Our study highlighted that the relationship between winter climate and fall mass could be reversed at high density, as shown by the positive and negative parabola observed in experimental and reference deer, respectively. The improved fall mass of experimental deer at low and high values of winter NAO likely corresponds to the positive parabola observed between winter NAO and forage abundance in experimental enclosures discussed in the previous paragraph, associated with the effect of forage abundance on fall mass. As we did not know spring mass of reference yearlings and forage abundance available to them, we could not determine which of those variables mediated the effect of winter climate on fall mass. Although the following hypothesis remains to be tested in our study system, the negative parabola observed in reference deer may result from a larger direct influence of winter climate on deer fall body mass at ambient density than at reduced densities, because higher forage abundance at reduced density may buffer the direct effects of winter climate. Such a quadratic direct effect of winter climate could result from lower costs of thermoregulation and locomotion during years of average winter NAO, because these costs could be higher during both years of high winter NAO, due to colder temperatures and higher sinking depth (Parker et al. 1984), and years of low winter NAO (warmer temperature), due to denser snow (Parker et al. 1984) and potential higher frequency of rain events (Parker 1988).

Carry-over effects of spring body mass

We showed that variations in spring mass are carried over into the fall, as found in domestic lambs (Mobæk et al. 2013) and reindeer (*Rangifer tarandus*; Bårdsen et al. 2010). We also predicted that variations in spring mass would be induced by winter NAO, as harsher winter may have induced higher costs of thermoregulation and movements in snow. Surprisingly, this prediction was not verified. Hence, our study provides support for the hypothesis that the effect of winter NAO on fall mass can be mediated by foraging conditions during the growing season (Mysterud et al. 2001), rather than by carry-over effects of winter climate mediated by spring mass. Yet, it cannot be excluded that other variables describing winter climate may affect spring mass, or that an effect of winter climate on spring mass may just be unveiled once other potential drivers of variations in spring mass (previous fall mass; Bårdsen et al. 2010) are taken into account.

In conclusion, combining experimental and hierarchical statistical approaches has proved instrumental to apply the mechanistic paradigm advocated by Krebs (1995). Those approaches allowed us to identify competition for limited forage as the potential mechanism induced by both intrinsic and extrinsic factors and explaining variation in fall mass. Ecologists are currently facing the challenge of better anticipating how temperate large herbivores will respond to ongoing global changes in intrinsic and extrinsic factors, such as the increase in large-herbivore abundance in temperate regions and climate change (Côté et al. 2004). Our findings and approaches can contribute to better tackle those questions, and the next step forward to increase our ability to predict such outcomes could be to scale-up from responses in life-history traits to those in population growth rates.

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LITERATURE CITED

- Austrheim, G., A. Mysterud, B. Pedersen, R. Halvorsen, K. Hassel, and M. Evju. 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. *Oikos* 117:837–846.

- Bårdsen, B. J., P. Fauchald, T. Tveraa, K. Langeland, N. G. Yoccoz, and 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, P. Fauchald, and K. Langeland. 2010. Observational evidence of risk-sensitive reproductive allocation in a long-lived mammal. *Oecologia* 162:627–639.
- Birch, L. C. 1957. The role of weather in determining the distribution and abundance of animals. *Cold Spring Harbour Symposia in Quantitative Biology* 22:203–218.
- Bonenfant, C., et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in ecological research* 41:313–358.
- Brook, B. W., and C. J. A. Bradshaw. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87:1445–1451.
- Brown, G. S. 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. *Journal of Animal Ecology* 80:1288–1298.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Choquetot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology* 72:805–813.
- Clough, Y. 2012. A generalized approach to modeling and estimating indirect effects in ecology. *Ecology* 93:1809–1815.
- Clutton-Brock, T. H., O. F. Price, S. D. Albon, and P. A. Jewell. 1991. Persistent instability and population regulation in Soay sheep. *Journal of Animal Ecology* 60:593–608.
- Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology and Systematics* 35:113–147.
- Coulombe, M.-L., S. D. Côté, and J. Huot. 2008. Experimental influence of population density and vegetation biomass on the movements and activity budget of a large herbivore. *Behaviour* 145:1167–1194.
- Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society of London Series B* 267:1771–1779.
- Creel, S., and M. Creel. 2009. Density dependence and climate effects in Rocky Mountain elk: an application of regression with instrumental variables for population time series with sampling error. *Journal of Animal Ecology* 78:1291–1297.
- Daniels, M. J., A. S. Chatterjee, and C. Wang. 2012. Bayesian model selection for incomplete data using the posterior predictive distribution. *Biometrics* 68:1055–1063.
- Dou, H., G. Jiang, P. Stott, and R. Piao. 2013. Climate change impacts population dynamics and distribution shift of moose (*Alces alces*) in Heilongjiang Province of China. *Ecological Research* 28:625–632.
- Environment Canada. 1982. Canadian climate normals, temperature and precipitation, 1951–1980, Québec. Atmospheric Environment Service, Ottawa, Canada.
- Environment Canada. 2006. Climate normals and averages daily data reports of Port-Menier's station from 1995 to 2005. Atmospheric Environment Service, Ottawa, Canada.
- Forchhammer, M. C., T. H. Clutton-Brock, J. Lindstrom, and S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* 70:721–729.
- Fryxell, J. M. 1987. Food limitation and demography of a migratory antelope, the white-eared kob. *Oecologia* 72:83–91.
- Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* 31:367–393.
- Garel, M., J.-M. Gaillard, J.-M. Jullien, D. Dubray, D. Maillard, and A. Loison. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *Journal of Mammalogy* 92:1112–1117.
- Gelman, A., and J. Hill. 2007. *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80:4–18.
- Herfindal, I., B. E. Sæther, E. J. Solberg, R. Andersen, and K. A. Hogda. 2006. Population characteristics predict responses in moose body mass to temporal variation in the environment. *Journal of Animal Ecology* 75:1110–1118.
- Hobbs, N. T., D. L. Baker, G. D. Bear, and D. C. Bowden. 1996. Ungulate grazing in sagebrush grassland: mechanisms of resource competition. *Ecological Applications* 6:200–217.
- Horsley, S. B., S. L. Stout, and D. S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98–118.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. *Science* 269:676–679.
- Krebs, C. J. 1995. Two paradigms of population regulation. *Wildlife Research* 22:1–10.
- Kreyling, J. 2010. Winter climate change: a critical factor for temperate vegetation performance. *Ecology* 91:1939–1948.
- Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* 65:653–670.
- Lebreton, J. D., and J. Clobert. 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. Pages 105–125 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hiron, editors. *Bird population studies*. Oxford University Press, Oxford, UK.
- Li, Q., and N. Lin. 2010. The Bayesian elastic net. *Bayesian Analysis* 5:151–170.
- Loison, A., and R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* 116:489–500.
- Mobæk, R., A. Mysterud, L. Leif Egil, Ø. Holand, and G. Austrheim. 2009. Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. *Oikos* 118:209–218.
- Mobæk, R., A. Mysterud, Ø. Holand, and G. Austrheim. 2013. Temporal variation in density dependent body growth of a large herbivore. *Oikos* 122:421–427.
- Mysterud, A., N. C. Stenseth, N. G. Yoccoz, R. Langvatn, and G. Steinheim. 2001. Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* 410:1096–1099.
- Mysterud, A., N. G. Yoccoz, R. Langvatn, N. Pettorelli, and N. C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philosophical Transactions of the Royal Society B* 363:2359–2368.
- Nicholson, A. J. 1933. Supplement: the balance of animal populations. *Journal of Animal Ecology* 2:131–178.
- Nielsen, A., N. G. Yoccoz, G. Steinheim, G. O. Storvik, Y. Rekdal, M. Angeloff, N. Pettorelli, Ø. Holand, and A. Mysterud. 2012. Are responses of herbivores to environmental variability spatially consistent in alpine ecosystems? *Global Change Biology* 18:3050–3062.
- Osborn, T. 2010. North Atlantic Oscillation index data. Climatic Research Unit, University of East Anglia, Norwich, UK.

- Parker, K. L. 1988. Effects of heat, cold, and rain on coastal black-tailed deer. *Canadian Journal of Zoology* 66:2475–2483.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. *Journal of Wildlife Management* 48:474–488.
- Patterson, B., and V. Power. 2002. Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia* 130:62–71.
- Pettorelli, N., J.-M. Gaillard, P. Duncan, J.-P. Ouellet, and G. Van Laere. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* 128:400–405.
- Plummer, M. 2011. rjags: Bayesian graphical models using MCMC. R package version 3-5. R Foundation for Statistical Computing, Vienna, Austria.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80:1322–1339.
- Potvin, F., P. Beaupré, and G. Laprise. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: a 150-year process. *Ecoscience* 10:487–495.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rochette, B., and A. Gingras. 2007. Inventaire aérien du cerf de Virginie de l'île d'Anticosti: Été 2006. Ministère des Ressources naturelles et de la Faune, Direction de l'aménagement de la faune de la Côte-Nord, Quebec City, Canada.
- Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. *Trends in Ecology and Evolution* 12:143–149.
- Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90:363–368.
- Simard, M.-A., J. Huot, S. de Bellefeuille and S. D. Côté. *In press*. Influences of habitat composition, plant phenology, and population density on autumn indices of body condition in a northern white-tailed deer population. *Wildlife Monographs*.
- Simard, M. A., T. Coulson, A. Gingras, and S. D. Côté. 2010. Influence of density and climate on population dynamics of a large herbivore under harsh environmental conditions. *Journal of Wildlife Management* 74:1671–1685.
- Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of Serengeti wildebeest: A test of the food hypothesis. *Oecologia* 65:266–268.
- Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. *Journal of Animal Ecology* 54:359–374.
- Solberg, E. J., P. Jordhøy, O. Strand, R. Aanes, A. Loison, B. E. Sæther, and J. D. C. Linnell. 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. *Ecography* 24:441–451.
- Spiegelhalter, D. J., N. G. Best, B. R. Carlin, and A. van der Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B* 64:583–616.
- Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. 2006. Herbivore optimization by North American elk: consequences for theory and management. *Wildlife Monographs* 167:1–24.
- Texeira, M., G. Baldi, and J. Paruelo. 2012. An exploration of direct and indirect drivers of herbivore reproductive performance in arid and semi arid rangelands by means of structural equation models. *Journal of Arid Environments* 81:26–34.
- Tremblay, J.-P., J. Huot, and F. Potvin. 2006. Divergent nonlinear responses of the boreal forest field layer along an experimental gradient of deer densities. *Oecologia* 150:78–88.
- Tremblay, J.-P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology* 83:1087–1096.
- Wipf, S., V. Stoeckli, and P. Bebi. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change* 94:105–121.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. CRC Press, London, UK.

SUPPLEMENTAL MATERIAL

Appendix A

Detailed results of the principal component analysis used to estimate the index of forage abundance ([Ecological Archives E095-114-A1](#)).

Appendix B

Detailed description and results of path analyses and hierarchical Bayesian analyses ([Ecological Archives E095-114-A2](#)).

Appendix C

Detailed results of the comparison between experimental and reference yearlings (model selection and parameter estimates) ([Ecological Archives E095-114-A3](#)).