

Winter severity modulates the benefits of using a habitat temporally uncoupled from browsing

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Abstract. Resources whose abundance is not affected by the density of the consumer population, namely donor-controlled resources, are ubiquitous. Donor-controlled resources can act as food subsidies when they sustain consumer populations at higher densities than what would be predicted without donor-controlled dynamics. Herbivore populations that have access to food subsidies may reach and maintain high densities, with potential major ecological and economic consequences. A better understanding of the roles of food subsidies on temperate herbivores will likely be achieved by simultaneously taking into account other drivers of demographic variations such as winter severity. Here, we tested the hypothesis that the use of a donor-controlled food resource that may act as a food subsidy, namely balsam fir (*Abies balsamea*), and winter severity act together to shape the patterns of overwinter mass loss in a large herbivore population (white-tailed deer, *Odocoileus virginianus*). We monitored weather conditions, diet, habitat use, and mass loss of female deer during two highly contrasted winters. During an exceptionally milder winter, characterized by shallower snow depth and warmer windchill temperatures, female deer shifted their diet toward resources usually covered by snow during typical winters. Surprisingly, the rate of body mass loss remained similar during the milder and the harsher winter. The rate of body mass loss rather decreased with the use of balsam fir stands during the harsher winter, but increased with that same variable during the milder winter. Our study revealed that deer can alleviate overwinter mass loss by using a donor-controlled habitat type temporally uncoupled from browsing, but that this benefit is climate dependent. This study represents an additional step to address the largely unexplored concept of how temporal uncoupling between resources and consumer dynamics may contribute to sustain consumer populations at higher densities than predicted without considering donor-controlled dynamics.

Key words: climate; diet; mass loss; *Odocoileus virginianus*; subsidy.

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INTRODUCTION

In classical trophic models, consumer density affects resource density (e.g., Oksanen et al. 1981, Turchin 2003). Because classical models cannot always predict the dynamics of trophic interactions (Polis and Strong 1996, Gauthier et al. 2004), increasing attention is being paid

to donor-controlled systems in which resource density controls consumer density, but not the reverse (Pimm 1982, reviewed by Polis et al. 1997). Donor-controlled dynamics can arise when there is an uncoupling between the abundance of food resources and the impact of the consumer population on those resources, either in space (reviewed by Polis et al. 1997) or in time (Miyaki

and Kaji 2004, Tremblay et al. 2005, Nelson and Reynolds 2014). On the one hand, spatial uncoupling can occur when consumers benefit from resources that originate from another ecosystem (allochthonous resources; reviewed by Polis et al. 1997, Stapp and Polis 2003, Abraham et al. 2005). On the other hand, temporal uncoupling can arise when there is a temporal delay between the effect of the consumer on the resource and the availability of that resource for the benefit of the consumer (Tremblay et al. 2005, Nelson and Reynolds 2014). Although an increasing number of studies are addressing the impacts of spatial uncoupling between donor-controlled resources and consumers on trophic dynamics (e.g., Jefferies et al. 2004, Killengreen et al. 2011, Giroux et al. 2012a), the impacts of temporal uncoupling between resource and consumer dynamics on trophic dynamics remain largely unexplored (but see Miyaki and Kaji 2004, Tremblay et al. 2005, Nelson and Reynolds 2014).

Donor-controlled resources can act as food subsidies when they sustain consumer populations at higher densities than what would be predicted without donor-controlled dynamics (Polis et al. 1997). For instance, it has been suggested that donor-controlled resources such as forage produced through agricultural activities may act as food subsidies that can contribute to supporting persistent, high densities of herbivores (Alverson et al. 1988, Jefferies et al. 2004, Gauthier et al. 2005). Forage produced through agricultural activities may indeed be largely independent of the grazing/browsing pressure. Because high herbivore densities can have major ecological and economic consequences (Côté et al. 2004), it is critical to better understand the interaction between herbivores and sources of forage that can act as food subsidies.

A better understanding of the roles of donor-controlled resources on herbivore populations will likely be achieved by simultaneously taking into account other drivers of demographic variations such as winter severity. Although a growing number of studies acknowledge that climatic and nutritional constraints outside winter influence the demography of large herbivores (Sæther 1997, Loison and Langvatn 1998, Cook et al. 2004, Brown 2011), constraints associated with winter remain key drivers of their demographic rates (survival: Loison and Langvatn 1998, Coulson

et al. 2001, Garrott et al. 2003; reproduction: Garrott et al. 2003, Apollonio et al. 2013; population growth rate: Post and Stenseth 1998, Hone and Clutton-Brock 2007). Climatic and nutritional constraints associated with winter can operate on demographic processes by modulating the body mass of large herbivores (Sæther 1997, Bårdsen et al. 2008, Parker et al. 2009). In temperate regions, body mass fluctuates seasonally, being highest at the end of autumn and lowest at the end of winter or in spring after parturition for reproductive females (Mautz 1978, Parker et al. 2009). A reduction in overwinter mass loss can be observed when energy requirements associated with locomotion in snow and thermoregulation decrease (Parker and Robbins 1985, Parker et al. 1999), for instance during winters with shallower snow and warmer temperatures (Loison and Langvatn 1998), and when forage quantity and quality are higher (Parker et al. 1999). Overwinter mass loss has been shown to affect the survival (Bartmann et al. 1992, Cook et al. 2004), reproduction (Festa-Bianchet et al. 1995, Milner et al. 2013), and fitness (Pelletier et al. 2007) of large herbivores.

We studied the influence of a donor-controlled forage resource on overwinter mass loss under contrasted winter conditions in a high-density white-tailed deer population (*Odocoileus virginianus*; hereafter “deer”). The population was introduced at the northeastern limit of the species distribution on a predator-free island in 1896 and 1897. It irrupted to high densities (> 20 deer/km² on average) and has since been exerting dramatic negative impacts on plant communities (Tremblay et al. 2005). Deciduous browse has almost disappeared from the winter feeding stratum (Tremblay et al. 2005), and nowadays, deer are constrained to feed mainly on coniferous forage, especially balsam fir (*Abies balsamea*), during winter (Lefort et al. 2007). Chronic browsing of balsam fir seedlings by deer has compromised the regeneration of balsam fir stands and led to their gradual replacement by white spruce (*Picea glauca*) stands (Potvin et al. 2003). Consequently, the main source of balsam fir accessible to deer during winter are windblown trees; needles and twigs in the litterfall can also become available but at lower abundance because snow regularly covers those resources, whereas lower branches of mature trees can also become available when snowpack is thick (Tremblay et al. 2005, Massé

and Côté 2012). Balsam fir browse has a low abundance on Anticosti Island (Tremblay et al. 2005, Massé and Côté 2012). Because the availability of windblown balsam fir trees and needles and twigs is independent of browsing over decades (senescence in balsam fir starts between 90 and 130 yr; Pothier and Savard 1998), this introduces a temporal uncoupling between the impact of deer browsing on balsam fir seedlings and the negative feedback from recruitment failure of mature balsam firs on the deer population (Tremblay et al. 2005). Tremblay et al. (2005) suggested that the use of such donor-controlled forage by deer on the island may explain the maintenance of high deer densities despite the persistent degradation of plant communities.

We aimed at better understanding whether the use of donor-controlled forage by an overabundant herbivore could act as a food subsidy, namely by benefiting the consumer of such forage. For that purpose, we tested the hypothesis that the use of donor-controlled resources that are uncoupled from browsing, namely balsam fir, acts in combination with winter severity to shape the patterns in overwinter mass loss. First, we predicted that the rate of body mass loss would decrease with the proportion of balsam fir in the diet, owing to the preference for this forage in our study area (Sauvé and Côté 2007). Second, we predicted that the rate of body mass loss would be higher during a harsher winter, characterized by higher snow depth and colder windchill temperatures, than during a milder winter. To test this hypothesis, we monitored mass loss, diet, and habitat use of female deer, as well as weather conditions, during two highly contrasted winters.

MATERIALS AND METHODS

Study area

We conducted the study during winters 2008–2009 and 2009–2010 in the western part of Anticosti Island in the Gulf of St. Lawrence, Québec, 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). Snowfall averages 328 cm annually, while rainfall averages 61 cm (Environment Canada 1982). We conducted the study during two winters characterized by highly contrasted snow

conditions, as shown by snow depth and snow sinking depth data from 1984–1985 to 2009–2010 (Fig. 1; Giroux 2014). Snow depth and snow sinking depth in winter 2008–2009 were among the highest recorded over the past decades, whereas in winter 2009–2010 they were by far the lowest recorded over the last 25 years. Long-term severe browsing by deer induced the decline of dominant deciduous tree species such as white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). In addition, the shrub layer is almost entirely absent, except for deciduous shrubs such as sweetgale (*Myrica gale*), shrubby cinquefoil (*Dasiphora fruticosa*), and leatherleaf (*Chamaedaphne calyculata*) in peatlands (Pellerin et al. 2006), and regenerating black and white spruce (Potvin et al. 2003) in forest stands. Deer extirpated the most palatable shrub species normally found in that region, such as mountain maple (*Acer spicatum*), redosier dogwood (*Cornus stolonifera*), beaked hazel (*Corylus cornuta*), and Canada yew (*Taxus canadensis*; Pimlott 1963, Potvin et al. 2003).

Weather data in reference stations

We collected weather data during the study in three reference stations located in each of the following habitat types: (1) balsam fir-dominated stands (balsam fir > 50% of the basal area), (2) white spruce-dominated stands (white spruce > 50% of the basal area), (3) black spruce-dominated stands (black spruce > 50% of the basal area), (4) peatlands, and (5) clearcuts. We randomly selected the location of reference stations within a 100-m buffer zone around roads (for logistical reasons), using 1:20,000 forest cover maps. Those maps were generated by delineating habitat polygons using 1:15,000 aerial photographs taken in 1997, to which we added recent clearcuts. We visited each station at six-day intervals on average (range: 1–20 d) in 2009 (from 15 February to 25 March) and 2010 (from 8 January to 31 March) to record snow depth, snow sinking depth, and wind speed, using a 1-cm graduated avalanche probe (Voilé Guide Probe, Salt Lake City, Utah, USA), a 1-cm graduated penetrometer (Verme 1968), and a handheld digital anemometer (Windmate 100; Speedtech Instruments, Toronto, Ontario, Canada), respectively. We automatically recorded hourly temperature from 30 November 2009 to 19 April

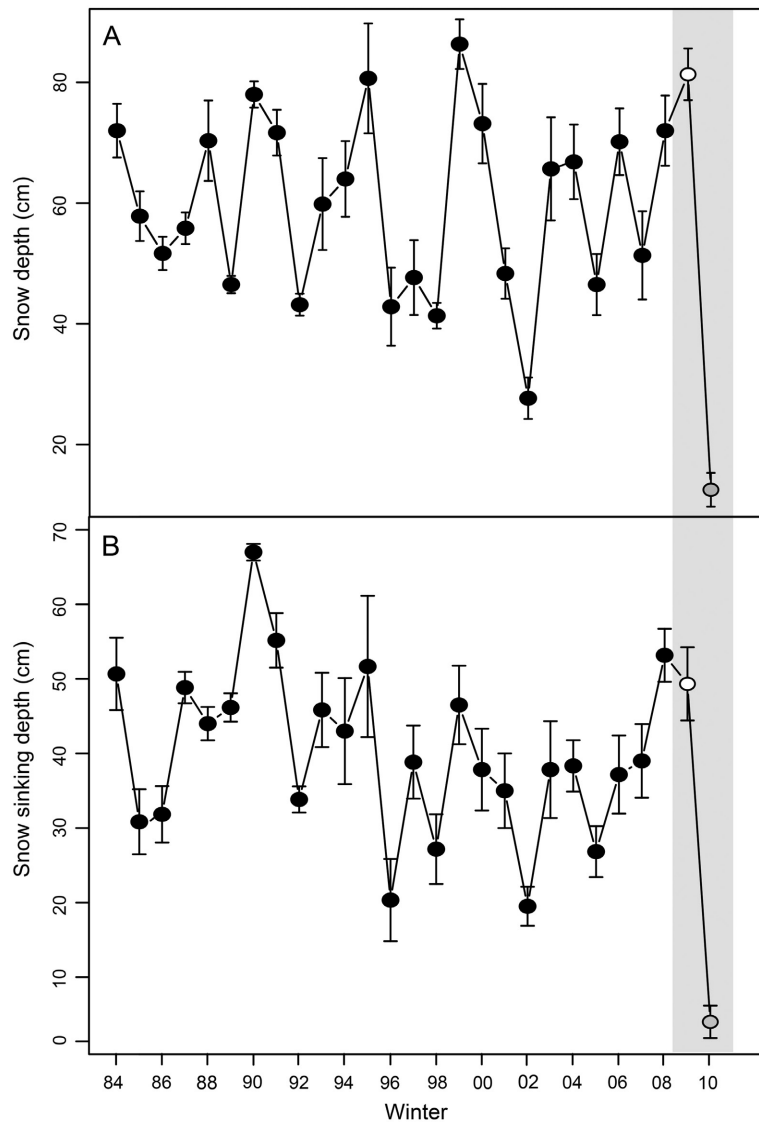


Fig. 1. Temporal trends in (A) snow depth and (B) snow sinking depth from 1984 to 2010 in a sampling station located in balsam fir stands on Anticosti Island (Québec, Canada). Each point represents the mean (\pm SD) of all measurements taken at two-week intervals from the beginning of January to the end of March. We illustrated the temporal window of our study with the light gray strip, and we highlighted the values corresponding to the harsher (2008–2009; white dot) and the milder (2009–2010; medium gray dot) winters.

2010, using one iButton device (Maxim Integrated, San Jose, California, USA) per reference station. Because we recorded wind data punctually throughout the entire study period and temperature data during only one winter, we developed regression models to predict hourly wind speed and temperature per habitat type throughout the entire study period. For that purpose, we regressed hourly wind speed and temperature

data collected at the reference stations against hourly wind speed and temperature data recorded continuously at the Port-Menier airport located approximately in the center of our study area (Environment Canada 2010; Appendix S1).

Deer captures and sampling

We captured 15 and 12 female deer during winters 2008–2009 (from 12 December to

9 January) and 2009–2010 (22 November–11 February), respectively, using Stephenson box traps, cannon nets, and net guns fired from a helicopter. We anesthetized deer by injecting a mixture of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine (Bimedamc Animal Health, Cambridge, Ontario, Canada) at doses of 3.2 and 1.6 mg/kg, respectively (Miller et al. 2003), administered with a syringe following physical contention. After chemical immobilization, we estimated deer full body mass with a spring scale (± 0.25 kg; hereafter “early winter mass”) and fitted them with GPS collars equipped with an Iridium satellite transmission device allowing the frequent reception of locations (Vectronic-Aerospace, Berlin, Germany). Prior to release, we administered yohimbine (Lloyd Laboratories, Shenandoah, Virginia, USA), an antagonist to xylazine, at doses of 0.2 mg/kg (Murray et al. 2000).

During winters 2008–2009 and 2009–2010, two and one collared females died from a natural cause during the study period. We estimated the full body mass (hereafter “late winter mass”) of those females (except one in 2008–2009, due to partial consumption by scavengers) using a spring scale (± 0.25 kg) within five days of death. We euthanized and estimated the full body mass or late winter mass of the remaining 13 and 11 female deer between 26 March 2009 and 7 April 2009, and between 6 April 2010 and 21 April 2010. We extracted the incisor teeth of all but one female to estimate their age using cementum layers in incisor teeth (Hamlin et al. 2000). During both winters, females averaged 7 years old (2008–2009: range = 2–12; 2009–2010: range: 3–14). We determined their reproductive status by verifying the presence of fetuses in the uterus in spring. Ten of the 14 females in 2008–2009 and 11 of the 12 females in 2009–2010 were pregnant at the end of winter.

Monitoring diet and habitat use

In a previous study, we showed that we could determine the diet of an individual by visiting GPS locations of that individual in the field and by collecting fecal pellets along single fresh snow tracks (Giroux et al. 2012b). Such tracks are frequently encountered on Anticosti Island because deer do not gather in yards (Lefort et al. 2007). To find single fresh snow tracks, we recorded one

telemetry location every five minutes during an eight-hour period, daily. We alternated daily between a morning (04:00–12:00 h) and an afternoon schedule (12:00 and 20:00 h). These schedules encompassed day and dusk, that is, the two periods of greatest deer activity during winter in this population (Massé and Côté 2013). Every 10 days, we transferred all telemetry locations of a given collared female received by e-mail to a handheld GPS (Garmin eTrex, Olathe, Kansas, USA) and visited recent locations shortly after their satellite transmission (average time interval between data recordings and field visits: 22 h, range: 5–36 h). We first visited a location randomly selected among the most recent locations recorded (up to 36 h) and then visited other locations in increasing and decreasing chronological order. At each location, we located single tracks found within the range of collar precision (5 m; Giroux et al. 2012b) and collected individual fecal samples along those tracks. We also collected a fecal sample from the digestive tract of marked individuals following mortality. We dried fecal samples at room temperature within six hours of collection and stored them at -4°C .

We determined the botanical composition of 87 and 53 fecal samples collected in 2008–2009 and 2009–2010, respectively, using microhistological techniques adapted from Sparks and Malechek (1968), Lefort et al. (2007), and Christianson and Creel (2008) (see details in Appendix S2). This corresponds to an average of 5.8 and 4.4 samples per individual in 2008–2009 (range: 3–8) and 2009–2010 (range: 2–7), respectively, that we collected every 12 and 15 days on average in 2008–2009 (range: 1–30) and 2009–2010 (range 5–43), respectively. We categorized the fragments observed into one of the following forage groups based on microhistological features: (1) lichens (arboreal or as litterfall), (2) *Abies balsamea*, (3) *Picea glauca*, (4) deciduous browse (mainly ericaceous shrubs, *Myrica gale*, and *Dasiphora floribunda*, but also *Betula* spp. and *Alnus* spp.), (5) graminoids, (6) forbs (*Cornus canadensis*, *Equisetum* spp., *Fragaria* spp., ferns, *Cirsium* spp., and unknown forbs), and (7) others (mosses and lycophods).

We assessed the proportion of locations in each habitat type using one telemetry location every hour for each collared deer. We associated each location with one of the following six habitat categories using forest cover maps: (1) balsam

fir stands (balsam fir >25% of the basal area), (2) white spruce stands (white spruce >50% of the basal area and balsam fir <25% of the basal area), (3) black spruce stands (black spruce >50% of the basal area and balsam fir <25% of the basal area), (4) peatlands, (5) clearcuts, and (6) others (lakes and other open habitats). This classification slightly differs from the one used to sample weather conditions in reference stations, in which balsam fir represented >50% of the basal area in balsam fir-dominated stands. We also considered stands where balsam fir represented 25–50% of the total basal area as balsam fir stands to estimate habitat use; balsam fir is a highly selected forage resource during winter on Anticosti Island (Sauvé and Côté 2007) that may influence deer habitat use even when available in low proportion (Lefort et al. 2007).

Statistical analyses

Comparison of weather conditions and diet between winters.—We described the climatic and ecological context of our study by comparing (1) snow depth, snow sinking depth, and wind chill temperatures observed among winters and habitats, and (2) deer diet between winters. We computed the wind chill temperature (W) using Eq. 1 when air temperature (T) was $\leq 0^\circ\text{C}$ and wind speed (V) ≥ 5 km/h and using Eq. 2 when air temperature was $\leq 0^\circ\text{C}$ and wind speed < 5 km/h (Environment Canada 2013):

$$W = 13.12 + 0.6215 \times T - 11.37 \times V^{0.16} + 0.3965 \times T \times V^{0.16} \quad (1)$$

$$W = T + \left[\frac{-1.59 + 0.1345 \times T}{5} \right] \times V \quad (2)$$

We modeled the variations in the response variables snow depth and snow sinking depth, respectively, using linear mixed models (LMMs) including year, habitat type, and their interactions as predictors. We specified reference station ID as a random variable. We modeled the variations in daily windchill temperature (average from the hourly data predicted from the airport data; Appendix S1) using linear models (LMs) including year, habitat type, and their interactions as predictors.

We compared the proportion of the following six forage types in deer diet between winters:

(1) balsam fir, (2) white spruce, (3) lichens, (4) deciduous browse, (5) graminoids and forbs (hereafter “herbaceous”), and (6) others (mosses and lycopods). We fitted a generalized LMM with quasibinomial errors (logit link; Zuur et al. 2009) to model the variations in the proportion of forage (response). We included the variables year, type of forage, and their interaction as predictors, and we specified feces ID nested within individual ID as random variables.

Rate of body mass loss.—We considered the proportion of balsam fir in diet and the proportion of locations in balsam fir stands as indices of balsam fir use by deer. In addition to indices of balsam fir use and winter, we included reproductive status and age as continuous covariables potentially affecting the rate of body mass loss. We computed the rate of body mass loss per day by subtracting the late winter mass from the early winter mass and then by dividing the result by the number of days between both measurements. We expressed the rate of body mass loss in kilograms lost per 100 d. We used a model selection approach (Akaike’s information criterion; Burnham and Anderson 2002) to identify the combination of these variables that best described the variations in the rate of body mass loss. We compared 30 candidate LMs with the rate of body mass loss as the response variable and up to four of the following predictors: the proportion of balsam fir in diet, the proportion of locations in balsam fir stands, winter, interaction between winter and either the proportion of balsam fir in diet or the proportion of locations in balsam fir stands, reproductive status, and age (see Appendix S3 for the full list of models). We conducted additional analyses to confirm that other covariates (e.g., dates of capture and of euthanasia, early winter mass, and the quadratic effect of age) did not better explain the variations in the rate of body mass loss than the variables included in the 30 candidate models (Appendix S4). We obtained similar results (best-fitting model and parameter estimates) when either running model selection without the female of unknown age or keeping that female and removing models including the variable age. We report parameters of the best model estimated with the data set including that female. In this analysis, we used the proportions of balsam fir

in diet or of locations in balsam fir stands averaged over the winter by individual deer. We detected one observation with a Cook's distance value larger than 1, indicating that it could be sufficiently influential to affect the results (Pardoe 2012). We ran analyses with and without this value, and decided to exclude it, because including it almost doubled the parameter estimates of each effect included in the best model, although it did not change the direction or significance of the effects. We performed all analyses using R 3.0.2 (R Development Core Team 2012).

Linking diet and habitat use.—To ease our interpretation of the results regarding the influence of diet and habitat use on the rate of mass loss, we also described the multivariate relationships among variables describing diet and habitat use using robust principal components analyses for compositional data (hereafter “robust PCAs”; function `pcaCoDa` in package `robCompositions`: Templ et al. 2015). Such approach takes into account that variables describing diet and habitat use are compositional data and thus correspond to the proportions summing to one. To solve the statistical problems associated with compositional data, the package `robCompositions` transforms these data, runs the PCA on transformed data, and then back-transforms the results (Templ et al. 2016). We performed a separate robust PCA for each winter, using the proportion of locations in all habitat types and of all dietary items in the analysis. We aggregated the habitat types (other habitats) and dietary items (other forage) that averaged less than 10% of forage or habitats used per year to reduce the number of variables while avoiding the inclusion of variables with many zero values. In 2008–2009, the variables included in the robust PCA were the proportion of balsam fir, of white spruce, and of other forages in the diet, as well as the proportion of locations in balsam fir stands, in white spruce stands, in peatlands, and in other habitats. In 2009–2010, these variables were the same as in 2008–2009, in addition to the proportion of deciduous browse and of herbaceous plants in the diet. In the robust PCAs, we used the proportion of dietary items estimated from each fecal sample, and we associated data from each fecal sample to the proportion of locations recorded for the given individual in the different habitat types during a

three-day period preceding feces deposition (estimated retention rate; see details in Appendix S2).

RESULTS

Comparison of weather conditions and deer diet between winters

Across habitats, snow depth and snow sinking depth were on average 86 and 22 cm higher (95% CI [78–94] and [17–28]), respectively, during winter 2008–2009 than during winter 2009–2010 (Fig. 2A, B). Snow depth did not vary among habitats during any winter (Fig. 2A). Snow sinking depth was on average 20 cm higher (95% CI [8–31]) in closed (i.e., forest stands) than in open (i.e., peatlands and clearcuts) habitats during winter 2008–2009. Snow sinking depth did not differ between habitat types during winter 2009–2010 (Fig. 2B). Wind chill temperatures were on average 5°C lower (95% CI [3–7]) during winter 2008–2009 than during winter 2009–2010 (Fig. 2C). Daily temperatures, which were also 5°C lower (95% CI [3–6]; Appendix S5) in 2008–2009 than in 2009–2010, drove these interannual variations in daily wind chill temperatures, because wind speed did not vary between years (difference between years: –0.3 km/h, 95% CI [–0.8 to 0.2]; Appendix S5).

The proportion of balsam fir in diet decreased by 36% (95% CI [0.28–0.44]) between 2008–2009 and 2009–2010, while that of white spruce and lichens remained similar between winters (difference between winters: white spruce = 0.03, 95% CI [–0.50 to 0.12], and lichens = 0.0, 95% CI [–3 to 4]; Fig. 3). The proportion of deciduous browse, herbaceous plants, and other resources (mosses and lycopods) in diet increased by 15% (95% CI [0.11–0.20]), 12% (95% CI [0.08–0.16]), and 7% (95% CI [0.02–0.11]), respectively, between winters 2008–2009 and 2009–2010. We have illustrated the variations in habitat use between years in Appendix S6.

Determinants of variations in the rate of body mass loss

In 2008–2009, early and late winter mass averaged 52.8 kg (range: 34.5–65.5) and 40.2 kg (range: 25.0–48.5), respectively. In 2009–2010, early and late winter mass averaged 48.9 kg (range: 41–56) and 38.2 kg (range: 32–46),

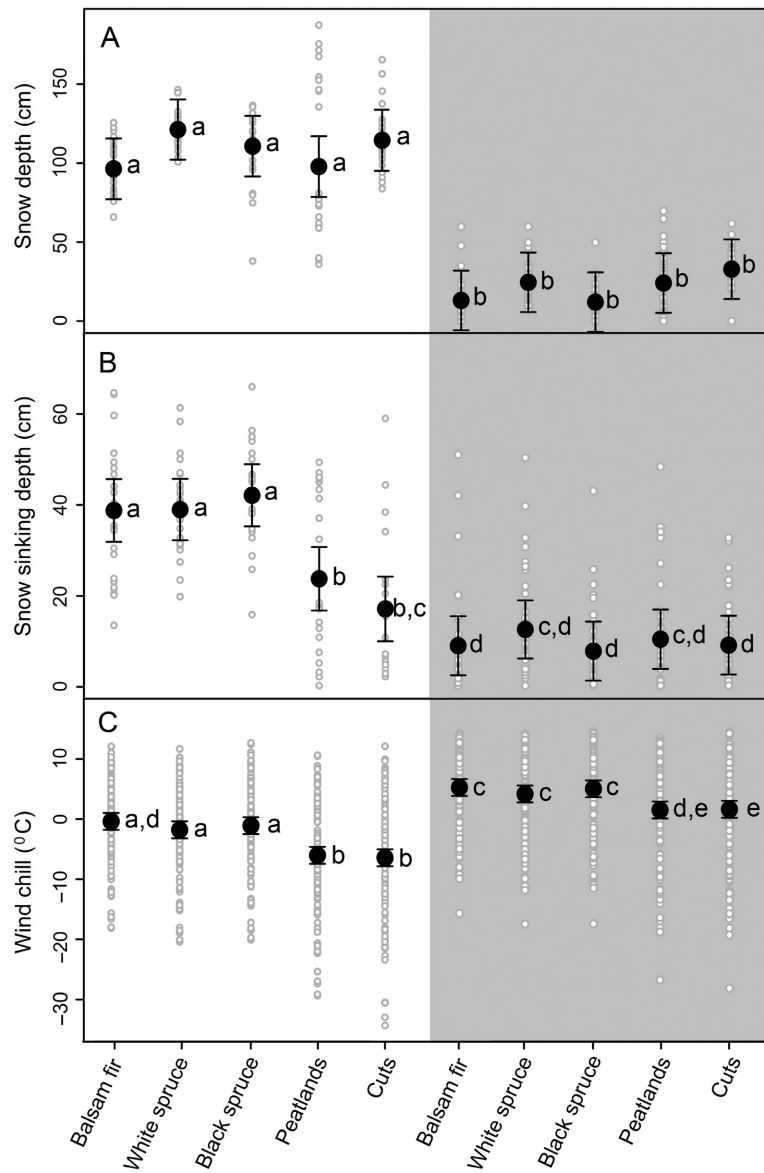


Fig. 2. (A) Snow depth, (B) snow sinking depth, and (C) wind chill temperatures for the main habitat categories used by white-tailed deer females on Anticosti Island (Québec, Canada) during a harsher (2008–2009; white background) and a milder (2009–2010; medium gray background) winter. For each variable, we show the predicted values (large black dots) and the 95% CIs obtained with linear models, along with the data used in the analyses (small white dots). Data used in analyses correspond either to the raw data collected in habitat-specific sampling stations (snow depth and snow sinking depth) or to the predicted values from the relationships between wind speed and temperature in habitat-specific sampling stations and at the airport of Port-Ménier (wind chill; Appendix S1). We identified habitat types with the same letter when 95% CIs overlapped.

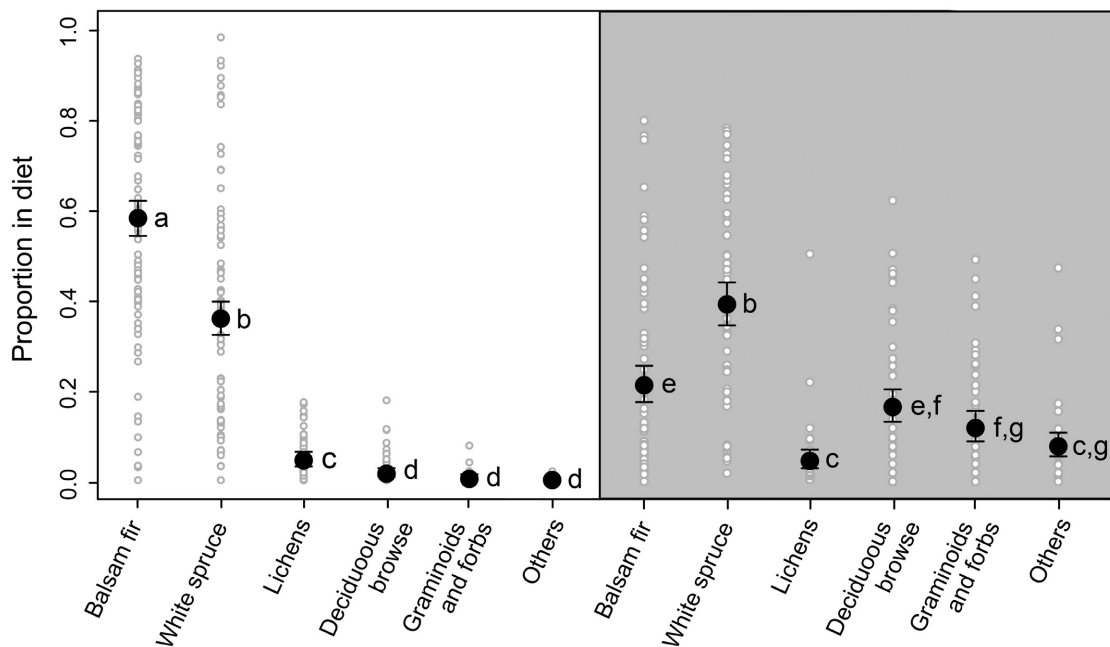


Fig. 3. Proportion of forage resources in the diet of white-tailed deer females on Anticosti Island (Québec, Canada) during the harsher (2008–2009; white background) and the milder (2009–2010; medium gray background) winters. We show the predicted proportions (large black dots) and their 95% CIs obtained using a generalized linear mixed model (GLMM) with quasibinomial errors, along with the raw data (for every forage resource, each white dot corresponds to the proportion of that resource in each fecal sample; $n = 87$ and 53 in 2008–2009 and 2009–2010, respectively). We identified habitat types with the same letter when 95% CIs overlapped.

respectively. Early and late winter mass did not differ between years (Appendix S4). The best model explaining the variations in the rate of body mass loss included the winter, the proportion of locations in balsam fir stands, and the interaction between both variables ($R^2 = 0.39$; Appendix S3). The rate of body mass loss was similar during both winters (2008–2009: 12.3 kg/100 d, 95% CI [11.0–13.6]; 2009–2010: 11.5 kg/100 d, 95% CI [10.2–12.9]). The rate of body mass loss decreased by 1.3 kg/100 d (95% CI [0.2–2.5]) and increased by 1.2 kg/100 d [0.2–2.2] with each 20% increase in the proportion of locations in balsam fir stands in 2008–2009 and 2009–2010, respectively (Fig. 4).

Relationships between variables describing diet and habitat use

The robust PCAs showed that the variations in diet were related to those in habitat use in 2009–2010, but not in 2008–2009 (Fig. 5). In 2008–2009, the first axis of the PCA explained 53% of the variation and discriminated fecal samples

associated with the use of white spruce stands and of peatlands vs. the use of other habitats (PCA loadings: white spruce stands = -0.39 , peatlands = -0.49 , other habitats = 0.77). The second axis of the 2008–2009 PCA explained 38% of the variation and discriminated fecal samples associated with the use of white spruce stands vs. the use of peatlands and of balsam fir stands (PCA loadings: white spruce stands = 0.76 , peatlands = -0.62 , balsam fir stands = -0.17). In 2009–2010, the first axis of the PCA explained 46% of the variation and discriminated fecal samples associated with the use of balsam fir stands and the consumption of balsam fir vs. those associated with the use of white spruce stands and of other habitats (PCA loadings: balsam fir stands = -0.79 , balsam fir in diet = -0.27 , white spruce stands = 0.37 , other habitats = 0.35). The second axis of the 2009–2010 PCA explained 22% of the variation and discriminated fecal samples associated with the use of other habitats vs. the use of white spruce stands (PCA loadings: other habitats = 0.76 , white spruce stands = -0.60).

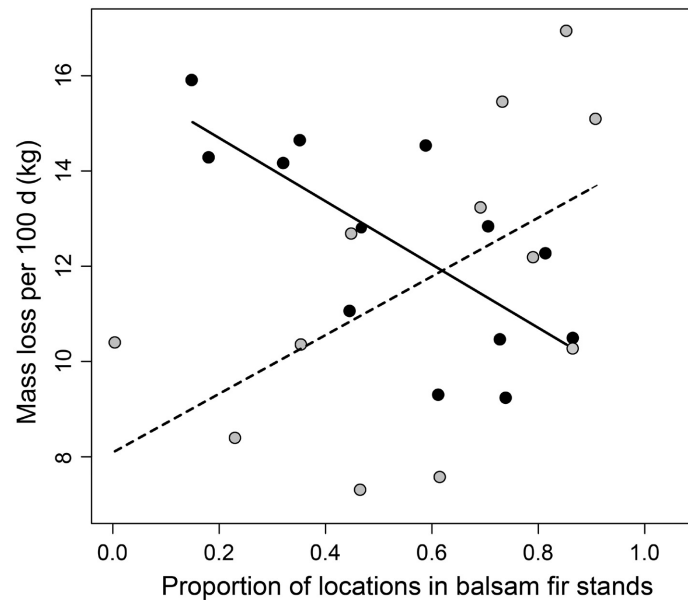


Fig. 4. Relationships between the rate of mass loss by female white-tailed deer on Anticosti Island (Québec, Canada) and the proportion of locations in balsam fir stands during the harsher (2008–2009) and the milder (2009–2010) winters, respectively.

DISCUSSION

During an exceptionally mild winter, characterized by the shallowest snow cover observed in the last 25 years on Anticosti Island, female white-tailed deer decreased their relative consumption of balsam fir and increased their relative consumption of deciduous browse and herbaceous plants compared to a harsher winter. Surprisingly, despite the highly contrasted snow conditions and wind chill temperatures between winters, deer lost body mass at a similar rate during both winters. The rate of body mass loss decreased with the use of balsam fir stands during the harsher winter, but the relationship was reversed during the milder winter. Our study shows that deer can alleviate overwinter mass loss by using a donor-controlled habitat that is temporally uncoupled from browsing pressure, but that this benefit disappears in milder conditions.

Foraging behavior between winters of contrasted severity

Winter severity can influence winter diet of large herbivores by modulating forage availability (Dumont et al. 2005, Christianson and Creel 2007, 2008). The consumption of herbaceous

plants (Christianson and Creel 2007, 2008) and shrub species (Dumont et al. 2005) usually buried under deep snow can increase in years with shallower snow. In our study, we observed a shift in diet between two winters characterized by highly contrasted snow conditions. The 27% increase in the relative importance of herbaceous plants and deciduous browse in diet as well as the 36% decrease in the proportion of balsam fir in diet during the milder winter likely resulted from the 86-cm shallower snow cover on average. Indeed, shallow snow cover rendered herbaceous plants and shrub species available (Dumont et al. 2005, Christianson and Creel 2007, 2008). Deep snow can also provide the support necessary to reach the lower branches of mature trees (e.g., balsam fir on Anticosti Island: Massé and Côté 2012). Yet, a companion study showed that the biomass of windblown balsam fir trees was six times higher than that of lower branches of mature trees along deer foraging paths, and that deer selected windblown balsam fir trees during the harsher, but not during the milder, winter (N. Courbin, C. Dussault, A. Veillette, M.-A. Giroux, and S. D. Côté, *unpublished manuscript*). Therefore, the difference in diet between winters likely resulted from the unusual availability of

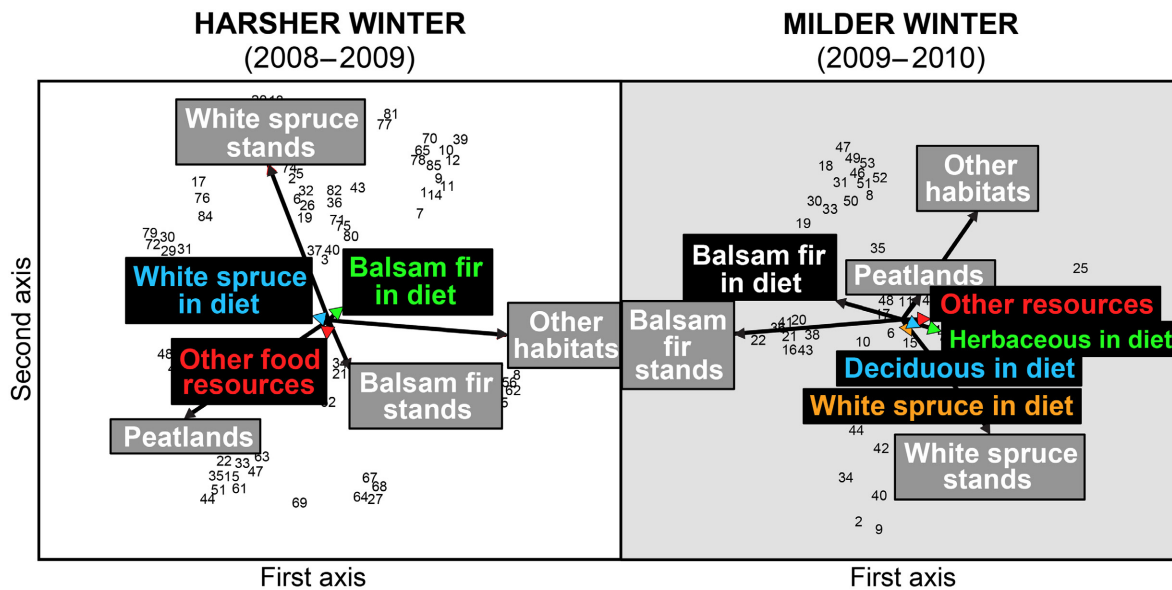


Fig. 5. Robust principal components analyses used to determine the multivariate relationships between the following variables describing diet and habitat use of white-tailed deer females on Anticosti Island (Québec, Canada) in 2008–2009 and 2009–2010: the proportion of balsam fir, white spruce, deciduous browse, herbaceous plants and other forages (e.g., lichens, mosses) in diet, as well as the proportion of locations in balsam fir stands, white spruce stands, peatlands, and other habitats (e.g., lakes, cuts). Variables describing diet and habitat use are shown in black and dark gray boxes, respectively.

herbaceous plants and shrub species during the milder winter and the selection of windblown balsam fir trees during the harsher winter.

Body mass loss between winters of contrasted severity

It is generally recognized that overwinter mass loss in large herbivores decreases with the ratio of energy intake to requirements (Parker et al. 1999), and thus, that mass loss can increase during harsher winters (Cederlund et al. 1991, Loison and Langvatn 1998). Yet, other studies showed that overwinter mass loss may not vary with winter harshness (Loison et al. 1999). In our study, the rate of body mass loss did not vary between winters, despite milder snow conditions (i.e., lower snow depth and sinking depth) and warmer temperatures that may have lowered energy requirements during the milder winter. It is unclear whether there were potential differences in energy intake between both winters. This is mostly due to the observation that during the milder winter, deer consumed resources that snow usually covers (herbaceous plants and

deciduous browse). So far, no study estimated the availability and quality of these resources during winter and compared them with typical winter forage in our study area. This hampered our ability to further interpret the similarity in the rate of mass loss between winters, and calls for further studies aiming at comparing forage availability and quality across a range of snow and forage conditions.

Temporal uncoupling between resource and consumer dynamics

The rate of mass loss decreased with the use of balsam fir stands, but only during the harsher winter. Balsam fir stands can be considered a donor-controlled habitat, because the abundance of the main source of balsam fir, namely windblown trees, is independent of browsing for decades and is on average almost fourfold higher in balsam fir stands than in other stands (N. Courbin, C. Dussault, A. Veillette, M.-A. Giroux, and S. D. Côté, *unpublished manuscript*). Surprisingly, the index of balsam fir use that best explained the variations in the rate of mass loss

during both winters was the proportion of locations in balsam fir stands, rather than the proportion of balsam fir in diet. This result raises interesting questions about the attributes of balsam fir stands that benefited deer. Indeed, the proportion of balsam fir in diet was not related to the proportion of locations in balsam fir stands during the harsher winter, and wind chill temperature and snow conditions in balsam fir stands did not differ from other forest stands (Fig. 2). Yet, a previous study showed that the density of deer tracks increased with the percentage of balsam fir in the forest stands during a typical winter on Anticosti Island (Lefort et al. 2007). Although the use of balsam fir stands could be associated with a higher deer density, which could reduce the availability of balsam fir browse or twigs per capita, deer could also benefit from the reduction in locomotion costs associated with a higher density of deer tracks (Parker et al. 1984). During the milder winter, the use of balsam fir stands was positively related to overwinter mass loss, suggesting that other foraging strategies may benefit deer when the snowpack is not thick enough to cover herbaceous plants and shrub species usually unavailable during winter in our study area.

The relationships between the use of balsam fir stands and overwinter mass loss bear interesting insights into the role of donor-controlled food resources uncoupled from browsing in the functioning of plant–herbivore interactions. Indeed, as overwinter mass loss can affect demographic parameters in large herbivores (Bartmann et al. 1992, Festa-Bianchet et al. 1995, Cook et al. 2004, Pelletier et al. 2007, Milner et al. 2013), our results suggest that the use of a donor-controlled habitat uncoupled from browsing pressure could influence demographic processes. Hence, the use of a donor-controlled habitat could contribute to explaining why previous studies did not observe a negative feedback between the deterioration of plant communities and the density of deer on Anticosti Island (Tremblay et al. 2005). Yet, because the relationship between the use of balsam fir stands and overwinter mass became positive during a mild winter, the role of a donor-controlled habitat on demographic processes in this population remains to be observed under a changing climate. We especially need such information as deer browsing pressure affects herbaceous plants and

deciduous browse (Tremblay et al. 2006), and the consumption of those resources increased during the milder winter. This suggests that climate can modulate temporal uncoupling between resources and consumer dynamics. Combined with previous studies (Miyaki and Kaji 2004, Tremblay et al. 2005), our study represents an additional step to better understand the impacts of donor-controlled dynamics arising from temporal uncoupling on herbivore populations living at high density.

In conclusion, our study brings interesting insights to better understand applied and fundamental questions related to the impacts of climate change and other global perturbations on wildlife populations. Our study suggests that the increased frequency of winter mild spells projected by climate models (Lemmen et al. 2008) may modify habitat–performance relationships (*sensu* Gaillard et al. 2010), but not the winter dynamics of body mass, at least in some populations. Yet, these climate models also project an increase in the amount of winter precipitation, albeit there are still uncertainties with respect to the form of these precipitations (snow, rain, or freezing rain: Lemmen et al. 2008), and hence on the predicted impacts of such changes on both habitat–performance relationships and winter dynamics of body mass. Ongoing monitoring of the habitat–performance relationships of wildlife populations under various climatic conditions could contribute to shed light on how they shall adjust to a changing climate. While working toward a better understanding of the impacts of climatic perturbations on wildlife populations, one must not overlook the impacts that other global changes such as agricultural activities, which can induce donor-controlled dynamics, can have on populations and natural ecosystems. Our study illustrates how we can address the simultaneous impacts of climate and donor-controlled dynamics on wildlife populations, therefore paving the way for further studies.

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