

The Effects of Decreasing Winter Diet Quality on Foraging Behavior and Life-History Traits of White-Tailed Deer Fawns

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Abstract

Many high-density populations of wild ungulates have exerted strong negative impacts on their habitat. A decrease in forage quantity and quality may affect individual growth, fecundity, and survival, especially under harsh winter conditions. On Anticosti Island, Québec, Canada, browsing by introduced white-tailed deer (*Odocoileus virginianus*) negatively affected boreal forest composition. Since the preferred contemporary winter forage of deer, balsam fir (*Abies balsamea*), has been almost completely extirpated from the island at browse height, deer are forced to increase the proportion of normally avoided forage, such as white spruce (*Picea glauca*), in their winter diet. We predicted that an increase in the proportion of white spruce in the diet would have detrimental effects on deer body condition and would affect their behavior and life history traits. We experimentally simulated a deterioration of winter forage quality in semi-natural enclosures by increasing the proportion of white spruce in the diet and examined the effects of winter diet quality on 1) forage intake, 2) body condition loss, 3) activity budget, and 4) survival of white-tailed deer fawns. Fawns fed the poor-quality diet maintained a higher forage intake rate throughout the winter than fawns fed the control diet, suggesting a compensatory response to the decrease of forage quality by consuming more forage during winter. Body mass decreased over the winter, but we did not observe any significant effects of diet quality on body mass loss. Diet quality did not influence the activity budget of fawns, but deer decreased activity in cold weather. The main determinant of overwinter survival was individual body mass in early winter. Our study suggests that deer have adapted to the extreme conditions encountered on Anticosti (i.e., harsh and long winters, low-quality browse, and a high-density population). Even though white spruce stands are gradually replacing balsam fir stands, our results suggest that deer on Anticosti could maintain a high-density population by increasing the amount of white spruce in their diet. However, future studies are necessary to address the long-term effects of a diet dominated by white spruce on deer body condition, survival, and reproduction under natural conditions. (*JOURNAL OF WILDLIFE MANAGEMENT* 70(5):1445–1454; 2006)

Key words

activity budget, Anticosti, body composition, density, diet, foraging behavior, life-history traits, nutrition, Odocoileus virginianus, survival, white-tailed deer, winter.

At high population density, herbivores can have a strong negative impact on the abundance of vegetation (Cooke and Farrell 2001, Jefferies and Rockwell 2002, Côté et al. 2004), which in turn may influence their growth, fecundity, and survival through a decrease in forage quantity and quality (Loison and Langvatn 1998, Andersen and Linnell 2000, Armstrong et al. 2005). Winter conditions are highly variable at northern and temperate latitudes and may add constraints on herbivores through both poor forage conditions and high-energy expenditures (Moen 1976). Forage is generally limited in quantity in winter as compared to summer (Verme and Ullrey 1972, Gray and Servello 1995) and, in ruminants, the low quality of available browse may not be sufficient to satisfy their nutritional and energetic requirements, especially at high population density (Torbit et al. 1985). In many high-density populations, mortality from starvation in winter is the main factor regulating population size, overriding predation (Potvin et al. 1981, Clutton-Brock et al. 1985, 1987, Bartmann et al.

1991). Those constraints have forced northern ungulates to adapt to extreme variations in seasonal conditions (Moen 1976, Suttie et al. 1983, DelGiudice et al. 1990, Loison and Langvatn 1998).

A multitude of factors influence forage intake in ruminants including digestibility, rate of passage through the gastrointestinal tract, local climatic conditions, forage quality, and forage availability (Welch and Hooper 1993). Studies have reported that most ungulates modify their foraging behavior in winter to minimize body mass loss and to meet their daily energy and nutritional requirements (Ozoga and Verme 1970, Ozoga and Gysel 1972), for example, by reducing their forage intake rate voluntarily (Thompson et al. 1973, Baker et al. 1979, Bartmann et al. 1991, Storeheier et al. 2003). A reduction in forage intake, however, may lead to body mass loss if a reduction in energy expenditures does not occur. Accordingly, ungulates may decrease energy expenditure in winter by modifying their activity rate, concentrating their active bouts during the warmer daylight hours, and foraging in habitats with little snow (Verme and Ozoga

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1980, Beier and McCullough 1990). Many studies have reported the reduction of activity in winter in ungulates (white-tailed deer [*Odocoileus virginianus*]: Ozoga and Verme 1970, Beier and McCullough 1990; red deer [*Cervus elaphus*]: Georgii 1981; roe deer [*Capreolus capreolus*]: Cederlund 1981; moose [*Alces alces*]: Renecker and Hudson 1989) and relate it to the decline in forage quality and availability, an increase of snow cover, and colder daily temperatures (Beier and McCullough 1990).

Energetic constraints may, however, lead to different body mass dynamics in winter (Cederlund et al. 1991) and force wild ungulates to survive on their body reserves or muscle protein (Torbit et al. 1985, DelGiudice et al. 1998, Jensen et al. 1999). Researchers have observed winter body mass losses ranging from 20–40% in wild ungulates (Cederlund 1981, Huot 1982, Festa-Bianchet et al. 1996, Parker et al. 1999). In deer, males weaken due to high-energy expenditure and low forage intake during the rut, and fawns are the most vulnerable segments of the population in winter (Dumont et al. 2000). Fawns usually face greater mortality in winter due to a higher metabolic rate per unit of body mass, larger surface area to mass ratio, and faster depletion of more limited body fat reserves compared to adults (Nordon et al. 1970, Moen 1976). Forage quality during the first winter of life can have long-term impacts on the body condition of fawns and can influence life-history traits such as survival, age at first reproduction, and even lifetime reproductive success (Solberg and Saether 1994, Stewart et al. 1999). Juveniles in better body condition have greater chances to survive their first winter (White et al. 1987, Côté and Festa-Bianchet 2001, Pettorelli et al. 2002) and usually show greater body mass as adults (Schultz and Johnson 1995). Study of winter body mass dynamics and foraging and activity patterns may provide insights into evolutionary adaptations to weather extremes.

On Anticosti Island, Québec, Canada, browsing by introduced and abundant white-tailed deer had negative impacts on boreal forest composition (Potvin et al. 2003). Preferred winter forage (deciduous browse) was almost completely eradicated 70 years ago and the alternative preferred forage (balsam fir [*Abies balsamea*]) is also being gradually extirpated from the island (Potvin et al. 2003, Tremblay et al. 2005). Due to over-browsing by deer, no balsam fir stands have regenerated since the 1930s (Potvin et al. 2003). The proportion of fir stands decreased from 40% to 20% since deer introduction and white spruce (*Picea glauca*) stands have gradually replaced fir stands (Potvin et al. 2003). Within the next 50 years, most of the balsam fir stands are expected to disappear from the island (Potvin et al. 2003). Although balsam fir usually is considered a starvation food (Ullrey et al. 1968), it is the main constituent of the winter diet of deer on Anticosti Island (Huot 1982, Lefort 2002). The decline in availability of fir, however, has forced deer to also forage on white spruce, a species normally not eaten by deer (Taylor 1965, Halls 1984, Sauvé 2005). Currently, the winter diet of deer on Anticosti is mainly composed of balsam fir (70%) and completed by white

spruce (20%) and lichens (Lefort 2002). This suggests a strong selection for balsam fir, which is scarce in the browse stratum (Tremblay et al. 2005) and is mostly available from litter-fall (12.7 ± 4.1 kg of twigs/ha; Tremblay et al. 2005) and wind-thrown trees. Given that white spruce stands gradually are replacing fir stands on Anticosti, deer likely will have to include a higher proportion of white spruce in their diet in the near future. White spruce may be considered a lower-quality browse because it contains more fiber and tannins than balsam fir (Sauvé 2005), but it is the only available alternative browse species on Anticosti Island and no information on the effects of increased proportion of white spruce in deer diet is available. A diet containing a higher proportion of white spruce could have detrimental effects on several behavioral parameters and life-history traits of deer, such as forage intake, body condition, activity budget, and overwinter survival.

We experimentally simulated in semi-natural enclosures a deterioration of winter forage quality caused by a high-density deer population and examined its effects on 1) forage intake, 2) body mass loss, 3) activity budget, and 4) survival of fawns. We predicted that deer fawns fed on a low-quality diet (a high proportion of white spruce) would have lower forage intake and greater body mass loss, spend less time active, and have a lower probability of survival than fawns fed on a higher-quality diet (a low proportion of white spruce).

Study Area

Anticosti is a 7,943-km² island located in the Gulf of St. Lawrence, Québec, Canada. The climate was sub-boreal and characterized by cool summers and long winters (Huot 1982). Land cover was comprised of boreal forest dominated by white spruce, balsam fir, and black spruce (*Picea mariana*; Potvin et al. 2003). There were no indigenous large herbivores on the island before the introduction of 220 white-tailed deer in the late 1800s. Since then, the population erupted due to lack of predators on the island. The Anticosti population was at the northern fringe of white-tailed deer distribution and a recent census estimated population size at >20 deer/km² (Potvin et al. 2004).

Methods

Captures

We captured 26 fawns (6–7 months old) in the autumn of 2002 ($n = 13$) and 2003 ($n = 13$). We physically restrained deer using Stephenson box traps, drop-nets, net guns, or canon-nets baited with balsam fir and commercial cow feed (Shur-Gain[®] prepartum cow feed, Agribrands, Purina Canada Inc., St. Hubert, Québec, Canada; Haulton et al. 2001). We also used chemical immobilization with a mixture of Telazol[®] (200 mg/ml; Fort Dodge Animal Health, Fort Dodge, Iowa) and Xylazine (100 mg/ml; Bimeda-MTC Animal Health Inc., Cambridge, Ontario, Canada) at doses of 6 mg/kg and 3 mg/kg, respectively, administered remotely with a rifle and radiotransmitter-equipped darts (Pneu-Dart Inc., Williamsport, Pennsylva-

nia; Miller et al. 2003). We used Yohimbine (2 mg/ml; LLOYD Laboratories, Shenandoah, Iowa) as an antagonist for Xylazine (Wallingford et al. 1996). We sexed and weighed fawns to the nearest 0.5 kg with a spring scale or an electronic scale. We measured hind foot length with a measuring tape (± 0.5 mm). We used foot length measured at capture as an indicator of structural size throughout the winter since dietary restriction does not allow structural growth of fawns during winter (Verme and Ozoga 1980). We individually marked all fawns with ear tags and relocated them in an outdoor enclosure. The Laval University Animal Care and Use Committee approved all procedures.

Experimental Design

We established an 80-m \times 150-m enclosure surrounded by a 4-m-high game fence in a natural and mature white spruce stand where trees did not have branches lower than 3 m and the shrub layer was absent, thereby excluding any uncontrolled food input into the enclosure except litter-fall. We further subdivided the enclosure in 3 sections of 80 m \times 50 m each with 30–40% of the initial forest maintained as cover. We built 3 wooden structures in each section to simulate wind-protected areas in the natural forest.

During the pre-experimental period (19 Dec 2002–11 Jan 2003 and 27 Dec 2003–8 Jan 2004), we grouped fawns together and fed them with the control winter diet (see next section for details). At the forest edge we placed food into a single feeding trough (2.5 m \times 30 cm \times 30 cm) that was large enough to allow access to food by all individuals simultaneously. We used spotting scopes (15–25 \times) and binoculars (8 \times 42) to conduct behavioral observations from elevated blinds located at 15 m from the enclosure fence.

At the beginning of January of each year, we divided fawns into similar groups by sex and body mass. We formed a control group (2003: 5 M, 2 F; 2004: 2 M, 5 F) and a poor-quality-diet group (2003: 4 M, 2 F; 2004: 3 M, 3 F) during both years. There was no difference in initial body mass (kg) between each group of fawns in 2003 (control diet: 28.2 ± 1.8 , poor diet: 28.8 ± 1.9 ; $t_{1,12} = -0.24$, $P = 0.81$) and 2004 (control diet: 26.9 ± 1.2 , poor diet: 26.4 ± 1.3 ; $t_{1,11} = 0.24$, $P = 0.81$).

The experimental diets were composed of a combination of white spruce and a mixture of balsam fir and arboreal lichens, in different proportions. The control diet represented the actual winter diet of free-ranging deer on Anticosti determined by micro-histological analyses of pellets (i.e., 70% balsam fir, 20% white spruce, and about 10% lichens; Lefort 2002). We corrected the percentage of lichens in pellets for the high digestibility of lichens (Côté 1998) by comparing lichen presence in pellets and in rumen contents (Lefort 2002). Lichens in the litter-fall can be an important source of forage for deer during winter on Anticosti (Tremblay et al. 2005). The poor-quality diet was 50% fir, 40% spruce, and 10% lichens. We harvested fir, spruce, and lichens in forest stands typical of Anticosti. Because very little browse <3 m from the ground was available (Tremblay et al. 2005), we felled mature balsam fir

trees twice a week and collected the branches (≤ 1 cm in diameter) as well as arboreal lichens growing on the branches. We harvested annual shoots (≤ 1 cm in diameter) of white spruce that were accessible to deer in winter (i.e., within 1–3 m in height). We shredded fir (with lichens) and spruce separately in a wood chipper (Yard Machines-5 HP wood chipper; MTD products Inc., Valley City, Ohio) that created a uniform mixture, which prevented fawns from selecting one of the diet components. To verify the homogeneity of the diet mixture, we collected 79 fresh pellet samples in the enclosures during winter 2003 and performed micro-histological analyses to evaluate the proportion of fir and spruce eaten by fawns (Holecheck et al. 1982, Hansen 1995, Lefort 2002). For each sample, we observed 2 slides of homogenized fecal material and identified 50 fragments of fir or spruce on each slide using the morphology of stomata (Lefort 2002). Fawns consumed the proportions of balsam fir and white spruce offered as the fecal percentages of spruce were $21.9 \pm 2.6\%$ in the control diet and $37.4 \pm 2.4\%$ in the poor diet (t -test testing the difference among the 2 diets: $t_{1,53} = 22.72$, $P < 0.0001$). We gave 2 kg of fresh food to each fawn daily, an amount considered sufficient to meet the daily metabolic needs of a 30-kg fawn (Huot 1982). We considered that the quality, not the quantity, of food limited fawns because there was always food left in the feeding troughs. Availability of snow made water accessible at all times.

Monitoring

We observed 2 sections of the enclosure simultaneously on a daily basis for approximately 6 hours. From January to mid-February, we watched deer during the complete daylight period (i.e., from about 0830–1530 hours). From mid-February to mid-April, we conducted observations alternatively during the morning (sunrise to 1200 hours) and the afternoon (1200 hours to sunset) to encompass the total daylight period. We performed 46 ± 2 observation periods per enclosure in 2003 and 53 observation periods per enclosure in 2004 (total observation time for 2003 was 707 hr and for 2004, 616 hr). During each observation period, we noted the time spent feeding at the trough for each individual (± 1 min) and weighed the amount of food (± 0.5 kg) eaten by the group at the end of the period. We estimated individual food intake from the product of the proportion of time spent feeding by an individual and the quantity of food eaten by the group during the observation period. We assumed all fawns had similar bite size and feeding efficiency while eating at the troughs. Finally, each morning we weighed the leftover from the previous day's ration to estimate the 24-hour food intake per group.

We estimated individual activity budget from instantaneous scan sampling every 10 minutes (Altmann 1974). We noted the main activity of each individual among foraging, interacting, standing, or lying at a bed site. We calculated daily activity rate from the ratio between active and inactive (i.e., lying at a bed site) periods. We measured body mass (± 0.5 kg) at least once a week for most individuals with an electronic scale baited once a day with <100 g of

commercial cow feed per group. We used body mass in all analyses. Dividing body mass (kg) by hind foot length (cm) to take into account structural size (Clutton-Brock and Pemberton 2004) or using the residuals of body mass regressed on hind foot length (Schulte-Hostedde et al. 2005) did not modify the results. For simplicity, we only present results for body mass.

We used mean daily temperature (T in $^{\circ}\text{C}$) and wind speed (W in km/hr) collected by Environment Canada (2004) at the Port Menier airport (1 km from the enclosures) to calculate a wind chill index (WCI) using the equation $\text{WCI} = 13.12 + (0.6215 \times T) - (11.37 \times W^{0.16}) + (0.3965 \times T \times W^{0.16})$. We used a wind chill index instead of temperature and wind speed alone because it included most of the variability in the weather data in only one parameter. We always tested wind chill index as a single factor in the statistical analyses.

When fawns died during the experiment, we performed necropsies to determine the cause of death and to measure subcutaneous, heart, kidney, visceral, and femur marrow fat contents. We analyzed marrow fat from 6 fawns in 2003 and 5 fawns in 2004. We collected and weighed (5.2 ± 1.9 g) a fresh sample of bone marrow from the left femur, then dried it at 50°C for 5 days and reweighed it. We attributed the difference between fresh (f) and dry (d) weight measurements to water loss and, therefore, we considered the remaining mass to be fat. We computed the percentage of femur marrow fat with the following equation (Neiland 1970):

$$\% \text{ fat} = 1 - \left[\frac{(f - d)}{f} \right] \times 100\%$$

The treatment ended when snow melted and patches of food started to appear in the forest around the enclosure. This indicated the beginning of spring and access to other food sources for free-ranging fawns occurred in mid-April in 2003 and at the end of March in 2004.

Statistical Analyses

Forage intake.—We used simple linear regressions to estimate the relationship between the total time spent eating by all individuals in a group and the amount of forage eaten by a group during an observation period (proc GLM, SAS institute 8.0). We did this to validate the use of forage intake estimates based on time spent feeding.

Our sampling design included repeated observations of the same individuals. To avoid pseudo-replication, we used mixed models with random coefficients (Littell et al. 1996). Our models were sensitive to multiple data arising from independent subjects and consisted of analyses of covariance with each subject treated as a covariable (Littell et al. 1996). In considering the subject as a random factor and repeated observations, we obtained linear models describing forage intake variations by individual.

We applied a square-root transformation to forage intake data to meet normality and homogeneity of variance. We tested the effects of wind chill index, winter progression (Julian days), diet quality, year, and interactions between day

\times diet, day \times year, and diet \times year on forage intake (Mixed procedure, SAS Institute 8.0). We did not include sex in the analyses because initial mass (kg) did not differ between sexes (2003: $M = 28.7 \pm 1.3$, $F = 29.6 \pm 2.7$; $t_{1,14} = 0.29$, $P = 0.78$ and 2004: $M = 28.4 \pm 1.3$, $F = 25.6 \pm 1.0$; $t_{1,11} = -1.7$, $P = 0.12$) and the sample size for each sex was too small.

We used a simple linear regression to estimate the relationship between forage intake per fawn over 24 hours and winter progression (Julian days; proc GLM, SAS institute 8.0).

Body mass and percentage of cumulative body mass loss.—We used mixed models to test the effects of winter progression (Julian days), diet quality, year, and all interactions on overwinter variation of body mass and percentage of cumulative body mass loss (Mixed procedure, SAS institute 8.0). We treated the individual as a random variable. We did not test the effect of wind chill index because it does not influence daily body mass and we were limited by the degrees of freedom of the number of parameters that we could test.

Activity budget.—We used mixed models to test the effects of wind chill index, winter progression (Julian days), diet quality, year, and interactions between day \times diet, day \times year, and diet \times year on overwinter variation of daily activity rate (Mixed procedure, SAS institute 8.0). We treated the individual as a random variable.

Survival.—We used a multiple logistic regression to assess the effects of year, diet quality, initial body mass, and all interactions on the probability of survival (Genmod procedure, SAS Institute 8.0). We performed t -tests to compare initial body mass and cumulative body mass loss rate between surviving and dead fawns each year. We also performed t -tests to compare femur marrow fat between dead fawns from the different diet-quality groups for the 2 years pooled.

We present all data as means \pm standard error (SE) and $\alpha = 0.05$.

Results

Forage Intake

There was a positive relationship between the total quantity of food eaten by a group and the total feeding time for all individuals during an observation period for each diet in 2003 (control diet: $r = 0.46$, $F_{1,38} = 9.76$, $P = 0.004$; poor diet: $r = 0.60$, $F_{1,40} = 22.31$, $P < 0.0001$) and 2004 (control diet: $r = 0.66$, $F_{1,48} = 36.64$, $P < 0.0001$; poor diet: $r = 0.49$, $F_{1,47} = 14.46$, $P = 0.0004$), indicating that our estimates of forage intake per individual were reliable.

Diet quality, as a main effect alone, did not affect forage intake, but we detected a significant effect of the interaction between diet quality and day on forage intake rate (Table 1). Fawns fed on the control diet decreased forage intake much more rapidly during the winter (slope = -0.11 ± 0.01 ; $P < 0.0001$) than fawns fed on the poor-quality diet (slope = -0.04 ± 0.01 ; $P = 0.01$; Fig. 1). This difference in the decrease of forage intake rate between diet qualities was similar for both winters (Table 1). The wind chill index did

Table 1. Mixed models testing the effects of year, diet quality, winter progression (Julian day), wind chill index (WCI) and interactions on forage intake rate, body mass, percentage of cumulative body mass loss, and activity budget of white-tailed deer fawns fed with different quality diets during the winters of 2003 and 2004 on Anticosti Island, Québec, Canada.

Factors	Effects ^a	df	F	P
a) Forage intake rate	WCI ^b	22	0.84	0.04
	Year	22	1.55	0.23
	Diet	22	2.76	0.11
	Day	22	55.31	<0.0001
	Diet × Day	22	14.26	0.0009
b) Body mass	Year	17	10.78	0.004
	Diet	17	1.55	0.23
	Day	17	737.25	<0.0001
c) % cumulative body mass loss	Year	17	5.03	0.04
	Diet	17	0.02	0.90
	Day	17	1,121.73	<0.0001
	Year × Day	17	3.94	0.06
d) Activity budget	WCI	22	298.8	<0.0001
	Year	22	63.8	<0.0001
	Diet	22	0.11	0.75
	Day	22	0.51	0.48
	Year × Day	22	38.29	<0.0001

^a Interactions that are not presented were not significant ($P > 0.05$) and not included in the final model.

^b WCI (°C) calculated from daily temperature (°C) and wind speed (km/hr). Note that it was not included in models b) and c).

not influence forage intake rate of fawns during both winters (Table 1).

Similar to the results obtained for groups during observation periods, in 2004 we observed a significant decrease in the forage eaten per fawn over 24-hour periods for the control diet ($r = 0.78$, $F_{1,46} = 68.5$, $P < 0.0001$) but not for the poor diet ($r = 0.05$, $F_{1,45} = 0.14$, $P = 0.71$; Fig. 2). The quantity of forage eaten by fawns fed on the control diet dropped from $1,480 \pm 40$ g/individual at the beginning of the winter to about $1,000 \pm 50$ g at the end of the winter, whereas it remained stable at 1200 ± 30 g for the group fed the poor diet (Fig. 2). Data from 2003 were not available for the whole winter periods and precluded the analysis of the effects of winter progression on 24-hour forage intake in that year.

Body Mass and Percentage of Cumulative Body Mass Loss

Not surprisingly, body mass decreased for all fawns during the winter. There were, however, no significant differences in the variation of body mass and the percentage of cumulative body mass loss during winter between the different diets for both years (Table 1). However, we detected a significant year effect on both the variation of body mass and the percentage of cumulative body mass loss (Table 1). Fawns were smaller in 2004 and presented a higher cumulative percentage of body mass loss than fawns in 2003 (Fig. 3). The near significant interaction between year and day on percentage of cumulative body mass loss (Table 1) suggests that fawns lost body mass at a slightly greater rate in 2004 (slope: 0.0032 ± 0.0001 , $P < 0.0001$) than during the winter of 2003 (slope: 0.0028 ± 0.0001 , P

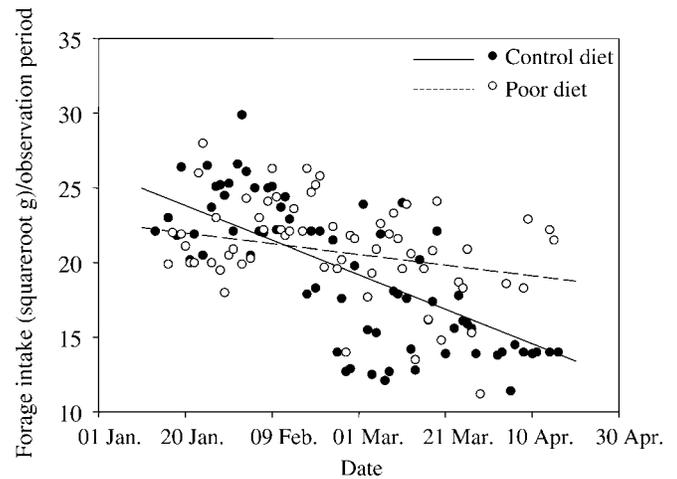


Figure 1. Change in forage intake rate during winter per observation period for groups of captive white-tailed deer fawns fed with 2 different quality diets on Anticosti Island, Québec, Canada. We pooled data for winter 2003 and winter 2004. Symbols represent the mean intake rate per observation period (mean length: $5:44 \pm 0:06$ hr) corrected for the number of fawns in a group.

< 0.0001 ; Fig. 3). The percentage of body mass loss for surviving fawns at the end of the experiment was relatively high for both years; it increased from 17% to 26% in 2003 ($n = 12$ fawns) and from 16% to 25% in 2004 ($n = 8$).

Activity Budget

There was no effect of diet quality on the proportion of time spent active by fawns, but we detected a significant year × day interaction (Table 1). Despite much variability, there was no significant variation in time spent active during the winter in 2003 (slope: 0.00033 ± 0.00034 , $P = 0.35$), whereas it increased significantly in 2004 (slope: 0.00305 ± 0.00037 , $P < 0.0001$). Fawns were more active in 2003 ($53 \pm 2\%$ of the observation periods) than in 2004 ($46 \pm 2\%$; year effect in Table 1). The WCI highly influenced time spent active because fawns reduced activity in cold weather (Table 1; Fig. 4). The proportion of time spent active increased with increasing WCI in both years (2003: slope: 0.0139 ± 0.0013 , $P < 0.0001$; 2004: slope: 0.0144 ± 0.0011 , $P < 0.0001$; Fig. 4).

Survival

Overwinter survival during the 2 years of the study was 63%. In 2003, 4 out of 13 fawns died (control diet: 2 of 7; poor diet: 2 of 6), whereas 5 out of 13 fawns died in 2004 (control diet: 2 of 7; poor diet: 3 of 6). Necropsies revealed that starvation was the likely cause of death as suggested by the absence of subcutaneous, heart, kidney, and visceral fat and low femur marrow fat content. There were no differences in femur marrow fat content between dead deer from 2003 ($6.8 \pm 0.4\%$, $n = 3$) and 2004 ($7.1 \pm 0.4\%$, $n = 6$; $t = 1.43$, $P = 0.21$), and between each diet for pooled data (control diet: $7.0 \pm 0.2\%$, $n = 4$; poor diet: $7.0 \pm 0.6\%$, $n = 5$; $t = 0.78$, $P = 0.21$). Year ($\chi^2 = 0.09$, $P = 0.77$), diet quality ($\chi^2 = 1.12$, $P = 0.29$), or the interaction year × diet quality ($\chi^2 = 0.01$, $P = 0.92$) did not affect the probability of survival

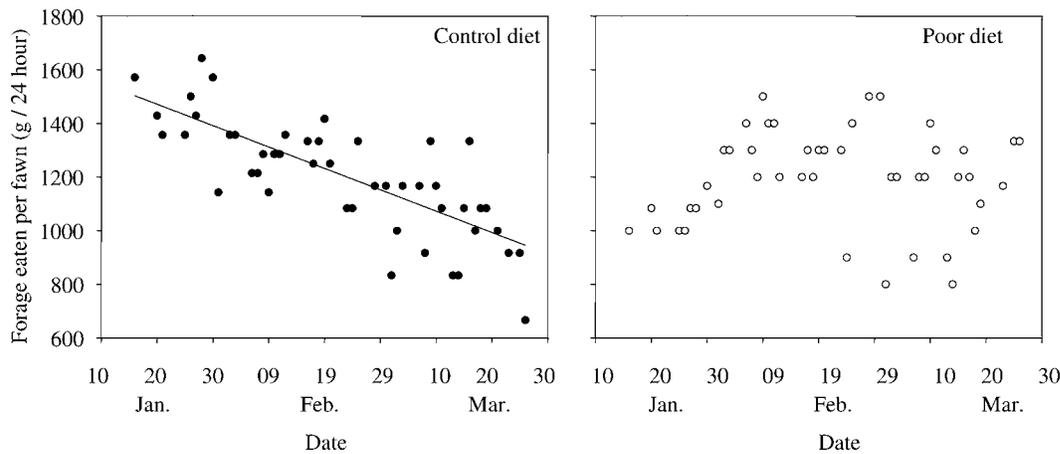


Figure 2. Forage eaten per fawn over 24-hour periods for captive white-tailed deer fawns fed with 2 diets of different quality in winter 2004, Anticosti Island, Québec, Canada.

of fawns, but survival was strongly and positively related to initial body mass (final model with body mass alone: $r = 0.74$, $\chi^2 = 15.15$, $P < 0.0001$). Fawns that survived had an initial body mass 25% greater than fawns that died in both winters (2003: alive: 31.2 ± 1.2 kg and dead: 24.0 ± 2.5 kg, $t_{1,9} = -2.25$, $P = 0.04$; 2004: alive: 28.4 ± 1.0 kg and dead: 23.8 ± 0.8 kg, $t_{1,11} = -3.72$, $P = 0.003$), but they lost body mass at the same rate during the winter (2003: alive: -0.076 ± 0.005 kg/day and dead: -0.074 ± 0.010 kg/day, $t_{1,9} = 0.18$, $P = 0.86$; 2004: alive: -0.089 ± 0.004 kg/day and dead: -0.076 ± 0.006 kg/day, $t_{1,9} = 1.78$, $P = 0.11$).

Discussion

We predicted that an increase in the proportion of low-quality white spruce in the winter diet would have detrimental effects on deer body condition and would affect behavior and life-history traits. Fawns fed the control diet decreased their forage intake at a greater rate than fawns fed the poor diet during both winters. Not surprisingly, body mass decreased over the winter, but we did not observe any significant effects of diet quality on body mass. Diet quality did not influence the activity budget of fawns, but deer decreased activity in cold weather. Finally, diet quality did not affect the probability of survival of fawns, but body mass at the onset of winter had a positive effect on survival.

Forage Intake

In wild ruminants, the primary constraints on forage intake in winter are forage availability and quality (Torbit et al. 1985, Gray and Servello 1995). These constraints often result in a negative energy balance and have led to physiological adaptation for energy conservation (Silver et al. 1969, Moen 1978). Forage availability was not a constraint since we provided homogenous forage ad libitum. On the other hand, we modified forage quality, which likely influenced the time required for rumination and the digestibility of forage (White 1983).

The marked reduction of voluntary forage intake observed in fawns fed the control diet is a common winter feeding

pattern that studies have reported in numerous ungulates (white-tailed deer: Thompson et al. 1973, Baker et al. 1979; mule deer [*Odocoileus hemionus*]: Bartmann et al. 1991; reindeer [*Rangifer tarandus tarandus*]: Skogland 1990, Storeheier et al. 2003). Ozoga and Verme (1970) observed high levels of forage intake in early winter followed by a marked reduction of intake in penned white-tailed deer fawns. The voluntary reduction of forage intake, often below maintenance, has been attributed to a physiological adaptation for energy conservation in harsh environments (i.e., under conditions of limited forage availability and quality, low ambient temperature, or high snow cover [Silver et al. 1969, Ozoga and Verme 1970, Thompson et al. 1973, Warren et al. 1981, Suttie et al. 1983, DelGiudice et al. 1990]). When the energetic cost associated with the digestion of winter forage is greater than the energy that it provides, it may be beneficial to favor energy conservation and reduce intake rate (Owen-Smith 1994). Even with a reduction of forage intake, the energetic balance may remain negative and necessitates the use of body reserves, which will lead to body mass loss.

Fawns fed the low-quality diet did not adopt the same strategy as the control fawns because their food intake rate per group decreased at a much lower rate during the winter than for the controls (Fig. 1), and the proportion of forage eaten daily by individual deer in the poor diet group remained relatively constant throughout the winter (Fig. 2). We suggest that a diminution of the diet quality, through an increase in the proportion of white spruce in the diet from 20% to 40%, may have forced fawns to adopt a near-constant forage intake rate throughout the winter to maintain rumen fill. Studies also have observed an increase of intake rate in response to a reduction of forage quality in horses (*Equus ferus przewalskii*; Berger et al. 1999) and domestic cattle (Hofmann 1989). Although the difference was not significant ($P = 0.07$, Table 1), fawns on the poor diet consumed on average about 10% more forage than fawns in the control group, probably in order to meet their energetic needs. The quality of forages clearly limits

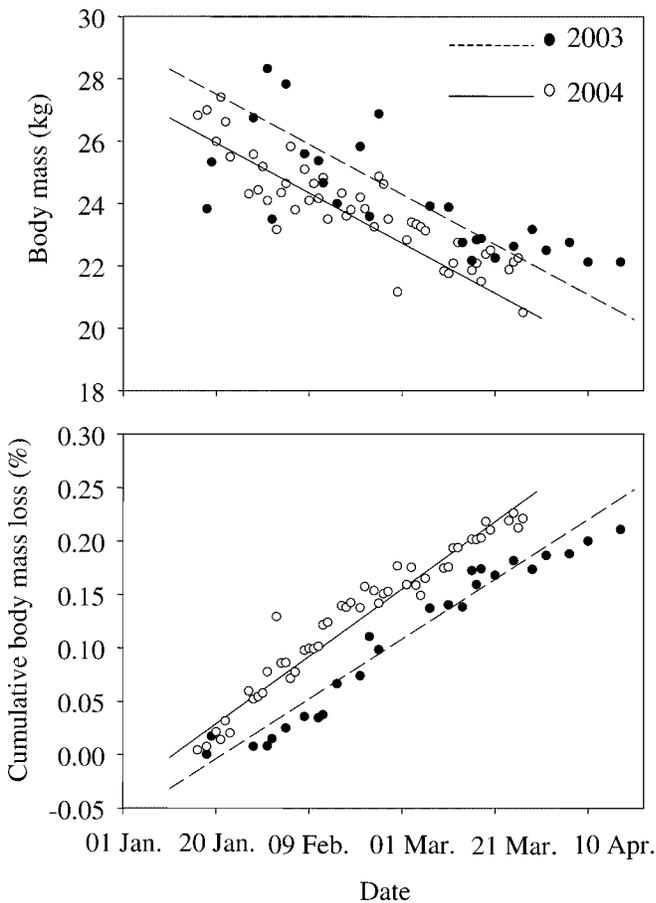


Figure 3. Body mass and percentage of cumulative body mass loss during the winters of 2003 and 2004 for captive white-tailed deer fawns on Anticosti Island, Québec, Canada. Since diet quality did not affect body mass and the percentage of cumulative body mass loss, we pooled the data for the 2 different quality diets. Symbols represent the mean body mass and percentage of cumulative body mass loss per observation period where $n \geq 3$ fawns.

consumption and digestion rates (Huston et al. 1986, Coleman et al. 1999), but by adopting a higher intake rate than control fawns, fawns on the lower-quality diet may have partly compensated for the lower nutrient content of forage and maintained a body mass loss similar to fawns from the control group. In nature, however, the increased energetic requirements to obtain forage (e.g., through locomotion in deep snow) may hasten the decline of body condition with the reduction of forage quality.

Decrease of Body Mass

Deer on Anticosti experience a negative energy balance in winter and lose 20–40% of their mass (Huot 1982). In our experiments, a decrease in diet quality did not result in an increased rate of body mass loss. The decline of deer body mass was slightly faster in 2004 than in 2003, but most of the variation in body mass was related to the progression of winter. Ungulate body mass is partly dependent on winter severity in temperate regions (Cederlund et al. 1991, Gaillard et al. 1996, Jensen et al. 1999) and harsh weather during winter may have a more profound impact on body mass dynamics than habitat quality in high-density

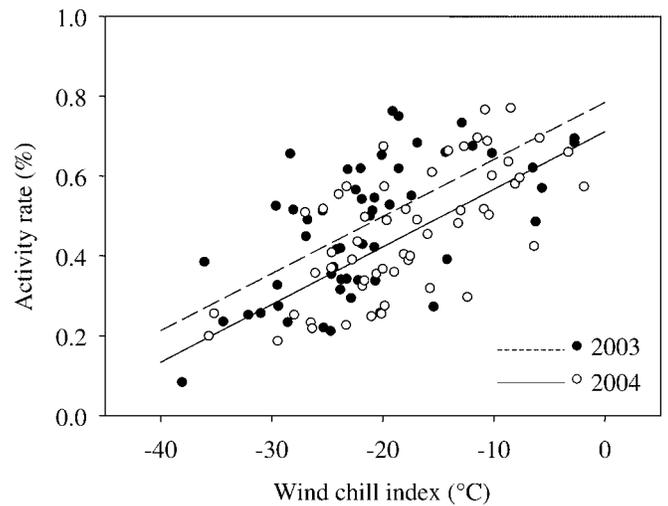


Figure 4. Relationship between the wind chill index and the daily proportion of time spent active during the winters of 2003 and 2004 for captive white-tailed deer fawns on Anticosti Island, Québec, Canada. We pooled data for 2 different quality diets. Symbols represent the mean proportion of time spent active per observation period.

populations (Cederlund et al. 1991, Gaillard et al. 1996, Pettorelli et al. 2002). Body condition decreases throughout the winter to meet increased energy demands for thermoregulation and locomotion in snow (DelGiudice et al. 1990, Parker et al. 1999); therefore, body mass at the onset of winter is critical for survival through the winter (Gaillard et al. 1996). A combination of stochastic events (e.g., weather) or perhaps cohort effects (Pettorelli et al. 2002) may explain the slight difference observed in the rates at which deer lost body mass between the 2 winters.

Activity Budget

Despite much variation in time spent active, fawns maintained a constant activity rate during the winter of 2003, whereas in 2004, activity increased through the winter. Diet quality did not affect the activity budget, suggesting that fawns did not compensate for the difference in forage quality by modifying activity rate. Studies have often interpreted the reduction of activity by ungulates observed in nature during winter as an adjustment to winter climatic conditions to favor heat conservation and limit energy expenditures caused by thermoregulation and locomotion in deep snow (Moen 1976, Verme and Ozoga 1980). Research has revealed a decrease of 20–50% of average active time from summer to winter in temperate ungulates (Georgii 1981, Georgii and Schröder 1983, Cederlund et al. 1989). Beier and McCullough (1990) generally considered snow depth to be the most important factor limiting activity in winter. In our experimental conditions, the abundance of forage, which we provided ad libitum, and limitations of movements of fawns in a few trampled trails in the enclosures may explain the absence of a diminution of activity during winter. We observed, however, that time spent active greatly increased in warmer days (Fig. 4). Diurnal activity patterns in northern ungulates often correlate with ambient temperatures (Ozoga and Verme 1970, Ozoga 1972, Berger 1977, Beier and

McCullough 1990). In the wild, deer significantly decrease their activity rate at the beginning of winter and during cold days concentrate their active bouts during the warmer daylight hours (Verme and Ozoga 1980, Beier and McCullough 1990, Parker et al. 1999). The modification of activity rate from year to year has been related to the harshness of winter conditions; lower activity rates occur during severe winters, as compared to mild winters (Cederlund 1981, White et al. 1987).

Survival

Deer on Anticosti face harsh winter conditions and the mortality rate during our study (37.5% overwinter) was high, irrespective of diet quality or year, but similar to survival rates observed under natural conditions on the island (Potvin et al. 1997). Although deer on Anticosti can withstand extreme body condition deterioration over winter, they showed very low femur marrow fat content at death, indicating that they likely died of starvation. Body mass at the beginning of the winter was the best predictor of overwinter survival of fawns, as other studies have also found (White et al. 1987, Skogland 1990, Bartmann et al. 1991, Cook et al. 2003). As food intake decreased and cumulative mass loss increased during winter, survival depended mainly on the stored body reserves and probably to a lesser degree on forage availability and quality (Mautz 1978). The great effect of body mass at the onset of winter suggests the possible influence of nutrition in late summer and autumn for growth and survival of fawns (Cook et al. 1996). Forage resources could be critical year-round, not just during the season of low availability (Parker et al. 1999). Moreover, Lesage et al. (2001) have shown that although white-tailed deer fawns on Anticosti Island are smaller than deer from the source population located approximately 200 km south on the mainland, they accumulate significantly more fat during summer. This strategy may be critical to survival throughout the long and harsh winters of Anticosti.

Our results suggest that forage quality in this experiment was not the most important factor affecting forage intake rate, body mass loss, activity budget, and survival of white-tailed deer fawns on Anticosti Island in winter. Fawns fed the poor-quality diet maintained a higher food intake rate than fawns fed the control diet during winter, suggesting that they can partly compensate for the decrease of forage quality by consuming more forage. Penned deer in our experiment, however, were facing different energetic requirements than wild animals. For example, there was a reduction in the energetic costs of locomotion because we provided forage *ad libitum* in feeding troughs. The amplitude of the variation in the response variables according to changes in diet quality may, thus, differ under natural conditions because of the different energetic requirements associated with the search for forage or cover.

The experimental design we used, however, allowed us to ask questions that could not be answered in a natural context, particularly the simulation of a decrease in winter diet quality that will occur when fir stands become rarer. By using wild-caught deer, outdoor pens, and controlling for the winter diet quality in an experimental design where only diet quality differed between the treatment and the control, we could directly make inferences about the effects of diet quality on deer body condition and foraging behavior.

The main determinant of overwinter survival was individual body mass in early winter. Other factors, such as the variability of winter conditions (e.g., snow-sinking depth) and the availability and quality of forage the preceding summer, also may be critical for fawn survival during winter. Available resources during summer and autumn could be critical for fawns to reach a minimal threshold body mass that will allow them to survive the winter. It remains to be determined whether white-tailed deer fawns of Anticosti Island have developed behavioral or physiological adaptations to enhance winter survival, such as a smaller body size and greater fat reserves (Lesage et al. 2001), or if observed differences are due to phenotypic plasticity.

Management Implications

Our results suggest that even though balsam fir stands are being gradually replaced by white spruce stands, deer on Anticosti may not be adversely affected in the short-medium term, particularly if they have access to wind-thrown trees and fallen twigs of balsam fir on the surface of the snow (Tremblay et al. 2005). However, we cannot rule out that an increase of white spruce to >40% of the winter diet, or a complete replacement of balsam fir by white spruce, may affect body mass loss and possibly reproductive success and survival of deer on Anticosti and elsewhere. We suggest, therefore, that wildlife and forest managers maintain balsam fir stands on the island.

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