Is winter diet quality related to body condition of white-tailed deer (*Odocoileus virginianus*)? An experiment using urine profiles

Daniel G. Sauvé and Steeve D. Côté

Abstract: During winter, boreal forest herbivores have access to only poor-quality forage. On Anticosti Island (Quebec, Canada), the ongoing reduction of balsam fir (*Abies balsamea* (L.) P. Mill.) owing to overbrowsing by white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) may force deer to include a higher proportion of white spruce (*Picea glauca* (Moench) Voss), a browse normally avoided, in their winter diet. We tested the hypotheses that (*i*) deer body condition during winter and (*ii*) the costs of detoxification of plant secondary metabolites in the winter diet could be estimated by monitoring the 3-methylhistidine / creatinine and glucuronic acid / creatinine ratios, respectively, in urine collected in snow from white-tailed deer fawns. Doubling the amount of white spruce in the winter diet of deer (from the current 20% under natural conditions to 40%) did not increase 3-methylhistidine / creatinine ratios but increased the glucuronic acid / creatinine ratio in urine, suggesting that a diet containing more spruce was more toxic. A weak positive relationship was observed between 3-methylhistidine and percent cumulative mass loss. There was no relationship between the 3-methylhistidine / creatinine ratio and the number of days left before death, as well as no relationship between the ratio of glucuronic acid / creatinine and percent cumulative mass loss. We conclude that the costs of detoxification of plant secondary metabolites in the winter diet of white-tailed deer in boreal forests could be monitored with glucuronic acid / creatinine ratios, but that 3-methylhistidine / creatinine ratios were weak indicators of deer body condition in winter.

Résumé : Durant l'hiver, les herbivores des forêts boréales se nourrissent de nourriture de faible qualité. Sur l'île d'Anticosti (Québec, Canada), la raréfaction graduelle du sapin baumier (*Abies balsamea* (L.) P. Mill.) causée par le surbroutement du cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) pourrait forcer ces derniers à ingérer en hiver plus d'épinette blanche (*Picea glauca* (Moench) Voss), une essence normalement évitée. Nous avons testé les hypothèses selon lesquelles (*i*) la détérioration de la condition corporelle des cerfs en hiver et (*ii*) les coûts de la détoxication des produits métaboliques secondaires des plantes dans l'alimentation d'hiver pouvaient être estimés par l'analyse de l'évolution des rapports 3-méthylhistidine / créatinine et acide glucuronique / créatinine, respectivement, dans l'urine de faons récoltée dans la neige. Doubler la proportion d'épinette blanche dans l'alimentation d'hiver (de 20 % en conditions naturelles à 40 %) n'a pas affecté le rapport 3-méthylhistidine / créatinine, mais a augmenté le rapport acide glucuronique / créatinine dans l'urine, suggérant qu'une alimentation plus riche en épinette blanche est plus toxique. Une faible relation positive a été observée entre la 3-méthylhistidine et le pourcentage cumulatif de perte de masse. La concentration de 3-méthylhistidine n'a pas augmenté quelques jours avant la mort. Aucune relation entre le rapport acide glucuronique:créatinine et le pourcentage cumulatif de perte de masse n'a été observée. Nous concluons que les coûts de détoxication des produits secondaires dans la diète hivernale des cerfs de Virginie de la forêt boréale peuvent être étudiés à l'aide du rapport acide glucuronique:créatinine, mais que le rapport 3-méthylhistidine / créatinine est un indicateur de faible qualité de la condition corporelle des cerfs en hiver.

Introduction

Wild northern ungulates regularly face severe winters, which may have important impacts on their body condition, survival, and future reproductive success (Gaillard et al. 2000), especially in high-density populations (Gaillard et al. 1996; Pettorelli et al. 2002). Under these harsh conditions, most ungulates, and particularly young individuals, experience high energy expenditures because of increased costs of thermoregulation and locomotion in deep snow and reduced forage abundance and quality (Jensen et al. 1999). Because body mass at the onset of winter is critical for winter survival of juveniles (Gaillard et al. 1996; Côté and Festa-Bianchet 2001; Taillon et al. 2006), wild ruminants must accumulate enough energy reserves as fat during summer and autumn to survive the winter, particularly when available browse in winter is insufficient to meet their daily nutritional and energetic needs.

During winter, boreal forest herbivores have access to poorer quality plants containing higher concentrations of

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secondary plant metabolites than in summer (Bryant et al. 1991; Tahvanainen et al. 1991). Secondary plant metabolites can negatively influence the digestibility and (or) palatability of plants, reducing preference and food intake by large herbivores (Robbins et al. 1987; Harborne 1991; Vourc′h et al. 2002). Conifers are particularly rich in plant secondary metabolites and have lower nutritive value than less-defended and more digestible deciduous browse (Tahvanainen et al. 1991).

Consuming a mixture of plant species usually reduces the effects of secondary plant metabolites found separately in each species, but the ingestion of such plants requires that the toxic compounds be detoxified through digestive or metabolic processes (McArthur et al. 1991; Mangione et al. 2001). One of the most common detoxification pathways is glucuronidation in the liver (McArthur et al. 1991). During this process, the toxic compound is conjugated to glucuronic acid and excreted in urine. Although the toxic compound may then become harmless, the process is costly (Sorensena and Dearing 2004). The excretion of glucuronic acid causes a loss in energy and a drop in urine pH, which may alter kidney function (Dearing and Cork 1999).

Wild ungulates such as white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) often mobilize their fat reserves during winter because of higher energetic costs and lower quality, and sometimes quantity, of forage available than in summer. When they have depleted most of their fat reserves and are still in negative energy balance, they must rely on other endogenous energy sources, such as body protein contained in the skeletal muscles. Their condition then declines rapidly (DelGiudice et al. 1998).

Since its introduction on Anticosti Island (Quebec, Canada) in the late 1800s, the white-tailed deer population has irrupted from roughly 200 to over 120 000 animals today (Potvin et al. 2003). Such a high-density (about 15–20 deer/km^2) population had an important impact on the island's vegetation and browsing has almost eliminated all deciduous shrubs (Tremblay et al. 2005). Before deer introduction, stands of balsam fir (*Abies balsamea* (L.) P. Mill.) were estimated to cover about 40% of the island's surface area. Today, this value is down to approximately 20% (Potvin et al. 2003). Although insect epidemics (e.g., spruce budworm (*Choristoneura fumiferana* (Clemens, 1865)) and hemlock looper (*Lambdina fiscellaria* (Guenée, 1857))) and forest fires have been partly responsible for the fir decline on the island, deer overbrowsing is the main factor owing to its suppressive effects on regeneration (Potvin et al. 2003). Potvin et al. (2003) predicted that most balsam fir stands will be replaced by stands of white spruce (*Picea glauca* (Moench) Voss) within the next 40–50 years on Anticosti. One critical consequence of past overbrowsing is that during winter (i.e., from mid-November to mid-April) on Anticosti, deer have access only to white spruce, which is highly available, and balsam fir, which is available only when trees are thrown down by wind or in the litterfall (Tremblay et al. 2005).

Although balsam fir is scarce compared with white spruce, fir twigs are the staple food for white-tailed deer in winter on Anticosti (Huot 1982), representing close to 70% of their diet, whereas white spruce represents about 20% of the winter diet (Lefort 2002). The diet is completed by arboreal lichens. Although both species of conifers are low-quality browse, balsam fir is of higher quality than white spruce. Fibre content (neutral detergent and acid detergent fibre) and condensed tannins are higher in white spruce than in balsam fir (Sauvé and Côté 2006), and Von Rudloff (1972) identified camphor as an abundant monoterpene in white spruce, whereas it is not found in balsam fir (Hunt and Von Rudloff 1974). Myrcene is also more abundant in white spruce than in balsam fir (Von Rudloff 1972; Hunt and Von Rudloff 1974). Higher fibre content and concentrations of plant secondary compounds in white spruce than in balsam fir may reduce its digestibility and possibly make it more costly to metabolize than fir.

Our objective was to experimentally test the effects of decreasing winter diet quality on the deterioration of deer body condition. We tested the hypothesis that deer body condition during winter could be estimated by monitoring the concentration of 3-methylhistidine in urine collected in the snow (i.e., snow-urine). Urine analyses have been widely used to evaluate body condition or nutrition quality of wild herbivores through the monitoring of catabolism of body protein and toxin detoxification (DelGiudice et al. 1988, 1998; White et al. 1995, 1997; Garrott et al. 1996; Servello and Schneider 2000). Some authors have reported that catabolism of skeletal muscle protein can be measured in urine through the concentration of 3-methylhistidine (Fitch et al. 1986; DelGiudice et al. 1998), although others have found conflicting results (Harris and Milne 1981; Rennie and Millward 1983; Cabanac et al. 2005). Urine analyses are particularly useful when repeated measurements are available on the same individual, i.e., when each animal can be compared with itself and when daily or weekly variations in urine metabolites can be assessed (DelGiudice et al. 1997). We predicted that 3-methylhistidine ratios in the snow-urine of deer fed a lower quality diet (i.e., a high proportion of white spruce) instead of a control diet similar to natural conditions would increase sooner in the winter, be associated with greater cumulative body mass loss, and increase more in the few days before death by inanition. We also tested the hypothesis that the costs of detoxification of plant secondary metabolites in the winter diet of deer could be estimated through the excretion of glucuronic acid. We predicted that fawns fed the control diet would have a lower concentration of glucuronic acid in their snow-urine than fawns fed a diet containing a higher proportion of white spruce.

Materials and methods

Study area

Anticosti Island (49°28′N, 63°00′W) is located in the Gulf of St. Lawrence, Quebec, Canada, and encompasses an area of about 8000 km^2. The climate is subboreal with a maritime influence, and the land is covered mainly by boreal forest (Huot 1982). The forest is dominated by white spruce, balsam fir, and black spruce (*Picea mariana* (P. Mill.) B.S.P.) (Potvin et al. 2003).

Capture and captivity

Between November and December 2002 and 2003, 32 white-tailed deer fawns (18 males and 14 females) were captured in the western part of the island using physical and chemical immobilization. We physically immobilized deer

with Stephenson traps, drop nets, and cannon nets baited with balsam fir and commercial cow feed (Shur-Gain®). For chemically immobilized deer, a mixture of Telazol® and xylazine (200 mg/mL) was administered using a Pneu-Dart rifle and radio-transmitter-equipped darts (Pneu-Dart Inc., Williamsport, Pennsylvania). Yohimbine was used as an antidote for xylazine in anaesthetized deer (Wallingford et al. 1996). Fawns were sexed and weighed to the nearest 0.5 kg with a spring scale or an electronic scale. For each individual, we calculated a body condition index by dividing body mass (kg) by hind foot length (cm). We used foot length measured at capture because dietary restriction does not allow winter growth of fawns (Verme and Ozoga 1980) in conditions such as those on Anticosti. All fawns were individually marked with ear tags and relocated in an outdoor pen (1.5 ha with three 0.5 ha subdivisions). The pen was established 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 litterfall (Taillon et al. 2006). About 40% of the initial forest was maintained as cover and three wooden structures were built in each section to simulate wind-protected areas in the natural forest. The animals were fed the natural winter diet of deer on Anticosti, i.e., a mixture of shredded balsam fir and white spruce at a proportion of 80% fir and 20% spruce until the beginning of the trials. Disturbance in the enclosures was kept to a minimum for at least 1 month before the beginning of the trials so that deer could habituate to the enclosure. Within a few days of capture, they readily came to the feeding troughs and their activity level did not differ from that of deer under natural conditions on the island (Coulombe et al. 2006; Taillon et al. 2006), suggesting that their level of stress was minimal.

Experimental diets

At the beginning of January of each year, fawns were divided into similar groups based on their body mass and sex (Taillon et al. 2006). Each group was fed a diet that consisted of white spruce and a mixture of balsam fir and arboreal lichens present on fir branches. The control diet (5 males and 2 females in 2003; 2 males and 5 females in 2004) consisted of 20% white spruce, which represents the natural winter diet of deer on Anticosti (Lefort 2002). The poor diet (4 males and 2 females in 2003; 3 males and 3 females in 2004) consisted of 40% white spruce, simulating a continuous decrease in the availability of fir on Anticosti (Tremblay et al. 2005).

Fir, spruce, and lichens were harvested within 1 km of the enclosure. We felled mature balsam firs, because only firs blown down by the wind are available to deer in winter on Anticosti (Tremblay et al. 2005). Fir trees were felled on a regular basis and the branches ≤1 cm in diameter were collected. We harvested annual shoots of white spruce that were accessible to deer in winter, i.e., 1–3 m above ground. We left lichens on the branches of felled firs.

Fir (with lichens) and spruce branches were shredded separately in a wood chipper (Yard Machines-5 HP), which allowed us to produce a uniform mixture to prevent selection by the fawns. Microhistological analyses of faeces confirmed that no selection for any of the diet components occurred (Taillon et al. 2006). Two kilograms of fresh food (i.e., about 1 kg dry) were given daily per fawn. This amount is considered to be the amount of food required to meet the basic metabolic needs of a 30 kg fawn (Huot 1982). We considered that fawns were limited by quality, and not quantity, of food. On average, 0.5 kg/deer of forage was left by the animals in the feeding troughs of each enclosure daily. No water was provided because snow was always available. Because we used natural diets of conifers from Anticosti Island and the enclosures were outside under 'natural' conditions, we expected to observe similar overwinter mortality rates as those seen under natural conditions (i.e., about 40% for fawns; Potvin et al. 1981, 1997). The mortality rates observed (37%; Taillon et al. 2006) were similar to those found under natural conditions, and body mass and mortality did not differ according to diet quality (Taillon et al. 2006). The animals were cared for in accordance with guidelines from the Canadian Council on Animal Care, and Laval University Animal Care and Use Committee reviewed and approved all procedures.

Data and sample collection

Daily air temperature and wind speed data were obtained from Environment Canada's weather station at Port Menier (1 km from the pen). We computed a wind chill index (W) with the following equation provided by Environment Canada:

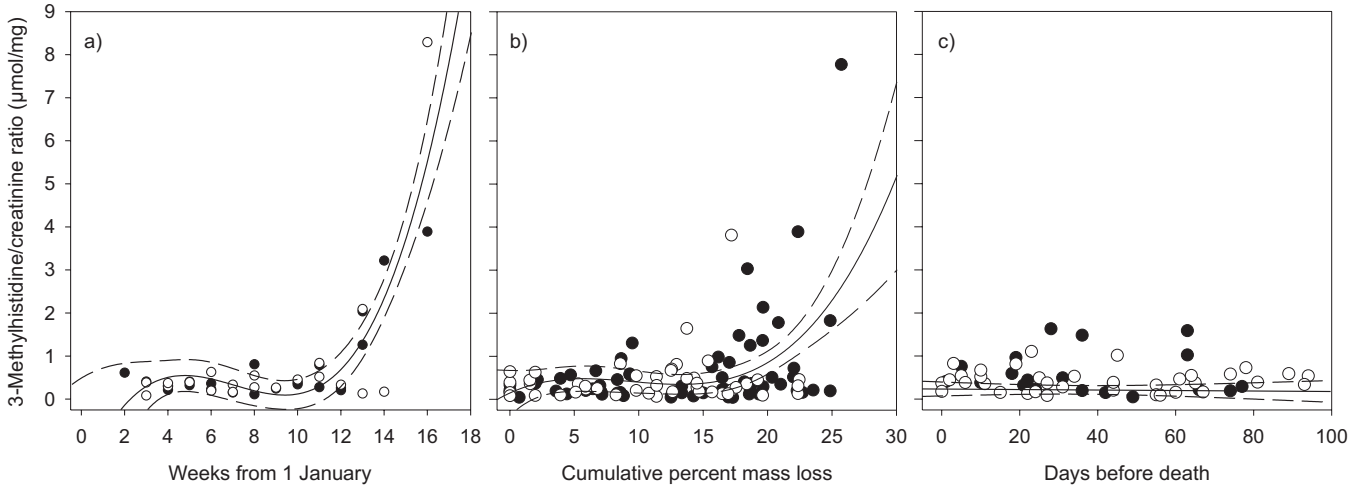
$$W = 13.12 + 0.6215T_{\text{air}} - 11.37V_{10\text{m}}^{0.16} + 0.3965T_{\text{air}}V_{10\text{m}}^{0.16}$$

where T_{air} is the air temperature (°C) and $V_{10\text{m}}$ is wind velocity (km/h) at 10 m from the ground, which is the standard height for an anemometer (Meteorological Service of Canada, Environment Canada).

Snow-urine samples were collected when a fawn was seen urinating. We tried to obtain at least one sample for each marked fawn every week. All samples (75 in 2003 and 99 in 2004) were frozen and stored until assayed in duplicate. We measured the concentration of creatinine, 3-methylhistidine, and glucuronic acid in the samples. We assayed creatinine and glucuronic acid directly from the thawed samples. For creatinine, we used commercially available kits from Catachem, Bridgeport, Connecticut (in 2003), and StanBio, Boerne, Texas (in 2004). The Catachem kits were discontinued in 2004. The methods for the determination of glucuronic acid are detailed in Mangione et al. (2001). Briefly, urine samples were mixed with a solution of borax and sulphuric acid and heated before a colorimetric reaction with phenylphenol. The absorbance of the samples was then compared with a standard curve made with pure glucuronic acid (Sigma-Aldrich Canada, Oakville, Ontario).

For the determination of the concentration of 3-methylhistidine, 25 mL of the thawed samples was lyophilized with 25 mL of sodium carbonate (2 mol/L) to volatilize ammonia, which may interfere with the colorimetric reaction (Fitch et al. 1986). We used 25 mL, instead of 8 mL as recommended by Fitch et al. (1986), to compensate for the dilution of urine in snow (P. Rioux, personal communication, 2002). The methods for the preparation of the samples and the determination of 3-methylhistidine with cationic-exchange resin (Dowex 50WX 8, 200–400 mesh) are described in Fitch et al. (1986). To compensate for the unknown hydration status of the animal and the dilution factor of the sample

Fig. 1. The dynamics of the 3-methylhistidine/creatinine ratio (μmol/mg) measured in snow-urine samples from captive white-tailed deer (*Odocoileus virginianus*) fawns fed different winter diets on Anticosti Island, in relation to the number of weeks since 1 January (*a*), the percentage of cumulative mass loss since early January (*b*), and the number of days left before death (*c*). Solid circles represent fawns on the control diet (20% white spruce, 80% balsam fir) and open circles represent fawns on the poor diet (40% white spruce, 60% balsam fir). The fitted curves (solid line) are third-degree polynomial regressions for the pooled data of both diets and the broken lines are the 95% confidence intervals.



in snow, the metabolites were computed as ratios of creatinine, because creatinine secretion is constant for 24 h periods and is relative to body mass (DelGiudice et al. 1988). The calculated ratios are expressed in micromoles/milligram and milligram/milligram for 3-methylhistidine / creatinine and glucuronic acid / creatinine, respectively.

Statistical analyses

A two-way ANOVA was performed to evaluate the differences in wind chill between the winters of 2003 and 2004, with year and week as fixed effects. We analysed urine data with mixed-effect, repeated-measures random coefficient models with each individual as independent subjects and the initial body condition index (initial body mass divided by tarsal length) as the covariate with a spatial power covariance structure (Proc Mixed in SAS release 8.02 (SAS Institute Inc. 1999–2001); Fujisawa 1996). Considering repeated measurements on the same individuals is a strong experimental design, because each animal can be compared with itself and variations in urine metabolites in time can be addressed independently of inter-individual differences (DelGiudice et al. 1997). We tested for the effects of year, time (weeks since 1 January), diet, initial body condition index, and all possible interactions on the log-transformed ratios of 3-methylhistidine / creatinine and glucuronic acid / creatinine.

To evaluate the relationships between urine metabolite ratios (3-methylhistidine / creatinine and glucuronic acid / creatinine ratios as dependent variables) and (*i*) time (weeks since 1 January), (*ii*) the percent cumulative mass loss of fawns during winter, and (*iii*) the number of days before death by inanition (as independent variables), we fitted third-degree polynomial regressions to the data. All data are means ± SE and we considered a P value ≤0.05 to be significant.

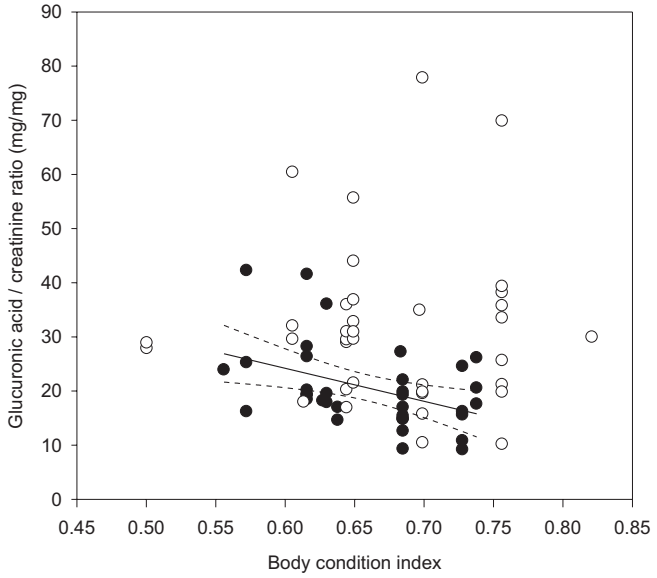
Results

The wind chill index differed between years (2003: –13.8 ± 0.7 °C; 2004: –11.7 ± 0.7 °C; $F_{[1,204]} = 15.15$, $r^2 = 0.02$, $P < 0.0001$) and between weeks ($F_{[17,204]} = 26.85$, $r^2 = 0.62$, $P < 0.0001$), and the interaction between year and week was significant ($F_{[16,204]} = 4.07$, $r^2 = 0.09$, $P < 0.0001$). These results indicated that the winter of 2003 was colder than the winter of 2004 and that the weekly winter variation of the wind chill index differed between the 2 years.

No year effect was noted on the 3-methylhistidine / creatinine ratios ($F_{[1,18]} = 3.05$, $r^2 = 0.10$, $P = 0.1$). Therefore, we used pooled data from the winters of 2003 and 2004 in subsequent analyses. Initial body condition index ($F_{[1,20]} = 0.54$, $r^2 = 0.02$, $P = 0.5$), diet quality ($F_{[1,20]} = 0.52$, $r^2 = 0.00$, $P = 0.5$), and the interaction between diet and weeks since 1 January ($F_{[11,69]} = 1.03$, $r^2 = 0.37$, $P = 0.4$) did not influence 3-methylhistidine / creatinine ratios. The 3-methylhistidine / creatinine ratios, however, increased during winter ($F_{[13,69]} = 2.52$, $r^2 = 0.33$, $P = 0.007$; Fig. 1*a*) and with cumulative mass loss ($F_{[3,107]} = 9.49$, $r^2 = 0.21$, $P < 0.0001$; Fig. 1*b*). We reanalyzed the relationship between week and 3-methylhistidine / creatinine ratios without the apparent outlier (Fig. 1*a*), and the relationship was still significant ($F_{[3,106]} = 3.22$, $r^2 = 0.30$, $P = 0.004$). No relationship was found between 3-methylhistidine / creatinine ratios and the number of days left before death ($F_{[3,52]} = 0.14$, $r^2 = 0.01$, $P = 0.9$; Fig. 1*c*).

Glucuronic acid / creatinine ratios did not differ between years ($F_{[1,14]} = 0.1$, $r^2 = 0.01$, $P = 0.8$), so we pooled data from the winters of 2003 and 2004. Deer on the poor diet had higher glucuronic acid / creatinine ratios (31.6 ± 2.5 mg/mg) than those on the control diet (20.6 ± 1.3 mg/mg) ($F_{[1,16]} = 18.65$, $r^2 = 0.21$, $P = 0.0005$). The initial body condition index of deer did not affect glucuronic acid / creatinine ratios alone ($F_{[1,69]} = 0.1$, $r^2 = 0.0$, $P = 0.7$), but it had an effect in interaction with diet quality. Glucuronic acid / creatinine ratios decreased with increasing initial body condition index in control deer ($F_{[3,31]} = 3.32$, $r^2 = 0.24$, $P = 0.03$; Fig. 2), but not in deer on the poor diet ($F_{[1,34]} = 0.0002$, $r^2 = 0.0$, $P = 0.9$, Fig. 2).

Fig. 2. The relationship between the glucuronic acid / creatinine ratio (mg/mg) measured in snow-urine and the initial body condition index (initial body mass / rear tarsal length) of white-tailed deer fawns fed two different diets. Solid circles represent fawns on the control diet (20% white spruce, 80% balsam fir) and open circles represent fawns on the poor diet (40% white spruce, 60% balsam fir). The relationship between glucuronic acid / creatinine and body condition index was significant for the control animals only (slope (solid line): –61.0 ± 22.5; $F = 7.4$; $r^2 = 0.18$; $P = 0.01$). The broken lines are the 95% confidence intervals.



Glucuronic acid / creatinine ratios did not vary through winter ($F_{[12,32]} = 1.01$, $r^2 = 0.16$, $P = 0.5$; Fig. 3*a*), and the interaction between weeks since 1 January and diet was not significant ($F_{[8,32]} = 1.67$, $r^2 = 0.49$, $P = 0.1$; Fig. 3*a*). Cumulative mass loss ($F_{[1,72]} = 0.1$, $r^2 = 0.0$, $P = 0.8$; Fig. 3*b*) and number of days left before death ($F_{[1,123]} = 3.2$, $r^2 = 0.03$, $P = 0.8$; Fig. 3*c*) did not affect glucuronic acid / creatinine ratios.

Discussion

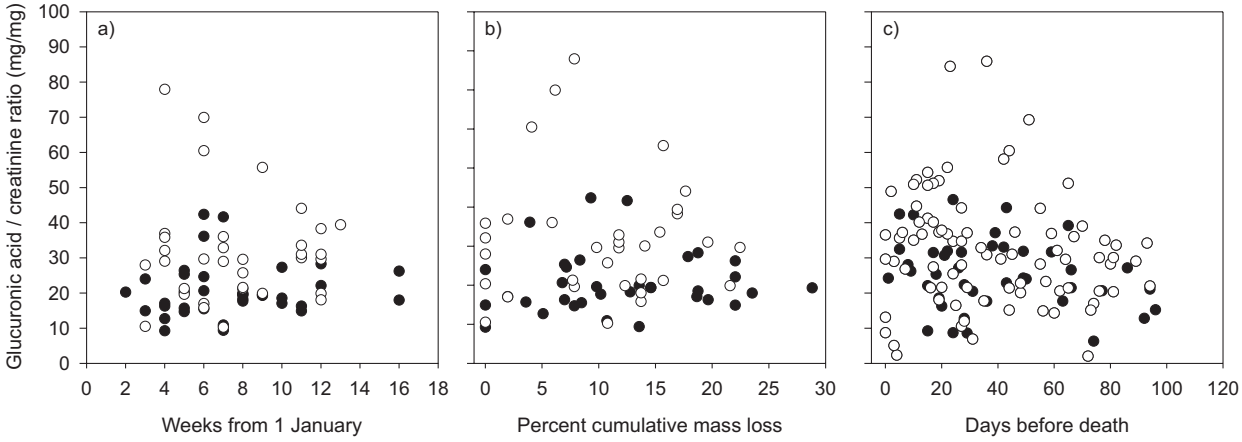
Our results showed that doubling the amount of white spruce (from 20% to 40% of the ration) in the diet of white-tailed deer on Anticosti Island increased its toxicity, as measured with the glucuronic acid / creatinine ratio. It had no significant effect, however, on the muscle protein breakdown of deer over winter estimated with 3-methylhistidine / creatinine ratios in snow-urine. Because of the dramatic decline in the availability of balsam fir winter browse on the island (Tremblay et al. 2005), the proportion of white spruce in the winter diet of deer should increase in the short term since no other browse, except black spruce, is available. White spruce contains more fibre, condensed tannins, and specific terpenes, such as camphor and myrcene, than fir (Von Rudloff 1972; Hunt and Von Rudloff 1974; Sauvé and Côté 2006). Contrary to our expectation, however, it appeared that an increase in the proportion of white spruce up to 40% in the winter diet of deer did not increase body protein catabolism or, alternatively, that we could not detect it with 3-methylhistidine / creatinine ratios. We cannot predict, however, the physiological effects of the complete eradication of balsam fir in the winter diet of deer on Anticosti, although we suspect that it will be detrimental to deer.

We found a significant, but variable, relationship between urinary 3-methylhistidine / creatinine ratios and the percent cumulative mass loss for deer on both diets (Fig. 1*b*). DelGiudice et al. (1998) observed a strongly significant curvilinear relationship between urinary 3-methylhistidine / creatinine ratios and the percent cumulative mass loss in food-restricted white-tailed deer compared with our experiment, where deer were fed ad libitum. Their results may differ from ours because they applied a quantitative restriction, whereas our experiment was based on a reduction of forage quality. Alternatively, 3-methylhistidine / creatinine ratios may not be a reliable indicator of muscle protein breakdown (Rennie and Millward 1983), particularly in species where a large amount of 3-methylhistidine is retained in muscles as the dipeptide balenine (Rathmacher and Nissen 1998), a scenario possibly occurring in white-tailed deer (Abe 2000). Within the diet quality range tested in our experiment, there seems to be no detrimental effects of diet quality on percent body mass loss of deer provided that they have access to sufficient browse. We have shown elsewhere that winter diet does not affect overwinter mass loss in deer from our study population (Taillon et al. 2006). Although Gray and Servello (1995) reported that deer on a winter browse diet could not meet energy requirements even on diets containing 88% of the daily digestible energy requirements, Jensen et al. (1999) have shown that deer feeding on low-quality browse can maintain an acceptable body condition provided that browse availability is sufficient. Although deer in our study lost substantial body mass during winter (up to 30% of their initial mass), the difference in quality between the experimental diets was not great enough to lead to differences in body condition deterioration that were detectable in urinary metabolites.

The 3-methylhistidine / creatinine ratios increased during winter (Fig. 1*a*), which is similar to the results of DelGiudice et al. (1998). With the progression of winter, body condition deteriorates and body fat reserves are depleted. Myosin contained in muscles is then broken down to supply energy to the animal under prolonged food restriction (DelGiudice et al. 1998; Vissiers et al. 2003). Although the increase of the 3-methylhistidine / creatinine ratio through winter was expected, it did not increase sooner for deer on a low-quality diet as we had predicted, suggesting that the mobilization of body reserves did not differ with the diet quality offered. Moreover, we did not detect an increase in 3-methylhistidine / creatinine in the few days preceding death by inanition. On Anticosti Island, winter forage is not necessarily limited in quantity but in quality and diversity — spruces are highly available, but no other species is available at browse height (Tremblay et al. 2005). Therefore, a large difference in food quality may be necessary to create a voluntary reduction of food intake. The difference in quality between our experimental diets was perhaps not great enough to observe a reduction that would lead to the deterioration of body condition and thus be reflected in 3-methylhistidine / creatinine ratios.

We found a weak negative relationship between body condition index and glucuronic acid / creatinine ratios for animals on the control diet only (Fig. 2). This interaction be-

Fig. 3. The dynamics of the glucuronic acid / creatinine ratio (mg/mg) measured in snow-urine samples from captive white-tailed deer fawns fed different diets on Anticosti Island, in relation to weeks since 1 January (*a*), the percentage of cumulative mass loss (*b*), and the number of days left before death (*c*). Solid circles represent fawns on the control diet (20% white spruce, 80% balsam fir) and open circles represent fawns on the poor diet (40% white spruce, 60% balsam fir).



tween diet quality and body condition index may indicate that the relative detoxification cost of forage is lower for animals in good body condition on the control diet than for those in low body condition. Alternatively, fawns in good body condition may have mounted a greater biochemical defense than fawns in lower condition. The detoxification costs for animals on the poor diet may be too high for all fawns, irrespective of body condition, thus reducing the ability of fawns with a high body condition index to better cope with higher concentrations of toxins.

The glucuronic acid / creatinine ratios were higher in samples from animals on the poor diet than from deer on the control diet. This result suggests that a diet containing 40% white spruce has significantly more secondary plant metabolites than a diet containing 20% spruce. These results are supported by our analyses of plant secondary metabolites in winter browse (Sauvé and Côté 2006) and by other studies (Von Rudloff 1972; Hunt and Von Rudloff 1974). Therefore, we can hypothesize that white spruce contains secondary plant metabolites that are more costly for white-tailed deer to detoxify than those of balsam fir. Generalist herbivores can cope with a mixture of plant secondary metabolites, whereas specialist herbivores have adapted to detoxify the metabolites found in specific plants (Dearing et al. 2000). By mixing white spruce with balsam fir and arboreal lichens, deer diversify the ingested secondary plant metabolites, thus possibly reducing the cost of the detoxification of separate metabolites (Dearing et al. 2000). It is possible that deer feeding solely on white spruce (or balsam fir) would experience higher costs related to the detoxification of the specific plant metabolic compounds found in spruce (or fir) than deer feeding on both species. Further research is needed to evaluate the physiological effects of feeding on a monospecific conifer diet in deer.

The glucuronic acid / creatinine ratios in snow-urine did not vary over winter. This suggests that the absolute metabolic cost of forage detoxification did not increase during winter. However, because the secondary plant metabolite load remained constant, but the metabolizable energy available to the detoxification pathway decreased in time as a result of the increase in the costs of other metabolic processes (e.g., thermoregulation and locomotion), the relative costs of detoxification may have increased. However, we did not measure the available metabolizable energy intake and we do not know the amount of energy allocated to the different metabolic processes. Therefore, it is not possible to determine the costs of detoxification in this experiment.

The glucuronic acid / creatinine ratios were not related to cumulative body mass loss or to the number of days left before death because the absolute cost of detoxification likely remained constant through winter because the diet composition did not change. This suggests that the secondary plant metabolite load was not the main factor explaining the deterioration of deer body condition observed over winter in our study. Although the detoxification costs added to the total metabolic costs, they were not high enough to influence body mass loss and, therefore, death by inanition.

In conclusion, our hypothesis that the body condition of deer fed a diet containing more white spruce than in the naturally occurring diet on Anticosti would deteriorate sooner in the winter than that of control deer was not supported. Although the diet containing 40% white spruce and 60% balsam fir contained more secondary plant metabolites than the diet containing 20% white spruce and 80% balsam fir, as revealed by glucuronic acid / creatinine ratios in snow-urine and plant chemical analyses, this difference was not great enough to lead to substantial physiological effects on body condition. We did, however, confirm the hypothesis that the 3-methylhistidine / creatinine ratios increased with time, possibly indicating that the body condition of deer deteriorated throughout the winter as found by DelGiudice et al. (1998).

Because weak effects of diet on body condition deterioration were detected in our study, one may be tempted to conclude that the difference in quality between balsam fir and white spruce may not be that great. However, available winter browse on Anticosti is almost exclusively composed of spruce (Potvin et al. 2003; Tremblay et al. 2005), yet the winter diet of deer is approximately 70% balsam fir. In addition, our results on glucuronic acid / creatinine ratios (above), on the chemical analyses of white spruce and fir (Sauvé and Côté 2006), and on preference tests (Sauvé and Côté 2006) all point in the same direction — fir is strongly

preferred over spruce. Further research is needed to evaluate the physiological effects on white-tailed deer of >40% white spruce in the diet. Such work would enable managers to evaluate the potential consequences of a winter diet shift towards white spruce on body condition, survival, and population dynamics of the white-tailed deer population of Anticosti Island.

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