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LES EFFETS DE LA DÉTÉRIORATION DE LA QUALITÉ DE L'ALIMENTATION D'HIVER SUR LA CONDITION CORPORELLE DU CERF DE VIRGINIE DE L'ÎLE D'ANTICOSTI

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Résumé

Le but principal de ce projet consistait à mesurer les effets de la diminution de la qualité de l'alimentation d'hiver sur la sélection et la prise alimentaire, le budget d'activité, la survie et la détérioration de la condition corporelle du cerf de Virginie de l'île d'Anticosti. Nous avons suivi la perte de masse de faons au cours de l'hiver et évalué leur condition corporelle à l'aide de métabolites urinaires.

Bien que nous ayons montré qu'une diète plus riche en épinette blanche (diète expérimentale) que celle observée présentement en nature (diète témoin) était plus riche en produits secondaires et plus fibreuse, ceci n'a pas influencé de façon marquée le budget d'activité, la perte de masse, le catabolisme des protéines musculaires, tel que mesuré par les métabolites urinaires, et la survie des faons. Cependant, les faons de la diète témoin ont diminué leur prise alimentaire pendant l'hiver contrairement aux faons de la diète expérimentale qui l'ont maintenue constante et plus élevée que les faons de la diète témoin. La masse corporelle au début de l'hiver s'est avérée le facteur déterminant pour la survie des cerfs.

Abstract

The main goal of this project was to evaluate the effects of the deterioration of winter diet quality on the food preference and intake, time budget, body mass loss, muscle protein catabolism and survival of white-tailed deer fawns on Anticosti Island. We evaluated body condition with the monitoring of body mass and snow-urine analyses throughout winter.

Although a diet richer in white spruce than that presently observed in nature contains more fibre and secondary plant compounds, this diet did not influence the activity budget, body mass loss, catabolism of body protein, measured with urine analyses, and survival of white-tailed deer fawns. However, fawns on a natural control diet decreased their forage intake over winter, while those on a poorer diet maintained a constant intake at a higher level than those on the control diet. Body mass at the onset of winter was critical for the winter survival of deer on Anticosti.

Avant-propos

Ce mémoire de maîtrise est le reflet de mon cheminement au cours des deux dernières années et demie. L'introduction et la discussion générale ont été rédigées en français, mais les 3 chapitres sont en anglais dans le format de publications scientifiques. Steeve D. Côté, qui est le co-auteur des articles, a énormément contribué à monter ce projet et a révisé les manuscrits. Joëlle Taillon, avec laquelle j'ai partagé le travail de terrain pendant les longs hivers d'Anticosti, a grandement contribué à l'analyse des données et à la rédaction du chapitre 2 dont elle est co-auteure. Ce chapitre est sous presse dans la revue *The Journal of Wildlife Management*.

Les captures, les hivers à Anticosti, les étés dans le laboratoire et les nombreuses « activités sociales » avec toute l'équipe ont fait de mon expérience au sein de la chaire de recherche CRSNG-PFA des années exceptionnellement enrichissantes. Cependant, rien de cela n'aurait été possible sans la confiance et le respect que mes supérieurs ont eu (et ont toujours…je présume) en moi. J'ai développé d'ailleurs une complicité particulière avec mon directeur Steeve Côté. Bien qu'il ait su me diriger, me guider et m'inspirer, il a aussi su me divertir, me nourrir et m'hydrater…ou me déshydrater! Steeve est pour moi un mentor, mais aussi un grand frère. Jean Huot, pour sa part, fut pour moi, comme pour bien d'autres avant, une référence, voir même une bible, de notions et concepts en écologie. Son encadrement et la confiance qu'il a envers les étudiants de la chaire ont fait de lui comme un père qui veille sur ses enfants.

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Je ne peux certainement pas garder sous silence la participation spéciale de certaines personnes. Bien que la participation directe de tous les membres d'une équipe à un projet soit essentielle à sa réussite, les interactions avec les autres étudiants de l'équipe sont primordiales. La dynamique retrouvée dans notre équipe de recherche est unique et irremplaçable. Que ce soit pour relire un manuscrit, se faire conseiller, se faire encourager, prendre une pause café ou pour trouver un prétexte à fêter, chaque étudiant de la chaire (ou non), est toujours là pour les autres. C'est ce qui fait que notre équipe est irremplaçable. Un gros merci à Joëlle Taillon, Jean-Pierre Tremblay, Ariane Massé, Marie-Lou Coulombe, Sandra Hamel, Vanessa Viera, Anouk Simard, Jean-François Therrien, Julien Mainguy, Martin Barrette, Antoine Saint-Louis, Valérie Harvey et Catherine Bajzak. Merci pour leurs encouragements, leur générosité et leur folie : Merci à ma deuxième famille.

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À Geneviève, Rosalie et Camille

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Introduction

L’étude des relations plantes/herbivores est un volet important de l’écologie terrestre qui permet de mieux comprendre les processus écologiques impliquant plusieurs niveaux trophiques. En l’absence de prédateurs, les grands herbivores peuvent atteindre de très fortes densités et avoir un impact considérable sur les communautés végétales en modifiant la diversité et l’abondance de certaines espèces ainsi que la structure des communautés (Potvin et al., 2003; Viera, 2003; Weisberg and Bugmann, 2003; Côté et al., 2004). De plus, lorsque les populations d’ongulés sont près de la capacité de support du milieu, la diversité et l’abondance des plantes peuvent avoir un effet de rétroaction négative sur les animaux en affectant leur condition corporelle, leur succès reproducteur et leur survie (Skogland, 1985; Gaillard et al., 2000).

En effet, une densité élevée au point de limiter les ressources peut affecter, entre autres, la masse corporelle à la naissance des ongulés, une caractéristique déterminante non seulement pour la survie hivernale du jeune, mais aussi pour la masse corporelle qu’il pourra atteindre à l’âge adulte (Gaillard et al., 2003). Les juvéniles ayant une plus petite masse corporelle sont moins aptes à compenser la perte de masse encourue pendant l’hiver plus tard dans leur vie (Gaillard et al., 1996), ce qui pourra influencer leur succès reproducteur (Gaillard et al., 2000; 2003).

Le régime alimentaire des herbivores est habituellement composé d’une bonne diversité d’espèces végétales, ce qui permet de minimiser les effets dissuasifs, toxiques ou anti-nutritifs de certaines plantes (Tixier et al., 1997; Illius et al., 2002). Avec une bonne diversité de plantes, les herbivores peuvent choisir les espèces végétales de meilleure qualité, éviter les plantes potentiellement toxiques ou diluer celles-ci avec des plantes moins toxiques. Cependant, au cours de l’hiver, la disponibilité de la végétation ayant une bonne qualité nutritive diminue grandement, et les seules plantes disponibles sont souvent munies d’adaptations anti-herbivores (Bryant et al., 1991; Tahvanainen et al., 1991). L’une de ces adaptations est la production de produits métaboliques secondaires qui défendent les plantes, entre autres contre le broutement, en leur conférant un mauvais goût ou en les rendant difficilement digestibles ou toxiques (Robbins et al., 1987a; 1987b; Reed et al., 2000). Ces produits métaboliques secondaires n'ont pas un rôle principal dans la physiologie de la plante (Burns, 1978; Taiz and Zeiger, 1991). Parmi les différents types de produits métaboliques secondaires retrouvés dans les plantes, il y a les phénols et les terpènes, des substances qui par leurs effets néfastes peuvent influencer la sélection des ressources alimentaires par les herbivores (Robbins et al., 1987a; Harborne, 1991; Vourc'h et al., 2002). Puisque les phénols réagissent avec les protéines, ceux-ci rendent les plantes astringentes et donc diminuent leur palatabilité (Fahey Jr. and Berger, 1993). Il est connu que la palatabilité influence négativement la prise alimentaire chez les ruminants (Grovum, 1993). En ce qui a trait aux terpènes, le signal est olfactif et gustatif, indiquant à l'herbivore que la plante est potentiellement toxique et donc à éviter (Harborne, 1991; Vourc'h et al., 2002).

En plus des produits secondaires, la prise alimentaire peut être influencée par plusieurs facteurs tels que la disponibilité, la palatabilité, la digestibilité et le taux de passage de la nourriture dans le tractus gastro-intestinal, ainsi que par l'appétit de l'animal et les conditions climatiques ambiantes (Welch et Hooper, 1993). Il est connu que les parois cellulaires des plantes, constituées principalement de cellulose et d'hémicellulose, sont indigestibles par les enzymes digestives des mammifères (Goering et Van Soest, 1970a). Bien que les ruminants aient la capacité d'extraire de l'énergie des plantes à l'aide de la fermentation microbienne dans le rumen (Yokoyama et Johnson, 1993), les plantes très fibreuses réduisent la digestibilité de la nourriture, le taux de passage à travers le tractus gastro-intestinal et donc le taux de prise alimentaire (Hanley, 1982; Gray et Servello, 1995). Les grands herbivores qui vivent sous des latitudes septentrionales ont généralement accès à de la nourriture de faible qualité ou peu abondante pendant l'hiver (Verme et Ullrey, 1972; Huot, 1982; Gray et Servello, 1995). Bien que la quantité de nourriture puisse ne pas être limitative, la faible disponibilité de nourriture de qualité peut faire en sorte que les grands herbivores n’arrivent pas à subvenir à leurs besoins énergétiques et nutritionnels (Torbit et al., 1985b), ce qui provoque souvent une perte de masse considérable pendant l’hiver (Huot, 1982; Festa-Bianchet et al., 1996; Côté et Festa-Bianchet, 2003). Pour tenter de minimiser cette perte de masse associée aux coûts énergétiques élevés pendant l’hiver, certains ongulés vont modifier leurs déplacements afin de réduire les coûts associés à la thermorégulation et à la locomotion dans la neige profonde (Ozoga et Verme, 1970; Ozoga et Gysel, 1972; Grenier et al., 1999; Lesage et al., 2001) et vont concentrer leurs périodes d’activité pendant les moments les plus ensoleillés de la journée (Ozoga et Verme, 1970; Verme et Ozoga, 1980; Beier et McCullough, 1990).

Malgré tout, les coûts énergétiques élevés et le manque à gagner en énergie et en nutriments peuvent forcer les animaux à puiser dans leurs réserves durant l’hiver (Torbit et al., 1985b; Jensen et al., 1999) et occasionner une forte détérioration de la condition corporelle pouvant causer la mort chez les individus les plus faibles, particulièrement les plus jeunes. En effet, les jeunes de l’année ont généralement un taux de mortalité hivernale plus élevé que les adultes puisqu’ils ne peuvent accumuler autant de gras corporel et qu’ils ont des exigences métaboliques plus élevées que les adultes (Nordon et al., 1970; Moen, 1976). Les jeunes en bonne condition corporelle à leur premier automne ont une plus grande probabilité de survivre à l’hiver que ceux en moins bonne condition (White et al., 1987; Côté et Festa-Bianchet, 2001; Pettorelli et al., 2002). De plus, les jeunes qui sont plus gros à leur premier hiver atteignent aussi une plus grande masse corporelle à l’âge adulte (Schultz et Johnson, 1995), ce qui pourrait affecter positivement leur succès reproducteur à vie et l’accès aux ressources.

Pour évaluer les effets de la restriction alimentaire hivernale sur la condition corporelle, il est possible de mesurer les variations de la masse corporelle (DelGiudice et al., 1994; Vagnoni et al., 1996; DelGiudice et al., 1997; DelGiudice et al., 1998; Cook et al., 2001). Cependant, la masse corporelle varie énormément de façon temporelle et entre les individus

(Gerhart et al., 1996). Conséquemment, l'utilisation de la masse corporelle seule n'est pas suffisante pour mesurer la condition corporelle et elle doit donc être utilisée conjointement avec d'autres indices comme l'analyse des variations de la concentration de certains métabolites urinaires (DelGiudice et al., 1990; Gerhart et al., 1996).

Auparavant, l'échantillonnage de l'urine d'un animal exigeait son immobilisation car l'échantillon se prenait à l'aide d'un cathéter (DelGiudice et al., 1987a; b; c). De nos jours, une méthode employée par plusieurs chercheurs permet d'analyser des échantillons d'urine récoltés sur la neige sans avoir à immobiliser et donc stresser les animaux (Mech et al., 1987; Garrott et al., 1996; Ditchkoff and Servello, 1999; Pils et al., 1999). Cependant, étant donné que les échantillons d'urine sont récoltés sur et à travers la neige, le facteur de dilution est inconnu et doit être pris en compte. La créatinine, un déchet métabolique issu de l'activité musculaire et libérée dans le sang, est sécrétée de manière relativement constante dans le temps (DelGiudice et al., 1987a; 1991) et sa concentration est proportionnelle à la masse musculaire de l'animal (DelGiudice et al., 1991). Il est donc possible d'utiliser la concentration de cette protéine pour calculer un rapport du métabolite à analyser, ce qui permet de corriger les concentrations des métabolites mesurés en fonction de l'hydratation et de la masse corporelle de l'animal ainsi que de la dilution de l'échantillon dans la neige (DelGiudice et Seal, 1988; DelGiudice et al., 1997).

En règle générale, lors de périodes de faible disponibilité de nourriture, les réserves de graisses sous-cutanées, viscérales ou de la moelle osseuse sont utilisées en premier lieu afin de subvenir aux besoins de l'animal mais le catabolisme des protéines musculaires (Torbit et al., 1985a; DelGiudice et al., 2000) peut également servir de source d'énergie. L'utilisation des réserves par les ruminants requiert généralement le catabolisme simultané de protéines musculaires étant donné que les acides aminés glycogéniques sont importants pour la mobilisation des triglycérides (Torbit et al., 1985b). Ceci se traduit par l'excrétion de la 3-méthylhistidine dans l'urine, puisque cette dernière n'est pas réutilisée dans le métabolisme des protéines (Emery et Preedy, 2003). La 3-méthylhistidine (calculée comme un rapport avec la créatinine) est donc considérée comme un bon indicateur d'une perte de masse musculaire causée par une restriction alimentaire prolongée (DelGiudice et al., 1998). La 3-méthylhistidine est un acide aminé qui compose la myosine, la protéine principale des muscles squelettiques (Lehninger, 1975). Conséquemment, la sécrétion de cet acide aminé dans l'urine est corrélée à la dégradation de la masse musculaire de l'animal (DelGiudice et al., 1998).

L'analyse d'autres métabolites urinaires peut aussi fournir différentes informations sur l'état physiologique des animaux. La glucuronidation est un processus métabolique de détoxication du foie qui permet de conjuguer une substance toxique, comme un produit secondaire des plantes, avec de l'acide glucuronique (dérivé du glucose), la rendant ainsi inoffensive (McArthur et al., 1991). Par contre, l'excrétion de l'acide glucuronique provoque une perte d'énergie puisque cet acide est produit à partir du glucose et que la réaction de conjugaison avec la substance toxique nécessite de l'énergie et une baisse du pH urinaire pouvant influencer le fonctionnement des reins (Dearing and Cork, 1999).

En résumé, l'analyse des rapports de la 3-méthylhistidine et de l'acide glucuronique sur la créatinine permet d'estimer la détérioration de la condition corporelle au cours du temps ainsi que le coût relatif associé à la détoxication de produits métaboliques secondaires dans la nourriture. En observant des animaux en captivité ou marqués, il est possible de connaître de quel animal provient chaque échantillon d'urine récolté sur la neige et ainsi réduire les effets confondants de la variabilité interindividuelle car chaque individu est comparé à lui-même au cours du temps (DelGiudice et al., 1997).

Problématique d'Anticosti

Au début du 20^e siècle, le cerf de Virginie (*Odocoileus virginianus*) s'est rapidement multiplié à la suite de son introduction sur l'île d'Anticosti (Huot, 1982; Potvin et al., 2003). D'environ 200 cerfs introduits, la population compte aujourd'hui plus de 125 000 têtes (Rochette et al. 2003). Comme il a aussi été observé ailleurs (Rooney, 2001; Côté et al., 2004), cette croissance démographique s'est rapidement traduite par de fortes pressions de broutement sur les communautés végétales des forêts de l'île, les espèces feuillues ayant même pratiquement disparues (Tremblay et al., 2005).

La pression de broutement exercée par le cerf transforme encore aujourd'hui les peuplements forestiers de l'île (Huot, 1982; Chouinard et Filion, 2001; Potvin et al., 2003). Néanmoins, la composition de l'alimentation hivernale des cerfs d'Anticosti était, et est toujours, constituée principalement de conifères (Huot, 1982; Potvin et al., 2003), ce qui est considéré comme étant une alimentation de faible qualité, faiblement digestible (Ullrey et al., 1968) et contenant beaucoup de produits métaboliques secondaires (Phillips et Croteau, 1999). Aucune autre nourriture alternative n'est disponible aux cerfs à Anticosti pendant l'hiver (Huot, 1982), rendant donc cette alimentation riche en conifères une diète de dernier recours.

Le broutement sélectif du cerf sur les semis de sapin baumier (*Abies balsamea*) empêche la régénération des sapinières qui sont graduellement remplacées par des pessières blanches pures (Potvin et al., 2003). Selon Chouinard et Filion (2001), 37 % des semis et 100 % des gaulis de sapin sont broutés par le cerf à Anticosti. Pour leur part, Potvin et al. (2003) ont observé que 26 à 48% des semis de sapin étaient broutés par année à Anticosti. Huot (1982) a noté que le sapin constituait environ 70 % du contenu du rumen des cerfs au cours de la saison hivernale. Il a aussi observé de l'épinette (*Picea spp.*) dans 99 % des rumens analysés mais l'épinette ne représentait que 10 % du contenu des rumens. Ces résultats suggèrent que le sapin baumier soit fortement préféré par le cerf en hiver à l'île d'Anticosti, car bien que beaucoup plus disponible que le sapin baumier, l'épinette blanche demeure faiblement utilisée (Huot, 1982).

La diminution de la superficie des sapinières sur l'île est un processus qui s'est accéléré au cours des dernières années puisque la majorité des sapinières ont atteint leur stade de maturité (Potvin et al., 2003) et que les arbres sont de plus en plus sujets aux chablis et aux maladies causées par les insectes. Puisque les cerfs broutent les semis, les sapinières ne se régénèrent pas. Bien que ces modifications à grande échelle soient bénéfiques à court terme car elles rendent plus de ramilles de sapin disponibles au sol (Tremblay et al., 2005), elles auront tôt ou tard pour conséquence de réduire la proportion de sapin disponible aux cerfs (Potvin et al., 2003).

Même s'il a été suggéré que le sapin soit préféré à l'épinette blanche par les cerfs (Chouinard et Filion, 2001), aucune étude n'offre une explication satisfaisante à ce choix. Il est possible que l'épinette blanche soit de qualité nutritionnelle inférieure au sapin. D'ailleurs, Huot (1982) a montré que le contenu du rumen de trois cerfs retrouvés morts, vraisemblablement d'inanition, était constitué de 75 %, 95 % et 100 % d'épinette blanche, respectivement. Ces observations suggèrent qu'une augmentation de la proportion d'épinette dans le régime alimentaire des cerfs puisse avoir des conséquences néfastes sur leur condition corporelle, et éventuellement sur leur survie et leur fécondité. Il est aussi possible qu'une augmentation de la proportion d'épinette dans l'alimentation des cerfs ait un effet sur la prise alimentaire et éventuellement le budget d'activité de ceux-ci.

Ce projet vise à estimer les effets de la réduction graduelle de la disponibilité de sapin baumier sur l'île d'Anticosti, et conséquemment de l'augmentation probable de la proportion d'épinette blanche dans l'alimentation hivernale des cerfs, sur le comportement de prise alimentaire, le budget d'activité, la condition corporelle et la survie des individus, de façon à pouvoir mieux prévoir les effets à long terme de ces changements sur la dynamique de la population de cerfs de l'île. Les objectifs poursuivis sont: (1) de tester expérimentalement les préférences alimentaires hivernales du cerf de Virginie d'Anticosti et de les expliquer par l'analyse de la teneur en fibres, en phénols totaux et en tannins condensés du sapin baumier et de l'épinette blanche, (2) d'évaluer les effets de la détérioration de la qualité de l'alimentation d'hiver, simulée par l'augmentation de la proportion d'épinette blanche dans la diète, sur la prise alimentaire, la perte de masse, le budget d'activité et la survie des cerfs et enfin, (3) de déterminer expérimentalement comment la qualité du régime alimentaire hivernale influence (a) la condition corporelle, par l'analyse du rapport 3-méthylhistidine:créatinine et (b) le coût associé à la détoxication des produits métaboliques secondaires des plantes par l'analyse du rapport acide glucuronique:créatinine dans l'urine de cerfs sauvages maintenus en enclos.

Pour rencontrer les objectifs énoncés, nous avons en premier lieu effectué une expérience de type cafétéria en offrant deux choix de nourriture aux cerfs afin d'évaluer la préférence alimentaire des cerfs captifs entre le sapin baumier et l'épinette blanche. Six cerfs ont eu à choisir parmi 6 combinaisons de sapin baumier et d'épinette blanche broyés ou intactes pendant des tests de 12 heures chacun.

Pour répondre au deuxième objectif, nous avons maintenu 32 faons en enclos pendant les hivers 2003 et 2004 et effectué des observations visuelles à partir de caches. Ces observations nous ont permis de mesurer le taux de prise alimentaire, la perte de masse, le budget d'activité et la survie des faons. Une balance électronique à plateau a été utilisée pour mesurer la masse corporelle.

En dernier lieu, des échantillons d'urine ont été récoltés dans la neige afin d'évaluer les effets de la détérioration de la qualité de l'alimentation d'hiver (exprimée par l'augmentation de la proportion d'épinette blanche dans la diète) sur la condition corporelle à l’aide de la variation des métabolites urinaires, comme la 3-méthylhistidine. Nous avons aussi mesuré l’acide glucuronique pour estimer le coût relatif de la détoxication des produits métaboliques secondaires retrouvés dans une alimentation plus riche en épinette blanche.

Ces objectifs nous ont permis de simuler les conditions susceptibles de survenir sur l’île d’Anticosti dans un avenir plus ou moins rapproché à la suite de la diminution des sapinières et à leur remplacement par des pessières blanches, et donc de l’augmentation graduelle de l’épinette blanche dans l’alimentation d’hiver des cerfs sur l’île d’Anticosti.

Why white-tailed deer prefer rare balsam fir over abundant white spruce as their main winter forage in boreal forests of Anticosti Island?

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RÉSUMÉ

Les cerfs d'Anticosti consomment le sapin baumier (*Abies balsamea*) et l'épinette blanche (*Picea glauca*) dans des proportions de 70 et 20 % respectivement de leur alimentation d'hiver même si l'épinette est beaucoup plus disponible que le sapin. Les cerfs expérimentaux avaient accès à des ramilles broyées ou intactes de sapin et d'épinette en quantités égales. Nous avons prédit que la sélection entre le sapin et l'épinette par les cerfs serait expliquée par la chimie et la texture foliaire. Les cerfs consommaient 90 % de sapin et 10 % d'épinette blanche bien que la disponibilité des deux essences était identique. La texture (broyée ou intacte) n'a pas influencé la sélection entre le sapin et l'épinette par les cerfs. Les concentrations de phénols totaux et de protéines ne variaient pas entre les essences. Les teneurs en fibres et en tannins condensés, par contre, étaient supérieures dans les ramilles d'épinette suggérant que ces paramètres étaient importants dans la sélection entre le sapin et l'épinette par les cerfs en hiver à Anticosti. La sélection pour le sapin par les cerfs pourrait être expliquée par la concentration de produits métaboliques secondaires mais d'autres études seront nécessaires afin d'élucider le rôle de ces derniers dans la sélection alimentaire des cerfs l'hiver.

ABSTRACT

We assessed winter food selection by white-tailed deer fawns (*Odocoileus virginianus*) on Anticosti Island, Quebec, using cafeteria feeding trials. Winter habitat on Anticosti is degraded and free-ranging deer at high densities consume 70% balsam fir (*Abies balsamea*) and 20% white spruce (*Picea glauca*) in their winter diet even though white spruce is much more available than balsam fir. Experimental deer had a choice between equally abundant balsam fir and white spruce twigs, shredded or not. We predicted that selection between balsam fir and white spruce could be explained by foliar chemistry and texture. Our results indicated that deer ate 89.9% balsam fir and 10.1% white spruce when the availability of both trees was equal. Deer did not eat shredded twigs more than intact twigs, suggesting that texture does not intervene in winter food selection between fir and spruce trees. Fibre content and condensed tannins were greater in white spruce than in balsam fir, suggesting that they may be important in explaining the differences in winter food selection by deer. The foliar concentrations of proteins and total phenol did not differ among tree species. The strong selection of balsam fir over white spruce could also be explained by other plant secondary metabolites, and future studies should be aimed at elucidating the role of these constituents in winter food selection by deer.

INTRODUCTION

Several factors may influence forage selection by wild herbivores, including the type of digestive system, mouth size, food abundance and diversity, and interactions between these parameters (Hanley, 1982). Forage selection may also be determined by the chemical composition of plants (Hanley, 1982; Berteaux et al., 1998; Shipley et al., 1998; Coleman et al., 2003), because the chemical constituents of plant tissue can affect the digestibility of forage (Robbins et al., 1987b). Although the cell content of plants is highly digestible, the cell walls are much less digestible because they are mainly composed of structural carbohydrates, such as cellulose and hemicellulose, which are not hydrolysable by any mammalian enzymes (Goering and Van Soest, 1970). Although ruminants can extract energy found in cellulose and hemicellulose through ruminal fermentation (Yokoyama and Johnson, 1993), highly fibrous plants (i.e. with a high cell wall content) reduce digestibility, rate of passage through the gastro-intestinal tract and intake rate of forage (Hanley, 1982; Gray and Servello, 1995).

Protein content may also influence forage selection (Berteaux et al., 1998). Although microbes are the main protein source for ruminants (Owens and Zinn, 1993; Dewhurst et al., 2000), the reticulo-rumen micro organisms must use nitrogen (N) in different forms (intact protein, amino acids or free N) from the substrate or through the rumen wall via the bloodstream (ammonia and/or urea), to form their own bodies, which will later be digested in the gastro-intestinal tract of ruminants (Maynard., 1969; Owens and Zinn, 1993; Bohnert et al., 2002). A minimum of 6% dry matter crude protein content in forage is necessary for the maintenance of a healthy rumen flora and fauna (Owens and Zinn, 1993).

Other compounds in plants, such as plant secondary metabolites, can reduce digestibility and/or palatability of forage (Robbins et al., 1987b; Harborne, 1991; Vourc'h et al., 2002). Phenols, such as condensed tannins, have been shown to reduce dry matter digestibility and protein availability in deer (Robbins et al., 1987a; b), whereas terpenoids can either be deterrent or toxic to deer and other mammals (Harborne, 1991; Vourc'h et al., 2002).

The physical characteristics of plants, i.e. soft versus prickly or spiny tissue, may also influence the palatability of forage, and therefore intake rate (Côté et al., 2004). For example, Illius *et al*. (2002) have shown that the presence of thorns in certain plant species can negatively influence bite size and foraging rate in roe deer (*Capreolus capreolus*). Very little is known on the effects of plant texture on handling time and food selection by ruminants, especially for coniferous browse.

To maximize digestible energy intake and to minimize the ingestion of possibly toxic or anti-nutritive compounds of plants, wild ruminants normally eat a diverse array of forage (Tixier et al., 1997; Illius et al., 2002). Wild herbivores have generally access to many plant species, allowing them to meet their daily energy and nutrient requirements (Shipley et al., 1998). However, in boreal forests during winter, ruminants must feed on poor quality and well defended plants with higher fibre content, lower protein content and higher concentrations of plant secondary metabolites than summer forage. These characteristics generally decrease the digestibility of plants and passage rate through the gastro-intestinal tract, increase fill rate and thus decrease intake rate and selection (Risenhoover, 1989; Van Soest, 1994; Gray and Servello, 1995).

Following its introduction on Anticosti Island in the late 1800's, the white-tailed deer (*Odocoileus virginianus*) population irrupted from roughly 200 to over 125 000 animals today (Potvin et al., 2000). Deer browsing gradually extirpated or severely reduced the abundance of all deciduous shrubs in the boreal forests of the island (Potvin et al., 2000; Chouinard and Filion, 2001). Before the introduction of deer, balsam fir stands were estimated to cover close to 40% of the island's surface. Today, that number has declined to 20% and fir stands are being replaced by white spruce stands (Potvin et al., 2003).

Although insect epidemics (e.g.: spruce budworm (*Choristoneura fumiferana*) and hemlock looper (*Lambdìna fiscellaria*) and forest fires may be partly responsible for the fir decline on the island, deer over browsing is the main factor that contributed to the decline by suppressing regeneration (Potvin et al., 2003). Nowadays, deer can only feed on three species during winter on Anticosti: white spruce (*Picea glauca*) and black spruce (*P. mariana*), which are highly available, and balsam fir (*Abies balsamea*), which is now only available when trees or small branches are thrown down by wind (Tremblay et al., 2005). No other browse is available on the island during winter (Tremblay et al., 2005), which spans from mid November to mid April.

Balsam fir is the staple food for white-tailed deer in winter on Anticosti representing 70% of the diet, while white spruce represents about 20% of the winter diet (Huot, 1982; Lefort, 2002). The diet is completed by arboreal lichens. Black spruce is not eaten. Anticosti Island is at the northernmost fringe of the distribution of white-tailed deer and the only known place where deer forage mainly on balsam fir and white spruce in winter. Mechanisms of forage selection between balsam fir and white spruce are important to understand because white spruce is gradually and rapidly replacing balsam fir across the whole island (Potvin et al., 2003).

The objectives of this study were to assess the preference of white-tailed deer for balsam fir and white spruce in winter and to determine whether plant constituents could explain the observed choice. In addition, we tested whether the texture of winter browse influences selection by white-tailed deer. We hypothesized that (1) white spruce is more fibrous and more chemically defended than balsam fir and that (2) shredded plant matter, i.e. less prickly, would be preferred over intact branches, especially for white spruce which appears much more prickly than balsam fir.

MATERIALS AND METHODS

Study area

Anticosti Island (49° 28’ N, 63° 00’ W) is a 7 943 km^2 island located in the Gulf of St. Lawrence, Quebec, Canada. The maritime climate is characterized by cool summers and mild but long winters (Huot, 1982). The boreal forest on the island is composed mainly of white spruce, balsam fir, and black spruce (Potvin et al., 2003).

Capture and captivity

From 1 to 25 December 2003, we captured 6 wild white-tailed deer fawns (4 males and 2 females). We physically immobilized deer with Stephenson box traps and canon-nets baited with balsam fir and commercial cow feed (Shur-Gain, Meunerie Cacouna inc., Cacouna Québec). Some deer were chemically immobilized with a mixture of Telazol® (4.5 mg/kg) and xylazine (2 mg/kg) that was administered via radio-transmitter equipped darts (Murray et al., 2000; Miller et al., 2003). Yohimbine was used as an antagonist for xylazine in anaesthetized deer. Deer were sexed and weighed to the nearest 0.5 kg with a spring scale or an electronic scale. All fawns were individually marked with ear tags and relocated to a 0.5 hectare outdoor pen. Individuals were fed their natural winter diet, i.e. a mixture of shredded balsam fir (80%) and white spruce (20%) twigs until the beginning of the feeding trials. The experimental protocol was approved by Laval University Animal Care Committee and met the principles and guidelines of the Canadian Council on Animal Care.

Food preference trials

In March 2004, each deer was isolated in an outdoor pen of 0.5 ha and underwent six preference-feeding trials that lasted 12 hours each. During each trial, deer had access to two large plastic containers (Rubbermaid storage bins) with 1000 g of fresh food in each. Deer were offered one of the following choices: 1) balsam fir and white spruce intact twigs, 2) balsam fir intact twigs and white spruce shredded twigs, 3) balsam fir shredded twigs and white spruce intact twigs, 4) balsam fir and white spruce shredded twigs, 5) balsam fir only (intact and shredded twigs), or 6) white spruce twigs only (intact and shredded). One of the six different combinations (in random order) was offered to each animal during a single trial. These combinations evaluated the selection between balsam fir and white spruce, and the effect of chipping twigs (i.e. removing the effects of texture) on winter food selection by white-tailed deer. The trees were harvested < 1km from the pens in mature fir stands. Fir trees were felled 1-2 days prior to testing and were kept outdoors in sub-zero temperatures. Spruce twigs were harvested with pruning shears as needed. Fir and spruce twigs were shredded separately in a gas-powered wood chipper (Yard Machines-5 HP wood chipper).

Dry matter intake was determined by subtracting the mass of orts from the initial mass of food placed in the troughs, corrected for the species-specific rate of water loss during the trials.

Vegetation collection and analysis

To evaluate the chemical composition of both tree species offered to deer, we collected two samples each of balsam fir and white spruce (annual shoots) in 8 different sites randomly chosen in mature balsam fir-white spruce stands (mean area ± S.E.: 13.2±2.6 ha) in mid-February 2004 for a total of 16 samples per tree species. The white spruce samples were hand collected between 0.5 and 3 m from the ground, whereas fir branches were cut with a 3 m tree pruner since no branches were accessible by hand due to deer browsing.

Half of all the samples (16 of 32) were kept frozen in doubly sealed plastic bags, while the other half was air-dried at 50°C until constant mass and kept at room temperature until analyzed. A total of 16 air-dried samples were shredded in a Willey mill (20 mesh size) and analyzed (8 samples for each species) for neutral detergent fibre (NDF), acid detergent fibre (ADF), and acid detergent lignin (ADL) (Goering and Van Soest, 1970). NDF and ADF fibre analyses were done using an Ankom 200 fibre analyzer (Ankom Technology, Macedon, New York), whereas ADL was determined according to the method of Goering and Van Soest (1970). All samples were analyzed in duplicate. Nitrogen content of all air-dried vegetation samples was determined in duplicates by the macro-Kjeldahl method, and results are expressed as crude protein content (nitrogen x 6.25).

The other fraction of the samples (8 balsam fir and 8 white spruce) was freeze-dried, ground with dry ice in a Willey mill (20 mesh size), and assayed for total phenol content using the Folin-Ciocalteu method (Yu and Dahlgren, 2000). We determined the concentration of condensed tannins using the HCl-butanol hydrolysis method (Yu and Dahlgren, 2000). We extracted total phenols and condensed tannins from 50 mg of plant material by placing each sample in a 70% (v/v) aqueous acetone solution for 24-hr in the dark, and then centrifuging the solution for 10 min and removing the extracts (Yu and Dahlgren, 2000).

Statistical analyses

The effects of texture and plant species on percent dry matter intake were evaluated using a 2-way ANOVA. To compare vegetation parameters (NDF, ADF, ADL, protein content, total phenols, condensed tannins) between species, we used two-sided t-tests. All data are presented as means ± SE.

RESULTS

Food preference

White-tailed deer fawns consumed both food types in every feeding trial and no differences in total dry matter intake were observed between tests ($F_{5, 66} = 1.79$, $P = 0.13$). All tests were therefore analyzed together in a 2-way ANOVA. Food texture did not influence selection for both tree species (texture: $F_{1, 44} = 1.75$, $P = 0.19$; texture*species interaction: $F_{1, 44} = 0.10$, $P = 0.76$; Figure 1). Deer showed a strong preference for balsam fir when the two species were offered simultaneously, irrespective of the texture of both foods ($F_{1, 22} = 11.31$, $P = 0.003$; Figure 1).

Vegetation analyses

Fibre (NDF and ADF) and condensed tannins content were greater in white spruce than in balsam fir (Table 1). Acid detergent lignin (ADL) tended to be greater in balsam fir than in white spruce, but the difference was not significant (Table 1). There were no differences in total phenols and crude protein contents between balsam fir and white spruce (Table 1).

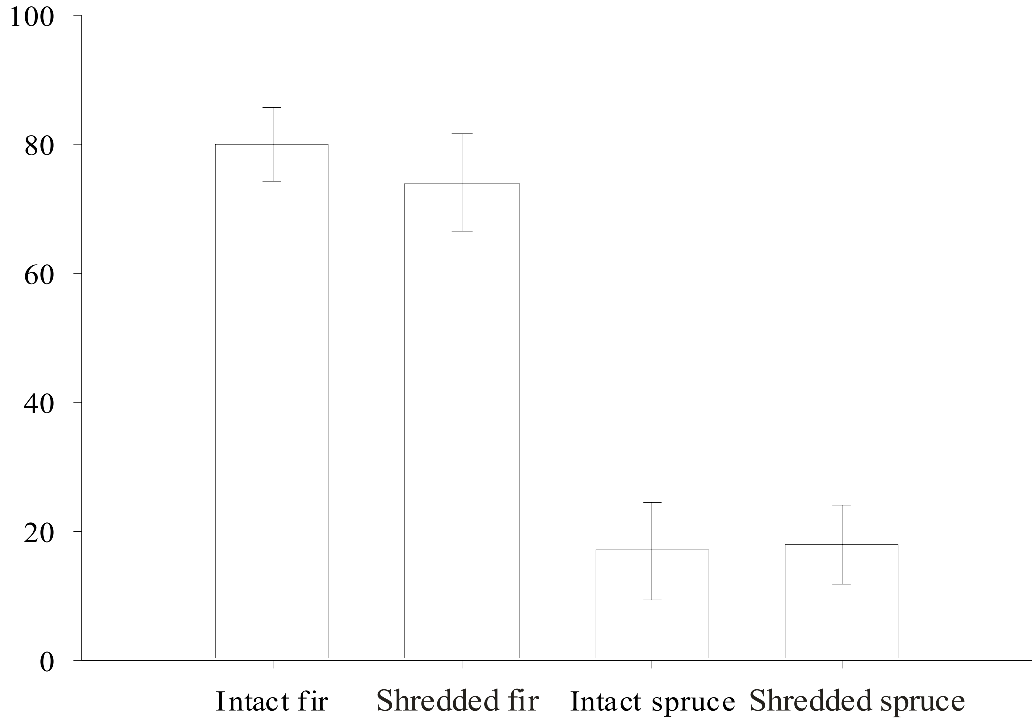

Figure 1: Percent dry matter intake of balsam fir and white spruce offered to white-tailed deer fawns from Anticosti Island (Quebec, Canada) during feeding trials conducted during March 2004. Different textures were offered, shredded and intact twigs. Standard errors of the mean are reported.

Table 1: Chemical composition of balsam fir and white spruce twigs from Anticosti Island (Quebec, Canada) during the winter of 2004. Dietary fibres (NDF, ADF, ADL) and protein content are expressed as percent dry matter, whereas total phenols and condensed tannins are expressed in mg/g dry matter. Data are presented as means ± standard error (in parentheses).

	Balsam fir	White spruce		p-values (two-tailed)
	Mean	Mean	t_{30}	
NDF	39.7 (1.2)	45.9 (1.2)	3.63	0.001
ADF	33.0 (0.5)	34.6 (0.6)	3.24	0.003
ADL	16.8 (0.5)	16.4 (0.4)	0.66	0.5
Crude proteins	5.3 (0.2)	5.2 (0.2)	0.32	0.8
Total phenols	2.1 (0.1)	2.2 (0.07)	0.87	0.4
Condensed tannins	0.098 (0.002)	0.11 (0.003)	2.32	0.03

DISCUSSION

The cafeteria-style experiments conducted in this study confirmed that white-tailed deer show a strong preference for balsam fir over white spruce. These results are consistent with observations of food selection by overwintering free-ranging deer on Anticosti Island (Lefort, 2002) where the availability of balsam fir is very low and that of white spruce is high (Tremblay et al., 2005). In the feeding trials, the availability of balsam fir and white spruce was identical, which may explain the higher percentage of balsam fir consumed in feeding trials (89.9%) compared to free-ranging deer where balsam fir comprised 70% of the diet. We believe that this difference is probably due to the low availability of balsam fir in natural forests of Anticosti, and that deer would likely eat more fir if it was more available. Free-ranging deer also consume approximately 10% arboreal lichens (Lefort, 2002). We did not measure arboreal lichens in our trials, but we left those present on the branches we fed to deer, both for trials with shredded and intact browse.

The chemical composition analyses revealed that white spruce was 5-10% more fibrous than balsam fir (Table 1). Because fibre content negatively influences dry matter digestibility (DMD) (Goering and Van Soest, 1970; Robbins et al., 1987b), white spruce is likely less digestible than balsam fir. Studies of ruminants have shown that fibrous forage can reduce the rate of food intake by decreasing the rate of passage of food through the gut (Hanley, 1982; Gray and Servello, 1995; Tixier et al., 1997). Factors other than, or in interaction with, dietary fibre may also be involved in DMD (Robbins et al., 1987a; b) and thus in the selection we observed. Fibre may affect DMD in subtle ways, and only through *in vitro* or *in vivo* digestibility trials conducted with deer inoculum could these effects be teased out (Pearson et al., 1980; Côté, 1998).

Our results also show that protein content was similar between balsam fir and white spruce (Table 1). Crude protein content for both tree species was below the 6% dry matter minimum threshold proposed by Owens and Zinn (1993). Brown *et al.* (1995) found that prolonged protein restriction negatively influences ruminal digestible energy. On the other hand, Asleson *et al.* (1997) did not find effects of seasonal protein restriction on antlerogenesis and body mass. However, both these studies (Brown et al., 1995; Asleson et al., 1997) had low-protein diets that included ≥ 7% crude protein, i.e. above the 6% proposed threshold. It appears therefore that wintering deer on Anticosti Island are protein deprived, as the only other constituents in their diet, arboreal lichens, are really low in proteins (Robbins, 1988).

Although it has been demonstrated that plant secondary metabolites can alter forage selection, intake rate and digestibility (Robbins et al., 1987a; b; Hagerman and Robbins, 1993; Shipley et al., 1998; Silanikove et al., 2001), our results suggest that total phenols cannot explain balsam fir selection over white spruce for white-tailed deer on Anticosti Island. However, the condensed tannins content was slightly but significantly greater in white spruce than in balsam fir, which may partly explain the selection for fir over spruce by deer. Although tannins are known to be anti-nutritive for ruminants (Robbins et al., 1987a; Silanikove et al., 2001), deer from the *Odocoileus* genus have large parotid glands which produce proline-rich proteins in the saliva (Hagerman and Robbins, 1993). These proline-rich proteins bind with tannins and form a precipitate, thus negating, at least in part, the adverse effect of tannins on protein digestibility. In addition, this precipitate seems to have no inhibitory effect on cellulolytic rumen micro-organisms (McArthur et al., 1991; Harborne, 2001).

However, it remains possible that we did not observe an effect of total phenols on food selection because our analyses were too coarse. Dosing specific phenols in forage is difficult, and limits the interpretation of the effects of these compounds on food preference and digestibility (Mole and Waterman, 1987a; 1987b). For example, Lawler *et al.* (1998) have shown that although total phenols and condensed tannins in certain eucalypts were not correlated with food intake by ringtail possums (*Pseudocheirus peregrinus*) and koalas (*Phascolarctos cinereus*), a specific group of phenolic compounds was negatively correlated with food intake.

Terpenes may also influence food selection in ruminants (Vourc'h et al., 2002). Although no analysis of terpenes was performed in our study, the terpene content of balsam fir and white spruce has been documented elsewhere (Wilkinson et al., 1971; von Rudloff, 1972; Hunt and von Rudloff, 1974). Von Rudolf (1972) identified camphor as an abundant monoterpene in white spruce, whereas it is not found in balsam fir (Hunt and von Rudloff, 1974). Camphor is known to be deterrent in red deer (*Cervus elaphus*), snowshoe hare (*Lepus americanus*) and voles (Harborne, 1991; 2001), and could also be involved in the preference for fir over spruce for white-tailed deer on Anticosti Island.

Our results showed that grinding the twigs did not alter food selection by white-tailed deer. We hypothesized that deer might prefer balsam fir over white spruce because the physical texture of fir is less abrasive and prickly than for spruce, and would therefore require less handling time to process or at least be more palatable than spruce. Although we did not measure handling time, there were no significant differences in dry matter intake between the intact and the shredded twigs for both species. These results suggest that the preference for balsam fir over white spruce by overwintering white-tailed deer on Anticosti Island is based on the chemical composition of plants rather than on their mechanical properties.

White-tailed deer preferred balsam fir to white spruce independently of texture. Although NDF, ADF and condensed tannin contents of balsam fir and white spruce were consistent with the preference observed, we cannot rule out that other factors may be involved in the strong preference of deer for balsam fir. Further studies should concentrate on the determination of other chemical constituents of balsam fir and white spruce, such as terpenes, to assess the strong selection observed for balsam fir over white spruce by white-tailed deer wintering in degraded boreal forests.

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The effects of decreasing winter diet quality on foraging behavior and life-history traits of White-tailed deer fawns

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RÉSUMÉ

La régénération du sapin baumier (*Abies balsamea*) à l'île d'Anticosti est compromise à cause de la pression de broutement par les cerfs. Présentement, l'alimentation hivernale des cerfs est composée de 70 % de sapin, de 20 % d'épinette blanche (*Picea glauca*) et de 10 % de lichens arboricoles. L'augmentation inévitable de la proportion d'épinette blanche dans la diète hivernale pourrait entraîner des effets négatifs sur la condition corporelle et les traits d'histoire de vie des cerfs. Nous avons simulé expérimentalement une détérioration de la qualité de l'alimentation hivernale et observé les effets sur la prise alimentaire, la condition corporelle et la survie des faons. Les faons recevant la diète pauvre (plus grande proportion d'épinette) avaient une plus grande prise alimentaire que les faons de la diète témoin, ce qui suggère une compensation face à une diminution de la qualité de la diète. La qualité de la diète n'a pas influencé la perte de masse et la survie des individus. Les cerfs semblent adaptés aux conditions restrictives d'Anticosti et pourraient se maintenir à haute densité malgré une proportion de 40 % d'épinette dans leur diète hivernale.

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. As 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 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 no significant effects of diet quality on body mass loss were observed. The activity budget of fawns was not influenced by diet quality, 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 winter, low quality browse and a high-density population. Even though balsam fir stands are being gradually replaced by white spruce stands, our results suggest that deer on Anticosti could maintain a high-density population by increasing the amount of white spruce in their diet. The long-term effects of a diet dominated by white spruce on deer body condition, survival and reproduction under natural conditions, however, remain to be addressed.

INTRODUCTION

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).

Forage intake in ruminants is influenced by a multitude of factors including digestibility, rate of passage through the gastrointestinal tract, local climatic conditions, forage quality and forage availability (Welch and Hooper 1993). It has been reported that most ungulates modify their foraging behavior in winter in order to minimize body mass loss and 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 energy expenditures are not reduced. 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 1980, Beier and McCullough 1990). The reduction of activity in winter has been reported in numerous ungulates (white-tailed deer: 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 is usually related 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). Winter body mass losses ranging from 20 % to 40 % have been observed 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 than 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 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 overbrowsing by deer, no balsam fir stands have regenerated since the 1930's (Potvin et al. 2003). The proportion of fir stands decreased from 40 % to 20 % since deer introduction and fir stands have been gradually replaced by white spruce 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 is usually 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 (*Picea glauca*) (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 litterfall (12.7 ± 4.1 kg of twigs/ha: Tremblay et al. 2005) and windthrown trees. Given that white spruce stands are gradually replacing fir stands on Anticosti, deer will likely 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 as it contains more fibre 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.

In this study, 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 (i.e. a high proportion of white spruce) would have lower forage intake, greater body mass loss, spend less time active and have a lower probability of survival than fawns fed on a higher quality diet (i.e. a low proportion of white spruce).

Study area

Anticosti is a 7943 km^2 island located in the Gulf of St.-Lawrence, Québec, Canada. The climate is sub-boreal and characterized by cool summers and long winters (Huot 1982). Landcover is 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 1800's. Since then, the population erupted due to lack of predators on the island. The Anticosti population is at the northern fringe of white-tailed deer distribution and a recent census estimated population size at >20 deer • km^{-2} (Potvin et al. 2004).

METHODS

Captures

Thirty-two fawns (6 to 7 months old) were captured in the falls 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® *pre-partum* cow feed) (Haulton et al. 2001). Chemical immobilization was also used with a mixture of Telazol® (200 mg/ml; Fort Dodge Animal Health, Fort Dodge, IA) and Xylazine (100 mg/ml; Bimeda-MTC Animal Health inc., Cambridge, ON) at doses of 6 mg/kg and 3 mg/kg respectively, administered remotely with a rifle and radio-transmitter equipped darts (Pneu-Dart Inc., Williamsport, PA) (Miller et al. 2003). Yohimbine (2 mg/ml; LLoyd Laboratories, Shenandoah, IA) was used as an antagonist for Xylazine (Wallingford et al. 1996). Fawns were sexed and weighed 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). Foot length measured at capture was used 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). All fawns were individually marked with ear tags and relocated in an outdoor enclosure. The Laval University Animal Care and Use Committee approved all procedures.

Experimental Design

An 80 m x 150 m enclosure surrounded by a 4 m-high game fence 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. The enclosure was further subdivided in 3 sections of 80 m x 50 m each with 30-40 % of the initial forest maintained as cover. Three wooden structures were built in each section to simulate wind-protected areas in the natural forest.

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

At the beginning of January of each year, fawns were divided into similar groups by sex and body mass. We formed a control group (2003: 5 males, 2 females; 2004: 2 males, 5 females), and a poor diet quality group (2003: 4 males, 2 females; 2004: 3 males, 3 females) during both years. There was no difference in initial body mass (kg) between each group of fawns in 2003 (control diet: 28.8 ± 1.9; poor diet: 28.2 ± 1.8; $t_{1,12} = -0.24$; $P = 0.81$) 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). The % of lichens in pellets was corrected for the high digestibility of lichens (Côté 1998) by comparing lichen presence in pellets and in rumen contents (Lefort 2002). Lichens in the litterfall can be an important source of forage for deer during winter on Anticosti (Tremblay et al. 2005). The poor diet quality was 50 % fir, 40 % spruce and 10 % lichens. Fir, spruce and lichens were harvested in forest stands typical of Anticosti. Because very little browse < 3 m from the ground was available (Tremblay et al. 2005), mature balsam fir trees were felled twice a week and the branches (≤ 1 cm in diameter) were collected 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. Fir (with lichens) and spruce were shredded separately in a wood chipper (Yard Machines-5 HP wood chipper, MTD products Inc., Valley city, OH) 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 microhistological 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 ± 2.6 % in the control diet and 37.4 ± 2.4 % in the poor diet (t-test testing the difference among the 2 diets: $t_{1,53} = 22.72$, $P < 0.0001$). Two kg of fresh food was given to each fawn daily, an amount considered sufficient to meet the daily metabolic needs of a 30 kg fawn (Huot 1982). We considered that fawns were limited by the quality and not by the quantity of food as there was always food left in the feeding troughs. Availability of snow made water accessible at all times.

Monitoring

Two sections of the enclosure were observed simultaneously on a daily basis for approximately 6 hours. From January to mid-February, the observations were made during the complete daylight period, i.e. from about 0830 to 1530 hours. From mid-February to mid-April, observations were conducted alternatively during the morning (sunrise to 1200) and the afternoon (1200 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 h and for 2004, 616 h). During each observation period, we noted the time spent feeding at the trough for each individual (± 1 minute) and weighed the amount of food (± 0.5 kg) eaten by the group at the end of the period. Individual food intake was estimated 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. All fawns were assumed to have 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 laying at a bed site. Daily activity rate was calculated from the ratio between active and inactive (i.e. laying 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 °C) and wind speed (W in km/h) 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: WCI: $13.12 + (0.6215*T) - (11.37*W^{0.16}) + (0.3965*T*W^{0.16})$. Wind chill index was used instead of temperature and wind speed alone as it included most of the variability in the weather data in only one parameter. Wind chill index was always tested as a single factor in the statistical analyses.

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

$$\% \text{ fat} = 1 - ((f - d) / f) \times 100\%$$

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 occurring 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). This was done 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 pseudoreplication, 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*diet, day*year and diet*year on forage intake (Mixed procedure, SAS Institute 8.0). Sex was not included in the analyses because initial mass (kg) did not differ between sexes (2003: males = 28.7 ± 1.3, females = 29.6 ± 2.7; $t_{1,14} = 0.29$, $P = 0.78$ and 2004: males = 28.4 ± 1.3, females = 25.6 ± 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). The individual was treated as a random variable. The effect of wind chill index was not tested here as it does not influence daily body mass and we were limited by the degrees of freedom of the number of parameters that could be tested.

Activity Budget

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

Survival

A multiple logistic regression was used 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 two years pooled.

All data are presented as means ± 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 diet quality (slope = -0.04 ± 0.01; $P = 0.01$) (Figure 2). This difference in the decrease of forage intake rate between diet qualities was similar for both winters (Table 2). The wind chill index did not influence forage intake rate of fawns during both winters (Table 2).

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 ($r = 0.05$; $F_{1,45} = 0.14$; $P = 0.71$) (Figure 3). The quantity of forage eaten by fawns fed on the control diet dropped from 1480 ± 40 g/individual at the beginning of the winter to about 1000 ± 50 g at the end of the winter, whereas it remained stable at 1200 ± 30 g for the group fed the poor diet (Figure 3). 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.

Table 2: 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. Interactions that are not presented were not significant (P > 0.05) and not included in the final model.

Factors	Effects	*df*	*F*	*p*
a) Food intake rate	Year	22	0.17	0.68
	Diet	22	3.72	0.07
	Diet*Year	22	2.24	0.15
	Day	22	56.37	<0.0001
	Year*Day	22	3.03	0.10
	Diet*Day	22	16.58	0.0005
	Diet*Year*Day	22	1.03	0.32
b) *BCI*	Year	17	0.77	0.39
	Diet	17	0.00	0.97
	Diet*Year	17	0.00	0.96
	Day	17	843.72	<0.0001
	Year*Day	17	4.69	0.04
	Diet*Day	17	0.09	0.77
	Diet*Year*Day	17	0.01	0.94
c) *Percentage of cumulative BCI loss*	Year	18	3.57	0.08
	Diet	18	0.45	0.51
	Diet*Year	18	0.74	0.40
	Day	18	721.13	<0.0001
	Year*Day	18	4.63	0.05
	Diet*Day	18	0.22	0.65
	Diet*Year*Day	18	0.15	0.71
d) *Activity budget*	WCI	22	308.85	<0.0001
	Year	22	66.84	<0.0001
	Diet	22	0.14	0.71
	Diet*Year	22	1.49	0.24
	Day	22	0.52	0.48
	Year*Day	22	38.23	<0.0001
	Diet*Day	22	0.02	0.88
	Diet*Year*Day	22	1.02	0.32

BCI: Body condition index (body mass (kg) / hind foot length (cm))

WCI: Wind chill index (C°) calculated from daily temperature (°C) and wind speed (km/h)

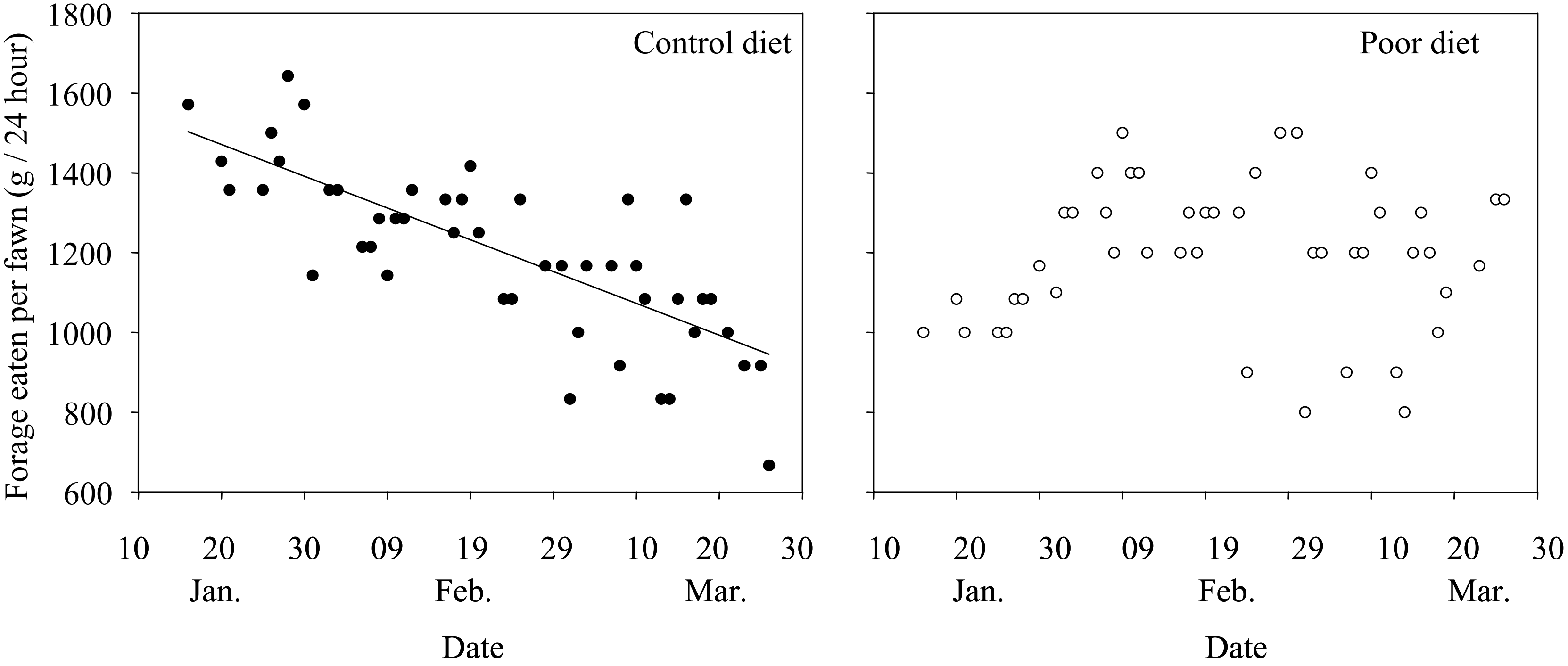

Figure 2: Decrease in forage intake rate during winter per observation period for groups of captive white-tailed deer fawns fed with 2 different quality diets on Anticosti Island, Québec, Canada. Data for winter 2003 and winter 2004 are pooled. Symbols represent the mean intake rate per observation period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

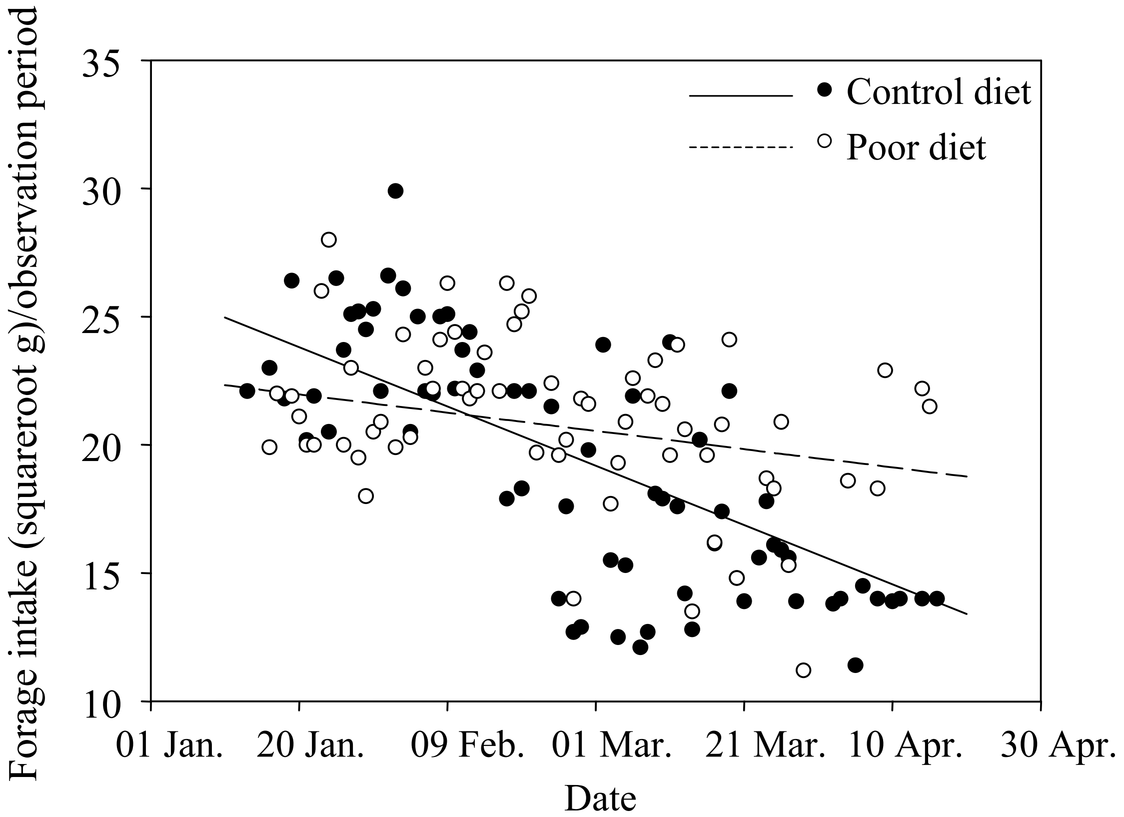

Figure 3: Forage eaten per fawn over 24-hour periods for captive white-tailed deer fawns fed with 2 diets of different quality in winter 2004, Anticosti Island, Québec, Canada.

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 2). However, we detected a significant year effect on both the variation of body mass and the percentage of cumulative body mass loss (Table 2). Fawns were smaller in 2004 and presented a higher cumulative percentage of body mass loss than fawns in 2003 (Figure 4). The near significant interaction between year and day on percentage of cumulative body mass loss (Table 2) 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; $P < 0.0001$) (Figure 4). The percentage of body mass loss for surviving fawns at the end of the experiment was relatively high for both years: 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 2). Despite much variability, there was no significant variation in time spent active during the winter in 2003 (slope: 0.00033 ± 0.00034, $P = 0.35$), while it increased significantly in 2004 (slope: 0.00305 ± 0.00037, $P < 0.0001$). Fawns were more active in 2003 (53 ± 2 % of the observation periods) than in 2004 (46 ± 2 %) (year effect in Table 2). Time spent active was highly influenced by the WCI as fawns reduced activity in cold weather (Table 1; Figure 5). 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, $P < 0.0001$) (Figure 5).

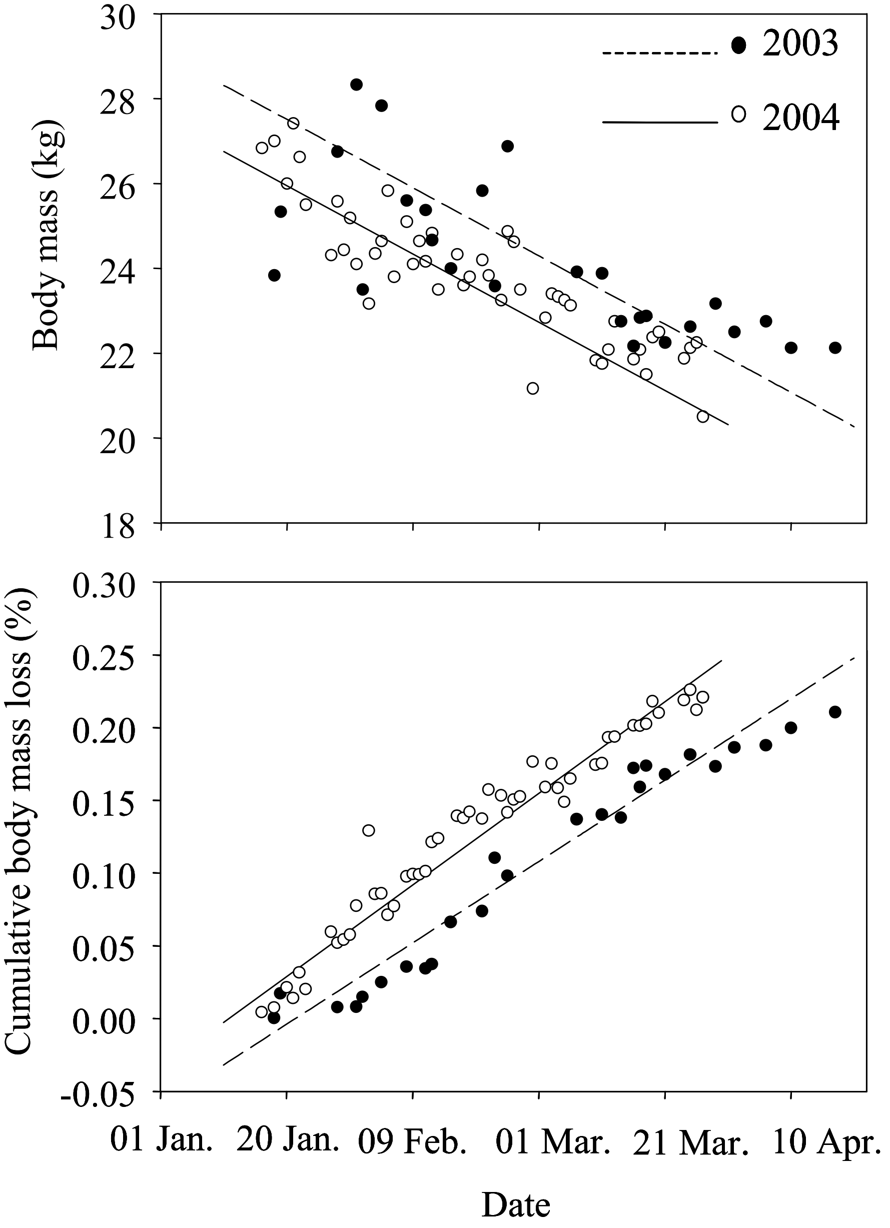

Figure 4: Body mass and percentage of cumulative body mass loss during the winters of 2003 and 2004 for captive white-tailed deer fawns on Anticosti Island, Québec, Canada. Since diet quality did not affect body mass and the percentage of cumulative body mass loss, the data for the 2 different quality diets were pooled. Symbols represent the mean body mass and percentage of cumulative body mass loss per observation period where n ≥ 3 fawns.

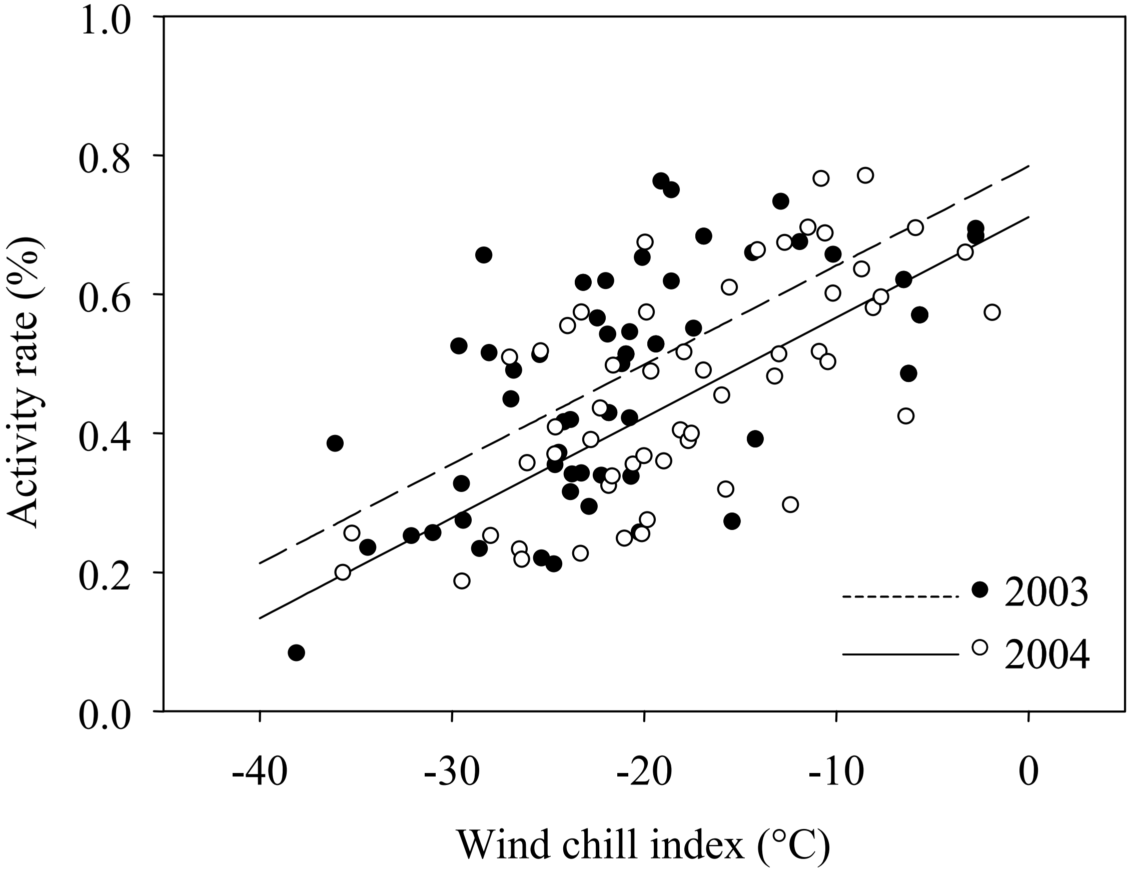

Figure 5: Relationship between the wind chill index (WCI) and the daily proportion of time spent active during the winters of 2003 and 2004 for captive white-tailed deer fawns on Anticosti Island, Québec, Canada. Data for 2 different quality diets were pooled. Symbols represent the mean proportion of time spent active per observation period.

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 death was very likely caused by starvation 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 ± 0.4 %, $n = 3$) and 2004 (7.1 ± 0.4 %, $n = 6$; $t = 1.43$, $P = 0.21$), and between each diet for pooled data (control diet: 7.0 ± 0.2 %, $n = 4$; poor diet: 7.0 ± 0.6%, $n = 5$; $t = 0.78$, $P = 0.21$).The probability of survival of fawns was not affected by year ($\chi^2 = 0.09$, $P = 0.77$), diet quality ($\chi^2 = 1.12$, $P = 0.29$) or the interaction year*diet quality ($\chi^2 = 0.01$, $P = 0.92$), but was strongly 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 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 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 no significant effects of diet quality on body mass were observed. The activity budget of fawns was not influenced by diet quality, but deer decreased activity in cold weather. Finally, the probability of survival of fawns was not affected by diet quality but was positively related to body mass at the onset of winter.

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 lead to physiological adaptation for energy conservation (Silver et al. 1969, Moen 1978). In our study, 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 has been 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 favour energy conservation and reduce intake rate (Owen-Smith 1994). Even when forage intake is reduced, 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 (Figure 1), and the proportion of forage eaten daily by individual deer in the poor diet group remained relatively constant throughout the winter (Figure 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. An increase of intake rate when forage quality was reduced has also been observed 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 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 when forage quality is reduced.

Decrease of Body Mass

Deer on Anticosti experience a negative energy balance in winter and lose 20 to 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 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). The slight difference observed in the rates at which deer lost body mass between the two winters may be explained by a combination of stochastic events (e.g. weather) or perhaps cohort effects (Pettorelli et al. 2002).

Activity Budget

Despite much variation in time spent active, fawns maintained a constant activity rate during the winter of 2003, while 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. The reduction of activity by ungulates observed in nature during winter has often been interpreted as an adjustment to winter climatic conditions to favour heat conservation and limit energy expenditures caused by thermoregulation and locomotion in deep snow (Moen 1976, Verme and Ozoga 1980). A decrease of 20 to 50 % of average active time from summer to winter has been observed in temperate ungulates (Georgii 1981, Georgii and Schröder 1983, Cederlund et al. 1989). Snow depth was generally considered the most important factor limiting activity in winter (Beier and McCullough 1990). In our experimental conditions, the abundance of forage, that was 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 (Figure 4). Diurnal activity patterns in northern ungulates are often correlated with ambient temperatures (Ozoga and Verme 1970, Ozoga 1972, Berger 1977, Beier and McCullough

1990). In the wild, deer have been observed to significantly decrease their activity rate at the beginning of winter and during cold days, and to 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 were observed during severe winters 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 was also found in other studies (White at 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 fall 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.

In conclusion, 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, the energetic costs of locomotion were reduced because forage was provided *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 will 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, inference about the effects of diet quality on deer body condition and foraging behavior could be directly made.

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, may also be critical for fawn survival during winter. Available resources during summer and fall 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

White-tailed deer on Anticosti Island are at the northern fringe of their range and experience high population density, long and harsh winter conditions and low availability of good winter forage (Huot 1982, Potvin et al. 2003, Plante et al. 2004). Although we doubled the proportion of white spruce in the winter diet, surprisingly deer did not loose more weight than those fed the natural winter diet. This suggests 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 windthrown 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 more than 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.

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Is winter diet quality related to deer body condition at high population density? An experiment using urine profiles

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RÉSUMÉ

La haute densité de cerfs observée sur l'île d'Anticosti (Québec, Canada), ainsi que la diminution graduelle du sapin baumier (*Abies balsamea*) causée par le surbroutement par le cerf de Virginie (*Odocoileus virginianus*) pourrait les forcer à inclure plus d'épinette blanche (*Picea glauca*) dans leur alimentation d'hiver. Nous avons évalué la détérioration de la condition corporelle et la détoxication des produits métaboliques secondaires des plantes par l'analyse des rapports 3-méthylhistidine:créatinine et acide glucuronique:créatinine dans l'urine récoltée dans la neige de faons sauvages captifs. Doubler la proportion d'épinette dans l'alimentation d'hiver (20% à 40%) n'a pas accéléré la détérioration de la condition corporelle mais a augmenté la concentration d'acide glucuronique dans l'urine, suggérant qu'une alimentation plus riche en épinette soit plus toxique. Une relation faiblement positive a été observée entre le rapport de 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 temps, le pourcentage cumulatif de perte de masse et le nombre de jours avant la mort n'a été observée. Nous concluons que les cerfs d'Anticosti peuvent s'adapter phénotypiquement à une diète de mauvaise qualité pendant l'hiver.

ABSTRACT

On Anticosti Island (Québec, Canada), the ongoing diminution of balsam fir (*Abies balsamea*) due to overbrowsing by white-tailed deer (*Odocoileus virginianus*) may force deer to include a higher proportion of white spruce (*Picea glauca*), a browse of low quality, in their winter diet. The deterioration of deer body condition and the detoxification of secondary plant metabolites were assessed with 3-methylhistidine:creatinine and glucuronic acid:creatinine ratios, respectively, in urine collected in snow from captive but wild caught white-tailed deer fawns. Experimentally doubling the amount of white spruce in the winter diet of deer (from the current 20% under natural conditions to 40%) did not increase the deterioration of body condition but increased the concentration of 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 3-methylhistidine:creatinine ratio and the number of days left before death, indicating that the 3-methylhistidine:creatinine ratio could not be used to detect approaching starvation for deer on Anticosti. Similarly, no relation were observed between the ratio of glucuronic acid:creatinine and date, percent cumulative mass loss or the number of days left before death. We conclude that white-tailed deer on Anticosti and possibly elsewhere at the northern fringe of their distribution could adapt to a winter diet of very low quality.

INTRODUCTION

Wild northern ungulates regularly face severe winters, which may have important impacts on their body condition, survival and 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 the increased costs of thermoregulation and locomotion in deep snow (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., 2005), 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 and well defended plants with higher concentrations of 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). It has been shown that conifers are particularly rich in plant secondary metabolites and have lower nutritive value than less defended and more readily digestible deciduous browse (Tahvanainen et al., 1991).

Consuming a mixture of plant species usually minimizes 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 pathway is the 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 (i.e. a loss of glucose and of the energy required for the reaction to occur) and a drop in urine pH, which may alter kidney function (Dearing and Cork, 1999).

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

Urine analyses have been used in the past as a tool to evaluate several parameters of body condition or diet quality of wild herbivores, such as catabolism of body protein and toxin detoxification (Garrott et al., 1996). The catabolism of skeletal muscle protein can be measured in urine through the concentration of 3-methylhistidine (Fitch et al., 1986; DelGiudice et al., 1998). The analysis of urine deposited in snow appears to be a reliable and non-invasive method to assess body condition, eliminating the necessity to immobilize wildlife (Mech et al., 1987; DelGiudice et al., 1988; White et al., 1995; White, 1997). Many studies in the recent past have used urinary metabolites to monitor different physiological processes successfully (DelGiudice et al., 1988; 1998; Pils et al., 1999; Servello and Schneider, 2000). The method is particularly useful when repeated measurements are available on the same individual, i.e. when each animal can be compared to itself and daily or weekly variations in urine metabolites can be assessed (DelGiudice et al., 1997).

Since its introduction on Anticosti Island (Québec, Canada) in the late 1800's, the white-tailed deer population irrupted from roughly 200 to over 120 000 animals today (Potvin et al., 2003). Such a high-density (about 15-20/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, balsam fir stands were estimated to cover about 40% of the island's surface area. Today, this value is down to about 20% (Potvin et al., 2003). Although insect epidemics (e.g.: spruce budworm *Choristoneura fumiferana* and hemlock looper *Lamdina fiscellaria*) and forest fires have been partly responsible for the fir decline on the island, deer overbrowsing is the main factor by its effects on suppressing regeneration (Potvin et al. 2003). Potvin et al. (2003) predicted that most balsam fir stands will be replaced by white spruce stands within the next 40 to 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 only access to white spruce (*Picea glauca*), which is highly available, and balsam fir (*Abies balsamea*), which is only available when trees are thrown down by the wind or in the litterfall (Tremblay et al., 2005).

Although balsam fir is scarcely available compared to 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 while white spruce represents about 20% of the winter diet (Lefort, 2002). Although both species are low quality browse, balsam fir is of higher quality than white spruce. Fibre content (NDF and ADF) and condensed tannins are higher in white spruce than in balsam fir, reducing its digestibility and possibly making it more costly to metabolize than fir (Chapitre 1). The diet is completed by arboreal lichens.

Our objectives were to evaluate the effects of increasing the proportion of white spruce in the diet of white-tailed deer fawns (1) on the deterioration of body condition measured through the concentration of 3-methylhistidine in snow-urine and (2) on the detoxification of plant secondary metabolites in the diet estimated through the excretion of glucuronic acid. We hypothesized that 3-methylhistidine ratios in the snow-urine of deer fed a diet containing a higher proportion of white spruce than those fed a control diet similar to natural conditions, would increase (1) sooner in the winter, (2) with cumulative body mass loss and (3) in the few days before death by inanition. We also hypothesized 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 is located in the gulf of St.-Lawrence, Québec, Canada (49° 28' N, 63° 00' W) and encompasses an area of about 8000 km². The climate is sub-boreal 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 (*P. mariana*) (Potvin et al., 2003).

Capture and captivity

In the falls of 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 canon-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 riffle and radio-transmitter equipped darts (Pneu-Dart Inc., Williamsport, PA). 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 (BCI), obtained by dividing body mass (kg) by hind foot length (cm), a measure of structural size. 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 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 Laval University Animal Care and Use Committee approved theses procedures. The animals were fed with a mixture of shredded balsam fir and white spruce at a proportion of 80% fir and 20% spruce until the beginning of the trials.

Experimental diets

At the beginning of January of each year, fawns were divided into similar groups based on their social rank, body mass and sex (Taillon, 2005). Each group was fed with a diet composed of different proportions of white spruce completed with 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), was composed 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) was composed of 40% white spruce, which simulated 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. within 1-3 m in height. 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 of one of the diets component. Microhistological analyses of faeces confirmed that no selection for any of the diets component occurred (Chapitre 2). Two kg of fresh food (i.e. about 1 kg dry) were given per fawn daily which 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 the quality and not by the 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 since snow was always available.

Data and sample collection

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

$$[1] \qquad W = 13.12 + 0.6215 \times T_{air} - 11.37 \times V_{10m}^{0.16} + 0.3965 \times T_{air} \times V_{10m}^{0.16}$$

where T_{air} is the air temperature in °C and V_{10m} is wind velocity in km/h at 10 m from the shredded, 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 (C), 3-methylhistidine (3-mh) and glucuronic acid (G) in the samples. We assayed C and G directly from the thawed samples. For the C, we used commercially available kits from Catachem (in 2003) and StanBio (in 2004). The Catachem kits were discontinued in 2004. The methods for the determination of G 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 to a standard curve made with pure glucuronic acid (Sigma-Aldrich Canada, Oakville, ONT.).

For the determination of the concentration of 3-mh, 25 ml of the thawed samples were lyophilized with 25 ml of sodium carbonate (2M) 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). The methods for the preparation of the samples and the determination of 3-mh 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 in snow, the metabolites were computed as ratios of creatinine (C), since C secretion is constant for 24h periods and is relative to body mass (DelGiudice et al. 1988). The calculated ratios are expressed in µmol:mg and mg:mg for 3-mh:C and G:C ratios, 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 (ID) as independent subjects and the initial body condition index (BCI; initial body mass divided by tarsal length) as the covariate with a spatial power covariance structure (proc mixed, SAS institute, V.8.0; (Fujisawa, 1996). Considering repeated measurements on the same individuals is a strong experimental design, because each animal can be compared to 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 BCI and all possible interactions on the log transformed ratios of 3-mh:C and G:C.

To evaluate the relationships between urine metabolite ratios (3-mh:C and G:C ratios as dependent variables) and 1) time (weeks since 1 January), 2) the percentage of cumulative mass loss of fawns during winter and 3) the number of days before death by inanition (as independent variables), we fitted third degree polynomial regressions to the data.

All data are presented as means ± standard errors (SE) and we considered a P-value ≤ 0.05 significant.

RESULTS

The wind chill index differed between years (2003: -13.8ºC±0.7; 2004: -11.7ºC ±0.7; $F_{1,204} = 15.15$, $r^2 = 0.02$, $P < 0.0001$), 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 two years.

Even though winter 2003 was colder than winter 2004, no year effect was noted on the 3-mh:C 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 BCI ($F_{1,20} = 0.54$, $r^2 = 0.02$, $P = 0.5$), 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-mh:C ratios. The 3-mh:C ratios, however, increased during the winter (Figure 8a; $F_{13,69} = 2.52$, $r^2 = 0.33$, $P = 0.007$) and with the cumulative mass loss ($F_{3,107} = 9.49$; $r^2 = 0.21$, $P<0.0001$), which was highly significant but dependent on only a few data points (Figure 8b). In figure 8a, one data point at the top right corner of the graph appears to have a great influence on the relationship between weeks from 1 January and the 3-mh:C ratio. However, we conducted the analysis without this data point and the relation was still significant ($F_{3,106} = 3.22$; $r^2 = 0.30$, $P = 0.004$). No relationship was found between 3-mh:C ratios and the number of days left before death ($F_{3,52} = 0.14$; $r^2 = 0.01$, $P = 0.9$; Figure 8c).

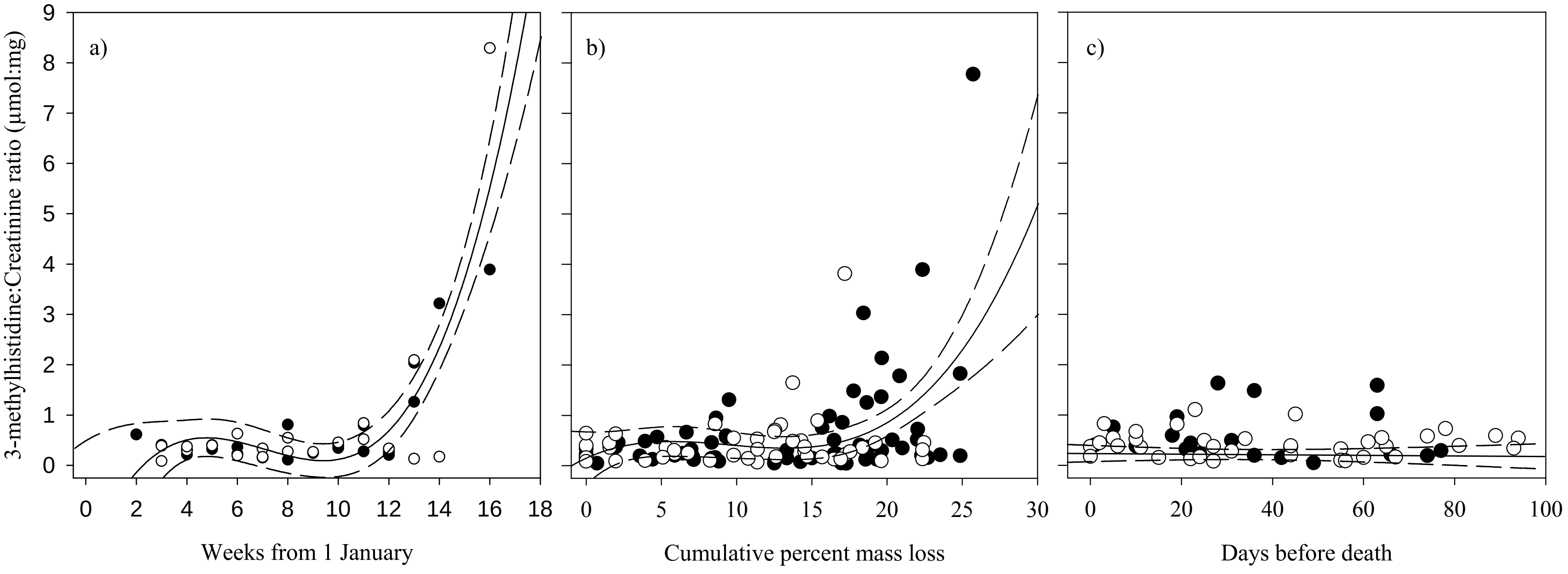

Figure 6: The evolution of 3-methylhistidine:creatinine ratio (µmol:mg) measured in snow-urine samples from captive white-tailed deer fawns fed different winter diet qualities on Anticosti Island, in relation to the number of weeks since 1 January (a), the percentage of cumulative mass loss since early January (b), and the number of days left before death (c). Full circles are for fawns on the control diet (20% white spruce, 80% balsam fir) and open circles are for fawns on the poor diet (40% white spruce, 60% balsam fir). The fitted curves (solid line) are 3rd degree polynomial regressions for the pooled data of both diets and the dashed lines are the 95% confidence intervals.

G:C 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 (31.6±2.5 mg/mg) had significantly higher G:C ratios than those on the control diet (20.6±1.3 mg/mg) ($F_{1,16}= 18.65$, $r^2 = 0.21$, $P = 0.0005$). G:C ratios decreased with increasing initial BCI in control deer ($F_{3,31} = 3.32$, $r^2 = 0.24$, $P = 0.03$, Figure 9). No relationship, however, was noted for deer on the poor diet ($F_{1,34} = 0.0002$, $r^2 = 0.0$, $P = 0.9$, Figure 9) or for pooled samples of both diets ($F_{1,69} = 0.1$; $r^2 = 0.0$, $P = 0.7$).

G:C ratios did not vary through the winter ($F_{12, 32} = 1.01$, $r^2 = 0.16$, $P = 0.5$, Figure 10a), and the interaction between weeks since 1 January and diet was not significant ($F_{8, 32} = 1.67$, $r^2 = 0.49$, $P = 0.1$, Figure 10a). Cumulative mass loss ($F_{1,72} = 0.1$, $r^2 = 0.0$, $P = 0.8$, Figure 10b) and number of days left before death ($F_{1,123} = 3.2$, $r^2 = 0.03$, $P = 0.8$, Figure 10c) did not affect G:C ratios.

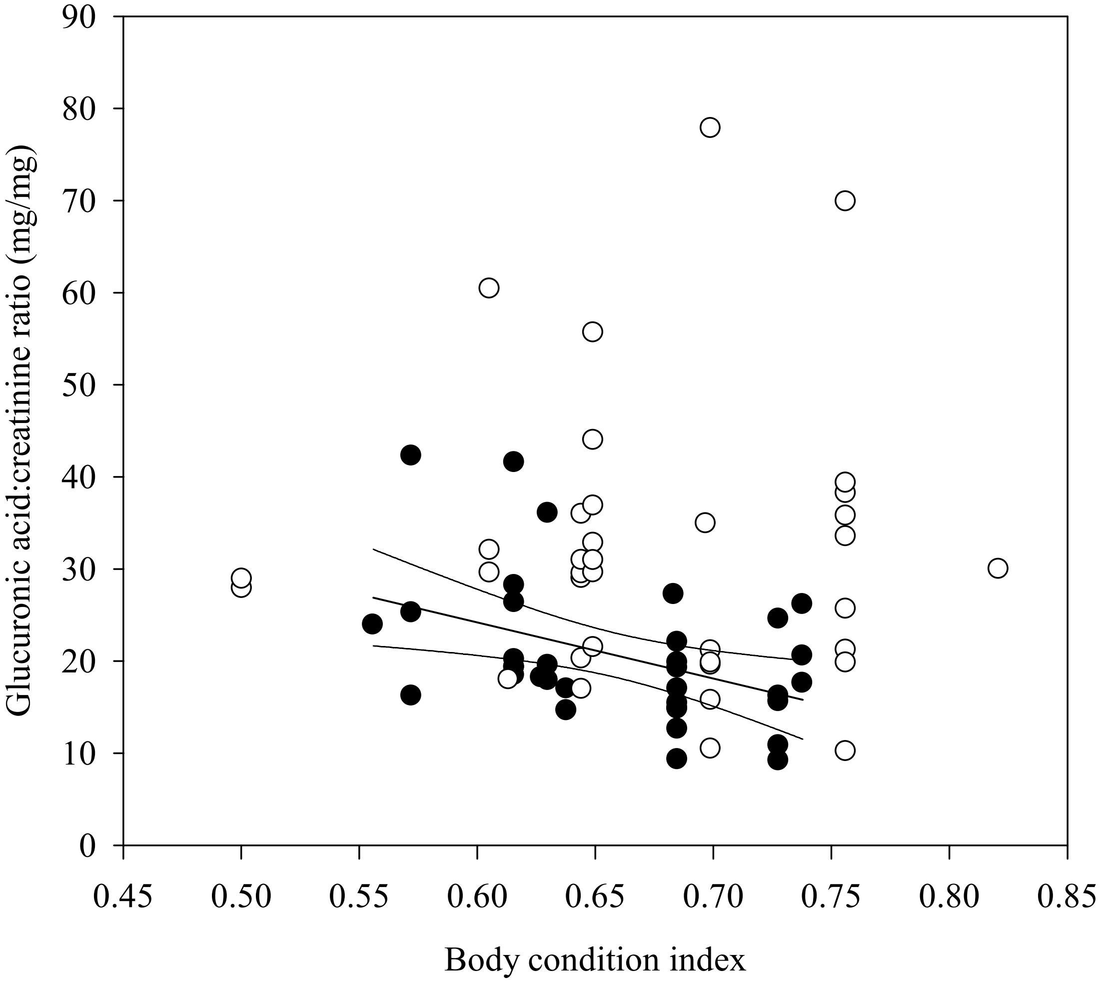

Figure 7: The relationship between the glucuronic acid:creatinine ratio (G:C; mg/mg) measured in snow-urine and the initial body condition index (BCI; initial body mass/rear tarsal length) of white-tailed deer fawns fed two different quality diets. Full circles are fawns on the control diet (20% white spruce, 80% balsam fir) and open circles are fawns on the poor diet (40% white spruce, 60% balsam fir). The relationship between G:C and BCI was significant for the control animals only (slope: -61.0±22.5; F = 7.4; r^2 = 0.18; P = 0.01).

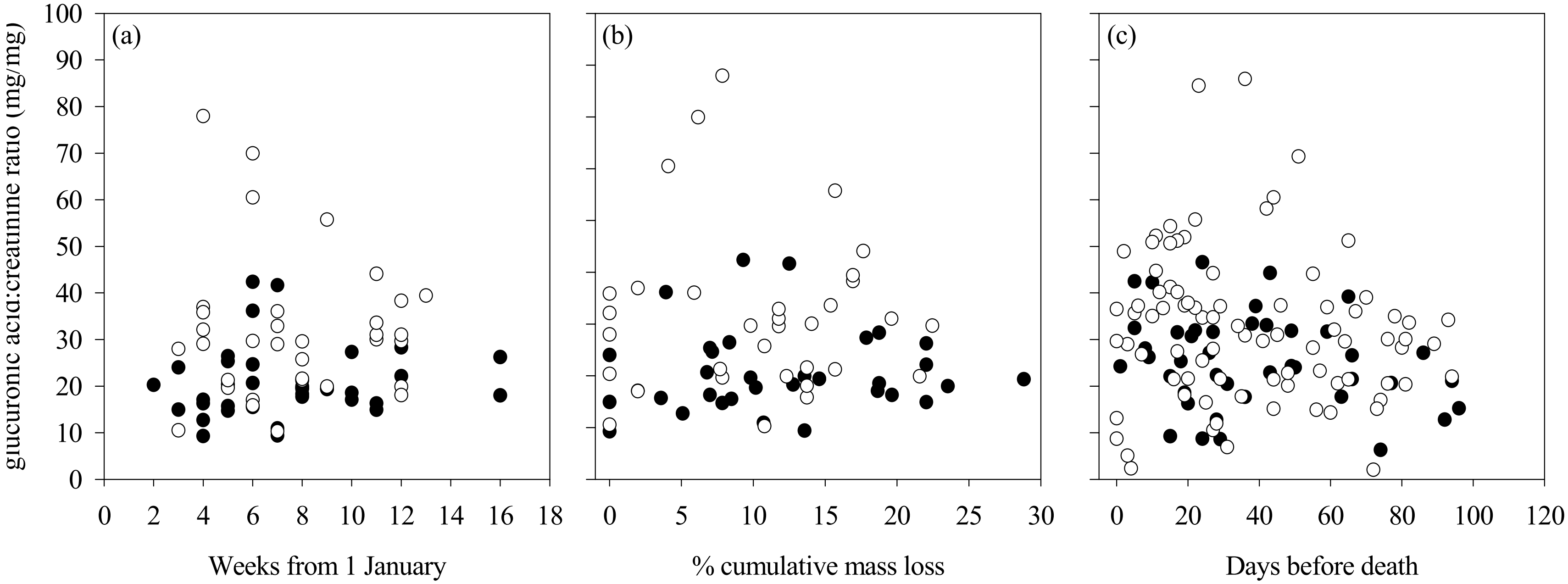

Figure 8: The evolution of glucuronic acid:creatinine ratio (mg:mg) measured in snow-urine samples from captive white-tailed deer fawns fed different quality diets on Anticosti Island, in relation to weeks since 1 January (a), the percentage of cumulative mass loss (b), and the number of days left before death (c). Full circles are for fawns on the control diet (20% white spruce, 80% balsam fir) and open circles are for fawns on the poor diet (40% white spruce, 60% balsam fir).

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 (G:C) ratio. It had no significant effect, however, on the absolute deterioration of body condition or the rate of decrease of condition over winter measured with 3-methylhistidine:creatinine (3-mh:C) ratios in snow-urine. Due to 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 as no other browse, except black spruce, is available. White spruce is of lower quality than fir, and contains more fibre and condensed tannins than fir (chapitre 1). Contrary to our expectation, however, it seems that an increase in the proportion of white spruce up to 40% in the winter diet of deer, does not increase body protein catabolism. We cannot, however, predict the physiological effects of the complete eradication of balsam fir in the winter diet of deer on Anticosti even though we suspect that it will be detrimental to deer.

We found a significant, but highly variable relationship, between urinary 3-mh:C ratios and the percent cumulative mass loss for deer on both diets (Fig. 8b). DelGiudice et al. (1998) observed a strongly significant curvilinear relationship between urinary 3-mh:C ratios and the percent cumulative mass loss in food restricted white-tailed deer compared to our experiment where deer were fed *ad libitum*. Their results likely differed from ours because they applied a quantitative restriction while our experiment was based on a reduction of forage quality. 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 sufficient access to browse. We have shown elsewhere that winter diet did not affect overwinter mass loss in deer from our study population (chapitre 2). 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. While deer in our study lost substantial amounts of body mass during winter (up to 30% of their initial body mass, chapitre 2), 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-mh:C ratios increased during winter (Fig. 8a), 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. Then, the myosin contained in muscles is 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-mh:C ratios through winter was expected (Fig. 8a), 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. Morever, we did not detect an increase in 3-mh:C in the few days preceding death by inanition (Fig. 8c). 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 (Huot, 1982; 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 such a reduction, which would lead to the deterioration of body condition and thus be reflected in 3-mh:C ratios.

We found a weak negative relationship between BCI and G:C ratios for animals on the control diet only (Fig. 9). This interaction between diet quality and BCI may indicate that the relative detoxification cost of forage is lower for larger animals on the control diet than for smaller animals. The detoxification costs for animals on the poor diet may be too high for all fawns, irrespective of body mass, thus cancelling the ability of larger fawns to better cope with higher concentrations of toxins.

The G:C ratios were significantly higher in samples for animals from the poor diet than from control deer. This 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 which showed that white spruce contained more fibre and condensed tannins than balsam fir on Anticosti (Chapitre 1). Therefore, we can hypothesize that white spruce contains secondary plant metabolites that are more costly for white-tailed deer to detoxify than 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 has been found that generalist woodrats (*Neotoma albigula*) lost more weight and had higher thermoregulation costs on a monospecific diet and on a diet containing one specific plant secondary metabolite than specialist woodrats (*N. stephensi*) (Dearing et al., 2000; McLister et al., 2004). 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.

As we hypothesized, the G:C ratios in snow-urine did not vary overwinter. This suggests that the absolute metabolic cost of forage detoxification did not increase during winter. However, since the secondary plant metabolites load remained constant and the metabolizable energy available to the detoxification pathway decreased in time, because of the increase in the costs of other metabolic processes (e.g. thermoregulation and locomotion), the relative costs of detoxification may have increased. However, since we did not measure the available metabolizable energy intake and we do not know the amount of energy allocated to the different metabolic processes, it is not possible to determine precisely the costs of detoxification in this experiment.

The G:C ratios were not related to cumulative body mass loss or to the number of days left before death since the absolute cost of detoxification likely remained constant through winter because the diet composition did not change. This suggests that the secondary plant metabolites load is not the main factor explaining the deterioration of the body condition observed over the winter. 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 verified. 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 G:C ratios in snow-urine and plant chemical analyses (Chapitre 1), this difference was not great enough to lead to substantial physiological effects on body condition. We did, however, confirm the hypothesis that the 3-mh:C ratios increased with time, indicating that the body condition of deer deteriorated throughout the winter, as found by DelGiudice et al. (1998).

Since no effect of diet on body condition deterioration was 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, since the availability of winter browse on Anticosti is almost exclusively composed of spruce (Potvin et al., 2003; Tremblay et al., 2005), but that the winter diet of Anticosti deer is approximately 70% balsam fir, it is clear that deer prefer fir. In addition, our results on G:C ratios shown above, on the chemical analyses of white spruce and fir (chapitre 1), and on preference tests (chapitre 1), 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 higher concentrations of white spruce in the diet than experimented here (i.e. >40%). This would enable managers to evaluate the potential consequences of a winter diet shift towards white spruce on body condition, survival and eventually the population dynamics of the white-tailed deer population of Anticosti Island.

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Conclusion

L’objectif principal de ce projet de recherche était de comprendre les interactions entre les cerfs de Virginie de l’île d’Anticosti et leur nourriture d’hiver. Nous avons tenté de déterminer les raisons qui pourraient expliquer la préférence des cerfs pour le sapin, une essence faiblement disponible comparativement à l’épinette blanche. Le broutement intense sur le sapin a pour effet d’empêcher la régénération des sapinières sur l’île et elle pourrait entraîner la disparition des sapinières à moyen ou long terme (Potvin et al., 2003). La réduction de la disponibilité du sapin pourrait ainsi forcer les cerfs à augmenter significativement leur consommation hivernale d’épinette blanche et leur occasionner plusieurs changements comportementaux ou physiologiques à court et à long terme.

Lors des expériences en captivité, nous avons constaté que bien que les cerfs aient eu accès au sapin baumier et à l’épinette blanche en quantités égales, ils préféraient de loin le sapin puisque celui-ci composait 90 % de la prise alimentaire, contre 10% pour l’épinette blanche. Les lichens arboricoles, généralement disponibles en petits fragments sur la surface de la neige comme source de nourriture hivernale (Tremblay et al., 2005), n’ont pas été inclus dans la nourriture offerte aux animaux en enclos mais étaient présents sur les branches de sapin offertes aux cerfs.

Nous avons observé que l’épinette blanche était significativement plus fibreuse que le sapin baumier, ce qui peut causer un ralentissement de la digestion et donc du taux de passage de l’épinette dans le tractus gastro-intestinal (Goering et Van Soest, 1970; Hanley, 1982; Robbins et al., 1987b; Tixier et al., 1997). De plus, une diminution de la digestibilité de la nourriture causée par une plus grande proportion de fibres peut diminuer l’extraction de l’énergie et de certains nutriments disponibles dans la nourriture pour le ruminant (Fahey Jr. et Berger, 1993; Ferrell, 1993). Nos résultats montrent également que la quantité de protéines dans le sapin et l’épinette ne semble pas être un facteur déterminant dans la sélection effectuée par le cerf. La végétation consommée par les ruminants doit contenir une quantité minimale de protéines afin d’assurer la présence dans le rumen d’une flore de micro-organismes adéquate (Owens et Zinn, 1993). Bien que la concentration en protéines dans le sapin et l'épinette blanche ait été similaire et ne peut donc pas expliquer la préférence du cerf pour le sapin, dans les deux cas, la concentration de protéines était inférieure au seuil minimum de 6 % reconnu par Owens et Zinn (1993) pour qu'une plante soit sélectionnée par un ruminant.

Nos résultats ont montré que les phénols totaux n'influençaient pas la sélection du sapin par rapport à l'épinette puisque leur concentration était similaire chez les deux essences. Dans la littérature, l'utilisation des phénols totaux comme indicateur de toxicité potentielle des plantes est contestée (Mole et Waterman, 1987a; 1987b; Lawler et al., 1998). Selon Lawler et al. (1998), la mesure des phénols totaux est trop grossière pour permettre d'expliquer la sélectivité d'un animal pour un certain nombre de plantes et seul certains phénols bien précis pourraient indiquer la présence de toxines néfastes par des signaux gustatifs.

Il semble aussi que certains phénols, comme les tannins condensés, puissent influencer la sélection alimentaire des ruminants (Robbins et al., 1987a; Silanikove et al., 2001). Cependant, d'autres études ont démontré que certains ongulés, comme le cerf de Virginie, sont peu affectés par les tannins, étant donné que des protéines riches en proline, présentes dans leur salive, leur permettent de précipiter et d'inactiver les tannins condensés (McArthur et al., 1991; Hagerman et Robbins, 1993; Harborne, 2001). Conséquemment, bien que l'épinette blanche contienne significativement plus de tannins condensés que le sapin baumier, les effets des tannins condensés sur la sélection alimentaire sont probablement faibles et s'additionnent simplement aux différences biochimiques qui existent entre le sapin et l'épinette. Enfin, tout comme pour les phénols totaux, Lawler et al (1998) croient que la mesure des tannins condensés n'est pas suffisante pour l'étude de la sélectivité. Une étude approfondie de la composition chimique précise des phénols, qui comprendrait les tannins condensés et hydrolysables et d'autres produits métaboliques secondaires du sapin et de l'épinette, pourrait possiblement expliquer davantage la sélection alimentaire observée pour le cerf en hiver.

L'analyse des terpènes, une autre classe de produits métaboliques secondaires, pourrait également permettre de mieux comprendre la sélection alimentaire hivernale du cerf à Anticosti (Harborne, 1991; 2001; Vourc'h et al., 2002). Par exemple, l'épinette blanche contient beaucoup plus de camphre que le sapin (von Rudloff, 1972; Hunt et von Rudloff, 1974), un terpène reconnu pour avoir un effet dissuasif sur le cerf rouge (*Cervus elaphus*), le lièvre d'Amérique (*Lepus americanus*) et certaines espèces de campagnols (*Microtus* spp) (Harborne, 1991; 2001). Il est possible que la plus forte concentration de camphre dans l'épinette blanche soit en partie responsable de la préférence du cerf pour le sapin baumier. Cette hypothèse mériterait d'être vérifiée.

Un résultat surprenant de notre étude est que même si la quantité de sapin offerte aux cerfs n'était pas limitée, ceux-ci consommaient tout de même un peu d'épinette blanche. Deux hypothèses alternatives pourraient expliquer ce résultat. Premièrement, il est possible que pour identifier l'épinette blanche, les cerfs doivent y goûter et donc en manger un peu. La deuxième hypothèse s'appuie sur le principe de dilution des produits métaboliques secondaires contenus dans les plantes. Bien que le sapin soit une nourriture de meilleure qualité que l'épinette blanche, il s'agit quand même d'une ressource de faible qualité qui contient des produits métaboliques secondaires potentiellement toxiques. Nos résultats appuient donc l'hypothèse selon laquelle les espèces généralistes, comme le cerf de Virginie, doivent varier leur diète afin de minimiser les coûts de détoxication associés à une diète monospécifique (Dearing et al., 2000).

Nous avons constaté que la diminution de la qualité de la diète par l'augmentation de la proportion d'épinette blanche dans celle-ci ne semblait pas influencer de façon très marquée la diminution de la prise alimentaire au cours de l'hiver. Pour leur part, Gray et

Servello (1995) ont remarqué que la prise de matière sèche était positivement corrélée à la teneur en énergie digestible. Nous pouvions donc nous attendre à ce que la prise alimentaire des cerfs ayant une diète de moins bonne qualité soit inférieure à celle des cerfs avec la diète témoin. Cependant, nous avons remarqué que les animaux ayant accès à une diète de meilleure qualité mangeaient moins que ceux qui se nourrissaient d'une diète de faible qualité pendant l'hiver 2004. Nous suggérons que les cerfs aient développé en quelque sorte une stratégie de compensation au cours de l'hiver en consommant plus de nourriture lorsque celle-ci était de faible qualité (Silver et al., 1969; Ozoga et Verme, 1970; Suttie et al., 1983).

Bien que leur masse corporelle ait diminué au cours de l'hiver, une réduction de la qualité de l'alimentation n'a pas accéléré la perte de masse. Kojola et al. (1998) ont constaté que les rennes (*Rangifer tarandus*) dans le nord de la Finlande ayant une alimentation plus pauvre pendant l'hiver perdaient plus de masse que ceux ayant une meilleure alimentation. Similairement, Pettorelli et al. (2001) ont observé que les chevreuils (*Capreolus capreolus*) avait une masse corporelle généralement supérieure dans un habitat de meilleure qualité. Par contre, dans notre étude, un effet de l'année a été observé sur la variation de la perte de masse et sur le pourcentage cumulatif de perte de masse. Les faons en 2004 étaient, en moyenne, plus petits et ont eu un pourcentage cumulatif de perte de masse supérieur à ceux de 2003. De plus, bien que non significative, l'interaction entre l'année et le temps (jours) suggère que les faons de 2004 ont perdu de la masse légèrement plus rapidement que ceux de 2003. Puisque l'hiver était plus rigoureux en 2003 qu'en 2004, nous n'avons pas d'explication pour ces résultats.

Nous avons aussi remarqué que les cerfs maximisaient la conservation d'énergie en concentrant leurs périodes d'activité quand il faisait moins froid, le taux d'activité étant relié négativement à l'indice de refroidissement éolien. La diminution du taux d'activité durant l'hiver a été observée chez l'orignal (*Alces alces*) par Cederlund et al. (1989). Cette stratégie permettrait aux faons de minimiser la perte d’énergie causée par la thermorégulation (Moen, 1976). Cependant, puisque les cerfs ont eu accès à de la nourriture fournie *ad libitum* et qu’ils ont entretenu un réseau de sentiers dans les enclos expérimentaux, ceux-ci n’ont pas eu besoin de limiter les déplacements reliés à la recherche de nourriture pour économiser l’énergie. Par conséquent, les coûts associés aux déplacements dans la neige profonde étaient minimisés, ce qui avait pourtant été proposé comme étant le facteur principal de diminution du niveau d’activité pendant l’hiver (Beier and McCullough, 1990). Contrairement à nos prédictions, la qualité de l’alimentation n’a pas influencé le budget d’activité.

Nous avons aussi constaté que le principal facteur déterminant la survie hivernale des faons à Anticosti était la condition corporelle initiale. Ce résultat correspond à ce qui est mentionné dans la littérature chez le cerf mulet (White et al., 1987; Bartmann et al., 1991), le wapiti (Cook et al., 2003) et le caribou (Skogland, 1985). Si les faons accumulent assez de gras pendant l’été et l’automne, ils augmentent leur chance de survivre à l’hiver (Lesage et al., 2001).

La diète plus riche en épinette blanche était plus toxique que la diète naturelle puisque les animaux nourris de la diète expérimentale avaient un rapport acide glucuronique:créatinine plus élevé que les témoins. Des résultats similaires ont été obtenus par Servello et Schneider (2000). Ils ont observé que les cerfs qui avaient une alimentation plus riche en sapin baumier que ceux ayant une alimentation commerciale avaient plus d’acide glucuronique dans leur urine, augmentant donc le coût associé à la détoxication des produits métaboliques secondaires contenus dans le sapin (Dearing et Cork, 1999; Mangione et al., 2001). Nos résultats ont aussi montré que le rapport acide glucuronique:créatinine ne variait pas dans le temps et qu’il n’était pas relié à la masse corporelle. Ceci peut s’expliquer par le fait que le niveau de toxicité au cours de l’hiver ne changeait pas pour chacune des diètes et que le coût de détoxication n’était pas proportionnel à la masse corporelle, du moins à l'intérieur de l'étendue de masses corporelles mesurées.

La concentration de 3-méthylhistidine a augmenté significativement au cours de l'hiver, ce qui correspond aux résultats observés par DelGiudice et al. (1998). Cependant, l'augmentation de la proportion d'épinette blanche, jusqu'à 40 % de la diète, ne semblait pas influencer le taux de catabolisme des protéines musculaires puisque la sécrétion de la 3-mh n'était pas plus élevée et n'a pas augmenté plus rapidement chez les cerfs nourris avec la diète expérimentale que chez les témoins. Ceci peut indiquer que la différence de qualité entre la diète témoin (80 % de sapin baumier et 20 % d'épinette blanche) et la diète expérimentale (60 % de sapin et 40% d'épinette) n'était pas assez grande pour influencer le taux de détérioration de la condition corporelle. Nous avons tout de même observé une faible relation significative entre le rapport 3-méthylhistidine:créatinine et le pourcentage de perte de masse cumulatif durant l'hiver, ce qui correspond à ce que rapporte la littérature (DelGiudice et al., 1998).

De manière surprenante par contre, le rapport 3-méthylhistidine:créatinine n'était pas relié au nombre de jours restant avant la mort. Étant donné que la sécrétion de la 3-mh est reliée au catabolisme des protéines musculaires et que les animaux en restriction alimentaire prolongée doivent puiser dans leurs muscles squelettiques afin d'assurer leur métabolisme, nous nous attendions à ce que le rapport 3-méthylhistidine:créatinine augmente de plus en plus quelques jours avant la mort, ce qui n'a pas été le cas. Il est possible que lorsque la condition de l'animal est détériorée au point de s'approcher ou de dépasser un seuil de non-retour, les fonctions métaboliques soient fortement réduites afin de conserver l'énergie le plus possible et de concentrer celle-ci vers les fonctions vitales, principalement les fonctions cérébrales (Whitney et Rolfes, 1999). Conséquemment, ceci pourrait se traduire par une diminution du catabolisme des protéines musculaires et expliquer que le rapport 3-

methylhistidine:créatinine n'ait pas augmenté quelques jours, voir même quelques semaines, avant la mort.

L’avenir du cerf à Anticosti

Selon nos résultats, nous pensons que le sort du cerf de Virginie de l’île d’Anticosti n’est pas compromis dans un avenir plus ou moins rapproché. Bien que les cerfs préfèrent le sapin baumier à l’épinette blanche et que cette préférence pourrait être reliée à une différence de qualité entre les deux espèces, l’augmentation de la proportion d’épinette blanche dans l’alimentation d’hiver du cerf, jusqu’à 40 % de sa diète, n’a pas influencé de façon marquée la prise alimentaire, le budget d’activité, la perte de masse (et donc la diminution de la condition corporelle) et la survie des individus. Par conséquent, la disparition graduelle du sapin de l’île, du moins à moyen terme, ne devrait pas influencer significativement les traits d’histoire de vie des cerfs. Nous pouvons donc spéculer que la dynamique de la population de cerfs à Anticosti ne devrait pas être influencée tant que la disponibilité du sapin au sol demeure suffisante pour permettre aux cerfs de conserver une proportion d’au moins 50 % à 60 % de sapin dans leur alimentation hivernale. Une fois de plus, le cerf de Virginie démontre ici sa grande adaptabilité phénotypique.

Dans l’avenir, il serait intéressant d’étudier la composition précise en tannins et en terpènes du sapin baumier et de l’épinette blanche afin de mieux comprendre pourquoi les cerfs préfèrent fortement le sapin à l’épinette. Des expériences visant à tester les préférences alimentaires du cerf en fonction des différents composés retrouvés dans ces deux essences pourraient aussi être réalisées. Une étude similaire à celle de Vourc’h et al. (2002) pourrait être entreprise à Anticosti afin de mieux comprendre la sélection observée entre le sapin baumier et l’épinette blanche par le cerf. Enfin, il serait pertinent de réaliser d’autres expériences mesurant les effets d’une diète encore plus « riche » en épinette blanche, afin de déterminer s’il existe un seuil critique de proportion d’épinette blanche dans l’alimentation hivernale où le comportement et la physiologie des cerfs seraient affectés. Il est cependant possible que les cerfs d’Anticosti aient la capacité de s’ajuster à une augmentation lente de la proportion d’épinette blanche dans l’alimentation en modifiant différents paramètres du tube digestif, comme la flore microbienne, et ainsi qu'ils puissent tolérer davantage d'épinette blanche dans leur diète. Ces informations permettraient aux gestionnaires de la faune de prendre une décision éclairée sur la façon de gérer la densité de cerfs à Anticosti en fonction de la composition végétale et de la régénération des forêts de l'île.

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