ALIMENTATION, DÉMOGRAPHIE ET CONDITION PHYSIQUE CHEZ UNE POPULATION DE COYOTES (*Canis latrans*) DANS LE GRAND ÉCOSYSTÈME DE KOUCHIBOUGUAC, NOUVEAU-BRUNSWICK, CANADA ©

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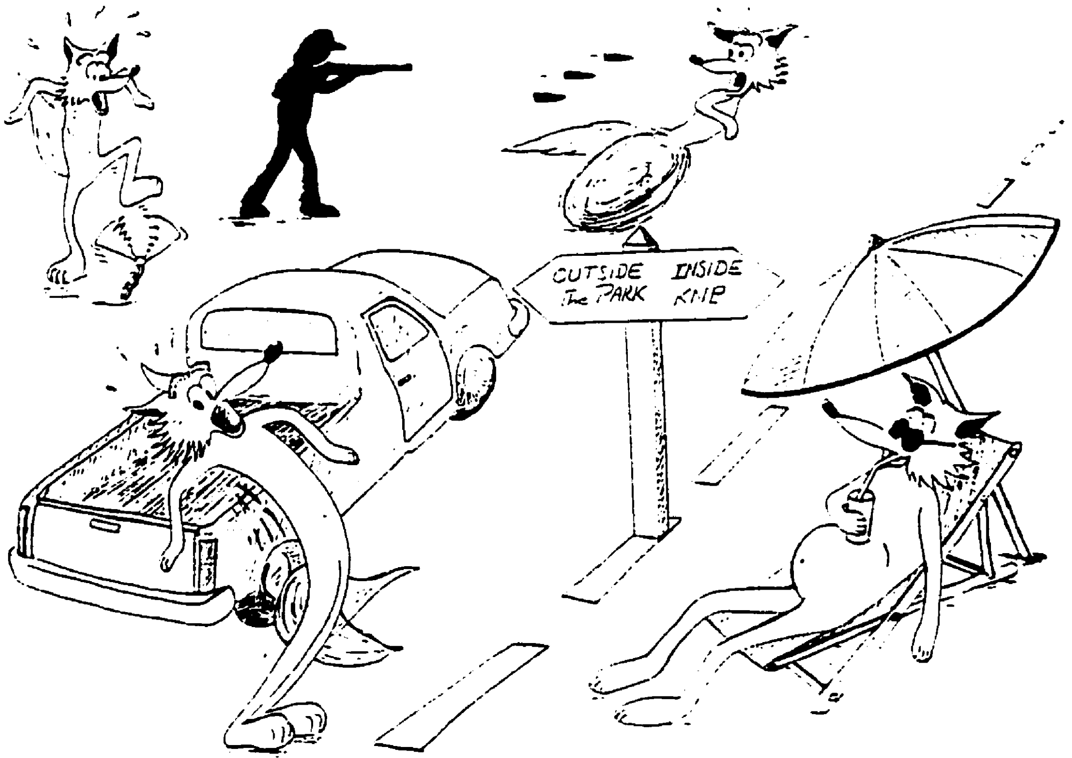
à Catherine, Daniel, Julien et Henriette...

... et aux coyotes



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RÉSUME GÉNÉRAL

C'est en grande partie grâce aux perturbations humaines sur l'habitat et la faune que le coyote a pu étendre considérablement son aire de répartition en Amérique du Nord mais il a aussi subit une exploitation et des programmes de contrôle plus ou moins intensifs selon les périodes et les régions. Étant donné les implications économiques et sociales liées aux intéractions entre le coyote et les activités humaines, il est important de mieux cerner les effets actuels des activités humaines sur le comportement et la démographie du coyote.

Cette thèse présente et discute les résultats d'une année et demi (octobre 1995-mars 1997) passée sur le terrain à récolter des fèces, des carcasses, des localisations, des indices du coyote dans la région du parc national Kouchibouguac, Nouveau-Brunswick, Canada.

Nous avons étudié la diète, les caractéristiques physiques, la démographie et la condition physique de coyotes dans le Grand Écosystème de Kouchibouguac, sur la côte est du Nouveau-Brunswick, durant une phase d'augmentation de la population de lièvres.

Les principaux éléments identifiés dans les fèces, étaient le lièvre d'Amérique, l'orignal et les fruits. Il existait une différence significative (P<0.01) de diète entre le Parc national Kouchibouguac et ses environs en septembre-octobre. Les coyotes utilisant le Parc consommaient significativement plus de fruits et moins de mammifères durant l'été comparé aux coyotes des régions adjacentes. De plus la diversité de l'alimentation était significativement plus élevée dans le Parc qu'à l'extérieur.

Les activités humaines peuvent avoir une influence sur le rythme d'activité et les habitats utilisés par les coyotes, ce qui peut influencer le comportement alimentaire. Le faible niveau de perturbation humaine dans le Parc permet probablement aux coyotes d'être plus actifs durant la journée tout en ayant accès aux milieux ouverts riches en fruits. Les fruits étant une source importante de glucides, ils pourraient avoir une importance dans la synthèse de réserves adipeuses avant l'hiver.

A partir de l'autopsie de 77 carcasses de coyotes récoltées entre novembre et mars dans les environs du Parc national Kouchibouguac, nous avons trouvé une diminution de condition corporelle entre novembre-janvier et février-mars chez les mâles adultes et chez les femelles comportant des cicatrices placentaires (*P*<0.05). Aucune variation n'était apparente au cours de l'hiver chez les femelles ne montrant pas de cicatrices placentaires. Chez les mâles adultes récoltés en fin d'hiver, plusieurs étaient atteint de la galle sarcoptique ce qui a probablement affecté leur condition physique. Les femelles pourraient, quant à elles, avoir subi un coût énergétique durant la période d'accouplement (février à mi-mars).

La population étudiée était caractérisée par une moyenne d'âge élevée (5.6±3.4 ans), une faible proportion de femelles reproductives (42.9%) et un faible nombre de cicatrices placentaires (5.7±2.0 cicatrices/femelle) comparé aux résultats des études précédentes. Ces caractéristiques peuvent être expliquées par une exploitation modérée par l'humain dans la région de l'étude. En effet, une faible exploitation par l'humain permet une stabilisation de la structure sociale limitant la reproduction.

Les perturbations humaines et l'intensité d'exploitation du coyote sont donc deux facteurs qui semblent influencer l'alimentation et la structure des populations de coyotes. Un faible niveau de perturbation et d'exploitation pourrait favoriser la consommation de fruits, diminuer le taux de natalité et renforcer les liens sociaux avec pour effet de stabiliser la population à un niveau relatif aux ressources alimentaires. D'un autre côté, étant donné les masses corporelles élevées des coyotes de cette région (13.9±2.7 kg, 9.5 à 22.0 kg), le renforcement des liens sociaux pourrait augmenter la prédation sur des animaux de grande taille tels les ongulés.

Ainsi, dans les conditions de cette étude, un faible degré de perturbation par l'humain et une faible intensité d'exploitation pourraient permettre de limiter la consommation de mammifères par le coyote durant l'été et de favoriser la stabilisation des liens sociaux entraînant un maintien de la population à des densités relativement faibles. Par contre, l'augmentation des liens sociaux pourraient entraîner une utilisation plus importante des ongulés, notamment comme proies hivernales.

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INTRODUCTION GÉNÉRALE

Lors de la colonisation du continent américain par les Européens, les écosystèmes ont été modifiés de façon substantielle. Les grands carnivores, tels le loup (*Canis lupus*), le couguar (*Felis concolor*) et l'ours grizzly (*Ursus arctos horribilis*), ont été persécutés par les colons, restreignant leurs aires de répartition aux zones moins peuplées de l'Amérique du Nord. La réduction des populations de grands carnivores et l'ouverture des forêts ont permis la formidable expansion de l'aire de répartition du coyote *(Canis latrans*) en créant des milieux plus favorables. Il y a 400 ans, le coyote occupait les régions du centre-ouest du continent, du nord du Mexique au sud des prairies canadiennes. Actuellement, il occupe la quasi-totalité de l'Amérique du Nord, du Mexique et de l'Amérique Centrale (Moore et Parker 1992). Le coyote a progressivement colonisé l'est du Canada durant les 50 dernières années, avec une première mention au Québec en 1944 (Young et Jackson 1951). La présence du coyote au Nouveau-Brunswick a été confirmée en 1958 (Squires 1968), puis il a été détecté en Nouvelle-Écosse en 1977 (O'Brian 1983), sur l'Île du Prince-Édouard en 1983 (Thomas et Diddlee 1986), et enfin sur l'Île de Terre-Neuve en 1987 (Moore and Parker 1992).

Durant cette expansion rapide de son aire, le coyote s'est adapté à de nouvelles conditions écologiques, résultant notamment en une augmentation de sa taille et de sa masse corporelle. Cette augmentation de masse suit un gradient longitudinal plutôt que latitudinal, comme la loi de Bergmann aurait pu le laisser penser (Thurber et Peterson 1991). Pour expliquer cette tendance morphologique, plusieurs facteurs ont été avancés, comme l'hybridation avec le loup (Schmitz et Kolenosky 1985a, Wayne et Lehman 1992) ainsi que l'augmentation de la taille des proies (Schmitz et Kolenosky 1985b, Larivière et Crête 1992).

Quels que soient les facteurs responsables de l'augmentation de la taille et de la masse du coyote dans le nord-est des États-Unis et l'est du Canada, il reste que les populations de coyotes de ces régions comptent les plus gros représentants de l'espèce (Voigt et Berg 1987), ce qui a des implications écologiques importantes au niveau des relations proies-predateurs et de la compétition avec les autres prédateurs.

Grâce à sa grande faculté d'adaptation, le coyote a su profiter des ressources disponibles dans chaque région de son aire de répartition. Au Mexique et dans le sud-ouest des États-Unis, sa diète est essentiellement constituée de petits mammifères, de lagomorphes, de reptiles et de végétaux (Litvaitis et Shaw 1980, Andelt 1985, Ortega-Rubio et al. 1995). Dans les régions forestières du nord-est de l'Amérique du Nord, la base de son régime alimentaire est généralement constituée par le lièvre d'Amérique (*Lepus americanus*) et le cerf de Virginie (*Odocoileus virginianus*) (Hilton 1976, Messier et al. 1986, Parker 1986, Patterson et al. 1998). Cette adaptabilité a également été démontrée à une échelle plus locale (Rose et Polis 1998). Ces qualités d'adaptation lui ont valu le qualificatif un peu simpliste d'espèce opportuniste. Néanmoins, il semble que les choix alimentaires du coyote ne soient pas uniquement dictés par l'abondance des proies (Patterson et al. 1998). Patterson et al. (1998) ont en effet constaté que la prédation sur le lièvre d'Amérique et sur le cerf de Virginie par le coyote semblait plus dictée par les conditions hivernales que par les densités de ces deux proies.

De nombreux facteurs peuvent influencer le comportement du coyote et la persistance de ses populations. Les activités humaines ont permis son expansion et favorisent encore ses populations malgré un contrôle intensif ou une persécution systématique dans de nombreuses régions. Plusieurs auteurs (Todd 1985, Crête et Lemieux 1994, Tremblay et al. 1998) ont suggéré que les milieux forestiers nordiques constituent des habitats suboptimaux pour le coyote, dont la persistance dépendrait étroitement des ressources provenant des milieux anthropiques adjacents. Un modèle de sources et fuites (Pulliam 1988) a été proposé pour expliquer cette relation dans l'est du Québec (Tremblay et al. 1998). Ces auteurs ont fondé leur argumentation essentiellement sur des données alimentaires et démographiques. Dans les milieux forestiers nordiques, la démographie semble plus étroitement reliée aux fluctuations des populations de lièvre, alors que dans les milieux plus anthropisés, les ressources en nourriture sont plus constantes au cours de l'année et d'une année à l'autre (Todd 1985). Ceci semble avoir des conséquences sur le potentiel reproducteur et sur la condition physique des animaux (Todd 1985, Tremblay et al. 1998). Todd et Keith (1983) et Todd (1985), dans une région forestière d'Alberta, ont trouvé que les réserves de gras, chez le coyote, diminuaient au cours de l'hiver, lorsque les populations de lièvre étaient en faible densité, suggérant un budget énergétique négatif. De plus, Poulle et al. (1995), à partir de données sur la condition physique de coyotes échantillonnés dans la péninsule Gaspésienne (Québec), ont suggéré que la période estivale pouvait être défavorable pour le coyote dans le nord-est, en raison d'une faible disponibilité de proies.

Dans l'est du Canada, la démographie, la condition physique et l'influence des activités humaines sur les populations de coyotes n'ont été encore que peu étudiées et des données supplémentaires sont nécessaires pour une meilleure compréhension des mécanismes régissant les populations de coyotes dans ces régions. D'octobre 1995 à mars 1997, j'ai effectué des travaux afin d'évaluer l'influence des activités humaines sur l'alimentation du coyote et documenter les caractéristiques physiques, la reproduction et la condition physique des coyotes dans l'est du Nouveau-Brunswick. Ces données m'ont également permis de discuter les implications de l'évolution morphologique et comportementale du coyote dans ces régions en ce qui concerne les relations avec les ongulés de grande taille comme l'orignal.

CHAPITRE 1

Contribution de l'étudiant à la préparation du manuscrit:

L'idée de cette étude est venue au cours de discussions entre les trois auteurs. Les données de terrain ont été récoltées par M. Dumond. Le traitement des données et la rédaction ont été effectuées par M. Dumond.

M.-A. Villard, É. Tremblay, ainsi les membres du jury de thèse ont participé à la révision des versions précédentes.

INFLUENCE OF A PROTECTED AREA ON SEASONAL VARIATION IN COYOTE DIET IN EASTERN NEW BRUNSWICK

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Abstract: Protected areas may be seen as a conservation tool, but also as refuges for species like the coyote, which are considered as pests by many humans. Do protected areas act as refuges for potential prey, or, on the contrary, do coyotes preferentially use out-boundary resources? To answer these questions, we compared seasonal variation in coyote diet composition between Kouchibouguac National Park, New Brunswick, Canada, and adjacent human-disturbed forested areas. Coyote scats were collected in these two areas over an entire year and diet was expressed as the percentage of items in the total volume of scats per two-month period. Snowshoe hare, moose, and fruits were the major components of coyote diet in both areas. Differences in diet occurred during July-August ($P<0.05$) and September-October ($P<0.01$). Park coyotes consumed significantly more fruits and less mammals (particularly snowshoe hare) than coyotes from adjacent areas. Diet diversity (Shannon-Wiener diversity index) was always higher in Park coyotes than in coyotes from outside. Several authors have suggested that, in boreal and northern temperate regions, coyote populations mainly depend on human-disturbed landscapes because forests may represent suboptimal habitats for coyotes at the northern edge of their range. Fruits may be a poor substitute to mammalian prey during summer as hypothesized by several authors, but they also represent a high source of carbohydrates. We suggest that the higher diversity in the Park coyote diet and particularly the high consumption of fruits during summer could reflect a behavioral response to the lower level of human disturbance, rather than a sign that the Park represents suboptimal habitat for coyotes.

INTRODUCTION

The classical role of national parks is to maintain ecological integrity, and to inform the public about natural history and conservation. To ensure that parks do not become islands of wilderness within human-disturbed landscapes, park managers have to work in partnership with local authorities and landowners (Cole and Landres 1996, Butler 1998). When national parks are perceived by the public as refuges for pest species like the coyote, the work of park managers becomes increasingly difficult, especially when wildlife management practices are influenced by political and economic issues (Bounds and Shaw 1994, Mech 1996). Do protected areas act as refuges for potential prey, or, on the contrary, do coyotes preferentially use out-boundary resources?

To answer these questions, we require knowledge on the differences in diet, foraging behavior, movements, activity, and social organization between protected and unprotected areas. McClure et al. (1995) found that suburban developments bordering Saguaro National Monument, in Arizona, provided alternative, supplemental sources of food to coyotes. Toweill and Anthony (1988) suggested that clearcutting may generate, directly and indirectly, an important supplemental source of food for coyotes by allowing fruit-bearing plants to grow, which in turn attracts potential prey species. Coyotes of the Grand Teton National Park (Wyoming) appeared to depend mainly on hunter-killed elk (*Cervus elaphus*) carrion during winter months (Bekoff and Wells 1986). Based on data on coyote food habits and demography, Todd (1985), Crête and Lemieux (1994), and Tremblay et al. (1998), suggested that boreal forests represent a suboptimal habitat for coyote populations, and that these populations are mainly supported by human-disturbed landscapes nearby. In a forest landscape of New Hampshire, Oehler and Litvaitis (1996) found an increase of wild canid (i.e. coyotes and foxes) density as the proportion of human-dominated habitats increased from 7 to 27 % of the landscape. Thus, if protected areas of the boreal and sub-boreal regions do represent suboptimal habitat for coyotes, we would expect coyotes from a protected area to forage in neighboring inhabited, disturbed areas.

Human-disturbed landscapes may represent a good source of food for coyotes but, on the other hand, these landscapes also are dangerous for coyotes. Human activities may influence coyote diet in other ways than by providing supplemental food sources. In many rural or forested inhabited areas, coyotes are hunted as a pest species, which may influence their foraging behavior and daily pattern of activity. Coyotes are considered more active from dusk until dawn (Ozoga and Harger 1966, Andelt and Gipson 1979). In a rural region of Alberta, coyotes preferred forested habitat and avoided open areas close to roads during daylight (Roy and Dorrance 1985). Conversely, lightly or unexploited coyote populations seem to exhibit more extensive daylight activity (Andelt 1985, Morton 1989, Fortin and Huot 1995, Patterson 1995, Gese et al. 1996a). This more extensive daylight activity in areas with low human disturbance may allow coyotes to have access to a greater diversity of food.

To assess the influence of a protected area on coyote populations, we compared seasonal and annual variations in coyote diet between Kouchibouguac National Park (New Brunswick Canada), and adjacent unprotected areas. We hypothesized that (1) coyote diet would differ between the Park and adjacent areas, and that (2) lower human pressure within the protected area would result in a higher diversity in coyote diet than in adjacent unprotected areas.

STUDY AREA

Our study area is located within the Greater Kouchibouguac Ecosystem, a large region centered on Kouchibouguac National Park (46°50' N, 65°00' W), in eastern New Brunswick, Canada (Fig. 1). The Greater Kouchibouguac Ecosystem is representative of the Maritime Plain Natural Region (Tremblay 1997). The physiography of the region is characterized by a flat terrain gently sloping towards Northumberland Strait (Desloges 1980). Road density for the Northumberland Coastal Ecodistrict is 0.79 km / km^2 (Ecosystem Classification Working Group. 1996, internal report, Department of Natural Resources and Energy, New Brunswick, Canada).

The climate is typical of the eastern coast of the continent, with an average annual temperature of 5°C and average precipitation of 979 mm (with 18.79 % as snow corresponding approximately to 1.8 meter). In summer (July to September), temperatures average 16.8°C and in winter (December to March) -7.1°C (Desloges 1980).

Our study area is divided in two distinct portions: one extensively overlaps Kouchibouguac National Park (hereafter called the "Park area") and the other is located outside the Park and will be referred to as the "unprotected area" (Fig. 1). We also refer to coyotes as Park coyotes and unprotected coyotes depending on the area where they dropped scats. Each area (Fig. 1) was delimited by a series of overlapping 5-km radii around each coyote scat collected. We chose a 5-km radius around each scat to encompass the probable landscape where a coyote fed before scat dropping. Both areas are dominated by woodland (Table 1). This region contains a range of forest types typical of the Acadian Forest, dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white cedar (*Thuja occidentalis*), trembling aspen (*Populus tremuloides*), gray birch (*Betula populifolia*), and red maple (*Acer rubrum*). Kouchibouguac National Park represent about a 10 km wide stripe on the coast and then is bordered on one side by the sea (Fig.1).

We compared the proportions of different land cover types and levels of human disturbance between the Park area and the unprotected area. These data were obtained from a reclassified LANDSAT-TM image of the Greater Kouchibouguac Ecosystem taken in 1993. The level of human disturbance was assessed by the distance (0 to over 500 meters) from anthropogenic areas (Fig. 1, Table 2). The two areas differed mainly in the intensity of human activities and resulting landscape alterations (Tables 1 and 2, Fig. 1). The landscape of the Park area (delimited with the 5-km radii around each scat) included about 93 km^2 of adjacent human-disturbed areas (Fig. 1). Anthropogenic areas (campground, trails and roads) within Kouchibouguac National Park accounted for less than 15 % of the anthropogenic area category, and forest regeneration within the Park accounted for about 31 % of the forest regeneration category. The Park area encompassed significantly more wetlands, while the unprotected area showed a significantly higher proportion of forest regeneration (Table 1). The Park area is characterized by a significantly higher proportion of its total area at least 500 m from the nearest anthropogenic area (Table 2).

The coyote population seemed to be at a relatively low density ($\leq$ 0.1 coyote / km^2) compared to previous years, and according to siren-elicited howling surveys conducted during the period of the study (Dumond 1997, Thébeau, unpublished data).

METHODS:

We collected coyote scats on dirt roads and trails, from 9 January 1996 to 1 January 1997, throughout the Park and the unprotected area. In the Park area, scats were exclusively collected within the Park boundaries. Each area was visited at least once a week by truck, bicycle, foot, snowshoe, or snowmobile, depending on season and accessibility. In the unprotected area, we mainly searched for scats along logging roads, while inside the Park we followed old dirt roads and hiking and biking trails. During winter, some scats were collected while snow-tracking coyotes. Coyote scat locations inside the Park and in the unprotected area were at least 10 km apart. We assumed that this 10 km buffer strip substantially reduced the probability of bias due to the movements of coyotes from one area to another. Usually, the eastern coyote travels less than 10 km in straight line per 24 hours (Person 1988, Fortin and Huot 1995, Dumond, unpublished data) and the time lapse between food intake and scat deposit is estimated to be between 12 and 24 hours (Huegel 1979, Danner and Smith 1980).

Each scat found was put in a plastic bag labeled with the location, date, and approximate age of the scat. Age was estimated according to aspect, date of previous survey and, in winter, depth and position in snow layers. Due to the relatively high density of red foxes (*Vulpes vulpes*), all scats less than 1.8 cm in diameter that were not associated with coyote tracks were discarded (Green and Flinders 1981, Rezendes 1993). Even though Bobcats (*Felis rufus*) were at low density in the study areas, care was taken to avoid any confusion by checking the texture and the color of scats as well as tracks and scratches associated with the scats (Murie 1989, Rezendes 1993). All scats were kept in a freezer and then oven-dried at 120°C for at least 12h (in order to kill parasites and coprophages) for subsequent analysis.

Scats were washed through a 1-mm sieve. Undigested remains (hair, bones, teeth, pieces of skin, seeds) were collected and identified. Macroscopic aspect and microscopic structures of hair (medulla and prints of scale patterns) were used to identify hair following identification keys (Adorjan and Kolenosky 1980, Moore et al. 1974) and a reference collection of dorsal and ventral hair of most of the mammal species present in the study area. Owing to the high similarity of their hair, red squirrel (*Tamiasciurus hudsonicus*) and chipmunk (*Tamias striatus*) were combined into a single category (Sciurids). For the same reason, voles and mice were classified in the small rodents' category. Due to the difficulty in identifying feathers, all feather and bird remains were classified into a single category (birds). Fruit seeds were identified at least to the genus by comparison with a reference collection constituted for the study. Other plant items were classified as other plant materials. Item category volumes in each scat were estimated to the nearest 5 percent.

We compiled data by area and by season. Biologically-meaningful seasons were determined based on meteorological condition and regional coyote phenology (Bekoff and Wells 1986, Dumond 1997): January-February (lowest temperature; low diversity in food resources; mating season); March-April (weather transition period; gestation); May-June (abundance of young of different prey species; end of gestation and den attendance); July-August (summer period, great variety of food, beginning of the fruit season; pup rearing); September-October (beginning of sport-hunting season; great mobility of the juveniles) ; November-December (sport-hunting and trapping seasons, decreasing temperature; decreasing of food resource diversity; independence of most juveniles).

Comparisons between successive seasons and between areas were made using G-tests with Williams'correction (G_{adj}) (Sokal and Rohlf 1981). Because we repeated this test several times, we set the significant level at P=0.01. Frequencies were compiled following the method of Messier and Crête (1985). We summed all the individual scat proportions of the volume for a given item to obtain a number of "rebuilt" scats that was used as frequencies. The advantage of this approach is that the sum of the frequencies of the different items is equal to the total number of scats. To avoid biases due to slight variations in prey availability between areas, most items were grouped into general categories: snowshoe hare (*Lepus americanus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), medium-sized rodents, small mammals, other mammals, birds, insects, fruits, other plant materials and miscellaneous.

Within each area (i.e. the Park and the unprotected area), the spatial distribution of the scat samples was clumped. We tested "within-area" homogeneity in coyote diet among four arbitrarily defined subareas, corresponding to the main sampling sites within each study area, during seasons for which we had large enough sample sizes, using G-tests. None of the comparisons among the four subareas within the Park and the unprotected area revealed a significant difference in coyote diet ($P > 0.05$), so we pooled data from all subareas within each area in our analysis.

We calculated the annual diet for each area as the mean of the different seasons (instead of the mean of the overall sample) to avoid biases due to unequal sample sizes among seasons and between the Park and the unprotected area. We also summarized our results for the same 11 food categories as in previous analyses in a hierarchical cluster analysis to produce a dendrogram representing the similarity in coyote diet among seasons and areas (Systat 8.0, SPSS Inc., 1998) using the (area/season)x(items) matrix. Because there is no satisfactory methods for determining the number of clusters (SAS Institute Inc. 1990), we estimated it arbitrarily.

Diet diversity was calculated separately for each season using the Shannon-Wiener diversity index. We used the 32 categories identified in coyote scats plus the unknown mammals, unknown insects, and miscellaneous items. Miscellaneous items included crustaceans, gasteropods, garbage, and unknown materials. Comparisons between areas and among seasons were made using t-tests (Zar 1996). The significance level was set at 0.01.

RESULTS

Overall Coyote Diet

We collected 313 scats inside the Park and 364 in the unprotected area. The largest seasonal sample was 98 scats in the unprotected area in May-June, while the minimum was 10 in the Park in January-February (Table 3). This discrepancy was partly due to lower sampling effort in the Park during winter and possibly also to increased coyote home range size during winter (Parker and Maxwell 1989, Patterson 1995).

Scat contents were generally dominated by mammals, and particularly by snowshoe hare (Table 3). Ungulates were well represented in coyote diet with an unusual high presence of moose. In the unprotected area, items representing at least 5% of the total volume of scats on an annual basis were, in order of decreasing importance, snowshoe hare, moose, beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), and blueberries (*Vaccinium* sp.). In the Park, these items were snowshoe hare, moose, apples (*Malus* sp.), white-tailed deer, small rodents, beaver, and blueberries (Table 3).

Seasonal Differences in Diet

Diet varied significantly among seasons in both areas, particularly between May-June and July-August (Table 3, Fig. 2). There also was a significant variation in diet between September-October and November-December inside the Park (Table 3, Fig. 2). The proportion of mammals in coyote diet decreased significantly from May-June to July-August in both areas (G_{adj} = 18.3 , df = 1, $P \leq 0.001$ inside the Park ; and G_{adj} = 9.0, df = 1, P = 0.003 in the unprotected area). There also was a significant increase in the proportion of mammals in coyote diet from September-October to November-December inside the Park (G_{adj} = 14.4 , df = 1, $P \leq 0.001$). Seasonal trends in the main categories, and particularly for snowshoe hare, were similar between areas (Fig. 2) when excluding the January-February sample. However, proportions of the different items in coyote diet within the Park during the January-February period are questionable owing to the very small sample size (n = 10). Ungulate proportion in coyote diet showed similar trends between areas, with a high consumption of moose from November to June and a low proportion of ungulates in July-August (Fig. 2). There was also an increase in white-tailed deer consumption in May-June, probably due to the availability of newborn fawns (we did not distinguish fawn from adult remains in coyote scats). The proportions of medium mammals, small mammals, and birds in coyote diet did not seem to follow a particular seasonal pattern except for beaver, whose proportion decreased steadily from January to October in the Park while it reached a maximum in spring and fall in the unprotected area (Table 3). Insects and fruits (Fig. 2) were consumed when available, mostly from May to October in the unprotected area and from July to December inside the Park.

Differences in Diet between Areas

There was a significant difference in diet between areas on an annual basis and during September-October (Table 3). Also, the diet tended to differ between areas during July-August ($P = 0.013$). Throughout the year, consumption of snowshoe hare was greater in the unprotected area than inside the Park. The proportion of snowshoe hare in coyote diet varied significantly between areas over the entire year ($G_{adj} = 33.7$, df = 1, $P \leq 0.001$) and during January-February ($G_{adj} = 6.7$, df = 1, $P = 0.010$), March-April ($G_{adj} = 7.1$, df = 1, $P = 0.008$), and July-August ($G_{adj} = 14.0$, df = 1, $P \leq 0.001$). In the unprotected area, snowshoe hare was the main food item throughout the year; inside the Park however, snowshoe hare proportion in the diet was lower than the proportion of fruits from July to October (Table 3, Fig. 2).

Ungulates were consumed in greater quantities in the Park area than in the unprotected area from January to June, but consumption was greater in the unprotected area from September to December (Fig. 2), a period corresponding to moose and deer hunting seasons. On an annual basis, park coyotes consumed significantly more small mammals, including Sciurids, voles, mice and shrews, than unprotected-coyotes ($G_{adj} = 9.7$, df = 1, $P = 0.002$).

When grouping together all mammal items, the proportion of mammals in coyote diet was significantly greater in the unprotected area on an annual basis ($G_{adj} = 65.8$, df = 1, $P \leq 0.001$), and during July-August ($G_{adj} = 17.1$, df = 1, $P \leq 0.001$) and September-October ($G_{adj} = 13.1$, df = 1, $P \leq 0.001$).

Inside the Park, insect percentage of volume in coyote scats tended to be higher than in the unprotected area ($G_{adj} = 4.3$, df = 1, $P = 0.038$). From July to September, Acrididae (e.g. grasshoppers) represented at least 29.9 % and 8.7 % of insect remains volume in coyote scats inside the Park and in the unprotected area respectively.

Fruits were consumed in lower quantity in the unprotected area. The proportion of fruits in scats inside the Park was almost constantly twice or more that observed in the unprotected area with a significant difference during July-August ($G_{adj} = 13.1$, df = 1, $P \leq 0.001$) and near the significant level during September-October ($G_{adj} = 6.1$, df = 1, $P = 0.014$). In both areas, blueberries, serviceberries (*Amelanchier* sp.), apples, and black huckleberries (*Gaylussacia baccata*) were the main fruit items found in coyote scats.

Although the proportions of crustaceans and fishes in the diet were higher in the Park (1.4 %) than in the unprotected area (0.1 %) on an annual basis, those items were minor in coyote diet. During all the seasons, human garbage represented no more than 0.5 % of coyote scat volume in both areas.

Cluster analysis

The dendrogram (Fig. 3) can be divided in three distinct clusters of season/area combinations. The exception is January-February in the Park area, for which we had a very small sample ($n = 10$). One cluster from January to August in the unprotected area and in May-June in the Park area corresponding with a high proportion of snowshoe hare in the diet, a second cluster during September-October in the unprotected area and from July to December in the Park area with a high consumption of fruits, and a third cluster during November-December in the unprotected area and March-April in the Park area, when moose proportion was the highest in the diet.

Diet Diversity

Diet diversity value was higher in the Park area than in the unprotected area throughout the year (Table 4, Fig. 4). The difference in diversity between areas was significant over the entire year, and during July-August and November-December periods (Table 4). Also, it was nearly significant during March-April ($P < 0.025$). Diet diversity was highest during September-October period in the unprotected area, and from July to December inside the Park. Diet diversity reached its lower value during March-April period in both areas. Coyote diet diversity increased significantly from May-June to July-August inside the Park and from July-August to September-

October in the unprotected area (Table 4, Fig. 4). In the unprotected area, diversity in coyote diet decreased significantly from September-October to November-December (Table 4, Fig.4).

DISCUSSION

Coyote diet differed significantly between the Park area and the unprotected area during September-October when diet diversity was the highest. Also, diet tended to differ between areas during July-August period. The divergence in diet between the two areas occurred after a significant seasonal change between May-June and July-August periods in both areas. This seasonal change led to an increase in diet diversity in both areas. Diet diversity was always higher for protected coyotes, with a significant difference over the entire year and specifically during July-August and November-December periods. The coastal location of Kouchibouguac National Park could have provided a supplemental food source from the sea but crustaceans and fishes were minor in Park-coyote diet and did not contribute to a substantial increase in diet diversity. In California, Rose and Polis (1998) found a significant difference between inland and coastal coyote diet, with marine food representing 40 to 50% of all food items found in coastal coyote scats. In our study area, food of marine origin was either less abundant or less available than along the California coast.

Protected coyotes globally consumed less mammals but more fruits, insects, and small mammals than unprotected coyotes. On an annual basis, the proportion of volume of mammal prey in coyote scats was significantly lower inside the Park, particularly from July to October. When we compared subareas within each area (great similarity of habitat and human disturbance), we did not find any spatial variation in coyote diet, which suggests that in our study, between-area variations in coyote diet were mainly influenced by the protected status of the Park which is the main difference between our study areas.

Although showing similar seasonal trends, the proportion of snowshoe hare in coyote diet was always lower inside the Park than in the unprotected area, possibly as a result of a lower density of hare within the Park. But, winter track transect sessions inside the Park (Richard 1996) and in the unprotected area (Thébeau, unpublished data) revealed comparable hare activity in both areas (14 *versus* 10 hare tracks / km, respectively). Human activities can cause habitat fragmentation for lagomorphs, which may result in an increased vulnerability to predators (Keith et al. 1993, Oehler and Litvaitis 1996, Villafuerte et al. 1997). This increased vulnerability could be one of the factors influencing the greater utilization of hare by coyotes in the unprotected area.

Several authors (Todd 1985, Crête and Lemieux 1994, Tremblay et al. 1998) suggested that northern forested habitat may be suboptimal for coyotes, and that coyote populations in those regions depend mainly on adjacent anthropogenic landscapes. Following that theory, the Park could be considered as a suboptimal habitat for coyotes owing to its low level of human disturbance and its high proportion of forested habitat. Nutritionally, fruits, insects, and small mammals can be considered as poor substitutes to lagomorphs. But because Kouchibouguac National Park is a narrow protected area (less than 10 km wide), coyote movements frequently extend beyond the Park boundary, at least during fall and winter (Dumond, unpublished data). This allows coyotes to have access to anthropogenic food sources adjacent to the Park. McClure et al. (1995) demonstrated the influence of suburban developments bordering Saguaro National Monument (Arizona) on coyote diet. Moreover, habitat selection by coyotes in relation to prey availability has been demonstrated in different parts of its range (Theberge and Wedeles 1989, Reichel 1991, Murray et al. 1994). Thus, we might expect that Park coyotes would make a greater use of the optimal habitat (i.e. adjacent human-disturbed areas) and take advantage of anthropogenic food sources. If that was the case, we would not expect to observe such a difference between coyote diets inside and outside the Park. Therefore, another factor must influence coyote diet diversification in the Park.

Usually coyotes exhibit nocturnal and crepuscular behavior in response to prey activity pattern (Andelt and Andelt 1981) but also in response to human disturbance (Andelt and Andelt 1981, Roy and Dorrance 1985). Human influence on coyote activity patterns is also suggested by the more extensive daylight activity in lightly or unexploited coyote populations (Andelt 1985, Fortin and Huot 1995, Patterson 1995, Gese et al. 1996a). This more extensive daylight activity in areas with low human disturbance could be a behavioral response to suboptimal environmental conditions to compensate for the low availability of medium and large mammals (e.g. lagomorphs, ungulates□). Protected areas also may be perceived by canids as areas relatively free of human activities as it was suggested by Nesbitt (1975) for feral dogs. In Kenai National Wildlife Refuge (Alaska), Thurber et al. (1994) have shown that wolf (*Canis lupus*) movements outside the refuge decreased significantly with increasing human settlement. Wolves also avoided roads that were frequently used by people. In urban environments in Washington State, Quinn (1997a) found that coyotes used significantly more habitats with least human disturbance level than expected according to their availability. If the Park is considered by coyotes to be a safe area (i.e. without lethal human encounters), this advantage could compensate for the supposed suboptimal food resources.

The fact that differences between areas were only significant during September-October, and nearly significant during July-August, may reflect limitations in Park-coyote movements due to pup rearing (Harrison and Gilbert 1985), reducing their accessibility to human food sources. Data on coyote movements were only available during fall and winter, but during this period resident pairs of Park coyotes frequently extended their movements beyond Park boundary (Dumond, unpublished data). Because these coyotes explored human-disturbed area adjacent to the Park, at least during fall and winter, den locations would have been found in the area with the hypothesized optimal source of food, i.e. the human disturbed area.

Conversely, the more frequent daylight activities of protected coyotes may be considered as a behavioral response to low human persecution and the higher consumption of fruits, insects, and small mammals could reflect an opportunistic choice by Park coyotes. The use of fruits as an optimal and opportunistic feeding strategy also was suggested by summer habitat and diet switching by coyotes in eastern Maine (Caturano 1983). Fruit consumption by coyotes probably occurs during the day (Tremblay et al. 1998), because vision is a major sense in coyote foraging behavior (Bekoff and Wells 1986). Fruits found in coyote diet were mainly species growing in the open or near forest edges (e.g. blueberry, black huckleberry, apple, serviceberry). Also, protected coyotes consumed more insects and particularly Acrididae (e.g. grasshoppers), that must have been caught during the daylight hours in open lands. Daylight foraging in open lands would expose coyotes to human persecution outside the Park boundary. In southeastern

Quebec, Tremblay et al. (1998) found that the proportion of fruits in coyote diet tended to be higher in the forested landscape than in the rural landscape from May to October. The proportion of fruits in coyote diet also was highest in a mixed forested-residential area than in a mixed agricultural-residential area (Quinn 1997b). These findings are consistent with our results which showed a higher proportion of fruits and a lower proportion of mammals in coyote diet where human activities were limited.

At least during winter, deer are usually an important food item for coyotes in southern boreal and northern temperate regions. However deer were not a major prey item in our study area except in the Park during the January-February period (28.5 %, n = 10), but this proportion is questionable due to the small sample size. The generally low proportion of deer in coyote diet contrasted with most of the other studies conducted in eastern Canada (Morton and Savoie 1983, LaPierre 1985, Moore and Millar 1986, Parker 1986, Parker and Maxwell 1989, Patterson 1995, see also Pekins 1992 for a review in northeastern U.S.A.). During the study, January and February were characterized by several above zero temperature periods with rain which reduced the snow depth. In turn, less snow could have increased coyote predation on hare and decreased vulnerability of deer to coyotes during winter (Dibello et al. 1990). Low deer density (Richard 1995) and the mild winter we experienced during this study could have been the main factors that reduced deer availability to coyotes. Conversely, moose proportion in coyote diet was higher than reported in most studies from northeastern U.S.A. and eastern Canada (Caturano 1983, Moore and Millar 1986, Morton 1989, Litvaitis and Harrison 1989, Dibello et al. 1990). Only a few studies reported relatively high consumption of moose by coyotes, at least during one season (Major and Sherburne 1987, Fortin and Huot 1995, Samson and Crête 1997). Density of moose was greater within than outside Kouchibouguac National Park (0.4 moose / km^2, Richard 1995 versus 0.2-0.3 moose / km^2, 1991 and 1993 moose survey of the Fish and Wildlife Branch, Department of Natural Resources and Energy, unpublished data) but was relatively high in both areas. In the Greater Kouchibouguac Ecosystem, moose seem to be an important source of food for coyotes during late fall and winter. This can lead to lower coyote predation on other species (Gese et al. 1996b) and compensate for the low deer density. Seasonal trends differed between the two areas. The high use of moose in the unprotected area seemed to reflect fall and early winter hunting activities while in the Park, consumption of moose was concentrated during winter and spring, probably in response to natural mortality. In the Park, the availability of moose carcasses during winter could have compensated for the relatively low consumption of snowshoe hare by coyotes compared to adjacent human-disturbed areas.

MANAGEMENT IMPLICATIONS

We suggest that the difference we observed in coyote diet between the Park and the adjacent unprotected area reflects differences in human disturbance. Human disturbance outside the Park (aggressive behavior toward coyotes) could restrict coyote daylight activities and, thus, the diversity of their diet. Lower human pressure inside the Park (non-aggressive encounters) apparently allowed protected coyotes to forage in open habitats during daylight, which means that they had access to a greater diversity of natural food resources given that sight is an important sense in food acquisition (Bekoff and Wells 1986). Our study suggests that if coyotes could safely use areas of high fruit production, this could significantly reduce, at least during summer and fall, coyote predation on medium and large mammals, especially on game species (e.g. hare, deer). Andelt et al. (1987) suggested that increasing plantation of appropriate fruiting species in a mixed grass shrubland area of Texas, could reduce coyote predation on mammals. Toweill and Anthony (1988) suggested that clearcuts may increase fruit availability to coyotes in a coniferous forest of Oregon. Our results suggest that in northern temperate areas, reduction of human pressure toward coyotes increases the diversity of their diet, and, thus, reduce predation on medium and large mammal species.

At least during summer, and based on diet data, the hypothesis stating that northern forested habitats are suboptimal due to low availability of food could be groundless. However, during winter, the generally low prey diversity and cold weather conditions in northern forests could negatively affect fecundity and body condition of coyotes. However, high moose densities and natural mortality could allow the maintenance of healthy coyote populations even during winter in northern regions. Studies on the influence of different type of human activities on coyote foraging movements, daily activity patterns and population dynamics would shed some light on the mechanisms underlying the dietary pattern we documented (especially between central part, peripheral and adjacent areas of large protected areas in coyote northern range). Also, our study suggests that further research on coyote/moose relationships is necessary in the northern temperate and boreal forest.

Table 1: **Percentage of the Park area and the unprotected area corresponding to different land cover types.**

Cover types (%)	Forest	Wetlands	Forest regeneration	Anthropogenic[a]	Miscellaneous	Area (km^2)
Park area	67.0	15.3	12.5	4.7	0.4	263
		*[b]	*			
Unprotected area	70.7	6.2	19.4	3.5	0.1	941

[a] Houses, campgrounds, roads, fields, clearcuts.

[b] Asterisks indicate significant differences between areas (G-tests with Williams' correction based on the surface of each category, df = 1, $P < 0.01$)

Table 2: **Degree of human disturbance in the Park area and in the unprotected area, according to the proportion of each area within different radii of closest human disturbance [a].**

Degree of human disturbance (%)	> 500 m	250 to 500 m	100 to 250 m	0 to 100 m	Road-100 m [c]	Anthropogenic	Area (km^2)
Park area	60.7	10.2	7.2	8.6	9.7	3.7	263
	* [b]	*					
Unprotected area	49.3	20.5	10.6	9.2	8.4	2.1	941

[a] Houses, campgrounds, fields, logging.

[b] Asterisks indicate significant differences between areas (G-tests with Williams' correction based on the surface of each category, df = 1, $P < 0.01$).

[c] Roads with a 100 m wide strip on each side.

Table 3 : Variations in composition (%) of coyote diet in the Greater Kouchibouguac Ecosystem, according to season and area.

	January-February		March-April		May-June		July-August		September-October		November-December		Annual	
ITEMS[a]	UA[b]	PA[b]	UA	PA	UA	PA	UA	PA	UA	PA	UA	PA	UA	PA
N	42	10	63	24	98	28	89	77	47	95	25	79	364	313
MAMMALS	89.5	82.5	90.5	86.3	91.8	89.1	75.8	44.5	69.1	36.9	80.2	63.6	82.8	67.2
Hare[c]	59.8	15.0	64.8	32.9	64.2	56.6	55.2	26.6	33.1	19.9	36.2	29.4	52.2	30.1
Ungulates	10.6	39.0	12.3	22.9	8.8	16.1	3.7	2.9	5.3	0.3	29.2	9.4	11.6	15.1
Moose[c]	10.6	10.5	8.6	22.5	2.8	11.6	1.0	0.3	3.2	0.1	29.2	6.2	9.2	8.5
Deer[c]		28.5	3.7	0.4	6.0	4.5	2.8	2.7	2.1	0.2		3.2	2.4	6.6
Medium Size Rodents[c]	11.2	22.0	9.3	14.6	16.2	8.4	8.9	4.0	14.5	0.9	11.6	5.4	11.9	9.2
Beaver	4.0	15.0	2.9	9.8	7.6	3.2	4.6	1.1	7.1	0.8	7.2	2.2	5.6	5.4
Muskrat	2.1		1.5	2.9			0.9		1.9				1.1	0.5
Porcupine	5.0	7.0	4.8	1.9	8.6	5.2	3.4	2.9	5.4	0.1	4.4	3.2	5.3	3.4
Small Mammals[c]	7.4	6.5	3.5	12.9	2.3	8.0	7.3	10.1	8.1	14.0	1.2	17.0	5.0	11.4
Siurids	2.6		2.1	4.2	1.7	5.4	4.8	4.0	5.1	7.6	0.4	4.6	2.8	4.3
Small Rodents	4.8	6.5	1.4	8.8	0.6	2.7	2.5	6.2	3.0	5.5	0.8	8.5	2.2	6.4
Shrews										0.8		3.9		0.8
Other Mammals[c]	0.6		0.6	2.9	0.4		0.7	1.0	8.2	1.8	2.0	2.3	2.1	1.3
Carnivores[d]			0.3	2.9	0.3		0.3	0.3	4.3			0.1	0.9	0.6
Livestock (pig)	0.5		0.1		0.1				1.6	0.5		1.1	0.4	0.3
Unknown Mammals	0.1		0.2				0.4	0.7	2.3	1.3	2.0	1.1	0.8	0.5

Table 3 (continued)

BIRDS [c]	4.9		0.6	1.5	1.7	0.5	4.0	1.9	0.5	2.7	2.6	2.3	2.4	1.5
INSECTS [c]	0.6		0.2	0.2	1.0	4.8	1.6	2.9	0.7	6.8	0.2	1.8	0.7	2.7
FRUITS [c]		1.0		1.5			17.6	43.1	27.1	48.6	9.4	23.2	9.0	19.6
Blueberries							13.8	24.0	14.6	4.7	2.0	1.4	5.1	5.0
Serviceberries							1.0	13.1	3.6	1.2			0.8	2.4
Apples		1.0						0.3	1.9	28.6	7.4	11.3	1.6	6.9
Black huckleberries				0.2				1.9	2.2	8.2		9.7	0.4	3.4
Others Berries [e]				1.3			2.8	3.8	4.8	5.9		0.7	1.3	1.9
OTHER PLANT MATERIALS [c]	4.0	13.0	2.6	0.8	2.4	4.7	0.1	3.2	1.5	1.5	7.6	2.9	3.1	4.3
MISCELLANEOUS [c]	1.0	3.5	6.1	10.2	3.1	0.9	0.9	4.2	1.0	3.6		6.2	2.0	4.8
DIFFERENCES BETWEEN AREAS [f]	G_{adj} (10)=5.8 P = 0.835		G_{adj} (10)=6.3 P = 0.789		G_{adj} (9)=5.9 P = 0.806		G_{adj} (10)=22.4 P = 0.013		G_{adj} (10)=25.0 P = 0.005		G_{adj} (10)=16.2 P = 0.095		G_{adj} (10)=58.7 $P \leq 0.001$	
SEASONAL VARIATIONS [g]														
G_{adj}	6.2	4.1	5.0	7.1	30.8	28.4	11.6	6.2	12.4	23.8	7.1	11.0	116.6	109.8
Df	9	10	9	10	10	10	10	10	10	10	9	10	50	50
P	0.724	0.943	0.831	0.715	≤ 0.001	0.002	0.311	0.797	0.259	0.008	0.628	0.357	≤ 0.001	≤ 0.001

Table 3 (continued)

[a] Expressed as the percentage of the total volume of coyote scats for each two-month period.

[b] UP = Unprotected area ; PA = Park area.

[c] categories used to test differences between areas and consecutive seasons (G-test with the Williams' correction, Sokal and Rohlf 1981, pp 745).

[d] striped skunk (*Mephitis mephitis*), domestic cat, raccoon (*Procyon lotor*), black bear (*Ursus americanus*), red fox.

[e] *Smilacina* spp., *Aralia* spp., *Prunus* spp., *Rubus* spp., *Viburnum cassinoides*, *Fragia* spp., *Cornus canadensis*.

[f] between sites within each season.

[g] between one two-month period and the next (e.g. January-February and March-April under the January-February column ; .... ; November-December and January-February under the November-December column).

Table 4 : **Variations in diet diversity of coyotes in the Greater Kouchibouguac Ecosystem according to season and area.**

	January-February		March-April		May-June		July-August		September-October		November-December		Annual	
	UA[a]	PA[a]	UA	PA	UA	PA	UA	PA	UA	PA	UA	PA	UA	PA
k[b]	15	9	16	19	17	15	26	27	31	28	14	29	38	36
n	42	10	63	24	98	28	89	77	47	95	25	79	364	313
H'[c]	0.68	0.86	0.62	0.91	0.63	0.77	0.79	1.04	1.09	1.13	0.8	1.13	0.84	1.23
H'_{max}	1.18	0.95	1.2	1.28	1.23	1.18	1.41	1.43	1.49	1.45	1.15	1.46	1.58	1.56
$J'=H'/H'_{max}$	0.58	0.9	0.51	0.71	0.51	0.66	0.56	0.73	0.73	0.78	0.69	0.77	0.53	0.79
Differences between areas[d]	$t_{(32)} = 1.37$ $P = 0.181$		$t_{(56)} = 2.36$ $P = 0.022$		$t_{(48)} = 1.16$ $P = 0.252$		$t_{(164)} = 2.82$ $P = 0.005$		$t_{(77)} = 0.34$ $P = 0.735$		$t_{(43)} = 3.13$ $P = 0.003$		$t_{(630)} = 8.72$ $P \leq 0.001$	
Seasonal variations[d, e]														
t	0.55	0.39	0.15	0.93	1.77	2.23	2.90	1.17	2.47	0.05	0.37	0.93		
df	92	29	133	51	182	44	110	154	58	161	62	18		
P	0.587	0.699	0.881	0.357	0.078	0.031	0.005	0.244	0.016	0.960	0.713	0.365		

Table 4 (continued)

[a] UA = Unprotected area; PA = Park area

[b] number of item categories

[c] Shannon-Wiener diversity index (H') for each season in each site.

[d] t-test for comparison between two diversity indices (H' ; Zar 1996).

[e] between one two-month period and the next (e.g. January-February and March-April under the January-February column ; .... ; November-December and January-February under the November-December column).

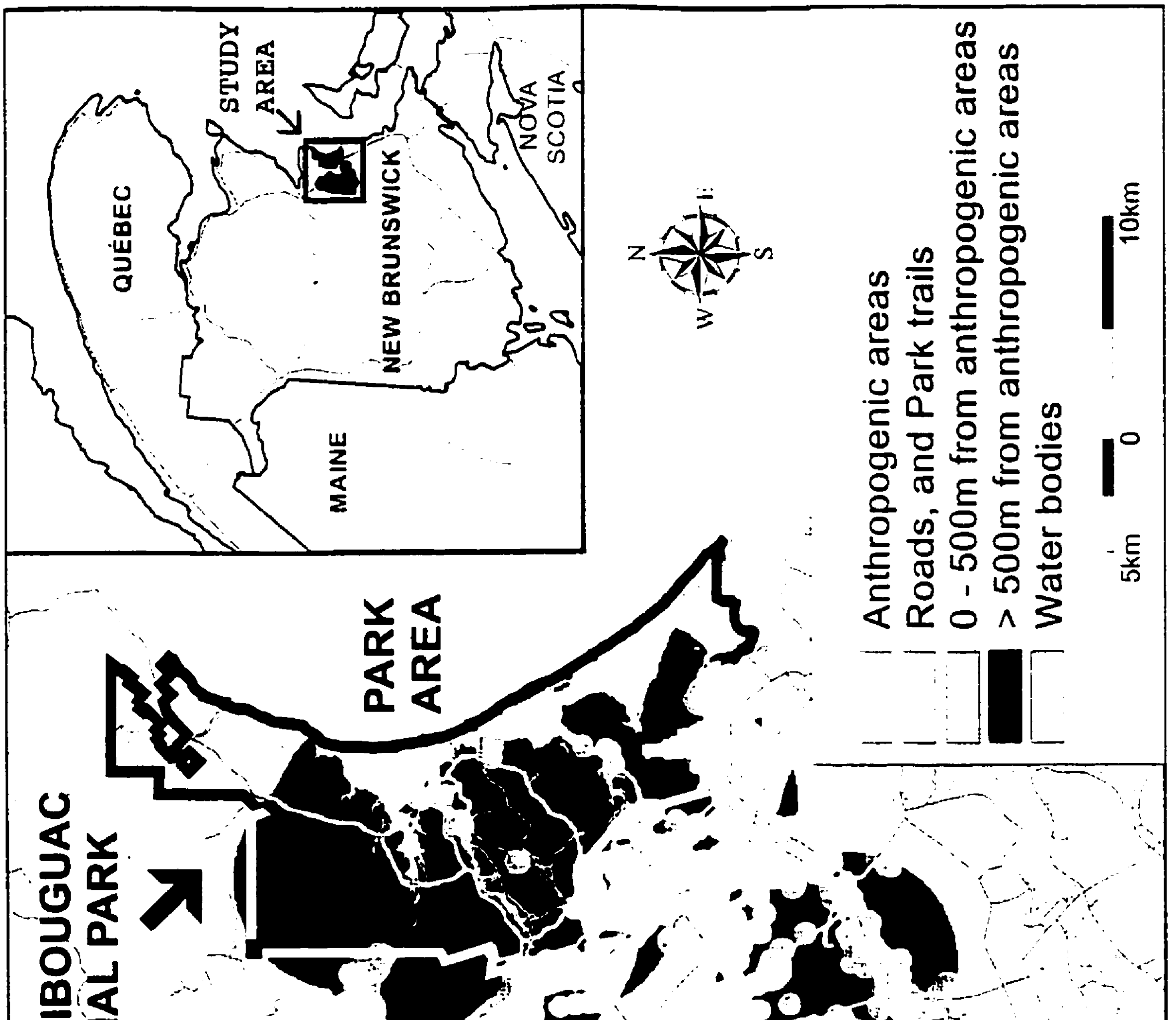
Figures

Figure 1: Location and landscape characteristics of the study area. Two areas are shown: a protected area comprising most of Kouchibouguac National Park (Park area), and an "unprotected area".

Figure 2: Seasonal variation in the main items of coyote diet in Kouchibouguac National Park (PA) and the adjacent unprotected area (UA).

Figure 3: Cluster analysis of seasonal coyote diet in Kouchibouguac National Park (PA) and adjacent unprotected area (UA).

Figure 4: Seasonal variation in coyote diet diversity in Kouchibouguac National Park (PA) and the adjacent unprotected area (UA).


UNPROTECTED AREA
KOUCHIBOUGUAC NATIONAL PARK
PARK AREA
QUÉBEC
STUDY AREA
NEW BRUNSWICK
MAINE
NOVA SCOTIA
N
E
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Anthropogenic areas
Roads, and Park trails
0 - 500m from anthropogenic areas
> 500m from anthropogenic areas
Water bodies
5km
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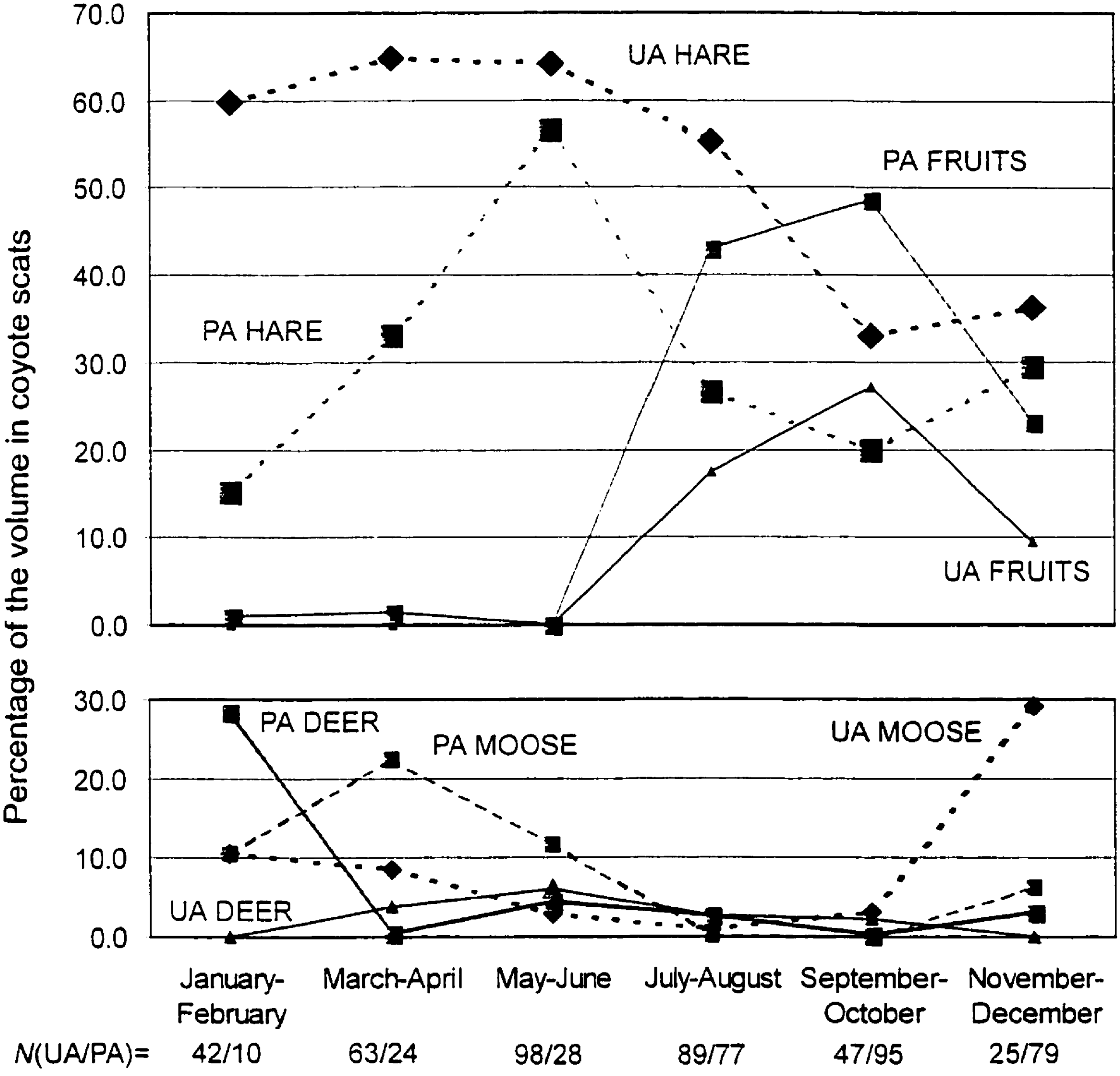
10km


70.0
60.0
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Percentage of the volume in coyote scats
UA HARE
PA FRUITS
PA HARE
UA FRUITS
PA DEER
PA MOOSE
UA MOOSE
UA DEER
January-February
March-April
May-June
July-August
September-October
November-December
N(UA/PA)=
42/10
63/24
98/28
89/77
47/95
25/79

Figure 2

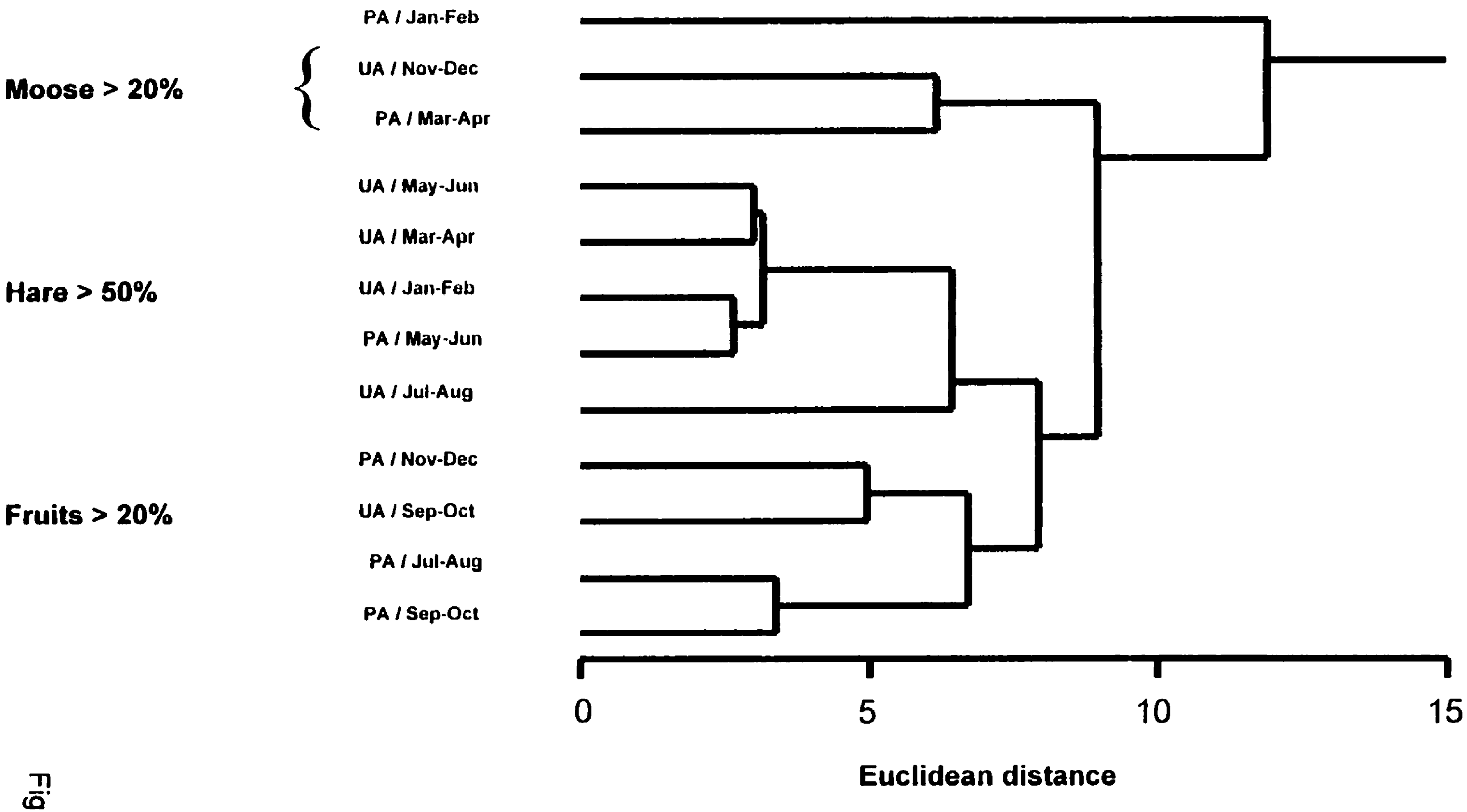
PA / Jan-Feb
Moose > 20%
UA / Nov-Dec
PA / Mar-Apr
UA / May-Jun
UA / Mar-Apr
Hare > 50%
UA / Jan-Feb
PA / May-Jun
UA / Jul-Aug
PA / Nov-Dec
Fruits > 20%
UA / Sep-Oct
PA / Jul-Aug
PA / Sep-Oct
0
5
10
15
Euclidean distance

Figure 3

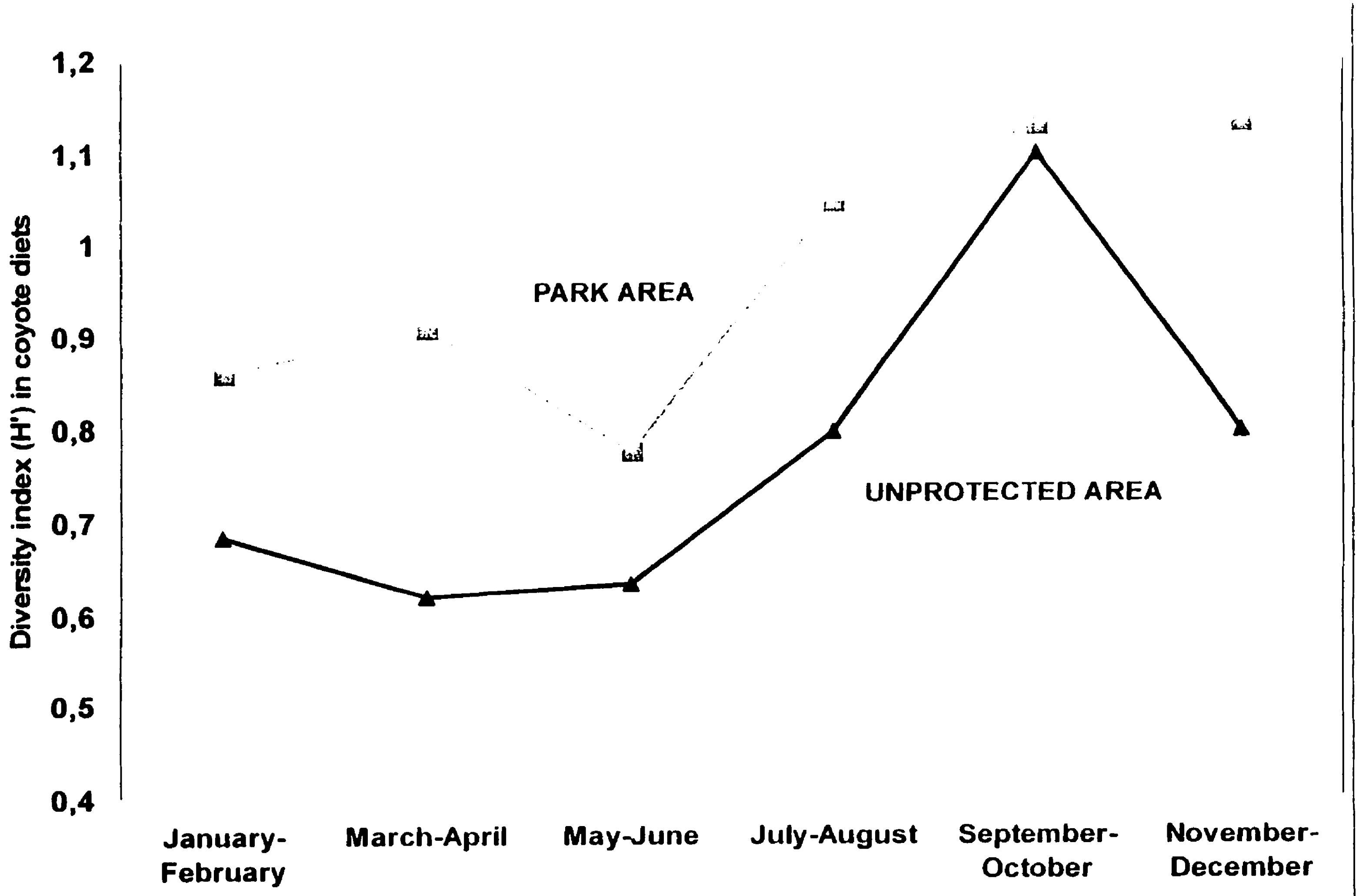
Diversity index (H') in coyote diets
1,2
1,1
1
0,9
0,8
0,7
0,6
0,5
0,4
PARK AREA
UNPROTECTED AREA
January-February
March-April
May-June
July-August
September-October
November-December

Figure 4

CHAPITRE 2

Contribution de l'étudiant à la préparation du manuscrit:

L'idée de cette étude a été suggérée par Christian Fortin. Les données de terrain ont été récoltées par M. Dumond. Le traitement des données et la rédaction ont été effectuées par M. Dumond.

M.-A. Villard ainsi que les membres du jury de thèse ont participé à la révision des versions précédentes.

DEMOGRAPHY AND BODY CONDITION OF A COYOTE (*Canis latrans*) POPULATION IN EASTERN NEW BRUNSWICK

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Abstract: We documented coyote demography and body condition using 77 carcasses collected in late fall and winter (1995-96 and 1996-97) during an increase in hare density in eastern New Brunswick. Physical characteristics were similar to those reported elsewhere in the northeastern portion of its range. Sex ratio did not differ significantly from 1:1. The population was unusually old (5.6 ± 3.4 years). Pregnancy rate was low (42.9% in adults), and placental scars (5.7 ± 2.0 scars / female) were only present in females > 5 years old. We compared November-January and February-March body condition according to sex and breeding status of females. Males experienced a significant depletion in fat reserves over the winter, maybe because a majority of individuals were affected by mange during late winter. Females with placental scars experienced a significant decrease in body mass over the winter, while non-reproductive adult females did not exhibit significant changes in body condition. Our results suggest that breeding females experience a negative energy budget during the mating season in eastern New Brunswick. Reproductive costs should be taken into account in future studies on demography and body condition.

Résumé: Nous avons étudié la démographie et la condition physique d'une population de coyotes de l'est du Nouveau-Brunswick à l'aide de 77 carcasses récoltées entre la fin de l'automne et la fin de l'hiver (1995-96 et 1996-97). Cette période correspondait à une phase d'augmentation de la densité du lièvre d'Amérique. Les caractéristiques physiques étaient similaires à celles rapportées précédemment dans le nord-est de l'aire de répartition du coyote. Le rapport des sexes n'était pas significativement différent de 1:1. La population était particulièrement âgée (5,6 ± 3,4 ans). La proportion de femelles reproductives était faible (42,9%) et seules les femelles de plus de 5 ans avaient des cicatrices placentaires (5,7 ± 2,0 cicatrices / femelle). Nous avons comparé la condition physique entre la fin de l'automne et la fin de l'hiver en fonction du sexe et du statut reproducteur des femelles. Les réserves de gras ont diminué significativement au cours de l'hiver chez les mâles peut-être parce que, à la fin de l'hiver, la majorité d'entre eux avaient la galle. La masse corporelle des femelles reproductices a diminué au cours de l'hiver alors qu'il n'y a eu aucune variation de condition physique chez les femelles adultes non-productives. Nos résultats suggèrent que, dans l'est du Nouveau-Brunswick, les femelles coyotes subissent un coût énergétique associé à la saison d'accouplement. Le coût reproducteur devrait être pris en compte lors des études futures portant sur la démographie et la condition physique du coyote.

INTRODUCTION

While increasing its range, the coyote (*Canis latrans*) has to face different climatic and ecological conditions, which in turn influence its demography. In the boreal forest of Alberta, Todd (1985) found that coyote populations were strongly dependent on cyclic snowshoe hare (*Lepus americanus*) populations, which influenced reproduction and body condition. In the same region, Todd et al. (1981) related a decrease in pregnancy rate in yearling female coyotes and in mean litter size among adult females to a decline in snowshoe hare density. In Alaska, wolf productivity also was positively related to nutritional status estimated from subcutaneous fat depth and prey availability (Boertje and Stephenson 1992). Todd and Keith (1983) and Todd (1985) found that coyote fat deposits decreased in a forested region of Alberta from early to late winter. Windberg et al. (1991) reported the same phenomenon in southern Texas. Todd and Keith

(1983) suggested that coyotes experienced a negative energy balance over the winter when hare were scarce.

In contrast with the studies mentioned above, fat depletion in coyotes occurred mostly between late winter and summer in eastern Québec, and not significantly over the winter (Poulle et al. 1995). Moreover, the reproductive status of female eastern coyotes seemed to be independent of fat deposits (Poulle et al. 1995). However, Todd et Keith (1983), Todd (1985), and Windberg (1995) conducted their studies during periods characterized by low prey availability or high coyote densities, which did not seem to be the case in Poulle et al. (1995). Poulle et al. (1995) explained late-winter to summer fat depletion by the fact that summer, in the northeast, is characterized by a low availability of prey. Crête and Lemieux (1994) also suggested that during summer, coyotes may encounter problems in locating prey species, which may negatively affect reproduction.

Forested areas at the northern edge of the range of the coyote (*Canis latrans*) are sometimes considered to represent suboptimal habitat for this species (Todd 1985, Crête and Lemieux 1994, Tremblay et al. 1998). These authors suggest that the viability of coyote populations in northern forested areas mainly depends on resources derived from human activities. Based on food habits and foraging behavior, Tremblay et al. (1998) suggested that northeastern coyote populations may represent a source-sink metapopulation whereby rural areas act as demographic sources and forested areas represent sinks. Coyotes tend to be heavier and larger (Tremblay et al. 1998), and fatter (Todd 1985) in rural landscapes than in forested landscapes. Then, one of the suboptimal characteristics of northern forested habitat would be a periodic low availability of prey, resulting in poor body condition compared to coyotes living in rural habitats.

In eastern Canada, only a few studies have documented coyote demography (Moore 1981, Jean and Bergeron 1984, Crête and Lemieux 1994, Poulle et al. 1995) and body condition (Fortin and Huot 1995, Poulle et al. 1995). Only one of these studies (Moore 1981) was conducted in New Brunswick. We require more data on northeastern coyote populations in relation to food availability under different levels of human activity in order to better understand coyote demography.

Our goals were (1) to document demography and body condition of a low density, lightly to moderately exploited coyote population in a forested landscape of eastern New Brunswick during an increase in snowshoe hare population, and (2) to compare coyote body condition between early and late winter with regards to sex and breeding status.

STUDY AREA

The study area is located in eastern New Brunswick, Canada, and extensively overlaps the Greater Kouchibouguac Ecosystem, a region centered on Kouchibouguac National Park (65°00'N, 46°50'W). Forests cover approximately 70% of the landscape and are dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white cedar (*Thuja occidentalis*), trembling aspen *(Populus tremuloides*), gray birch (*Betula populifolia*), and red maple (*Acer rubrum*). The landscape also is characterized by the presence of wetlands, clearcuts, villages, and roads. Logging and peat extraction are the main human activities outside the Park. The physiography of the region is flat to gently sloping (Deloges 1980). The average annual temperature is 5°C, and precipitations average 979 mm (18,8 % of which falls as snow, corresponding to 1.8 m). The average winter temperature (December to March) is -7.1°C. The lowest temperatures are usually recorded in January or February (Desloges 1980), and the maximum snow depth usually is reached in March (Fortin et al. 1999).

MATERIALS AND METHODS

Population trends were estimated for coyote, red fox, bobcat (*Felis rufus*), snowshoe hare, moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) using a questionnaire sent to trappers, hunters, and Kouchibouguac National Park wardens during January 1997. We asked which year(s), in the 1985-1996 period, each species reached its maximum and minimum densities, and what was the trend of the population over the last five years in our study area (increasing, decreasing, or stable). For each species, we assigned +1 for each year considered to be a density peak, and -1 for each year considered to be a density low. The sum for each year gave the relative abundance of a species for each year between 1985 and 1996. Similarly to

Lindström et al. (1994), we assigned a value of +1, 0, and -1, when the population of a given species was considered to increase, to remain stable, or to decrease, respectively. The average was calculated and used as an index of the trend over the last five years. Additional information was obtained from Kouchibouguac National Park track-transect reports, and the ungulate surveys of the Department of Natural Resources and Energy.

Seventy-seven coyote carcasses were collected from trappers, hunters, and forest rangers from November 1995 to March 1996 and from December 1996 to February 1997. Coyotes were captured using foot traps and snares, or were killed by hunters or through collisions with vehicles. All carcasses were kept frozen until March of each winter for necropsies at the Atlantic Veterinary College (Charlottetown, Prince Edward Island, Canada). We recorded body length to the nearest 0.5 cm from the tip of the nose to the base of the tail (BTL) and from the tip of the nose to the last vertebra of the tail (TL). We weighed each carcass to the nearest 0.5 kg. Because we had skinned (SBM) and unskinned (BM) body mass, we standardized body mass data using the regression equation BM (kg)= 1.09 x SBM (kg) + 0.45 (R^2=0.99, n=49, Poulle et al. 1995). Inferior canines were extracted after boiling the entire head for a few minutes. Age was determined by counting canine cementum annuli (Bio-Tech Enr., Charlesbourg, Québec). Coyotes of 0.5 to 1, 1.5 to 2, and over 2 years old were classified as juveniles, yearlings, and adults respectively. We removed and weighed both kidneys and attached fat, and calculated the kidney fat index (KFI): KFI = (kidney fat mass x 100 / kidney mass). Both femurs were removed and a 3-cm long piece of marrow was weighed, and then air-dried, and weighed again. We calculated the percentage of fat in the marrow (FMF). The fat was estimated to constitute most of the air-dried marrow (Neiland 1970). FMF=[(air-dried marrow mass)*100/(marrow mass)]. For the KFI and the FMF we used the mean of the right and the left samples. As suggested in Huot et al. (1995), we calculated the kidney - femur fat index (KFFI): KFFI = FMF + KFI. We also estimated the percentage of fat in the body (PF) using the regression equation proposed by Huot et al. [1995 ; PF = (7.18 x 10^{-2}) KFFI + 0.46]. The uterus (from the cervix to the ovaries) was removed from each female and opened to count placental scars from the previous spring. Generally, mating season peaks during February, lasting through March (Hilton 1978, Chambers

1992), thus we compared BM, TL, BTL, KFI, FMF, KFFI, and PF between November-January and February-March separately for males and females, and for reproductive (with placental scars of previous spring) and non-reproductive (without placental scars) females. For sex ratio, length and body mass, additional data were obtained from coyotes captured in October-November 1995 (n = 5) and February 1996 (n = 4) for telemetry purposes.

Since our goal was to obtain an overall picture of population structure, reproduction, and physical condition rather than to document population dynamics, we pooled the two fall-winter samples. We examined differences in physical characteristics and body condition between sex, seasons, breeding status, and among age classes using t-tests. We tested the hypothesis of a balanced sex-ratio with a G-test. We used an alpha level of 0.05 for all statistical tests. Sample size varied among tests owing to missing values for certain individuals. We summarized sample sizes for the different variables and comparisons in Table 1.

RESULTS

Population trends

We received 27 (25% of 108 sent) questionnaires adequately completed, i.e. we excluded questionnaires where the same year(s) was (were) indicated for both maximum and minimum densities of a species. Based on the results from these questionnaires, we plotted the estimated trends in the populations of each species over the 1985-1996 period (Fig. 1) and we calculated the trend over the last five years (Table 2). The relationships among species followed the expected patterns. For example, coyote population trends usually are inversely correlated with those of red fox and bobcat, and so are trends of white-tailed deer and moose. Winter track transects in Kouchibouguac National Park (1982, 1992, and 1996) also showed similar trends (Morton and Savoie 1983, Richard 1992, 1996). During our study (1995-1997), coyote populations declined or remained stable at a relatively low density, and snowshoe hare populations increased. Coyote density was estimated to be ≤ 0.1 coyote/km^2 (Dumond 1997, Thébeau, unpublished data). Moose abundance was relatively stable (Table 2) and we estimated a density of approximately 0.3 moose / km^2 in the study area according to the 1995 aerial ungulate survey in Kouchibouguac National Park (Richard 1995), and aerial surveys of 1991 and 1993 in adjacent areas by the Department of Natural Resources and Energy. Deer were at a relatively low density. Red foxes were numerous in the study area, and bobcats were slightly increasing after a long period of low density.

Sex ratio and age structure

For the overall coyote sample, sex ratio did not differ from 1:1 ($G = 0.01$, $df = 1$, $P=0.915$, Table 3). The population was old, averaging 5.9 ± 3.1 years for females and 5.3 ± 3.7 for males (Table 3). Juveniles, and yearlings represented only 15.6% (n=12) of the population, and 64.9% of the individuals were over 4.0 years old (Fig. 2). The major mode was approximatly 5.5-7.5 years old (39.0% of the population, n=30, Fig. 2), which were born during the high coyote population density period of 1988-1990 (Fig. 1). Individuals over 10 years old represented 9.1 %.

and the oldest male and female were 16.5 and 15.5 years old respectively (Fig. 2).

Physical characteristics

Physical characteristics (body length and body mass) of our coyote population were similar to those reported in other studies in northeastern United States (Richen and Hugie 1974, Hilton 1976) and eastern Canada (Moore 1981, Poulle et al. 1995, Fortin and Huot 1995). Males were heavier ($t_{(85)} = 2.577$, $P = 0.012$) and longer (TL, $t_{(84)} = 3.419$, $P = 0.001$) than females (Table 3). Average body mass and length seemed to increase with age until they reached a plateau for coyotes over 6 years old (Fig. 3), but the high intra age-class variations resulted in a poor correlation between age classes and body mass or length ($R^2 < 0.50$). When grouped together, juveniles and yearlings had a significantly lower body mass ($t_{(75)} = 3.754$, $P \leq 0.001$), and shorter body length ($t_{(74)} = 2.177$, $P = 0.033$) than adults.

Pregnancy rate and placental scars

Pregnancy rate, as estimated by the presence or absence of placental scars, was only 42.9% among adult females, which is low but comparable to that reported by Crabtree (1989) for an unexploited coyote population (40%). The pregnancy rate increased with age (Table 3). No female younger than 5.5 years had placental scars, which means that no female younger than 4.5 years had reproduced during the previous breeding season. The average number of placental scars was 5.7 ± 2.0 (Table 3), which falls in the lower range (5.9 to 7.9 scars per adult female) of those reported in other northeastern coyote populations (Moore 1981, Jean and Bergeron 1984, see Chambers 1992 for a review). The average number of placental scars per reproductive female did not vary significantly among reproductive age classes (> 5 years old), but was highest in females over 8 years old (Table 3).

Change in body condition over the winter

We compared overwinter (November-January versus February-March period) variation in body mass (BM), body length (TL and BTL), KFI, FMF, KFFI, and PF for males and females and specifically for adult males and females (Table 4). For same-sex comparisons, with all ages > 2 years pooled, none of the differences in body length were significant. Therefore, differences in other variables apparently referred directly to changes in body condition. Among males (Fig.4), there was a significant decrease between November-January and February-March for KFI ($t_{(35)}$ = 2.685, $P = 0.011$), FMF ($t_{(35)}$ = 4.557, $P \leq 0.001$), KFFI ($t_{(35)}$ = 3.522, $P = 0.001$) and PF ($t_{(35)}$ =3.522, $P = 0.001$). However, these results have to be considered with caution owing to the fact that the majority of males collected during February-March were affected by sarcoptic mange. It follows that, for males, our data may not reflect the trend that would be observed in a healthy coyote population. Also, our small sample size of males during February-March reduces the generality of our findings. For all females and for adult females separately, none of the comparisons were significant ($P > 0.2$).

Relationships between breeding status and body condition

We compared body mass (BM), body length (TL and BTL), KFI, FMF, KFFI, and PF between periods (November-January versus February-March) and among reproductive and non-reproductive adult females. There was no significant difference in body length between periods or between breeding status (reproductive *versus* non-reproductive females). Females with placental scars were significantly heavier ($t_{(33)}$ = 2.064, P= 0.047) than females without scars during November-January (Table 4). During February-March, there was no significant difference in body condition between reproductive and non-reproductive females, but all the variables had a higher value in non-reproductive females than in reproductive females. Nevertheless, mass and pregnancy rate seemed to increase with age, and the early-winter difference in mass between reproductive and non-reproductive females could be an effect of age. Average body mass in reproductive females decreased significantly (14%, Fig.4) between November-January and February-March ($t_{(13)}$ = 2.483, $P = 0.027$), but there was no significant decrease in KFI, FMF, KFFI, and PF (Table 4). For non-reproductive females (Fig.4), there was no difference in body condition between periods (P>0.5 for all variables).

DISCUSSION

The coyote population under study was unusually old, with a low number of placental scars per female and a very low pregnancy rate. Previous studies reported that coyote populations were clearly dominated by juveniles and yearlings, with an average age lower than 3 years (Nellis and Keith 1976, Andrews and Boggess 1978, Berg and Chesness 1978, Todd et al. 1981, Jean and Bergeron 1984, Stephenson and Kennedy 1993, Crête and Lemieux 1994). Fortin and Huot (1995) also studied an old coyote population (mean = 7.0 years) in the Gaspé Peninsula (Québec). Crabtree (1989) reported an average age of 3.5 years in a population from south-central Washington. He suggested that the older age structure was due to the absence of exploitation, a low immigration rate, and a high mortality rate among pups.

In our study area, coyote trapping was light to moderate with occasional shooting by hunters but there was no eradication program. The low proportion of young coyotes (< 4 years), low pregnancy rate, and low number of placental scars per female in our population either indicated that (1) recruitment, and/or immigration of juveniles, yearlings and young adults were low, or (2) emigration in the younger age classes was high. Also, (3) pup mortality may have been high but we had no data to confirm this.

Crabtree (1989) found that only territorial females bred successfully and that territories could be occupied by the same female for several years, even though it did not breed successfully every year. Among non-territorial females with embryo implantation, none successfully whelped. Thus, he concluded that social behavior could affect demography (Crabtree 1989). When the level of coyote exploitation is low, it seems to increase social and territorial behavior and reduce the proportion of reproductive females (Andelt 1985, Crabtree 1989). This may contribute to stabilize the population at the saturation level (Andelt 1985). Although coyote density was relatively low, our study area may be saturated in terms of territory availability. Prey scarcity can induce an increase in the area of coyote territories (Mills and Knowlton 1991). In our study area, consecutive years of low hare density could have resulted in large coyote territories whose boundaries remained unchanged during the increasing phase of hare population cycle. This would have limited territory availability regardless of the availability of food. Low pregnancy rate and small litter size are generally associated with saturated populations (Knowlton 1972) or with low levels of exploitation (Jean and Bergeron 1984, Crabtree 1989). On the other hand, low reproduction parameters could also indicate that our heavily forested study area only provides suboptimal habitat for coyotes.

During the study, body condition in males and reproductive females decreased over the winter, whereas body condition in non-reproductive females remained similar between early and late winter. Poulle et al. (1995) did not find any significant decrease in male and female body condition from early (December-January, n=21) to late winter (March, n=8), but they did not test for a variation in body condition between reproductive and non-reproductive females over the winter. In the arctic fox (*Alopex lagopus*), Prestrud and Nilssen (1992) found that fat deposits were gained from August to November. They did not find significant fat depletion between November and March, but fat deposits were significantly depleted between March and May. In that same study, female arctic foxes that had reproduced the previous spring were significantly leaner than other foxes, suggesting an energetic cost of reproduction. Conversely, in our study, reproductive female coyotes were heavier than non-reproductive females in early winter. This contrasts also with the findings of Poulle et al. (1995), which suggested that for female coyotes, reproduction was independent of fat deposits. However, our results could be an artifact of the difference in average age between reproductive and non-reproductive females.

Compared to arctic foxes (Prestrud and Nilssen 1992) and coyotes from the Gaspé Peninsula (Poulle et al. 1995), female coyotes in eastern New Brunswick may have more opportunities to regain their body condition during early fall because climatic conditions are more favorable and there is probably a greater food availability. In the red fox, fat deposits were correlated with the consumption of fruits (Lindström 1983). During our study, fruits were an important component of coyote diet from July to October (Dumond et al. unpublished manuscript). The energetic cost of gestation and whelping may have been compensated by the high consumption of fruits. Also, mammalian food may not have been a limiting factor, as snowshoe hare densities and moose carcass availability were relatively high. Poulle et al. (1995) rejected the hypothesis that a fruit diet alone can be responsible for the important fat deposition during fall referring to the fact that fruits were mainly consumed in July and August in their study area (Crête and Lemieux 1994). The fact that Crête and Lemieux (1994) described coyote diet only from May to late August restricts considerably the argumentation of Poulle et al. (1995). In the Gaspé peninsula, Samson and Crête (1997) reported a percentage of volume of fruits in coyote scats over 40% during September and October. Poulle et al. (1995) considered summer as the period from the end of May to early September. Due to the small sample size (n=24), a bias could result from an unequal distribution of the sample during the period. Also, from June to August, adults expend energy to feed their young but, after this period, juveniles become more independent and can participate in foraging activities. During September and October, consumption of fruits was still high in our study area and may have contributed directly to fat deposition.

In coyotes, reproductive females are usually territorial, at least in unexploited populations (Crabtree 1989, Windberg 1995), and can breed for several consecutive years (Bekoff and Wells 1986). We can assume that the majority of females with placental scars (i.e. that mated successfully the previous winter) mated or would have mated during the winter of their capture. Mating peaks during February (Hilton 1978, Andrews and Boggess 1978, Bekoff and Wells 1986). Body mass decreased between early winter (before mating season) and late winter (during or after mating). Therefore, the overwinter decrease in reproductive-female body mass probably reflects an energetic cost incurred during the mating season rather than a cumulative cost associated with breeding the previous year and/or whelping activities. The fact that fat indices did not decrease significantly over the winter could indicate that mass loss was mainly due to protein and water loss. Kreeger et al. (1997) found that during consecutive fasting and refeeding, captive wolves quickly regained lost body mass but body composition changed. Most of the regained mass was in fat, while proteins and water were only partly regained. Non-reproductive females did not experience any significant decrease in body condition over the winter, which supports the idea that weight loss in reproductive females probably was related to their reproductive activities. These findings suggest that breeding status and reproductive costs should be considered in future studies on coyote body condition.

The level of exploitation seems to influence population densities, social behavior, and reproduction in coyote populations (Knowlton 1972, Crabtree 1989, Windberg 1995). Variations in coyote density among habitats or landscape types could reflect different levels of exploitation by humans, which in turn could influence social, territorial and reproductive patterns in coyote populations. Although body condition might be a good indicator of habitat quality for coyote, researchers must account for the sex and breeding status of the individuals. Data on sociodemographic patterns, exploitation level, and seasonal variation in body condition will be necessary to determine whether coyote populations from rural and forested habitats are structured as a source-sink metapopulation in the northeast.

Table 1: Sample sizes (number of coyotes sampled) for the different variables.

	Overall population (age classes)						Males			Females						
	Total	0.5-2.0	2.5-4.0	4.5-6.0	6.5-8.0	> 8.0	Overall	Adults		Overall	Adults Nov-Jan			Adults Feb-Mar		
								Nov-Jan	Feb-Mar		Overall	With placental scars	Without placental scars	Overall	With placental scars	Without placental scars
Age	77	12	15	18	19	13	38	33	5	39	22	9	13	12	6	6
BM	87	12	15	18	19	13	44	35	7	43	22	9	13	13	6	6
TL	86	11	15	18	19	13	43	34	7	43	22	9	13	13	6	6
BTL	86	11	15	18	19	13	43	34	7	43	22	9	13	13	6	6
Females	43	4	7	10	11	7				43	22	9	13	13	6	6
FWPS [a]	15	0	0	4	5	6				15	9	9		6	6	
KFI [b]	75	12	14	17	19	13	37	33	4	38	22	9	13	11	5	6
FMF [b]	75	12	14	17	19	13	37	33	4	38	22	9	13	11	5	6
KFFI [b]	75	12	14	17	19	13	37	33	4	38	22	9	13	11	5	6
PF [b]	75	12	14	17	19	13	37	33	4	38	22	9	13	11	5	6

[a] Females with placental scars.

[b] Kidney Fat Index (KFI), Femur Marrow Fat (FMF), Kidney-Femur Fat Index (KFFI), Percentage of Fat (PF).

Table 2: Population trends of several mammals in eastern New Brunswick (1992-96) as estimated from 27 questionnaires filled out by trappers, hunters and park wardens in January 1997.

Population trends (n = 27)	Coyote	Red Fox	Bobcat	Hare	Moose	Deer
Index	-0.44	0.33	0.15	0.30	0.15	-0.48
Decrease	59[a]	4	26	19	19	52
Stable	26	59	33	33	48	44
Increase	15	37	41	48	33	4

[a] Percentage of answers per species

Table 3: Coyote population characteristics in eastern New Brunswick from late-fall and winter samples 1995-1997.

	Sex-ratio	Age	BTL (cm)	TL (cm)	BM (kg)	Number of Placental scars	Pregnancy rate (%)[a]	KFI	FMF	KFFI	PF
Females		5.9 (3.1)	89.2 (4.7)	123.3 (5.4)	13.1 (1.9)	5.7 (2.0)	38.5	84.4 (48.8)	75.8 (11.8)	160.2 (54.6)	12.0 (3.9)
Males		5.3 (3.7)	91.7 (6.1)	128.5 (8.2)	14.6 (3.1)			72.3 (39.9)	69.5 (18.2)	141.8 (53.9)	10.6 (3.9)
Total	0.51	5.6 (3.4)	90.6 (5.6)	125.9 (7.4)	13.9 (2.7)			78.4 (44.8)	72.7 (15.5)	151.1 (54.7)	11.3 (3.9)
Age class (years)											
0.5-2.0	0.67		86.1 (4.0)	121.1 (5.5)	11.3 (1.0)	0.0	0.0	67.3 (33.0)	65.1 (12.5)	132.4 (42.9)	10.0 (3.1)
2.5-4.0	0.53		88.7 (6.7)	123.3 (7.6)	12.5 (1.9)	0.0	0.0	74.3 (46.2)	69.3 (16.0)	143.6 (56.5)	10.8 (4.1)
4.5-6.0	0.44		90.2 (4.3)	125.4 (5.0)	13.8 (2.2)	5.0 (3.0)	40.0	76.7 (36.8)	78.3 (9.7)	155.1 (42.3)	11.6 (3.0)
6.5-8.0	0.42		92.0 (5.1)	127.2 (7.6)	14.9 (2.7)	4.3 (2.9)	45.5	80.3 (57.3)	72.1 (18.7)	152.4 (67.8)	11.4 (4.9)
> 8.0	0.46		92.3 (4.7)	127.2 (6.4)	15.2 (2.8)	6.7 (3.0)	85.7	92.5 (44.3)	77.1 (16.5)	169.5 (56.6)	12.6 (4.1)

[a] Because pregnancy rate was estimated from the presence placental scars, it actually corresponds to the period 1994-1996.

Note: *standard deviations are shown in brackets.*

Table 4: Overwinter variation in coyote body condition in eastern New Brunswick (1995-1997).

			Age	BM	TL	BTL	KFI	FMF	KFFI	PF
Males	Overall	Nov-Jan	5.5 ± 3.8	14.7	128.3	91.9	78.0	73.3	151.3	11.3
							*	***	***	***
		Feb-Mar	3.7 ± 2.4	13.8	129.8	91.0	25.6	38.1	63.7	5.0
	Adults	Nov-Jan	6.7 ± 3.4	15.4	129.1	92.6	80.7	75.1	155.8	11.6
							*	***	**	**
		Feb-Mar	4.5 ± 1.8	14.3	131.4	92.0	30.3	39.7	70.1	5.5
Females	Overall	Nov-Jan	6.0 ± 3.7	13.2	123.8	89.5	88.7	76.6	165.2	12.3
		Feb-Mar	5.9 ± 1.7	13.0	123.2	90.2	74.7	74.3	149.1	11.2
	Adults	Nov-Jan	6.9 ± 3.4	13.8	125.0	90.4	90.1	77.8	167.9	12.5
		Feb-Mar	5.9 ± 1.7	13.0	123.2	90.2	74.7	74.3	149.1	11.2
Adult females with		Nov-Jan	8.9 ± 3.2	15.0	125.6	91.1	96.2	80.6	176.9	13.2
placental scars				•						
		Feb-Mar	7.0 ± 1.5	12.9	122.4	88.8	64.9	72.0	136.9	10.3
Adult females without		Nov-Jan	5.4 ± 2.7	13.0	124.6	90.0	85.9	75.8	161.7	12.1
placental scars		Feb-Mar	4.8 ± 1.0	13.1	123.8	91.3	83.0	76.3	159.2	11.9

Note : asterisks show significant differences between November-January and February-March (* $P < 0.05$, ** $P < 0.01$, ***$P \leq 0.001$)

Figures

Figure 1 : Relative abundance of the coyote, sympatric carnivores, and its main prey from 1985 to 1996 in eastern New Brunswick, as estimated from 27 questionnaires filled out by trappers, hunters, and Kouchibouguac National Park Wardens in January 1997.

Figure 2 : Age structure of a coyote population from eastern New Brunswick based on two late-fall-winter samples (1995-1997, n=77).

Figure 3 : Variation in mean body length and body mass (±SD) according to age class during late-fall and winter in eastern New Brunswick (1995-1997). Sample sizes appear in brackets.

Figure 4: Overwinter variations of body masse and Kidney-Femur Fat Index (KFFI) in adult coyotes according to sex and breeding status of the females.

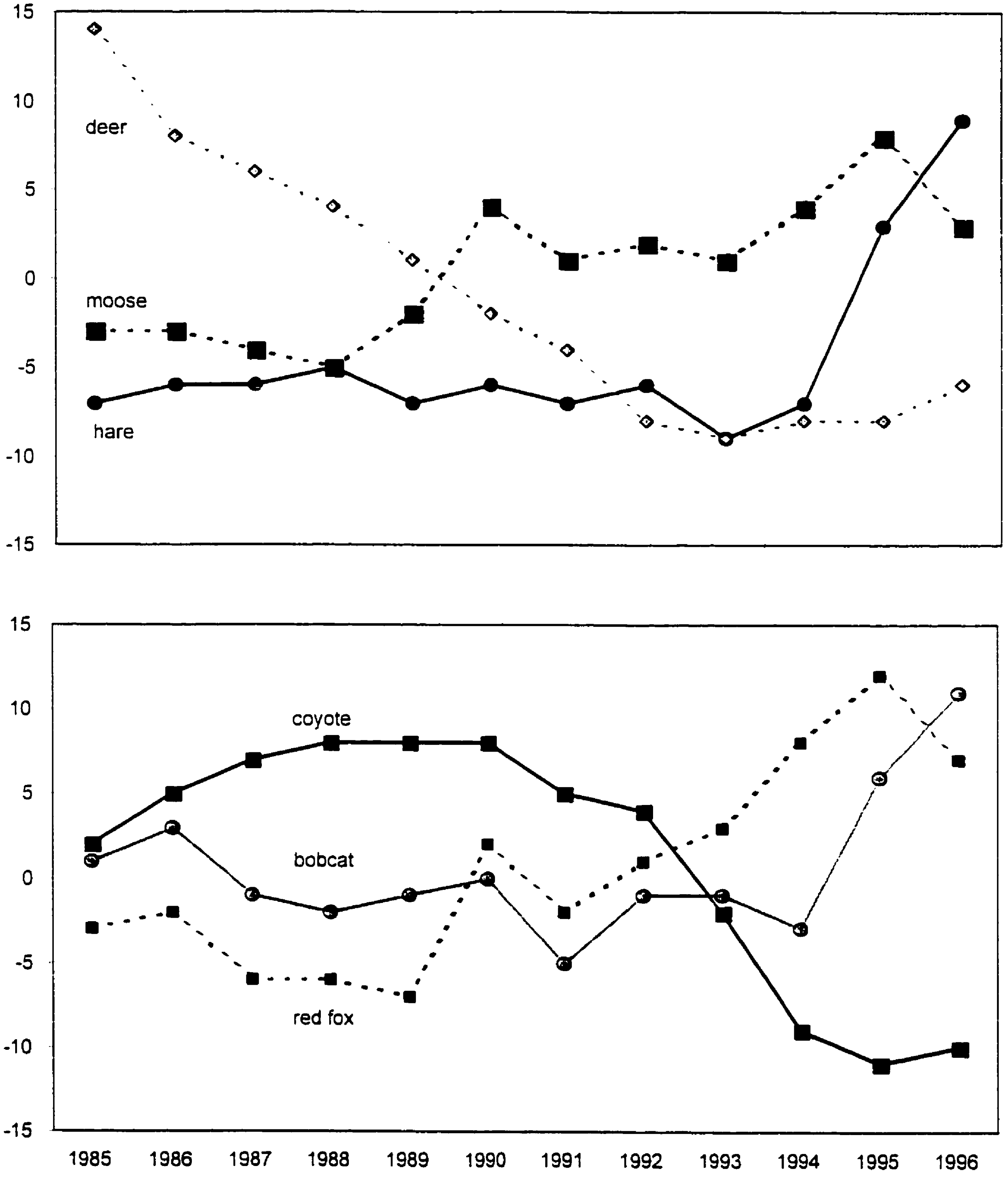

15
10
5
0
-5
-10
-15
deer
moose
hare
15
10
5
0
-5
-10
-15
coyote
bobcat
red fox
1985
1986
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996

Figure 1

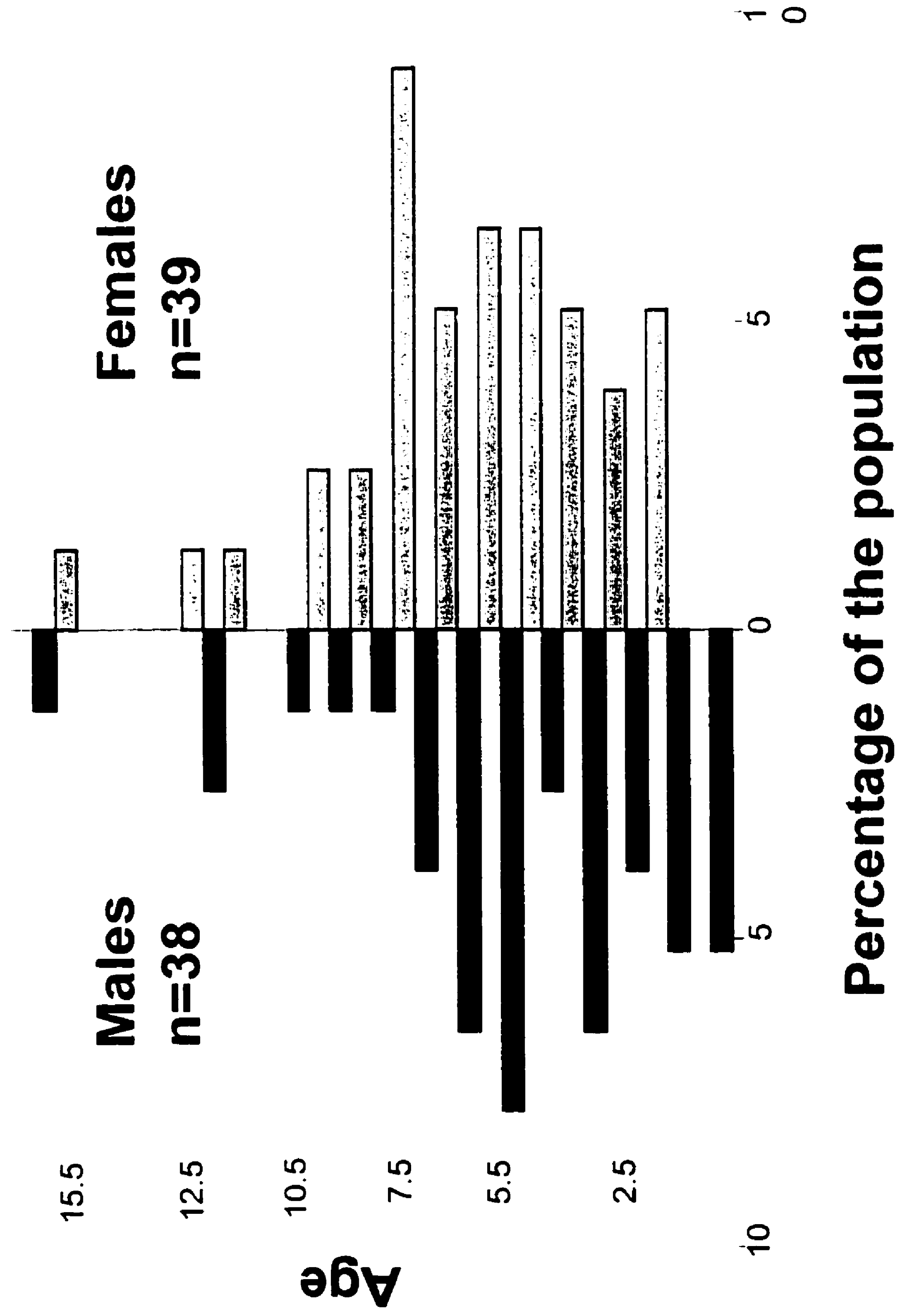
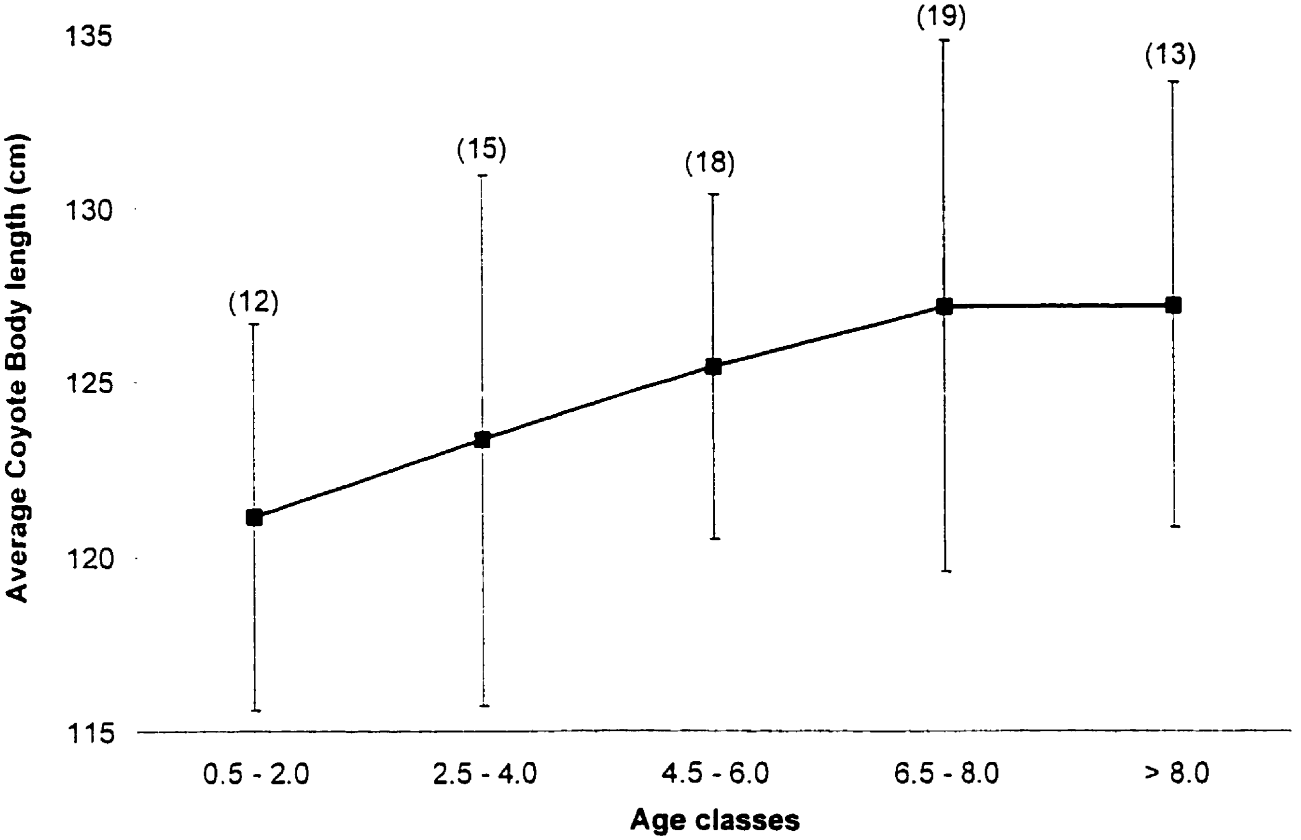

Females
n=39
Males
n=38
Age
15.5
12.5
10.5
7.5
5.5
2.5
Percentage of the population
10
5
0
5
10

Figure 2


Average Coyote Body length (cm)
135
130
125
120
115
(12)
(15)
(18)
(19)
(13)
0.5 - 2.0
2.5 - 4.0
4.5 - 6.0
6.5 - 8.0
> 8.0
Age classes

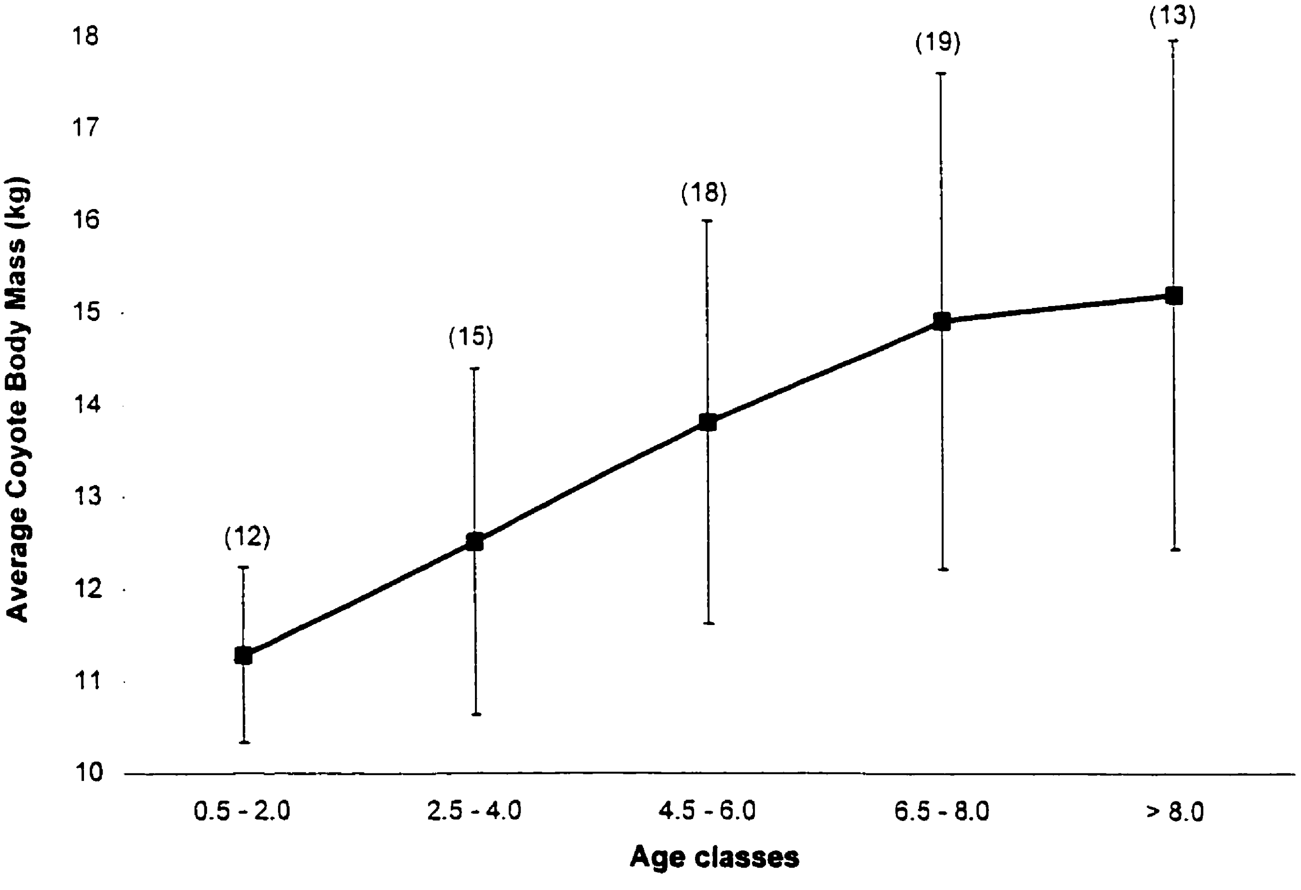

Average Coyote Body Mass (kg)
18
17
16
15
14
13
12
11
10
(12)
(15)
(18)
(19)
(13)
0.5 - 2.0
2.5 - 4.0
4.5 - 6.0
6.5 - 8.0
> 8.0
Age classes

Figure 3

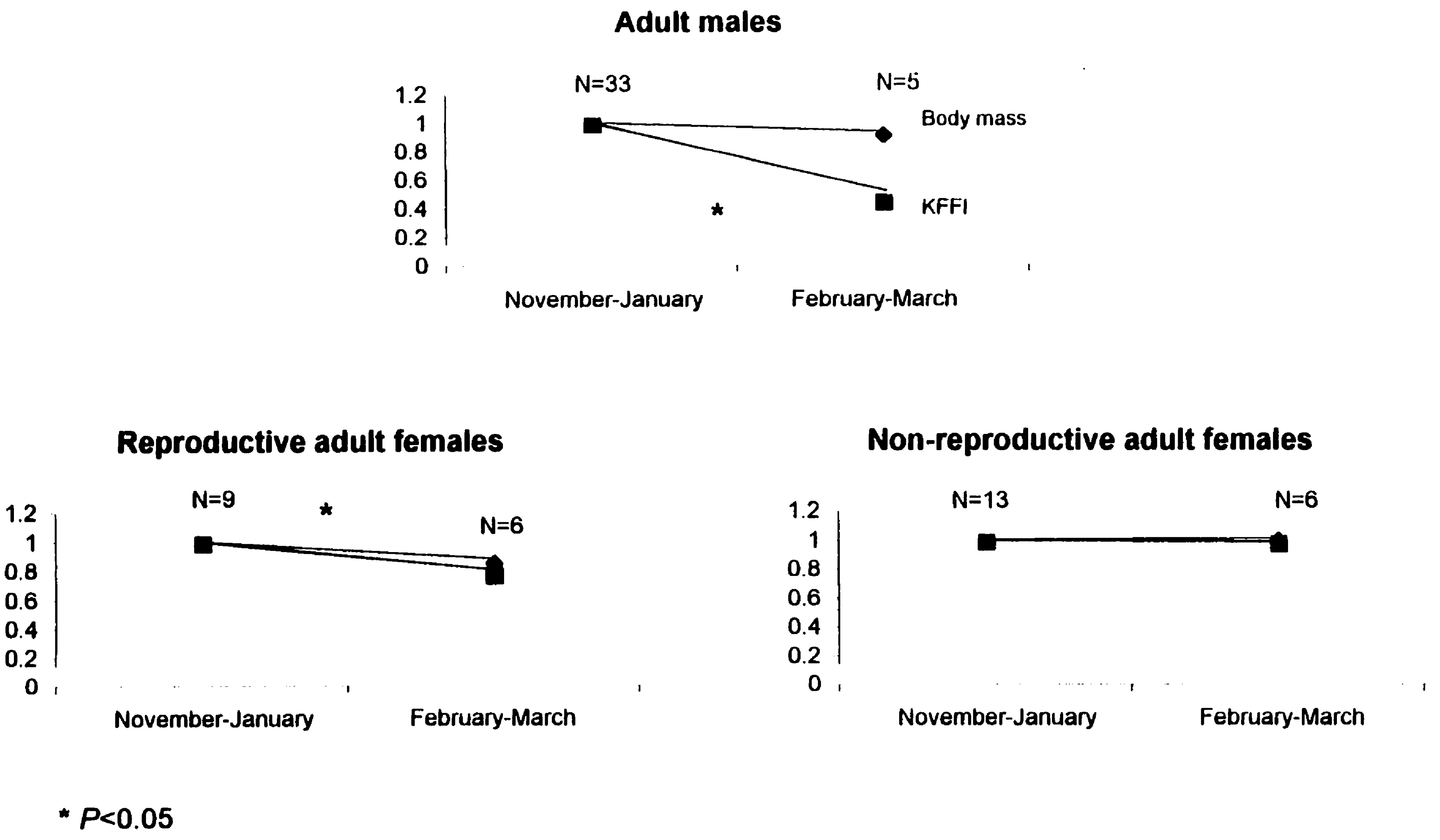

Adult males
N=33
N=5
Body mass
KFFI
*
1.2
1
0.8
0.6
0.4
0.2
0
November-January
February-March
Reproductive adult females
N=9
*
N=6
1.2
1
0.8
0.6
0.4
0.2
0
November-January
February-March
Non-reproductive adult females
N=13
N=6
1.2
1
0.8
0.6
0.4
0.2
0
November-January
February-March
* P<0.05

Figure 4

CHAPITRE 3

Contribution de l'étudiant à la préparation du manuscrit:

L'idée de cet article, la récolte des données sur le terrain, le traitement des données et la rédaction ont été effectuées par M. Dumond.

M.-A. Villard, É. Tremblay, ainsi que les membres du jury de thèse ont participé à la révision des versions précédentes.

COYOTE-MOOSE RELATIONSHIPS: SCAVENGING OR PREDATION?

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Soumis à ALCES mai 1999

Abstract: Over the last 200 years, the coyote has extended its range and adapted to new ecological conditions. In northeastern North America, new prey availability, climatic conditions, and possibly hybridization with wolves have resulted in an increase in coyote body size. This phenomenon and the relatively low diversity of prey in forested habitats during the winter have made predation on ungulates, such as white-tailed deer, relatively more frequent. With the decrease in deer populations in many northeastern portions of its range and the cyclic decline in snowshoe hare, coyote persistence depends on its ability to switch to new prey species. During my study in eastern New Brunswick, moose was found to be an important item in coyote diet during winter and spring (28.3% of occurrence in coyote scats from November to June). Moose density was approximately 0.3 moose/km^2 in the area, and many carcasses may have been available to coyotes from natural mortality, hunting, and vehicle collisions. The highest proportion of moose in coyote diet was reached in November-December (37.5% of occurrence in coyote scats), and was assumed to be associated with a high availability of carcasses from hunting and roadkills. However, moose represented 63.8% of volume in coyote scats collected around a moose carcass in March-April compared to 35.0% in December, suggesting that coyotes were more dependent on moose during late than early winter. Over the entire study area, two other peaks of moose proportion occurred in coyote diet in March (37.2% of occurrence) when snow cover was the deepest with several crusted snow layers, and in June (35.8% of occurrence) during the period of calving. These two peaks suggest that coyote predation on moose, at least on fawns, should be considered possible or even frequent. During this study, coyote body mass ranged from 9.5 to 22.0 kg (n=87), with 46.7% of adult males weighing from 15 to 22 kg (n=30). Coyote body mass overlapped that of moose-hunting wolves in southwestern Québec. The size

of coyote groups in eastern New Brunswick also overlapped that of moose-hunting wolf packs. Based on field data and previous studies, I suggest that moose may represent a key species in the diet of the northeastern coyotes, and that coyote may already, or in the near future, prey on moose.

INTRODUCTION

Coyote (*Canis latrans*) predation on small ungulates like mule deer (*Odocoileus hermionus*), white-tailed deer (*Odocoileus virginianus*), and pronghorn antelope (*Antilocapra americana*), is a common event where these species are available (Bowen 1981, Parker 1989, Poulle et al. 1993, Patterson 1995). In southeastern Québec, caribou (*Rangifer tarandus*) population survival is threatened by coyote predation (Crête and Desrosiers 1995). Although it is not common in the literature, coyote predation on larger ungulates such as elk (*Cervus elaphus*) has also been reported (Weaver 1977, Koehler and Hornocker 1991). Gese and Grothe (1995) studied coyote predation behavior toward elk in Yellowstone National Park, Wyoming. Coyote mainly killed calves, but predation on adult females occurred. In Jasper National Park, Bowen (1981) found elk to be one of the major food items in coyote diet but he considered predation to be rare.

Coyotes have dramatically extended their range over the last 200 years (Moore and Parker 1992). During their colonization northward and eastward, they adapted to new ecological conditions (climate, habitat, and new prey). Also, in some areas, hybridization with wolves (*Canis lupus*) probably occurred (Hilton 1978, Schmitz and Kolenosky 1985a, Wayne and Lehman 1992). Availability of larger prey (Schmitz and Kolenosky 1985b, Larivière and Crête 1992), and probably the lack of competitors such as wolves in most northeastern range, have resulted in an increase in coyote body size and mass. Coyotes in northeastern USA and eastern Canada are considered to be the largest representatives of the species in the wild (Voigt and Berg 1987), averaging of 15.2 and 16.6 kg for adult females and males, respectively, in New Brunswick and Nova Scotia (Moore 1981), and reaching occasionally 23 to 27 kg (Parker 1995). In the northeastern part of its range, the coyote encounters a lower diversity of available prey, particularly during winter. In the early stages of colonization, coyotes took advantage of the availability of white-tailed deer (Hilton 1978) but within a few decades, deer populations decreased in many areas of their northeastern range. When density of deer is low, coyotes are more dependent upon fluctuations of snowshoe hare (*Lepus americanus*) populations (Parker 1986), and thus could evolve in hunting new prey species.

Coyote predation on moose (*Alces alces*) does not seem to be a common event, considering the absence of observations reported in the literature. In the northeast, only a few studies reported moose in coyote diet at a proportion over 10 % of occurrence or volume in scats, at least during one season (Major and Sherburn 1987, Fortin and Huot 1995, Samson and Crête 1997). Natural moose mortality during winter and human-induced mortality (hunting and vehicle collisions) mostly during fall could provide a large amount of moose carcasses to coyotes. With the recent decrease in deer populations and the fluctuations in snowshoe hare population densities in eastern Canada, moose could become more of a staple food for coyotes, especially in high moose density areas. Previous studies have considered the coyote only as a scavenger of moose carcasses (Hilton 1978, Parker and Maxwell 1989). Hilton (1978), suggested that when large prey are more or less exclusively available, direct predation on deer may become proportionately more frequent. It is now known that coyotes prey frequently on white-tailed deer (Messier et al. 1986, Parker and Maxwell 1989, Dibello et al. 1990, Lavigne 1992, Poulle et al 1993, Patterson 1995), and that a solitary coyote can kill female adult deer with good femur marrow fat index (> 80%) in deep snow (Patterson 1994). The common perception that coyotes could only scavenge could only scavenge on white-tailed deer (Ozoga and Hager 1966, Hamilton 1974, Richens and Hugie 1974, Hilton 1976) was refuted by recent studies, and so could the notion that they cannot prey on moose.

In La Vérendrye reserve in southwestern Québec, wolf body weight averages 29.6±1.1 and 26.6±1.3 kg for adult males and females, respectively (Messier 1987). Moose (0.37 moose/km^2) was the major prey for wolves in that area. In adjacent areas, wolves averaged 25.2±1.4kg and 21.7±1.1kg for adult males and females respectively, and also mainly preyed on moose (0.25 to 0.21 moose/km^2, Messier 1987). In Algonquin provincial Park, male wolves weighed from 19.5 to 36.7 kg and averaged 27.7 kg, while females ranged from 17.7 to 31.7 kg (Pimlott et al. 1969). The sligth overlap in the range of body mass between coyotes and wolves would support the hypothesis that coyotes can reach the physical capability to kill at least a moose calf.

Moose hunting by wolves, except for newborn fawns, requires cooperative hunting by the pack (Mech 1970). Within and outside La Vérendrye reserve, wolf pack size averaged 5.7 (range 2 to 8) and 3.7 (range 2 to 6) individuals respectively (Messier 1985). Messier and Barrette (1982), and Dumond (1997) found coyote packs ranging from 3 to 5 individuals between mid-November and April in southern Québec and eastern New Brunswick respectively. In Jasper National Park, Bowen (1981) found that during winter, 59% of the coyotes lived in packs composed of three to eight related adults, yearlings, and independent young. In National Elk Refuge, Wyoming, Camenzind (1978) reported that 61% of the resident coyotes belonged to packs ranging from 3 to 7 individuals. Also, temporary aggregations from 7 to 22 transients were observed (Camenzind 1978). During winter snowtracking in Nova Scotia, Sabean (1993) reported coyote group sizes of 3 to 6 individual. As was the case for body mass, coyote pack size overlaps that of moose-hunting wolves.

In this paper, I discussed the hypotheses that (1) moose could become a key species in the diet of the northeastern coyotes, and that (2) evolution of coyote physical characteristics and cooperative foraging behavior may result in predation upon moose. I used data on coyote diet and physical characteristics in eastern New Brunswick from October 1994 to February 1997, and previous studies in eastern Canada and northeastern USA.

METHODS:

The study was conducted in Kouchibouguac National Park (46°50'N, 65°00'W) and the surrounding area in eastern New Brunswick, from October 1994 to February 1997. The study area is part of the Maritime Plain Natural Region and contains a range of forest types typical of the Acadian Forest, associated freshwater systems and extensive peatlands (Tremblay and

Beach 1993). Logging and peat extraction were the main human activities outside the Park. The physiography of the region is characterized by a flat terrain gently sloping towards Northumberland Strait (Deloges 1980). The climate is typical of the eastern coast of the continent, with an average annual temperature of 5°C and average precipitation of 979 mm (with 18,8 % as snow corresponding to 1.8 meter). Winter temperatures (December to March) average -7.1°C (Desloges 1980).

I collected coyote scats from 9 January 1996 to 1 January 1997 ($n = 677$) for a comparative study on coyote diet within Kouchibouguac National Park, and in adjacent human-disturbed areas. Methods for field sampling and scat analysis are described in Dumond et al. (1999, submitted paper). Since differences in coyote diet between Kouchibouguac National Park and adjacent human-disturbed areas were found during July-August (P=0.013) and September-October (P=0.005, Dumond et al. submitted paper), diet for the region was characterized by the mean of the two areas. I also collected scats around two moose carcasses within Kouchibouguac National Park during March-April and December 1996. These scats were analyzed separately to avoid over-estimation of the proportion of moose in coyote diet. The first carcass (March) was discovered several days after coyotes had started feeding on it, according to the numerous tracks and bed sites found around the carcass, and the amount of meat missing on the carcass. The second carcass (December) was left in the woods by park wardens after a road kill. To allow comparison with other studies, diet data are shown as frequency of occurrence and percentage of total volume of scats, seasonally and on an annual basis.

I also collected coyote carcasses from trappers, hunters, and provincial forest rangers from November 1995 to March 1996 ($n = 52$) and from December 1996 to February 1997 ($n = 25$). Coyotes were captured using leghold traps and snares, or were killed by shooting or by vehicle collision. For each carcass, I recorded the sex, the age (cementum annuli count), and the total body length from the tip of the nose to the last vertebra of the tail. I also weighed each carcass with or without the skin. Because I had unskinned (BM) and skinned (SBM) body weight, I standardized weight data using the regression equation BM (kg)= 1.09 x SBM (kg) + 0.45 (Poulle et al. 1995). For length and body mass, additional data were obtained from October-

November and February live-capture sessions conducted as part of a telemetry study (n = 10).

In 1994-96, the coyote population density was estimated to be ≤ 0.1 coyote / km^2 within Kouchibouguac National Park using track counts and siren census techniques (Dumond 1997, Thébeau, unpublished data), and moose population density was calculated to be 0.4 moose / km^2 in the same area, based on helicopter census (Corbett 1995), and probably was slightly lower outside the Park (0.2-0.3 moose / km^2) according to surveys conducted by the New Brunswick Department of Natural Resources and Energy in 1991 and 1993 (unpublished data).

RESULTS

Ungulates in coyote diet:

Moose occurred frequently in coyote scats from November-December to May-June (over 20% of occurrence in scats, Table 1). The occurrence of deer in coyote scats was always lower than 15% except in January-February, when it reached a maximum of 20% (Table 1, Fig.1). On an annual basis, moose percentage (volume and occurrence) in coyote diet was very similar between Kouchibouguac National Park and adjacent human-disturbed areas (Table 2). Moose consumption by coyotes was mainly restricted to the months of March, when snow cover was at his deepest with layers of crusted snow (Fortin et al. 1999, Kouchibouguac National Park, unpublished data), June, during the fawning period, and November-December, when many carcasses remain from hunting season (Fig. 1). Percentage of deer in coyote diet followed similar fluctuations, but with a maximum in January-February rather than March (Fig.1).

I collected 16 and 28 coyote scats around a moose carcass in March-April and December respectively (Fig. 2). The food items found in March-April scats were, by order of decreasing importance, moose, grass, beaver *(Castor canadensis)*, muskrat (*Ondatra zibethicus*), fishes, porcupine (*Erethizon dorsatum*), snowshoe hare, birds, and garbage (Fig. 2). In December, food items were, by order of decreasing importance, moose, snowshoe hare, grass, deer, other plant materials, small mammals, porcupine, fruits, birds, and garbage (Fig. 2). During March-April, coyotes seemed to feed more exclusively on moose carcass than in December (Fig. 2). During March-April 1996, at least three coyotes were feeding on the carcass. In April 1995, a minimum of three coyotes were also associated with a moose carcass monitored (Dumond 1997). In December, I was unable to estimate the number of coyotes present at the carcass due to the absence of snow.

Coyote physical characteristics:

The coyote population under study area was older than most other populations documented in the literature (Table 3). The range of weight in this coyote population (Table 3) slightly overlapped that of wolves in southwestern Québec (25.2±1.4kg and 21.7±1.1kg for males and females, respectively) (Messier 1987) and Algonquin Provincial Park, Ontario (ranging from 19.5 to 36.7 kg, and 17.7 to 31.7 kg for males and females, respectively) (Pimlott et al. 1969). Forty-seven percent of adult males weighed 15 kg or more (Table 3), and 11,4% weighed more than 19 kg.

DISCUSSION

Based on the fact that (1) the percentage of moose in coyote diet was high from November to June, and (2) the use of moose carcasses seemed to be more exclusive during late winter, I suggest that moose may represent an important food item for coyotes in eastern Canada. When available, moose carcasses provide a large amount of food, especially during late winter when coyote probably experience a negative energy budget (Pekins and Mautz 1990, Dumond and Villard, unpublished manuscript). During late fall and early winter, moose hunting and death related to vehicle collisions probably increased the availability of moose carcasses for coyotes, while during late winter, natural mortality was probably the main source of carcasses. Snow cover usually is deepest during late winter (Fortin et al. 1999, Kouchibouguac National Park, unpublished data). Deep, dense, and crusted snow could reduce moose mobility and accessibility to food sources, resulting in a lower physical condition (Franzmann 1978). The frozen layers in the snow cover also cause lesions on the legs that could affect moose mobility, while coyotes often can walk over these layers. Wolf predation on moose (Peterson and Allen 1974) and elk (Carbyn 1983, Huggard 1993) has been found to be related to snow conditions. The body mass range of the coyote population in eastern New Brunswick slightly overlaps that of wolves in Ontario (Pimlott et al. 1969) and southwestern Québec (Messier 1987). Because wolves in southwestern Québec mainly preyed on moose (Messier 1987), this further supports the possibility of moose predation by coyote in eastern New Brunswick.

During March 1995, and March-April 1996, a minimum of three coyotes were present around moose carcasses, indicating that this food source might allow an increase in the sociability of coyotes, which is consistent with previous studies (Camenzind 1978, Bekoff and Wells 1980, Bowen 1981). Fox (1975) described the coyote social system as a transitional type between solitary and social hunters. Coyote social organization usually consists of a mating pair that can be more or less permanent and their offspring that may remain with their parents after being physically independent (Bekoff and Wells 1980). Gittleman (1989) discussed the factors that could influence group living in carnivores. He pointed out two major functional explanations for group living, i.e. anti-predatory defense and exploitation of food. Since coyotes do not have many predators in northeastern North America due to the extirpation of the wolf and the cougar from most of those areas, anti-predatory defense is irrelevant. In terms of food exploitation, two main forces could lead to an increase in sociability in carnivores: hunting more efficiently and protecting a kill from competitors (Lamprecht 1981). Sociability in coyote has been shown to increase with prey size (Camenzind 1978, Bowen 1981) and carcass defense (Bekoff and Wells 1980, Bowen 1981). Bowen (1981) favored the increase in hunting success as the main driving force behind an increase of group size. Messier and Barrette (1982) suggested that group living in coyotes may result from the fact that it may be advantageous for juveniles to remain in their parents territory and thus benefit for food and protection. Messier and Barrette (1982), and Gese et al. (1988) argued that increased prey size is more an effect of already existing coyote groups than a cause for the increase in group size. Messier and Barrette (1982) suggested that coyote group size may rather reflect delayed dispersal by juveniles in high-density populations, when habitat is saturated. Camenzind (1978) and Bowen (1981) attributed the formation of coyote groups with an abundant. clumped, and defendable winter food source. However, whatever the driving force leading to an increase of group size, coyotes living in groups have access to a greater diversity of food because they can combine solitary hunting on small prey and group hunting on larger prey.

Large pack formation, with a mated pair and several generations of descendants, like for wolves, would be the next step that is occasionally reached during atypical ecological conditions such as an abundance of larger prey and a lack of competition from rival predators and conspecifics (Fox 1975). In wolf-free areas, an increasing moose density and a low availability of alternate food when hare populations are at the low density phase of their cycle might provide the coyote with such atypical ecological conditions. The use of moose carcasses seemed to be more exclusive during March-April (63.8 % of scat volume) than during December (35.0 % of scat volume), a period when the diversity of food available to coyotes is still high. In Yellowstone National Park, Gese et al. (1996) found that coyotes spent more time feeding on ungulate carcasses when snow depth and carcass biomass increased. Consistently with Gese et al. (1996), in this study, coyotes seemed to be more dependent on moose carcasses during the period when snow was deepest, and predation on weak moose would be possible for coyote group hunting in deep, crusted snow. Also, the increase in moose frequency in coyote scats during June could be related to the availability of newborn fawns, as is the case for deer (see Fig. 1), and, thus, associated with predation.

Of course, these results do not prove that coyote foraging behavior is evolving toward predation on moose. However, they do suggest that moose is an important food item for coyotes, at least during winter, and that coyotes may already or in the near future prey upon moose in eastern Canada. I suggest research on the use of moose carcasses by coyotes in the northeast, and further investigations of winter and spring coyote foraging behavior in areas of high moose density and deep snow cover.

Table 1 : **Seasonal and annual diet of coyotes in Kouchibouguac Greater Ecosystem, New Brunswick, Canada.**

Seasons	Jan-Feb		Mar-Apr		May-Jun		Jul-Aug		Sep-Oct		Nov-Dec		Annual	
n KNP / n OP [a]	10/42		24/63		28/98		77/89		95/47		79/25		313/364	
	%vol [b]	%occ [b]	%vol	%occ	%vol	%occ	%vol	%occ	%vol	%occ	%vol	%occ	%vol	%occ
Ungulates	24.8	39.5	17.6	33.0	12.5	30.6	3.3	11.1	2.8	5.3	19.3	40.0	13.4	26.6
Moose	10.5	24.5	15.5	27.8	7.2	23.5	0.6	3.7	1.6	3.7	17.7	37.5	8.9	20.1
Deer	14.3	20.0	2.1	5.3	5.2	8.9	2.7	7.4	1.2	1.6	1.6	3.8	4.5	7.8
snowshoe hare	37.4	54.5	48.9	62.6	60.4	73.0	40.9	53.5	26.5	45.6	32.8	50.3	41.1	56.6
other mammals	23.8	46.7	21.9	38.3	17.6	31.1	16.0	42.4	23.7	64.5	19.8	46.5	20.5	44.9
Fruits	0.5	5.0	0.7	4.2	0	0	30.4	49.8	37.9	73.0	16.3	34.8	14.3	27.8
Miscellaneous	13.5	29.5	11.1	33.2	9.6	40.3	9.4	48.6	9.2	49.1	11.8	36.1	10.8	39.5

[a] n KNP = number of coyote scats collected within Kouchibouguac National Park, New Brunswick, Canada.

n OP = number of coyote scats collected outside the Park.

[b] %vol = mean percentage of the total scat volume collected in the study area.

%occ = mean percentage of occurrence in coyote scats collected.

Table 2 : **Relative importance of moose in coyote diet within (KNP) and outside (OP) Kouchibouguac National Park, New Brunswick, Canada.**

Periods	Annual			Nov-Jun			Jul-Oct		
Area	n	%vol [a]	%occ [a]	n	% vol	% occ	n	% vol	% occ
KNP	313	8.5	20.7	141	12.7	29.5	172	0.2	3.1
OP	364	9.2	19.5	228	12.8	27.1	136	2.1	4.3
KGE [b]	677	8.9	20.1	369	12.7	28.3	308	1.1	3.7

[a] %vol = percentage of the total volume of coyote scats ; %occ = percentage of occurrence in coyote scats.

[b] Kouchibouguac Greater Ecosystem (mean between KNP and OP).

Table 3 : Physical characteristics of a coyote population in eastern New Brunswick, Canada.

	n m/f [a]	Males (range)	Females (range)	Total (range)
Age (years)	38/39	5.3 (0.5-16.5)	5.9 (1.5-15.5)	5.6 (0.5-16.5)
Length (cm)	43/43	129 (110-146)	123 (110-132)	126 (110-146)
Weight (kg)	44/43	14.6 (9.5 - 22.0)	13.1 (9.7 - 16.8)	13.9 (9.5 - 22.0)
Adult [b] weight (kg)	30/35	14.9 (9.5 - 22.0)	13.4 (9.7 - 16.8)	14.1 (9.5 - 22.0)
Adult [b] coyotes ≥15 kg	30/35	46.7 %	25.7 %	35.4 %

[a] number of males (m) and females (f).

[b] individuals > 2 years old.

Figures

Figure 1: Monthly variations in the occurrence (——) and percentage of volume (- - -) of moose (black lines) and deer (gray lines) in coyote scats, in 1996 in Kouchibouguac Greater Ecosystem, New Brunswick . Sample sizes of scats collected in Kouchibouguac National Park and in adjacent areas are shown in brackets.

Figure 2: Percentage of volume of the different food items found in coyote scats collected around a moose carcass in March-April, and in December 1996 in Kouchibouguac National Park, New Brunswick.

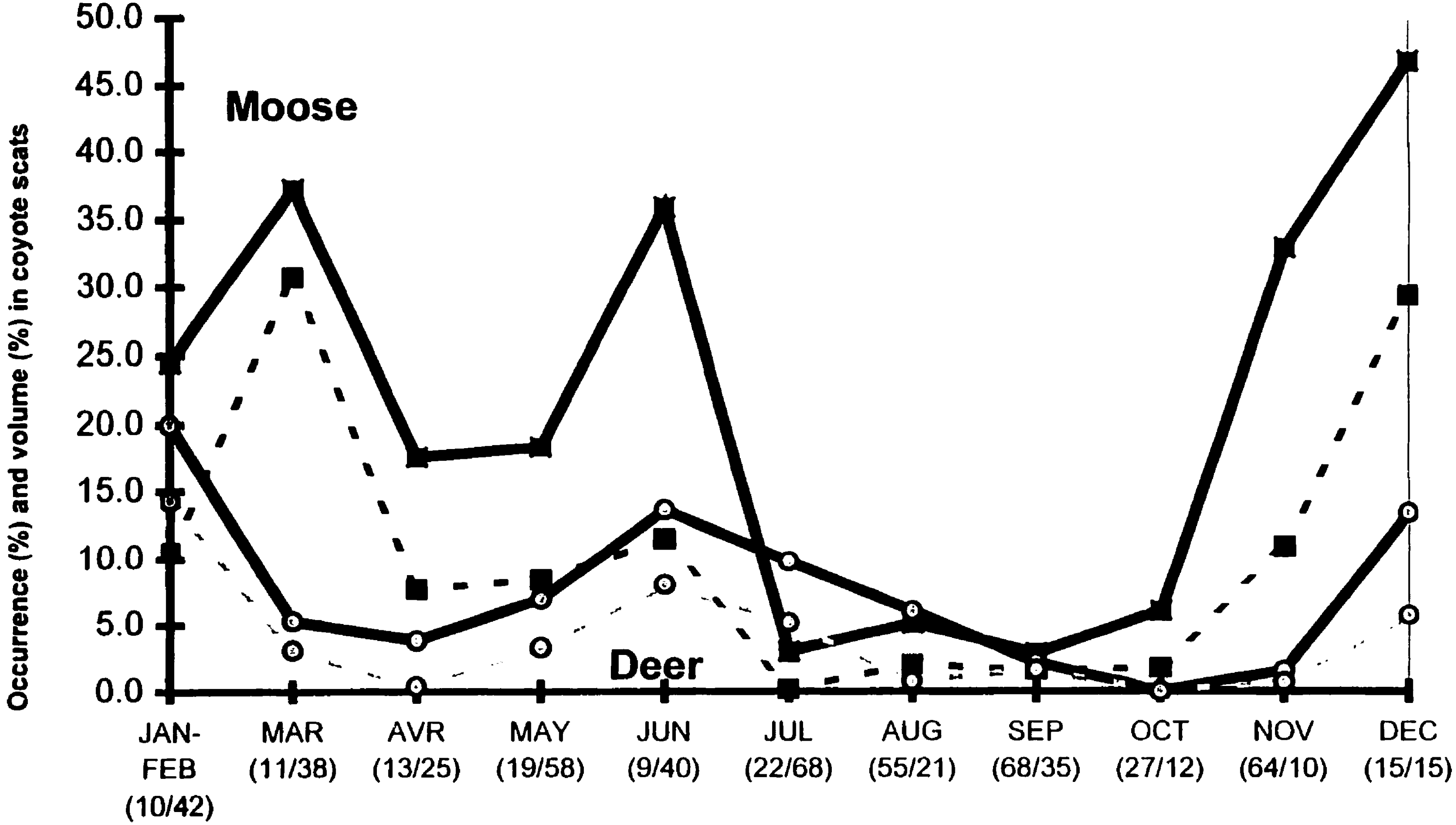
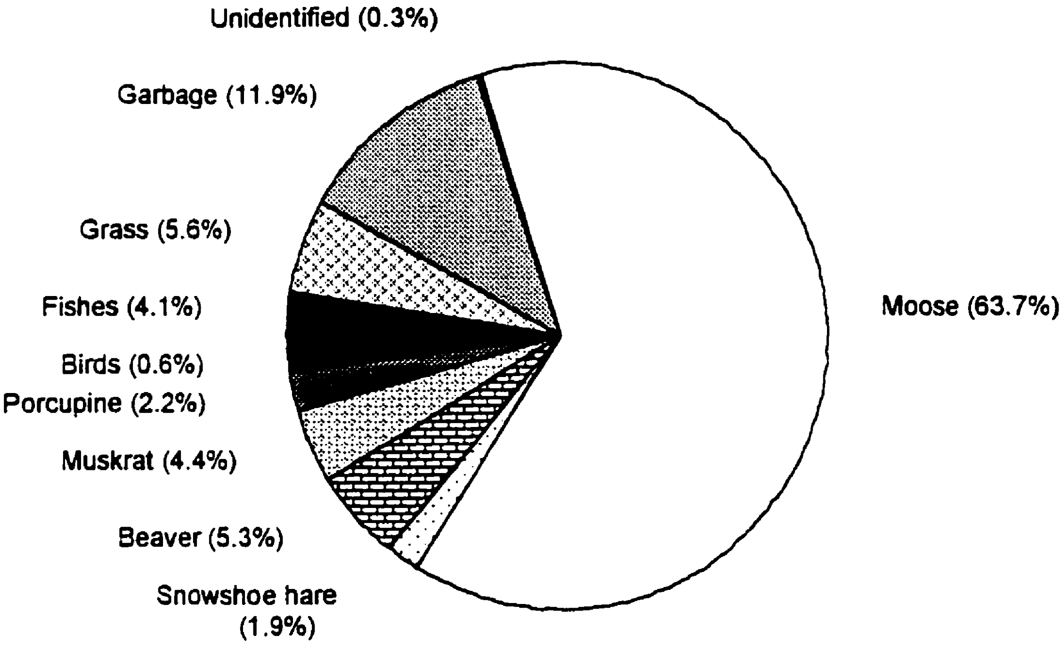
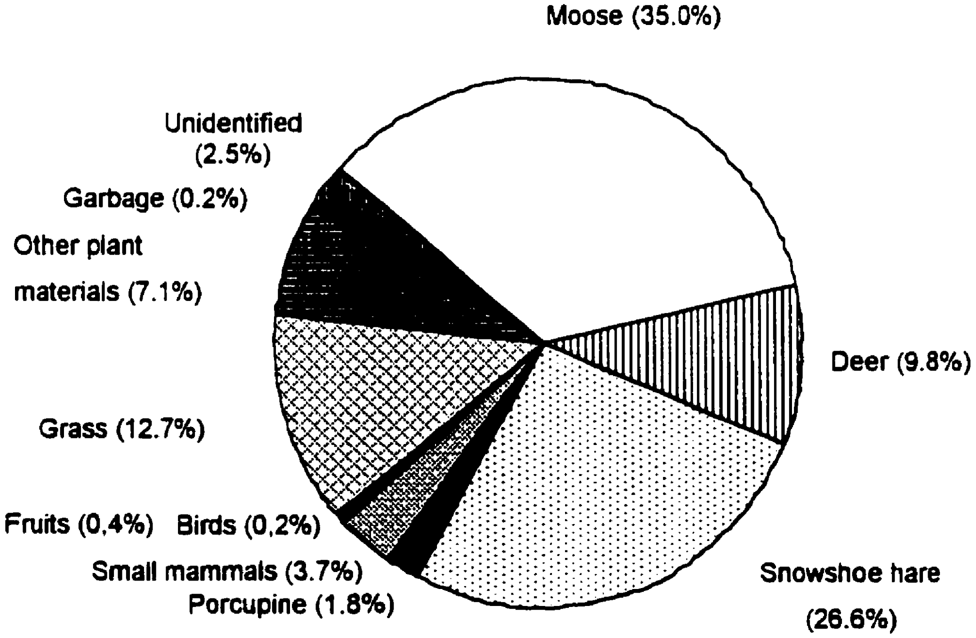

Occurrence (%) and volume (%) in coyote scats
50.0
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Moose
Deer
JAN-FEB (10/42)
MAR (11/38)
AVR (13/25)
MAY (19/58)
JUN (9/40)
JUL (22/68)
AUG (55/21)
SEP (68/35)
OCT (27/12)
NOV (64/10)
DEC (15/15)

Figure 1



March-April 1996, n = 16 scats



December 1996, n = 28

Figure 2

CONCLUSION GÉNÉRALE

L'alimentation du coyote semble refléter les opportunités et les préférences alimentaires, mais son rythme d'activité (chapitre 1). Le niveau de perturbation par l'humain semble influencer l'alimentation du coyote en restreignant plus ou moins l'accès aux ressources alimentaires exploitables durant la journée dans des habitats ouverts, ce qui est le cas des fruits et de certains insectes (ex: Orthoptères). De plus, les activités humaines ont pour conséquence de modifier la configuration des paysages, ce qui peut influencer la vulnérabilité relative de certaines espèces à la prédation. Plusieurs études ont conclu qu'une augmentation de la prédation sur le lièvre d'Amérique ou le lapin à queue blanche était due à la diminution de la superficie des fragments forestiers au sein d'un paysage (Keith et al. 1993, Oehler and Litvaitis 1996, Villafuerte et al. 1997).

Dans le cadre de cette étude, le lièvre était plus utilisé par les coyotes à l'extérieur du Parc que dans le Parc ce qui pourrait être expliqué par la différence de configuration des deux paysages. En effet, les activités de coupe forestière ou d'agriculture, à l'extérieur du Parc, entraînaient des lisières plus marquées et des fragments forestiers plus petits. D'un autre côté, les relevés de pistes effectués durant l'hiver 1996 montraient une activité similaire du lièvre entre le Parc et ses environs. L'augmentation de la vulnérabilité du lièvre en raison de la fragmentation de l'habitat étant essentiellement causée par l'augmentation des distances parcourues par ceux-ci (Villafuerté et al. 1997), on peut estimer que les relevés de pistes rendent compte de ce facteur et donc que la disponibilité du lièvre pour le coyote était équivalente dans les deux portions de l'aire d'étude. De plus, durant cette étude, les coyotes utilisant le Parc se déplaçaient fréquemment dans les zones exploitées adjacentes au Parc, au moins d'octobre à mars (Dumond, données non publiées). De janvier à avril, la consommation de lièvre était pourtant significativement moins élevée dans le Parc ($P < 0.01$). Le lièvre pourrait donc ne pas constituer la source optimale de nourriture des coyotes dans l'est du Nouveau-Brunswick. Dans le Parc, de janvier à avril, l'orignal constituait également une source importante de nourriture pour les coyotes. L'utilisation du lièvre était également significativement moins élevée dans le Parc durant juillet-août ($P \leq 0.001$) ce qui, sur la base d'une disponibilité équivalente comme pour l'hiver, suggère qu'une autre source de nourriture présentait des avantages pour les coyotes du Parc. Dans le Parc, les coyotes consommaient significativement moins de mammifères de juillet à octobre ($P \leq 0.001$) et plus de fruits durant juillet-août ($P \leq 0.001$). Le Parc représentant une zone d'échantillonnage de petite superficie, les risques d'échantillonner de façon répétée des sites de rendez-vous, et donc de récolter une proportion importante de fèces provenant de jeunes coyotes, étaient plus grands ce qui aurait pû biaiser la comparaison entre les deux zones d'études (Cypher et al. 1996). Néanmoins, au Maine, les seules différences significatives significative d'alimentation entre les jeunes et les adultes concernaient essentiellement le cerf de Virginie et le lièvre (Harrison et Harrison 1984). Les fruits semblaient utilisés de façon équivalente entre les jeunes et les adultes mais les jeunes avaient une diète moins diversifiée que les adultes.

Dans l'est du Nouveau-Brunswick, durant juillet-août, la diète des coyotes était significativement plus diversifiée ($P = 0.005$) dans le Parc qu'à l'extérieur. Toutefois, de juillet à octobre, il n'y avait pas de différence significative entre les valeurs de diamètre maximal des fèces récoltés dans le Parc et à l'extérieur ($t_{(177)} = 0.589$, $P = 0.278$). Au moins durant juillet-août, si il y avait eu une récolte plus importante de fèces de jeunes coyotes dans le Parc, la comparaison des diamètres aurait dû indiquer une différence significative ce qui n'était pas le cas ($P=0.144$). Ainsi, la consommation plus importante de fruits semble plutôt refléter une opportunité offerte grâce au degré de perturbations humaines plus bas dans la zone protégée que constitue le Parc national Kouchibouguac.

Une réduction des perturbations humaines semble donc permettre au coyote de diversifier sa diète et d'exploiter plus intensivement les fruits en permettant une activité diurne plus importante et une utilisation plus intensive des milieux ouverts riches en fruits. Plusieurs études ont également suggéré une influence du degré de perturbation par l'humain sur le rythme d'activité du coyote et les habitats utilisés (Andelt 1985, Gese et al. 1989, Quinn 1997a). La diminution des perturbations humaines semble permettre au coyote d'être plus actif le jour et/ou utiliser des habitats ouverts. Ceci a pour effet non seulement de réduire la prédation sur les mammifères de moyenne et de grande taille durant l'été par une consommation plus importante de fruits, mais vraisemblablement aussi, comme chez le renard roux (Lindström 1983), d'augmenter la synthèse de réserves adipeuses.

L'accumulation de tissus adipeux peut être un facteur important de survie durant la période hivernale. La rigueur de la période hivernale pour le coyote dépend essentiellement de la disponibilité en nourriture, de la température et de l'épaisseur et du type de neige. L'activité reproductrice, c'est à dire l'accouplement (chapitre 2), la gestation et l'élevage des jeunes (Poulle et al. 1995), semble également avoir un impact sur les variations de masse chez le coyote. Une bonne condition physique produiraient plus de jeunes viables. Le succès reproducteur des femelles dépend également du statut social (Crabtree 1989). Les femelles territoriales dominantes sont plus aptes à mener la gestation à terme et d'élever des jeunes avec succès (Andelt 1985, Crabtree 1989).

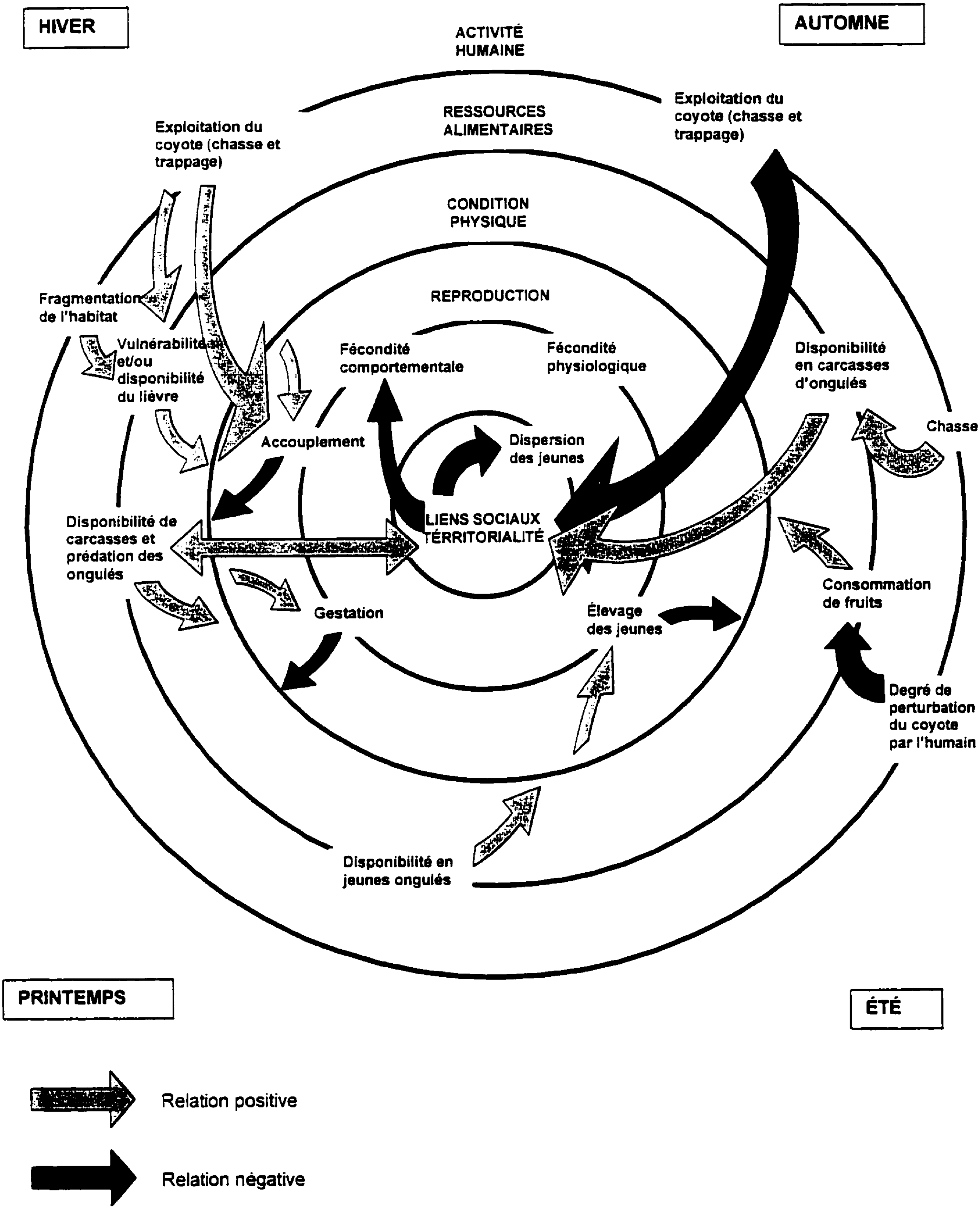
L'exploitation des populations de coyotes par l'humain entraîne une rupture de la structure sociale et un déséquilibre démographique (Knowlton 1972, Crabtree 1989). Les programmes de contrôle ne font bien souvent qu'extirper les jeunes classes d'âge de la population, dont les capacités reproductrices sont limitées, laissant ainsi une plus grande ressource alimentaire au individus reproducteurs restants. De plus, la rupture de la structure sociale régissant les populations de coyotes entraîne une diminution des inhibitions reproductives chez les individus hiérarchiquement inférieurs.

Le degré de sociabilité chez le coyote est influencé par différents facteurs dont il a été discuté au chapitre 3. La structure sociale et la territorialité entraînent une plus grande stabilité des populations de coyotes, maintenant leur densité à un haut niveau (0,8 – 0,9 coyote/km^2, Andelt 1985), ou à un niveau relativement bas (0,4 coyote/km^2, Crabtree 1989 ; $\leq$ 0,1 coyote/km^2, cette étude) selon la disponibilité des ressources alimentaires. Dans l'est du Canada, le coyote a profité, entre autres, de la niche écologique laissée vacante suite à l'extermination du loup. La structure sociale et le comportement alimentaire du coyote pourraient se rapprocher de plus en plus de ceux du loup, maintenant ainsi, dans les milieux peu perturbés par l'humain, des populations régies par de forts liens sociaux et se stabilisant à de relativement faibles densités.

Le schéma de la page 77 tente de résumer les différents résultats obtenus dans le cadre de cette étude et complétés par les résultats d'études précédentes citées tout au long de cette thèse. Je pense que les liens sociaux sont une des bases possibles pour expliquer les relations du coyote avec son environnement. L'exploitation du coyote par l'humain tend à déstabiliser ces liens sociaux, à diminuer les inhibitions comportementales des femelles de rang inférieur, à augmenter la disponibilité en nourriture et donc la condition physique des individus survivants. Cela a pour conséquence d'augmenter la fécondité et le taux de survie des chiots maintenant ainsi des populations estivales plus denses. De plus, les perturbations humaines réduisant l'accès à certaines ressources alimentaires tels les fruits, cela entraîne une utilisation plus importante des mammifères par le coyote. Donc, inversement, la réduction des perturbations humaines entraînent une consommation plus importante de fruits durant l'été mais d'un autre côté, une réduction de l'exploitation permet la formation plus durable de groupes qui sont aptes, notamment en hiver, à chasser des proies de plus grande taille tels les ongulés.

Figure

Synthèse schématique des mécanismes régissant les populations de coyotes dans l'est du Canada et discutés dans cette thèse.


HIVER
AUTOMNE
PRINTEMPS
ÉTÉ
ACTIVITÉ HUMAINE
RESSOURCES ALIMENTAIRES
CONDITION PHYSIQUE
REPRODUCTION
Exploitation du coyote (chasse et trappage)
Exploitation du coyote (chasse et trappage)
Fragmentation de l'habitat
Vulnérabilité et/ou disponibilité du lièvre
Fécondité comportementale
Fécondité physiologique
Disponibilité en carcasses d'ongulés
Chasse
Accouplement
Dispersion des jeunes
LIENS SOCIAUX TERRITORIALITÉ
Disponibilité de carcasses et prédation des ongulés
Consommation de fruits
Gestation
Élevage des jeunes
Degré de perturbation du coyote par l'humain
Disponibilité en jeunes ongulés
Relation positive
Relation négative

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