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M. Dumond and M.-A. Villard

Abstract: We documented the demography and body condition of coyotes (*Canis latrans*), using 77 carcasses collected in late fall and winter (1995–1996 and 1996–1997) during an increase in snowshoe hare (*Lepus americanus*) density in eastern New Brunswick. We compared body condition at the beginning (November–January) and end of winter (February–March) in relation to breeding status. Physical characteristics of coyotes were similar to those reported elsewhere in the northeastern portion of its range. The sex ratio did not differ significantly from 1:1. The population was unusually old $(5.6 \pm 0.4 \text{ years of age (mean } \pm \text{SE)})$. The parturition rate was low (40.9% in adult females), and placental scars were present only in females >5 years old $(6.6 \pm 0.6 \text{ scars per female})$. There was no significant decrease in the body condition of adult females over the winter but the body mass of those females with placental scars tended to decrease over the winter (P = 0.012). Also, during November–January, reproductive females (with placental scars) were significantly heavier (P = 0.007) than non-reproductive adult females (without placental scars). Our results suggest that in the coyote populations in eastern New Brunswick, breeding status and reproductive costs should be taken into account in future studies of demography and body condition. Also, the low level of coyote exploitation by humans may be responsible for the old age structure of the population and the low parturition rate. The exploitation level should be considered when analyzing coyote sociodemographic data.

Résumé : Nous avons étudié les caractéristiques physiques, la structure de la population, la fécondité et la condition physique d'une population de Coyotes (Canis latrans) 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 (1995-1996 et 1996-1997) durant une phase d'augmentation de la densité du Lièvre d'Amérique (Lepus americanus). Nous avons comparé la condition physique au début (novembrejanvier) et à la fin (février-mars) de l'hiver en fonction du statut reproducteur des femelles. Les caractéristiques physiques étaient semblables à celles signalées précédemment dans le nord-est de l'aire de répartition du Coyote. Le rapport males : femelles n'était pas significativement différent de 1 : 1. La population était particulièrement âgée $(5,6 \pm 0.4 \text{ ans})$ (moyenne ± erreur type)). La proportion de femelles reproductives était faible (40,9% des femelles adultes) et seules les femelles de plus de 5 ans avaient des cicatrices placentaires (6,6 ± 0,6 cicatrices par femelle). Il n'y avait pas de variation significative de la condition physique des femelles adultes au cours de l'hiver mais la masse corporelle des femelles portant des cicatrices placentaires tendait à diminuer au cours de l'hiver (P = 0.012). En début d'hiver, les femelles comportant des cicatrices placentaires avaient une masse corporelle plus élevée que les femelles adultes sans cicatrices placentaires (P = 0.007). Nos résultats indiquent que le statut reproducteur et les coûts reliés à la reproduction devraient être pris en compte lors d'études futures sur la démographie et la condition physique du Coyote. De plus, le faible degré d'exploitation du Coyote par l'humain semble être responsable de la moyenne d'âge élevée et du faible taux de parturition. Il faudrait tenir compte du degré d'exploitation lors de l'analyse de données sociodémographiques concernant le Coyote.

Introduction

The coyote (Canis latrans) has shown a spectacular expansion of its distribution over the last 200 years (Moore and Parker 1992). This expansion has exposed the species to new ecological conditions that influence population processes. In the boreal forest of Alberta, Todd (1985) found that coyote populations were strongly dependent on cyclical populations of the snowshoe hare (Lepus americanus), which influenced their reproduction and body condition. In the same region, Todd et al. (1981) related a decrease in the pregnancy

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rate in yearling female coyotes and in mean litter size among adult females to a decline in snowshoe hare populations. In Alaska, wolf (*Canis lupus*) productivity was also 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 fat deposits in coyotes decreased from early to late winter in a forested region of Alberta. Windberg et al. (1991) reported the same phenomenon in southern Texas. Todd and Keith (1983) suggested that coyotes experienced a negative energy balance over winter when hare were scarce.

In contrast with the studies mentioned above, fat depletion in the coyote populations of eastern Quebec occurred mainly between late winter and summer, but not significantly over winter (Poulle et al. 1995). Moreover, the reproductive status of eastern female coyotes seemed to be independent of fat deposits (Poulle et al. 1995). However, Todd and Keith (1983), Todd (1985), and Windberg (1995) conducted their studies during periods characterized by low prey availability

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or high coyote densities, which did not seem to be the case in Poulle et al.'s (1995) study. Poulle et al. (1995) explained the depletion of fat in late winter to summer by the fact that in the northeast, summer is characterized by low prey availability. Crête and Lemieux (1994) also suggested that coyotes may encounter problems in locating prey during summer, which may negatively affect reproduction.

Forested areas at the northern edge of the coyote's distribution are considered by some authors to represent suboptimal habitat for the species (Todd 1985; Crête and Lemieux 1994; Tremblay et al. 1998). Those authors suggest that the viability of coyote populations in northern forested areas depends mainly on resources derived from human activities. Based on their food habits and foraging behaviour, Tremblay et al. (1998) suggested that northeastern coyote populations may represent a source-sink metapopulation, with rural areas acting as demographic sources and forested areas representing sinks. Coyotes tend to be larger, heavier (Tremblay et al. 1998), and fatter (Todd 1985) in rural landscapes than in forested landscapes. Thus, one of the suboptimal characteristics of northern forested habitat would be periodic low availability of prey, resulting in poor body condition compared with 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 Moore's study (1981) was conducted in New Brunswick. More data on northeastern populations of coyotes with regard to food availability and different levels of human activities are required in order to gain a better understanding of population mechanisms. The objectives of this study were (i) to document the demography and body condition of a low-density, lightly to moderately exploited population of coyotes in a forested landscape in eastern New Brunswick during an increase in the snowshoe hare population and (ii) to compare coyote body condition between early and late winter with regard to breeding status.

Study area

The study area is located in eastern New Brunswick 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 is also characterized by the presence of wetlands, clearcuts, villages, and roads. Logging and peat extraction are the main human activities. The physiography of the region is flat to gently sloping (Desloges 1980). The average annual temperature is 5°C and precipitation averages 979 mm (18.8% of which falls as snow, corresponding to 1.8 m). The average winter temperature (December-March) is -7.1°C. The lowest temperatures are usually recorded in January or February (Desloges 1980) and maximum snow depth is usually reached in March (Fortin et al. 1999).

Materials and methods

Population trends were estimated for coyote, red fox (Vulpes vulpes), bobcat (Lynx 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) within the 1985-1996 period each species reached its maximum and minimum densities, and what was the trend (increasing, decreasing, or stable) of the population of each species in our study area over the previous 5 years. For each species we assigned +1 to each year in which density was considered to reach a peak and -1 to each year in which it was considered to reach a low. The sum for each year gave the relative abundance of a species for each year between 1985 and 1996. We assigned a value of +1, 0, or -1 when the population of a species was considered to have increased, remained stable, or decreased, respectively. The average was calculated and used as an index of the trend over the previous 5 years. Similar questionnaires were used by Todd and Keith (1983) and Lindström et al. (1994). Additional information was obtained from Kouchibouguac National Park track-transect reports and from the ungulate surveys of the Department of Natural Resources and Energy. During fall 1994 (Dumond 1997), 1995, and 1996 (N. Thébeau, unpublished data), and winter 1995 (Dumond 1997) and 1996 (N. Thébeau, unpublished data), coyote-howling surveys were conducted following the method of Wenger and Cringan (1978). From November 1994 to March 1995, all observed coyote signs (faeces, tracks, visual or aural detection) were recorded and mapped, to estimate the density of the population, and the results were compared with those from surveys of siren-elicited howling (Dumond 1997).

Seventy-seven coyote carcasses were collected from trappers, hunters, and forest rangers between November 1995 and March 1996 and between December 1996 and February 1997. Coyotes were captured using foot traps and snares or were killed by hunters or through collisions with vehicles. All the carcasses were kept frozen until March of each winter for necropsy at the Atlantic Veterinary College (Charlottetown, Prince Edward Island). 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) and body mass to the nearest 0.5 kg. Because we had skinned body mass (SBM) and unskinned body mass (BM), we standardized body mass data using the regression equation BM (kg) = $1.09 \times SBM$ (kg) + 0.45 ($R^2 = 0.99$, n = 49; Poulle et al. 1995). The inferior canines were extracted after the entire head was boiled for a few minutes, and age was estimated by counting canine cementum annuli (Bio-Tech Enr., Charlesbourg, Quebec). Coyotes 0.5-1, 1.5-2, and >2 years of age were classified as juveniles, yearlings, and adults, respectively. We also classified adults into four age-classes for body condition, pregnancy rate, and sex ratio data (2.5-4.0, 4.5-6.0, 6.5-8.0, and >8.0 years). We removed and weighed both kidneys and attached fat and calculated the kidney-fat index: KFI = kidney-fat mass \times 100/kidney mass. Both femurs were removed and a piece of marrow 3 cm long was weighed, air-dried, and reweighed. We calculated the percentage of fat in the marrow: FMF = air-dried marrow mass × 100/marrow mass. The fat was assumed to constitute most of the air-dried marrow (Neiland 1970; Huot et al. 1995). For KFI and FMF we used the mean of the right and left samples. As suggested in Huot et al. (1995), we calculated the kidney fat – femur fat index: KFFI = FMF + KFI. Using the regression equation proposed by Huot et al. (1995), we also estimated the percentage of fat in the body: PF = (7.18×10^{-2}) KFFI + 0.46. The uterus (from the cervix to the ovaries) was removed from each female and opened to count the placental scars. Litter size was estimated from the number of placental scars from the previous breeding season. The parturition rate was estimated from the presence of placental scars. Litter size and parturition rate were estimated from females killed before 31 January. Reproductive status (reproductive versus non-reproductive females) was assessed from the presence of placental scars, regardless of their number. We compared BM, BTL, and KFFI between November-January and February-March separately for reproductive (with

placental scars) and non-reproductive (without placental scars) females. For sex ratio, length (BTL and TL), and body mass (BM), additional data were obtained from coyotes captured for telemetry purposes in October–November 1995 (n = 5) and February 1996 (n = 4).

Because our goal was to gain an understanding of population structure, reproduction, and physical condition rather than to document population dynamics, the two fall-winter samples were pooled. There was no significant difference (G test, P > 0.05) between the two samples with regard to the dates of death (November-January versus February-March) or the cause of death (snared versus shot, hit by a vehicle, or trapped). Most of the coyotes we obtained were snared (77.9%), which is comparable to other studies conducted in northern forested areas (Jean and Bergeron 1984; Poulle et al. 1995). Therefore, although our sample may not exactly represent the actual population structure, it is accurate enough for comparison with previous studies. We compared our variables between sex, time periods, and breeding status and among age-classes by means of t tests. A α level of 0.01 was used for all statistical tests to account for the large number of tests performed. Sample size varied among tests because values were missing for certain individuals.

Results

Population trends

We received 27 (25% of the number sent out) usable questionnaires. We excluded questionnaires in which the same year(s) was (were) selected for both maximum and minimum densities of a species. We plotted the population trends for each species over the period 1985-1996 (Fig. 1) and calculated the trend over the previous 5 years (Table 1). Wintertrack 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 population was declining or remaining stable at a relatively low density and snowshoe hare population was increasing. The density of the coyote population was estimated to be <0.1/km² according to a winter-indices survey (Dumond 1997) and fall and winter surveys of siren-elicited howling (Dumond 1997; N. Thébeau, unpublished data). Moose abundance was relatively stable (Table 1); we estimated moose density to be approximately 0.2-0.3/km² from the 1995 aerial ungulate survey in Kouchibouguac National Park (Richard 1995) and aerial surveys in 1991 and 1993 in adjacent areas by the Department of Natural Resources and Energy. Deer were at a relatively low density. Red foxes were abundant in the study area, and bobcats were increasing slightly in abundance after a long period of low density.

Sex ratio and age structure

The sex ratio of the coyote population did not differ from 1:1 (Table 2). In the juvenile and yearling (0.5-2.0 years) and young adult (2.5-4.0 years) classes, the sex ratio indicated that there were more males, but in all year classes over 4.0, females were slightly more common. However, sex ratios never differed significantly from 1:1. These slight variations among age-classes might reflect the population dynamics of previous years or differential susceptibility to trapping. The population was relatively old, the average age for females being 5.9 years and for males being 5.3 years (Table 2). Juveniles and yearlings represented only 15.6% of the sample (n = 77), and 64.9% of the individuals were older

than 4.0 years (Fig. 2). The major cohorts were represented by coyotes 5.5–7.5 years old (39.0% of the population; Fig. 2), which were born during the period of high coyote density (Fig. 1). Individuals older than 10 years represented 9.1% of the sample and the oldest male and female were 16.5 and 15.5 years of age, respectively (Fig. 2).

Physical characteristics

The physical characteristics (BTL, TL, SBM, and BM) of this coyote population were similar to those reported in other studies conducted in the northeastern United States (Richens and Hugie 1974; Hilton 1976) and eastern Canada (Moore 1981; Fortin and Huot 1995; Poulle et al. 1995). When five individuals (three males and two females) affected by mange were removed from the analysis, males were significantly heavier ($t_{[80]} = 3.095$, P = 0.003) and longer (TL, $t_{[79]} = 4.049$, P < 0.001) than females (Table 2). Individuals with mange were collected during late winter; they were characterized by a significantly lower KFFI ($t_{[13]} = 3.839$, P = 0.002) than other individuals during late winter. These five individuals were removed from the sample used for analyzing the variation in body condition over winter.

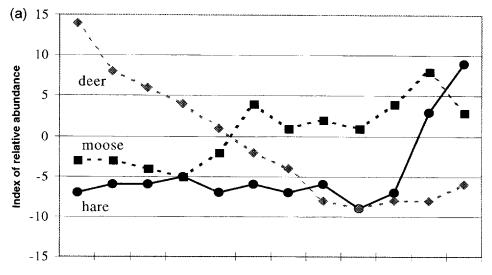
Parturition rate and placental scars

The parturition rate, estimated as the presence or absence of placental scars, was only 40.9% among adult females killed between November and 31 January (n = 22), comparable to that reported by Crabtree (1989) for a lightly exploited coyote population. The parturition rate reached a maximum in the oldest age-class (Table 2). No female younger than 5.5 years had placental scars, indicating that, at least in the previous year, no female under 4 years old had bred successfully. The number of placental scars was 6.6 ± 0.6 (mean \pm SE; n = 9).

Relationship between breeding and body condition over winter

We compared BM, BTL, and KFFI between November-January and February-March and among reproductive and adult non-reproductive females (excluding two individuals affected by mange) (Table 3). No significant differences in BTL were found between periods or according to breeding status (reproductive versus non-reproductive females), therefore differences in other variables apparently were a direct result of changes in body condition. Regardless of breeding status, body condition of adult females did not vary significantly over the winter. During November-January, females with placental scars were significantly heavier ($t_{1201} = 3.017$, P = 0.007) than adult females without placental scars (Table 3). During February–March, there was no significant difference in body condition (P > 0.5) between reproductive and non-reproductive adult females. Nevertheless, BM and pregnancy rate reached their maximum values in the oldest age-class, and the early-winter difference in BM between reproductive and non-reproductive females could be an effect of age. Average BM in reproductive females tended to decrease (14%) between November-January and February-March $(t_{1121} = 2.956, P = 0.012)$, though not significantly (Table 3). For non-reproductive females there was no difference in body condition between periods (P > 0.5 for all variables). We did not test for variation in the body condition of

Fig. 1. Relative abundance of coyotes, main prey (a), and sympatric carnivores (b) in eastern New Brunswick from 1985 to 1996, based on a survey questionnaire.



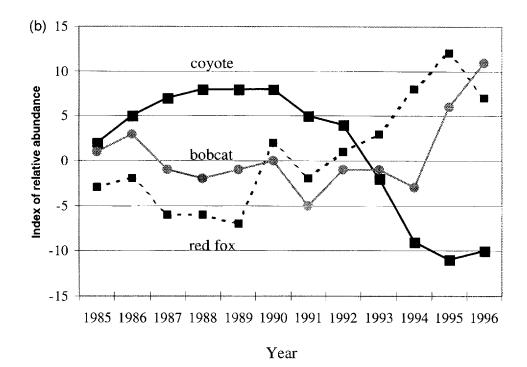


Table 1. Population trends for several mammal species in eastern New Brunswick during 1992–1996, based on a survey questionnaire.

Population trend	Coyote	Red fox	Bobcat	Hare	Moose	Deer
Index ^a	-0.44	0.33	0.15	0.3	0.15	-0.48
Decreasing	59^{b}	4	26	19	19	52
Stable	26	59	33	33	48	44
Increasing	15	37	41	48	33	4

Note: Data are based on 27 usable questionnaires.

"For the method of calculation see the text.

^bPercentage of questionnaire answers represented by the species.

males because the majority of individuals collected in late winter were affected by mange.

Discussion

The coyote population under study was unusually old, with a very low parturition rate. Previous studies have usually reported that coyote populations were clearly dominated by juveniles and yearlings with an average age of less 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). 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 low level of exploitation, a low immigration rate, and a high mortality rate among pups.

In our study area, coyote trapping was light to moderate and there was no eradication program. The low proportion of young coyotes (<4 years old) and the low parturition rate in our population indicate that recruitment and (or) immigration of juveniles, yearlings, and young adults were low, and (or) that emigration in the younger age-classes was high. Also, pup mortality might 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 she did not breed successfully every year. Among nonterritorial females with embryo implantation, none successfully whelped, thus he concluded that social behaviour could affect demography (Crabtree 1989). A low level of coyote exploitation seems to increase social and territorial behaviour and reduce the proportion of reproductive females (Andelt 1985; Crabtree 1989). This may stabilize a covote population at the saturation level (Andelt 1985), or below that level, as a result of an increase in territorial behaviour. 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 generated large covote territories, the boundaries of which could then have remained unchanged during the increasing phase of hare populations. In California, White and Ralls (1993) reported that even when prey were abundant, kit foxes (Vulpes macrotis mutica) maintained large and relatively non-overlapping home ranges that corresponded to their survival requirements during prey scarcity. This would have limited territory availability regardless of food availability. A low parturition rate and small litter size are generally associated with saturated populations (Knowlton 1972) or a low exploitation level (Jean and Bergeron 1984; Crabtree 1989). The population under study may be regulated by social behaviour and the use of large territories as a result of the low exploitation level.

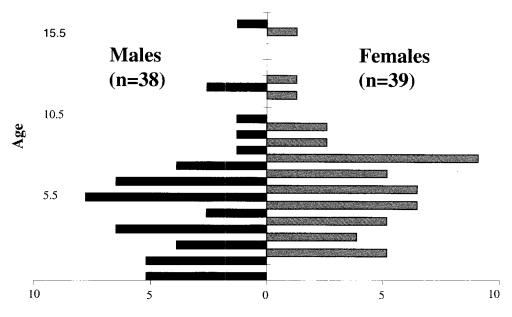
Conversely, the low parturition rate could indicate that our extensively forested study area represents suboptimal habitat for the coyote. A lower availability of food would have reduced fecundity and (or) survival of pups, which would explain the low percentage of the younger age-classes in this population. However, like Poulle et al. (1995), we found no

Fable 2. Characteristics of the coyote population in eastern New Brunswick (late fall and winter 1995–1997).

	Sex ratio Age	Age	BTL (cm)	TL (cm)	BM (kg)	PR (%) KFI	KFI	FMF	KFFI	PF
All females		5.9±0.5 (39)	89.5±0.7 (43)	123.4±0.8 (43) 13.1±0.3 (43)	13.1±0.3 (43)		84.4±7.9 (38)	75.8±1.9 (38)	75.8±1.9 (38) 160.2±8.9 (38)	12.0±0.6 (38)
All males		5.3 ± 0.6 (38)	91.7 ± 0.9 (43)	128.5±1.3 (43)	14.6±0.5 (44)		72.3±6.6 (37)	69.5±3.0 (37)	141.8±8.9 (37)	10.6 ± 0.6 (37)
All individuals	0.51 (87)	5.6±0.4 (77)	90.6±0.6 (86)	125.9 ± 0.8 (86)	13.9±0.3 (87)		78.4±5.2 (75)	72.7±1.8 (75)		11.3 ± 0.5 (75)
Mange coyotes	0.60(5)	4.3 ± 1.3 (5)	89.3±4.8 (5)	125.3 ± 5.8 (5)	12.7 ± 1.1 (5)		22.0 ± 7.9 (5)	35.4±7.4 (5)	57.4 ± 14.4 (5)	4.6 ± 1.0 (5)
Age-class (years)										
0.5-2.0	0.67 (12)		86.1 ± 1.2 (11)	121.1±1.7 (11)	11.3 ± 0.3 (12)		67.3 ± 9.5 (12)	65.1 ± 3.6 (12)	132.4 ± 12.4 (12)	10.0 ± 0.9 (12)
2.5-4.0	0.53 (15)		88.7±1.7 (15)	123.3 ± 2.0 (15)	12.5±0.5 (15)		74.3 ± 12.3 (14)	69.3±4.3 (14)	143.6±15.1 (14)	10.8±1.1 (14)
4.5–6.0	0.44 (18)		90.2 ± 1.0 (18)	125.4 ± 1.2 (18)	13.8 ± 0.5 (18)	50.0 (4)	76.7±8.9 (17)	78.3±2.4 (17)	155.0±10.3 (17)	11.6±0.7 (17)
6.5-8.0	0.42 (19)		92.0±1.2 (19)	127.2±1.8 (19)	14.9 ± 0.6 (19)	28.6 (7)	80.3±13.1 (19)	72.1 ± 4.3 (19)	152.4±15.6 (19)	11.4±1.1 (19)
>8.0	0.46 (13)		92.3±1.3 (13)	127.2 ± 1.8 (13)	15.2 ± 0.8 (13)	83.3 (6)	92.5±12.3 (13)	77.1 ± 4.6 (13)	169.5±15.7 (13)	12.6±1.1 (13)

Note: Values are given as the mean ± standard error of the mean (SE), with the sample size in parentheses. BTL, body length from the tip of the nose to the base of the tail; BM, body mass; PR, parturition rate (based on females killed prior to 31 January); KFI, kidney fat index; FMF, femur marrow fat; KFFI, kidney-femur fat index; PF, percentage of fat in the body.

Fig. 2. Age structure of two winter samples (November 1995 – March 1996 and December 1996 – February 1997) of coyotes in eastern New Brunswick.



Percentage of the sample

Table 3. Over-winter variation in body condition of adult female coyotes^a in eastern New Brunswick (1995–1997).

	Period	Age (years)	BTL	BM	KFFI
All adult females	NovMar.	6.5±0.5 (33)	89.6±0.8 (33)	13.4±0.3 (33)	165.8±9.8 (32)
	NovJan.	6.9±0.7 (22)	90.1±0.8 (22)	13.7±0.4 (22)	167.9±12.2 (22)
	FebMar.	5.9±0.5 (10)	89.2±1.8 (10)	12.7±0.5 (10)	162.2±19.4 (9)
Adult females with placental scars ^a	NovJan.	8.9±1.1 (9)	91.1±0.8 (9)	15.0 ± 0.3 (9)	176.9±17.6 (9)
	FebMar.	6.9±0.7 (5)	88.0±2.7 (5)	$12.5\pm1.0(5)$	151.2±43.3 (4)
Adult females without placental scars ^a	NovJan.	5.4±0.7 (13)	89.5±1.1 (13)	12.8±0.6 (13)	161.7±17.0 (13)
•	Feb.–Mar.	4.9±0.5 (5)	90.4±2.5 (5)	13.0±0.4 (5)	171.0±13.6 (5)

Note: Values are given as the mean ± SE, with the sample size in parentheses. BTL, body length from the tip of the nose to the base of the tail; BM, body mass; KFFI, kidney-femur fat index.

"Individuals affected by mange (2) were excluded.

significant difference in body condition over winter among adult females. Therefore, it is not obvious that our study area represented a suboptimal habitat, at least during winter. Nevertheless, we found that reproductive females were significantly heavier than non-reproductive adult females during early winter. Conversely, Poulle et al. (1995) found no significant difference in body condition between reproductive and non-reproductive females during this period. Prestrud and Nilssen (1992) found that in the arctic fox (Alopex lagopus), fat deposits were gained between August and November. They found no significant fat depletion between November and March, but fat deposits were significantly depleted between March and May. In this study, female arctic foxes that had reproduced the previous spring were significantly leaner than other foxes, suggesting an energetic cost of reproduction. However, our results could be an artifact of the difference in average age between reproductive and non-reproductive females. Compared with 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 improve their body condition during early fall, owing to more

favourable climatic conditions and greater food availability. In the red fox, fat deposits were correlated with the consumption of fruits (Lindström 1983). We found that fruits were an important component of the coyote diet from July to October (Dumond 1999). The energetic cost of gestation and whelping may have been compensated for by the high consumption of fruits. Also, mammalian food may not have been a limiting factor, as the snowshoe hare population and moose-carcass availability were relatively high. Moreover, in Yellowstone National Park, Gese et al. (1996) found that foraging behaviour was influenced by social status, with alpha coyotes spending more time feeding on ungulate carcasses than subordinate coyotes. In eastern New Brunswick during our study, the percentage of moose in coyote diet was maximal in November-December, reaching 29% of coyote scat volume (Dumond 1999). The higher BM of reproductive females in early winter may be a consequence of concentrating their foraging behaviour around ungulate carcasses.

In coyotes, reproductive females are usually territorial, at least in lightly exploited populations (Crabtree 1989; Windberg 1995; Sacks et al. 1999), 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 had reproduced successfully the previous winter) mated or would have mated during the winter of their capture. Mating reaches a peak during February (Andrews and Boggess 1978; Hilton 1978; Bekoff and Wells 1986; for a review see Chambers 1992). Although the body condition of females did not vary significantly between periods according to breeding status, BM of reproductive females tended to decrease (P = 0.012) between November–January (before the mating season) and February–March (during or after mating). It is important to test the hypothesis that an energetic cost is incurred during the mating season using larger sample sizes and under different environmental conditions. However, we suggest that breeding status and reproductive costs be considered in future studies of body condition in coyotes.

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

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References

- Andelt, W.F. 1985. Behavioral ecology of coyotes in south Texas. Wildl. Monogr. No. 94.
- Andrews, R.D., and Boggess, E.K. 1978. Ecology of coyotes in Iowa. *In Coyotes*: biology, behavior, and management. *Edited by*M. Bekoff. Academic Press, New York. pp. 249–265.
- Bekoff, M., and Wells, M.C. 1986. Social ecology and behavior of coyotes. Adv. Study Behav. 16: 251–336.
- Berg, W.E., and Chesness, R.A. 1978. Ecology of coyotes in Northern Minnesota. *In* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York. pp. 229–247.
- Boertje, R.D., and Stephenson, R.O. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Can. J. Zool. 70: 2441–2443.

- Chambers, R.E. 1992. Reproduction of coyotes in their northeastern range. *In* Ecology and management of the eastern coyote. *Edited by* A.H. Boer. University of New Brunswick, Fredericton. pp. 39–52.
- Crabtree, R.L. 1989. Sociodemography of an unexploited coyote population. Ph.D. thesis, University of Idaho, Moscow.
- Crête, M., and Lemieux, R. 1994. Dynamique de population des coyotes colonisant la péninsule gaspésienne. Ministère de l'environnement et de la faune, Québec, Que.
- Desloges, C. 1980. Les resources naturelles du Parc national Kouchibouguac. Parcs Canada—Région de l'Atlantique, Halifax, N.S.
- Dumond, M. 1997. Densité, répartition et alimentation du coyote (*Canis latrans*) au Parc national Kouchibouguac de Novembre 1994 à Mars 1995. Parcs Canada—Rapport technique en Science des Ecosystèmes No. 5, Parcs Canada—Region Atlantique, Halifax, N.S.
- Dumond, M. 1999. Alimentation, démographie et condition physique d'une population de coyotes (*Canis latrans*) dans l'est du Nouveau-Brunswick, Canada. M.Sc. thesis, Université de Moncton, Moncton, N.B.
- Fortin, C., and Huot, J. 1995. Ecologie comparée du Coyote, du Lynx et du Renard roux au Parc national Forillon. Parcs Canada, Patrimoine Canadien and Université Laval, Ste.-Foy, Que.
- Fortin, G., Granberg, H., and Dubois, J.-M. 1999. Etude préliminaire du couvert nival dans le Parc national Kouchibouguac au Nouveau-Brunswick (1974–1998). Bulletin de recherche, Département de Géographie et Télédétection, Université de Sherbrooke, Sherbrooke, Que.
- Gese, E.M., Ruff, R.L., and Crabtree, R.L. 1996. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool. **74**: 769–783.
- Hilton, H. 1976. The physical characteristics, taxonomic status and food habits of the eastern coyote in Maine. M.Sc. thesis, University of Maine, Orono.
- Hilton, H. 1978. Systematics and ecology of the eastern coyote. *In* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York. pp. 209–228.
- Huot, J., Poulle, M.-L., and Crête, M. 1995. Evaluation of several indices for assessment of coyote (*Canis latrans*) body composition. Can. J. Zool. 73: 1620–1624.
- Jean, Y., and Bergeron, J.-M. 1984. Productivity of coyotes (*Canis latrans*) from southern Québec. Can. J. Zool. **62**: 2240–2243.
- Knowlton, F.F. 1972. Preliminary interpretations of coyote population mechanics with some management implications. J. Wildl. Manage. 36: 369–382.
- Lindström, E. 1983. Condition and growth of red foxes (*Vulpes vulpes*) in relation to food supply. J. Zool. (1965–1984), **199**: 117–122.
- Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Sköld, K., and Swenson, J.E. 1994. Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. Ecology, 75: 1042–1049.
- Mills, L.S., and Knowlton, F.F. 1991. Coyote space use in relation to prey abundance. Can. J. Zool. 69: 1516–1521.
- Moore, G.C. 1981. A comparative study of colonizing and longer established eastern coyote (*Canis latrans*) populations. M.Sc. thesis, University of Western Ontario, London.
- Moore, G.C., and Parker, G.R. 1992. Colonization by the eastern coyote (*Canis latrans*). *In* Ecology and management of the eastern coyote. *Edited by* A.H. Boer. University of New Brunswick, Fredericton. pp. 23–37.
- Morton, L.D., and Savoie, M. 1983. Les mammifères du parc national Kouchibouguac. Service canadien de la faune, région de l'Atlantique, Sackville, N.B.

- Neiland, K.A. 1970. Weight of dried marrow as an indicator of fat in caribou femurs. J. Wildl. Manage. 34: 904–907.
- Nellis, C.H., and Keith, L.B. 1976. Population dynamics of coyotes in central Alberta, 1964–68. J. Wildl. Manage. 40: 389–399.
- Poulle, M.-L., Crête, M., and Huot, J. 1995. Seasonal variation in body mass and composition of eastern coyotes. Can. J. Zool. 73: 1625–1633.
- Prestrud, P., and Nilssen, K. 1992. Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. J. Wildl. Manage. 56: 221–233.
- Richard, B. 1992. Relevé de pistes (track transects) dans le Parc national Kouchibouguac. Parc national Kouchibouguac, Service canadien des parcs, Environnement Canada, Kouchibouguac, N.B.
- Richard, B. 1995. Recensement des Ongulés du parc national Kouchibouguac. Parc national Kouchibouguac, Service canadien des parcs, Patrimoine canadien, Kouchibouguac, N.B.
- Richard, B. 1996. Relevé de pistes (track transects) dans le Parc national Kouchibouguac. Parc national Kouchibouguac, Service canadien des parcs, Patrimoine canadien, Kouchibouguac, N.B.
- Richens, V.B., and Hugie, R.D. 1974. Distribution, taxonomic status, and characteristics of coyotes in Maine. J. Wildl. Manage. **38**: 447–454.
- Sacks, B.N., Jaeger, M.M., Neale, J.C., and McCullough, D.R. 1999. Territoriality and breeding status of coyotes relative to sheep predation. J. Wildl. Manage. 63: 593-605.
- Stephenson, S.W., and Kennedy, M.L. 1993. Demography of a coy-

- ote population in western Tennessee. J. Tenn. Acad. Sci. 68: 122-124.
- Todd, A.W. 1985. Demographic and dietary comparisons of forest and farmland coyote, *Canis latrans*, populations in Alberta. Can. Field-Nat. 99: 163–171.
- Todd, A.W., and Keith, L.B. 1983. Coyote demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. 47: 394– 404.
- Todd, A.W., Keith, L.B., and Fischer, C.A. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. J. Wildl. Manage. 45: 629–640.
- Tremblay, J.-P., Crête, M., and Huot, J. 1998. Summer foraging behaviour of eastern coyotes in rural versus forest landscape: a possible mechanism of source–sink dynamics. EcoScience, 5: 172–182.
- Wenger, C.R., and Cringan, A.T. 1978. Siren-elicited coyote vocalizations: an evaluation of a census technique. Wildl. Soc. Bull. 6: 73–76
- White, P.J., and Ralls, K. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. J. Wildl. Manage. 57: 861–867.
- Windberg, L.A. 1995. Demography of a high-density coyote population. Can. J. Zool. 73: 942-954.
- Windberg, L.A., Engeman, R.M., and Bromaghin, J.F. 1991. Body size and condition of the coyote in southern Texas. J. Wildl. Dis. 27: 47–52.