

# Summer foraging behaviour of eastern coyotes in rural *versus* forest landscape: A possible mechanism of source-sink dynamics<sup>1</sup>

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**Abstract:** Following wolf (*Canis lupus*) extinction and opening of the forest landscape, coyotes (*Canis latrans*) progressively colonized eastern North America. In southeastern Québec, coyotes occur in two contiguous landscape types: rural and forest. We tested the hypothesis that forest landscapes were marginal habitats for coyotes in summer, as opposed to rural landscapes. Ten coyotes were radio-tracked during the 1995 snow-free period (rural:  $n = 4$ , forest:  $n = 6$ ) and morphological measurements were obtained for 25 additional ones were handled (rural:  $n = 9$ , forest:  $n = 16$ ). Analysis of undigested residues in scats ( $n = 562$ ) showed that during the den attendance period (1 May to 15 July), coyotes in both landscapes mostly consumed animal flesh. However, during pup initiation (15 July to 1 October), forest coyotes consumed more wildberries than rural coyotes. During den attendance, rural coyotes had higher activity and movement rates than forest coyotes. We observed the opposite trend in late summer; forest coyotes were more active than rural animals and traveled at a higher rate. Finally, rural coyotes were heavier than their forest counterparts in late summer. Our results support the hypothesis that forest landscapes of southeastern Québec are sub-optimal habitats for coyotes. Difference in foraging behaviour and performance between the two habitats may affect survival and/or fecundity, thus creating a source/sink population dynamics.

**Keywords:** activity, coyote (*Canis latrans*), food habits, movement, source/ sink.

**Résumé:** À la suite de l'extermination du loup (*Canis lupus*) et de l'ouverture des paysages forestiers, le coyote (*Canis latrans*) a progressivement colonisé l'est de l'Amérique du Nord. Dans l'est du Québec, le coyote a accès à deux types de paysage : le milieu agro-forestier et le milieu forestier. Dix coyotes ont fait l'objet d'un suivi télémétrique au cours de l'été 1995 (agro-forestier:  $n = 4$ , forestier:  $n = 6$ ) et 25 individus additionnels ont fourni des mesures morphologiques (agro-forestier :  $n = 9$ , forestier :  $n = 16$ ). Le régime alimentaire estival a été déterminé par l'examen des résidus non digérés de 562 fèces. Lors de la période d'élevage des jeunes (1<sup>er</sup> mai - 15 juillet), les coyotes des deux paysages ont présenté un régime alimentaire à dominance carnée. Au cours de cette période, les coyotes agro-forestiers ont été plus actifs et se sont déplacés à un taux supérieur à celui des coyotes forestiers. Par contre, lors de la période d'initiation des jeunes à la chasse (15 juillet - 1<sup>er</sup> octobre), les coyotes forestiers ont consommé un volume plus important de fruits sauvages ; ils ont adopté un comportement plus actif et présenté des taux de déplacement plus importants. Ils présentaient aussi une masse corporelle et une longueur totale inférieures aux coyotes agro-forestiers. Nos résultats suggèrent que le paysage forestier constitue un milieu de qualité inférieure pour le coyote en comparaison avec le milieu agro-forestier ; l'efficacité de la quête alimentaire et la performance reproductrice pourraient affecter la survie et/ou la fécondité, créant une dynamique de population de type «production/ absorption».

**Mots-clés:** activité, coyote (*Canis latrans*), mouvement, production/absorption.

## Introduction

Prior to European settlement, coyotes (*Canis latrans*) were confined to the open plains and arid regions of the western half of North America (Young & Jackson, 1951; Nowak, 1979; Moore & Parker, 1992). The species was excluded from forested areas by the wolf (*Canis lupus*) (Richens & Hugie, 1974; Fuller & Keith, 1981; Paquet, 1991). Massive landscape changes resulting from development of agriculture, forestry and urbanization, allowed coyotes to extend their distribution northward and eastward, to progressively fill the ecological niche left unoccupied after the extermination of the wolves over vast areas.

Coyotes reached the southwestern border of Québec by 1944 (Rand, 1945) and its southeastern portion in the early 1970's (George, 1975). Mixed forest-agriculture (rural) areas and boreal forests represent the main landscapes in southeastern Québec (Larivière & Crête, 1992). The rural landscape possesses many features of the original range occupied by coyotes. It also presents greater habitat diversity, prey choice and prey availability than boreal forests (Pekins, 1992). In a comparison of farmland and woodland coyotes, Todd (1985) found that farmland coyotes had different food habits, a higher fat index and a more stable demography than their woodland counterparts. Other studies reached similar conclusions (Todd & Keith, 1976; Todd, Keith & Fischer, 1981). However, those studies did not focus on the foraging strategies used by coyotes in those two landscapes. Furthermore, ecological conditions differed markedly from those found in southeastern Québec.

<sup>1</sup>Rec. 1997-04-04; acc. 1997-11-28.

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The boreal forest currently represents the northern limit of coyote distribution in northeastern North America. Climate characterizing this biome differs from that found in the original coyote range mainly by the depth and persistence of snow cover. Poulle, Crête & Huot (1995) observed significant fat and protein losses during summer in coyotes inhabiting the boreal forest of the Gaspé peninsula. They also reported a very low fecundity rate and hypothesized that there could be a mechanism of fat regulation in coyotes to reduce energy expenditure during the warm season.

Here, we test the hypothesis that the forest landscape of southeastern Québec is a marginal habitat, or sink, for coyotes in summer, whereas the rural landscape constitutes a source habitat. The source and sink dynamic model developed by Pulliam (1988) assumes that individuals occur in landscapes that differ in terms of relative quality. Reproductive success is greater than mortality in sources and individuals produced in excess are forced to emigrate to less productive sinks. Several studies, mostly on birds and small mammals, compared demographic rates of one species in different landscapes (see review by Pulliam, 1996), but few have clearly demonstrated the existence of sources and sinks. Further modeling of source and sink dynamics has recently shown that source and sink populations cannot be identified by simple comparisons of demographic rates (Watkinson & Sutherland, 1995). Causal factors that influence birth and death rates must be considered because habitat quality and individual behaviours interact to influence population dynamics (Meffe & Carroll, 1994). Difference in food supply was proposed to explain variation in survival rate among landscapes for tree squirrels (*Tamiasciurus spp.*), meadow voles (*Microtus pennsylvanicus*), and deer mice (*Peromyscus maniculatus*) (Smith, 1968; Grant, 1975; Van Horne, 1982). We hypothesized that foraging efficiency of coyotes in the rural landscape exceeded that in forest landscape, with higher survival and/or fecundity rate in the former, ultimately creating source and sink dynamics.

The greater production of prey in rural landscapes relative to that in forests should affect food habits and foraging behaviour. Fuller (1989) found an inverse relationship between home-range size and prey density of wolves. Variations in composition of diet were also proposed for differences in home-range size of coyotes (Person & Hirth, 1991), red foxes (*Vulpes vulpes*) (Macdonald, 1987; Lovari, Valier & Ricci Lucchi, 1994), Blandford's foxes (*Vulpes cana*) (Geffen *et al.*, 1992), marten (*Martes americana*) (Thompson & Colgan 1987; 1994), badger (*Meles meles*) (Kruuk, 1978; Kruuk & Parish, 1982), and many other carnivores (Gittleman & Harvey, 1982). Some studies (Todd, Keith & Fischer, 1981; Gese, Rongstad & Mytton, 1988) revealed that prey availability affected movements and activity of coyotes. On the other hand, Mech (1977) observed that wolves adopted an energy-saving strategy by reducing movements when prey were scarce.

The objective of our study was to test if source and sink dynamics could apply to coyote populations occupying rural and forest landscapes in southeastern Québec, based on variation in foraging efficiency. We predicted that, in summer, diet would differ between landscapes, being of an higher relative quality for coyotes in rural than in forest

landscape. Following this prediction, we also anticipated that home-range size would be larger and that movement rate and activity would be greater in the forest landscape than in the rural landscape.

## Material and methods

### STUDY AREA

The study area covers 1200 km<sup>2</sup> of rolling hills on the south shore of the St-Lawrence river in southeastern Québec (Figure 1). The altitude varies between 220 m and 660 m. Precipitation averages 1105 mm in the center of the study area, with 33% falling as snow (Environment Canada, 1993). Snow cover persists from early December to late April.

The amount of agricultural activity has been diminishing since the 1950s. As a result, the rural landscape appears as a mosaic of old and cultivated fields, covering 40% of the study area (Temiscouata County, 1986), interspersed with numerous woodlots. Contiguous forest blocks covered the rest of the study area.

The study area occupies a transition zone between the northern hardwood forest and the boreal forest (Rowe, 1972; Marie-Victorin, 1964). Logging has been very important since the colonization of the area and has affected forest stand composition.

Coyotes were likely at a density of  $\leq 0.1$  animal/km<sup>2</sup> at the time of the study (M. Crête, unpubl. data). Large mammals common in the study area are moose (*Alces alces*; 0.12/km<sup>2</sup>; Courtois, 1991), white-tailed deer (*Odocoileus virginianus*;  $\sim 1-2$ /km<sup>2</sup>; Ministère de l'Environnement et de la Faune, unpubl. data) and black bear (*Ursus americanus*;  $\sim 0.4$ /km<sup>2</sup>; Lamontagne, Jolicoeur & Lafond, 1996, unpubl. data). Other predators include red fox, fisher (*Martes pennanti*), marten, Canada lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*). Snowshoe hare (*Lepus americanus*) and several species of small mammals form the prey base.

### FOOD HABITS

Food habits were determined by the identification of undigested fragments of food items remaining in scats. Coyote scats were distinguished from fox scats using color and diameter parameters. Scats were collected from 1 May to 30 October 1995 by patrolling two permanent networks of secondary gravel roads and trails with an all-terrain vehicle running at low speed. The first network ran across rural landscape and covered 57 km, whereas the forest landscape network measured 108 km. At their closest point, the two networks were 25 km apart. Each network was patrolled every other week. We found 263 and 299 scats in the rural and the forest landscapes, respectively. For the analysis, we divided the study period into two parts: den attendance (1 May-15 July) and pup initiation (15 July-1 October). In the rural landscape, 149 scats were collected during the den attendance period and 114 during the pup initiation period, while corresponding figures were 97 and 202 in the forest landscape. Prior to the beginning of scat collection in May, we cleaned up the two circuits in order to collect only fresh material of known age.

All scats were oven-dried at 70°C for 24 hours and rinsed through a 0.5 mm sieve. Macroscopic and microscopic

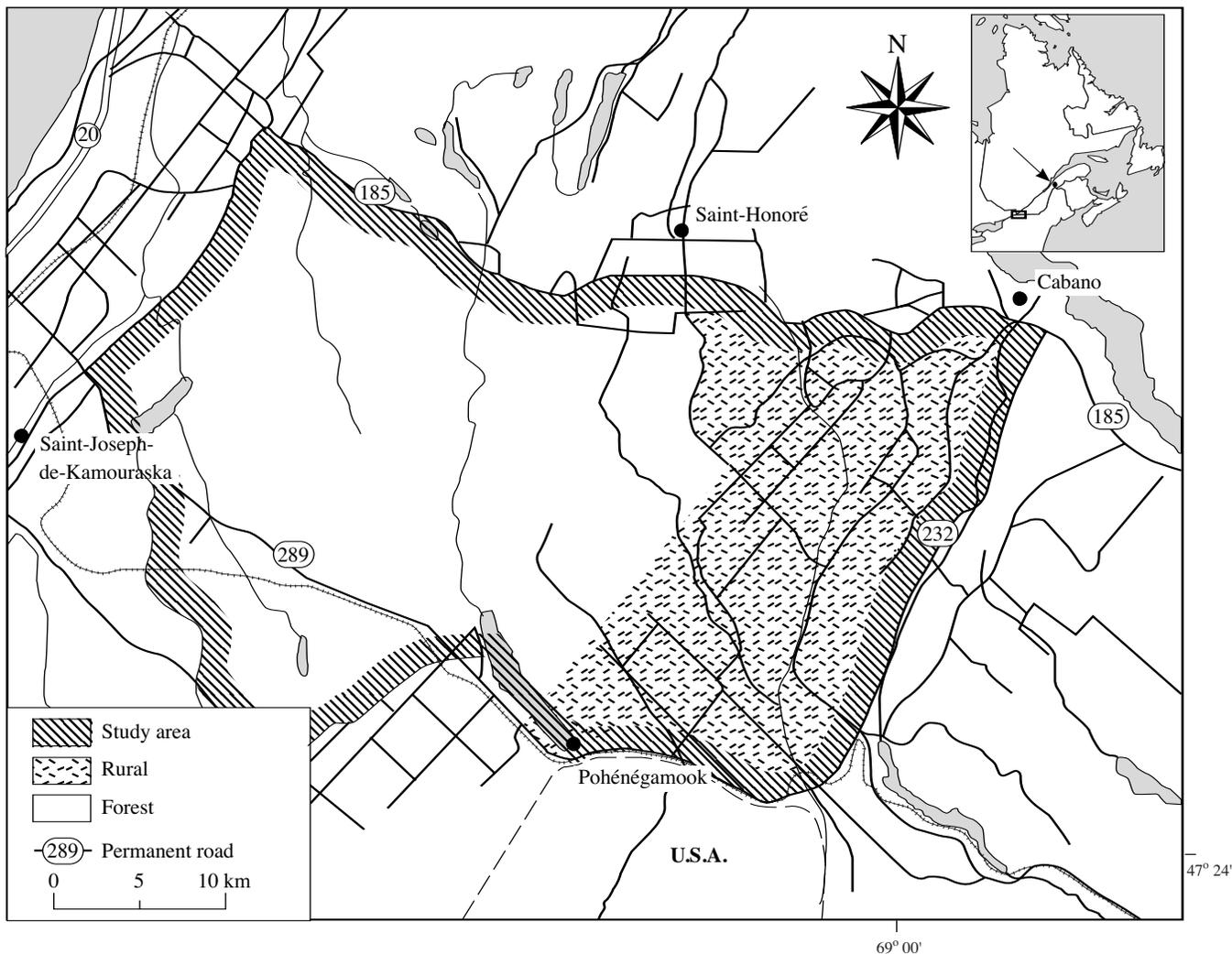


FIGURE 1. Location of the study area in southeastern Québec, and distribution of forest and rural landscapes.

examination of the whole undigested residues of bones, teeth, hairs and seeds allowed us to identify diet composition by species or group of species (Aborjan & Kolenowsky, 1969; Moore, Spence & Dugnolle, 1974). We examined the microscopic structure of hair medulla to discriminate between cervidae and other mammalian hairs, and the microscopic pattern of cervidae hair scales (Korschgen, 1980) to distinguish between white-tailed deer and moose. Results were expressed in terms of frequency of occurrence and percent volume in scats. In the latter option, percent of volume occupied by fragments of each food item in a scat was estimated visually to the nearest five percent.

#### SPACE USE

During late summer 1994 and 1995 and spring 1995, 16 coyotes were fitted with radio collars (Holohil Systems Ltd., Ontario). In addition, 19 pups were captured, measured and ear-tagged in August 1994, 1995 and 1996. All coyotes were trapped using Victor # 3 coil spring steel traps with padded and offset jaws (Woodstream Corp., Pennsylvania). Each trap included a 5-m chain ending with

an anchor so that captured animals could drag the trap and conceal themselves in vegetation when the anchor entangled. Traps were visited daily and captured coyotes were restrained using a noose pole; they were weighed, measured, sexed, aged by tooth wear (Gier, 1968), ear-tagged and then immediately released. Our animal-handling procedure was approved by the "Comité de protection des animaux de l'Université Laval". Based on the trapping period and body size, we classified coyotes as pups (5-6 months), yearlings (17-18 months), or adults (> 24 months). At the beginning of the study (1 May 1995), 10 radio-collared coyotes were present in the study area (six adult males, three adult females and one yearling).

Two terrestrial mobile tracking systems were used to estimate the position of animals by triangulation. The first one consisted of a nine-element yagi antenna mounted through the roof of a vehicle (Amlaner & Macdonald, 1979; Lovallo *et al.*, 1994) coupled to an Azimuth 1000 Digital Compass (KVH Industries Inc., Rhode Island; Lovallo *et al.*, 1994). The second mobile system consisted of a seven-element yagi antenna mounted on an all-terrain vehicle and

a hand-held compass. SRX 400 receivers (Lotek Engineering Inc., Ontario) were used with the two systems. The position of each station used for triangulation was determined using a Global Positioning System model 55 AVD (Garmin International Inc., Kansas).

We aimed at monitoring each coyote once a week for a 6-hour session, at the rate of one location per 30 minutes. Circadian variations of space use (Smith, Cary & Rongstad, 1981) were taken into account by sampling each coyote alternately during the day and at night as determined by sunrise and sunset (Environment Canada, weather data). Because the analysis of radio-tracking data usually relies on independent observations (White & Garrott, 1990), we selected only those relocations  $\geq 12$  hours apart (Reynolds & Laundré, 1990) to estimate home-range size. However, movement and activity rates are estimated more accurately by sampling frequently (Swihart & Slade, 1985). Movement rate was calculated by averaging the distance traveled between relocations separated by more than 30 minutes and less than 120 minutes over a 6-hour tracking session (Laundré & Keller, 1981). Activity rate was defined as the proportion of observations recorded as active in a tracking session with more than 3 valid relocations over a single circadian period (Larivière, Huot & Samson, 1994).

We used the Maximum Likelihood Estimator (Lenth, 1981) computed by LOCATE II software (Pacer, Nova Scotia) to determine animal position and estimate confidence ellipses. The Maximum Likelihood Estimator uses bearing standard deviance to estimate the confidence ellipse and, as this factor can be influenced by triangulation conditions, we calculated an OSD for every combination of tracking system, landscape and activity levels. Usually, we estimated the animal position with three bearings  $\bar{x} \pm SD = 3.1 \pm 0.4$  bearings/fix,  $n = 565$ ), with at least two of them intersecting at angles greater than  $30^\circ$ . We rejected locations for which bearing readings were separated by more than 15 minutes (Schmutz & White, 1990;  $\bar{x} \pm SD = 10 \pm 5$  minutes,  $n = 109$ ). We also rejected triangulation fixes with confidence ellipses exceeding  $0.3 \text{ km}^2$   $\bar{x} \pm SD = 0.007 \pm 0.008 \text{ km}^2$ ,  $n = 565$ ). Using blind tests, we estimated the accuracy of our locations from ground telemetry to  $242 \pm 195 \text{ m}$  ( $n = 27$ ) as determined with transmitters placed in known locations. Additional coyote relocations ( $n = 280$ ) were obtained twice a week by aerial tracking from a fixed-wing aircraft (Mech, 1983). Precision of aerial fixes averaged  $660 \pm 550 \text{ m}$  ( $n = 33$ ) based on blind tests.

The home-range size of coyotes was estimated by the Adaptive Kernel Method (Worton, 1987; 1989). The 95% confidence area was calculated using CALHOME software (Kie, Baldwin & Evans, 1994). CALHOME computes an optimal smoothing parameter ( $H_{opt}$ ) of the distribution function. However, by varying  $H_{opt}$ , the Least Square Cross-Validation value (LSCV) described by Worton (1995) can still be reduced. There is no standard mathematical method to minimize the smoothing parameter, so we repeated the analysis with smaller values of  $H$  up to a maximum reduction of  $0.8 H_{opt}$  (Worton, 1995), in order to reduce LSCV without creating excessive break-up of the home-range polygon (Kie, Baldwin & Evans, 1994). The use of the Adaptive Kernel Method to estimate home-range requires

between 30 and 100 independent relocations (Anderson, 1982). Number of locations often dropped below 30 when dividing the summer in two periods; we then used the 95% Minimum Convex Polygon methods (Mohr, 1947) to estimate the extent of space used by coyotes during the den attendance ( $21.5 \pm 2.5$  relocations/coyote) and the pup initiation ( $19.7 \pm 2.7$  relocations/coyote) periods.

Coyotes were assigned to specific landscapes *a posteriori*, based on habitat composition of their home-ranges. We classified rural coyotes as those whose home-ranges included  $\geq 25\%$  of old or cultivated fields and urban areas. The surface occupied by those habitats was estimated with a metric Bryant transparent grid (Mosby, 1980). The home-range of one yearling female included 15% of agricultural land but it was contiguous to a small town (3215 inhabitants), and therefore we classified this animal as a rural coyote. All forest coyotes had  $> 99.5\%$  of forested habitats in their home-ranges.

#### STATISTICAL ANALYSIS

Comparison of food habits among landscapes and time periods were performed using log-linear model analysis (SAS Institute Inc., 1988). Percent volume per prey item ( $\Sigma$  relative volume per scat/total number of scats) served as the basis to calculate the frequencies of occurrence for used in log-linear models (Messier & Crête, 1985). The absence of several food items from each scat precluded compositional analysis of food habits based on exact percentage (Reynolds & Aebischer, 1991). Miscellaneous food items were dropped from the analysis to reduce interdependence between food items. Beaver occurrence was also dropped from the analysis since it was absent from the diet of rural coyote. We first built a general model with all variables (landscape, period and food item) and their interactions. Interactions were deleted one at a time, from higher to lower levels, until only significant interactions remained (Christensen, 1990). This procedure was repeated until we reached the simplest model which still fitted the data. At each step, the reduced model was compared with the previous one with a likelihood ratio  $\chi^2$  test ( $G^2$ ; SAS institute Inc., 1988). In log-linear analyses, estimation of log-linear parameters (comparison of the response variable for the different explanatory variables and interactions retained in the model) follows a standard normal distribution ( $Z$ ).

Comparisons of movement and activity rates among landscapes, time periods and parts of the day (day/night) were performed using split-plot in time ANOVA (Milliken & Johnson, 1984; SAS Institute Inc., 1988). Split-plot design was used because we repeated measurements on the same individuals at different periods (Table I). Data from males and females were pooled for those analyses, because there was no significant effect of sex in the models in which this source of variation was included. Morphological measurements were compared among sex and landscape using two-way ANOVA (SAS Institute Inc., 1988). Capture dates were compared between landscapes with the Student *t*-test. *A posteriori* comparisons of activity rate, movement rate and morphological characteristics were conducted using least square means procedure (Student *t*-test), and only pre-planned comparisons were kept (SAS Institute Inc., 1988).

TABLE I. Typical design of the split-plot in time ANOVA used for comparing activity and movement rate of coyotes, and degrees of freedom associated with the different sources of variation

| Sources of variation                           | Degree of freedom |
|--|-------------------|
| BETWEEN SUBJECTS                               |                   |
| Landscape                                      | 1                 |
| Coyote(landscape)                              | 8                 |
| WITHIN SUBJECTS                                |                   |
| Period   | 1                 |
| Circadian period                               | 1                 |
| Period × circadian period                      | 1                 |
| Landscape × period                             | 1                 |
| Landscape × circadian period                   | 1                 |
| Landscape × period × circadian period          | 1                 |
| Period × circadian period × coyote (landscape) | 24 <sup>1</sup>   |

<sup>1</sup>Satterthwaite approximation was used to calculate the degrees of freedom (which are sometimes non-integer) appropriate for the different *F* statistics (Montgomery, 1991).

For all ANOVAs, we tested for homogeneity of variance through visual examination of residuals, and for departure from normality with the Shapiro-Wilk test. Departure from normality for data on movement rate was corrected with a logarithmic transformation. All means are reported with standard deviation (SD).

**Results**

**FOOD HABITS**

The reduced log-linear model which best fitted the data on food habits combined the interactions between landscapes and food items as well as between periods and food items (Goodness-of-fit :  $G^2_{(1)}=0.30, P=0.58$ ). In this model, both landscape and period contributed to explain difference in food habits (landscape × food item,  $G^2_{(10)}=46.43, P<0.001$ ; period × food item,  $G^2_{(10)}=53.93, P<0.001$ ).

During den attendance, small mammals (*Microtus spp.*, *Peromyscus spp.* and *Sorex spp.*) dominated the diet of both rural and forest coyotes (Figure 2a). According to our model, this prey type tended to be less important for forest coyotes (24%) than for rural ones (49%; Table II). Forest coyotes also relied almost equally on snowshoe hare (19%), beaver (*Castor canadensis*) (14%) and white-tailed deer (16%), but only white-tailed deer consumption was significantly higher for forest coyotes than for rural ones (0.2%). Beside small mammals, only woodchuck (*Marmota monax*; 18%) exceeded 10% of scat volume for rural coyotes, and consumption of this food item was significantly higher for rural than for forest coyotes. Plant matter, mainly plant detritus, contributed little to rural and forest coyote diet during the period of den attendance.

During the period of pup initiation, woodchuck and white-tailed deer were again the only element of the diet that statistically differed between landscapes, based on our model. However, small mammals and fruits dominated the diet (Figure 2b). Although not statistically significant, small mammals tended to occupy a larger volume in rural scats than in those collected in the forest landscape (rural = 53% versus forest = 18%), whereas it was the opposite for fruits (rural = 25% versus forest = 43%).

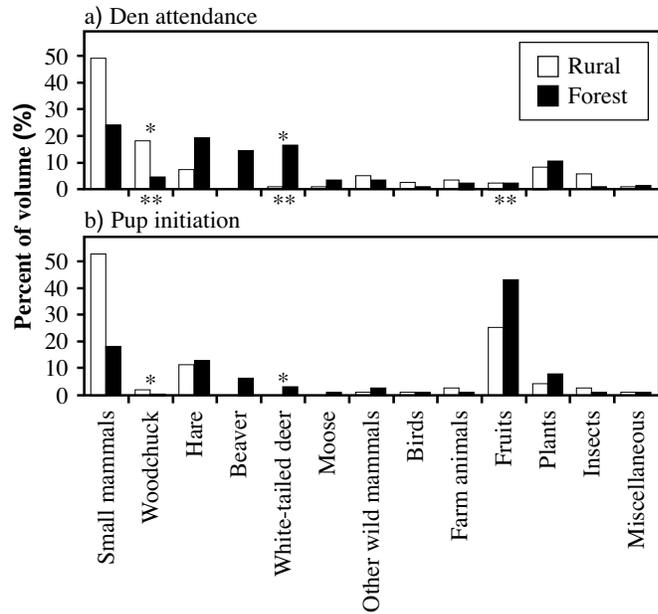


FIGURE 2. Food-habits of rural (*n* = 263 scats) and forest (*n* = 299 scats) coyotes expressed as percent volume, according to the period of scat collection. a) Den attendance: 1 May-15 July, b) Pup initiation: 15 July-1 October. Single asterisks indicate significant differences between landscapes and double asterisks identify significant changes from one period to the other (Likelihood-ratio  $\chi^2, \alpha = 0.10$ ).

TABLE II. Estimation of standard parameters for the log-linear models kept to explain variations in food items of coyotes according to landscape and summer period (landscape × food item,  $G^2_{(10)}=46.43, P<0.001$ ; period × food item,  $G^2_{(10)}=53.93, P<0.001$ )<sup>1</sup> and food types (landscape × food type,  $G^2_{(1)}=8.04, P=0.005$ ; period × food type,  $G^2_{(1)}=39.74, P<0.001$ )<sup>2</sup>

| Food type          | Food item          | Landscape |      | Period |      |
|--------------------|--------------------|-----------|------|--------|------|
|                    |                    | Z         | P    | Z      | P    |
| ANIMAL             |                    | 2.84      | 0.05 | 6.30   | 0.00 |
|                    | Small mammals      | 1.74      | 0.08 | 1.91   | 0.06 |
|                    | Woodchuck          | 2.17      | 0.03 | 2.60   | 0.01 |
|                    | Snowshoe hare      | 1.16      | 0.88 | 1.18   | 0.24 |
|                    | White-tailed deer  | 2.02      | 0.04 | 1.93   | 0.05 |
|                    | Moose              | 1.19      | 0.88 | 0.47   | 0.63 |
|                    | Other wild mammals | 0.27      | 0.79 | 1.25   | 0.21 |
|                    | Birds              | 0.49      | 0.62 | 0.55   | 0.58 |
|                    | Farm animals       | 0.71      | 0.48 | 0.52   | 0.60 |
|                    | PLANT              |           | 2.84 | 0.05   | 6.30 |
| Fruits             |                    | 1.11      | 0.29 | 6.49   | 0.00 |
| Plant matter       |                    | 0.89      | 0.38 | 0.18   | 0.86 |
| OTHER <sup>3</sup> |                    |           |      |        |      |
| Insects            | 1.30               | 0.19      | 0.31 | 0.76   |      |

<sup>1</sup>Goodness-of-fit:  $G^2_{(1)}=0.30, P=0.58$ .

<sup>2</sup>Goodness-of-fit:  $G^2_{(1)}=1.37, P=0.24$ .

<sup>3</sup>Miscellaneous food items were dropped from the analysis to reduce interdependence between food habits data.

When comparing the two periods, the log-linear model indicated that fruits became more abundant in both landscapes during the pup initiation period, whereas woodchuck and white-tailed deer were less abundant (Figure 2, Table II). The consumption of small mammals also tended to differ between periods.

The pooling of food items into two broad categories, *i.e.*, animal and plant food types, resulted in a log-linear model similar to the previous one (landscape × food type,  $G^2_{(1)}=8.04$ ,  $P=0.005$ ; period × food type,  $G^2_{(1)}=39.74$ ,  $P<0.001$ ; Goodness-of-fit :  $G^2_{(1)}=1.37$ ,  $P=0.24$ ). Rural coyotes made higher use of animal food than forest coyotes (Table II). The difference was very small during the period of den attendance for animal prey (rural=85% *versus* forest=84%) as well as for plant items (rural=9% *versus* forest = 12%). However, diet composition differed significantly between periods. During the second part of the summer, consumption of animal prey decreased in both landscapes, but especially in the forest (rural = 68% *versus* forest=46%) whereas plant food type became more important (rural=29% *versus* forest=51%).

HOME-RANGE SIZE

On average, areas used by forest coyotes always exceeded those used by rural animals, for all possible combinations of sexes and time periods, either with the Minimum Convex Polygon or the Adaptive Kernel method (Table III). Home range size of rural coyotes averaged  $58.2 \pm 7.6$  km<sup>2</sup> and  $30.1 \pm 9.3$  km<sup>2</sup> ( $n=2$ ) for the entire study period (95% Adaptive Kernel and Minimum Convex Polygon, respectively), which were smaller than the average of  $142.1 \pm 91.1$  km<sup>2</sup> and  $101.4 \pm 67.1$  km<sup>2</sup> ( $n=4$ ) for forest coyotes. Sample size was too small to justify statistical analysis. Core areas estimated with the 30% Adaptive Kernel followed the same pattern (rural:  $2.4 \pm 0.6$  km<sup>2</sup>,  $n=2$ , forest:  $8.9 \pm 12.9$  km<sup>2</sup>,  $n=4$ ). The core areas used during den attendance and pup initiation were approximately the same in both landscapes. When combining sexes, the area used by rural coyotes averaged  $23.0 \pm 13.3$  km<sup>2</sup> ( $n=3$ ) and  $14.3 \pm 11.8$  km<sup>2</sup> ( $n=3$ ) for the first and the second periods, respectively, compared to  $42.0 \pm 23.4$  km<sup>2</sup> ( $n=6$ ) and  $41.2 \pm 26.3$  km<sup>2</sup> ( $n=4$ ) for forest coyotes.

MOVEMENT AND ACTIVITY RATES

The movement rate of coyotes exhibited large variations among individuals of the same landscape (coyote × landscape:  $F_{(7,2058)}=2.86$ ,  $P=0.03$ ). No statistical difference was found between diurnal and nocturnal movement rates ( $F_{(1,2643)}=3.05$ ,  $P=0.09$ ) and therefore, we did not further consider time in our analyses. During den attendance, rural coyotes traveled, on average,  $760 \pm 660$  m/hour while forest coyotes covered  $290 \pm 390$  m/hour ( $t_{(19)}=1.82$ ,  $P=0.04$ ). This pattern was reversed during pup initiation, when rural coyotes moved at a rate of  $190 \pm 190$  m/hour on average, compared to  $830 \pm 1620$  m/hour for forest coyotes ( $t_{(19)}=0.55$ ,  $P=0.29$ ). The observed movement rates of rural coyotes were higher during den attendance than during pup initiation ( $t_{(19)}=2.02$ ,  $P=0.03$ ), but the higher movement rates of forest coyotes during pup initiation did not differ statistically from those estimated during den attendance ( $t_{(19)}=-0.24$ ,  $P=0.59$ ).

During den attendance, rural coyotes were active during  $66 \pm 32\%$  of daytime fixes compared to  $23 \pm 28\%$  for forest coyotes ( $t_{(20)}=2.27$ ,  $P=0.03$ ). During this period, rural animals were as active during daylight as at night ( $76 \pm 31\%$ ,  $t_{(20)}=-0.11$ ,  $P=0.54$ ) whereas forest coyotes were mostly nocturnal, with  $71 \pm 31\%$  of their time active at night ( $t_{(20)}=3.21$ ,  $P=0.002$ ). This pattern reversed during pup initiation, when rural coyotes decreased their activity during the day compared to den attendance ( $18 \pm 23\%$ ,  $t_{(20)}=1.90$ ,  $P=0.04$ ). They kept the same activity rate at night ( $78 \pm 22\%$ ), which was significantly higher than during the day ( $t_{(20)}=3.85$ ,  $P<0.001$ ). By contrast, after den attendance, forest coyotes increased their activity during daytime ( $51 \pm 36\%$ ) though not significantly ( $t_{(20)}=0.76$ ,  $P=0.23$ ), which was approximately equal to activity during this period at night ( $60 \pm 28\%$ ,  $t_{(20)}=-0.14$ ,  $P=0.56$ ). The overall pattern of activity rate created a significant landscape × time period × circadian period interaction

TABLE III. Home range sizes (km<sup>2</sup>) of rural and forest coyotes in southeastern Québec during the period of den attendance (1 May - 15 July) and pup initiation (15 July - 1 October), according to two estimators: 95% Minimum Convex Polygon (MCP) and Adaptive Kernel (AK)

| Landscape | Period          | Sex                   | Number of fixes<br>( $\bar{x} \pm$ SD) | MCP 95%<br>( $\bar{x} \pm$ SD) | AK 95%<br>( $\bar{x} \pm$ SD) | AK 30%<br>( $\bar{x} \pm$ SD) |
|-----------|-----------------|-----------------------|--|--------------------------------|-------------------------------|-------------------------------|
| Rural     | Den attendance  | Male (3) <sup>1</sup> | 21 ± 4                                 | 23.0 ± 13.3                    | N.A. <sup>2</sup>             | N.A.                          |
|           |                 | Pup initiation        | Male (2)                               | 22 ± 1                         | 17.9 ± 14.1                   | N.A.                          |
|           |                 | Female (1)            | 21                                     | 7.1                            | N.A.                          | N.A.                          |
|           |                 | Pooled (3)            | 21 ± 1                                 | 14.3 ± 11.8                    | N.A.                          | N.A.                          |
|           | Combined period | Male (2)              | 44 ± 1                                 | 30.1 ± 9.3                     | 58.2 ± 7.6                    | 2.4 ± 0.6                     |
| Forest    | Den attendance  | Male (3)              | 23 ± 2                                 | 52.3 ± 25.5                    | N.A.                          | N.A.                          |
|           |                 | Female (3)            | 20 ± 1                                 | 31.7 ± 20.1                    | N.A.                          | N.A.                          |
|           |                 | Pooled (6)            | 22 ± 2                                 | 42.0 ± 23.4                    | N.A.                          | N.A.                          |
|           | Pup initiation  | Male (2)              | 21 ± 1                                 | 36.8 ± 1.7                     | N.A.                          | N.A.                          |
|           |                 | Female (2)            | 16 ± 1                                 | 45.6 ± 44.6                    | N.A.                          | N.A.                          |
|           |                 | Pooled (4)            | 19 ± 3                                 | 41.2 ± 26.3                    | N.A.                          | N.A.                          |
|           | Combined period | Male (2)              | 44 ± 2                                 | 136.7 ± 67.7                   | 200.2 ± 73.8                  | 2.8 ± 0.7                     |
|           |                 | Female (3)            | 36 ± 3                                 | 66.2 ± 62.9                    | 84.1 ± 77.3                   | 14.7 ± 18.8                   |
|           |                 | Pooled (5)            | 40 ± 5                                 | 101.4 ± 67.1                   | 142.1 ± 91.1                  | 8.9 ± 12.9                    |
|           |                 |                       |  |                                |                               |                               |

<sup>1</sup>Number of monitored animals.

<sup>2</sup>Not computed due to inadequate number of fixes.

(Landscape × Period × Circadian period.:  $F_{(1, 27.12)} = 7.75$ ,  $P = 0.01$ ).

REPRODUCTION

Monitoring of marked animals suggested that more rural coyotes may have reproduced than forest animals. At least two adult males out of the four marked rural coyotes seemed to have raised young according to site fidelity (potential den sites were not visited to minimize disturbance) and observation of pups in the same area during trapping in late summer. Only one adult female out of the six marked forest coyotes appears to have raised pups. One pair of forest coyotes showed a strong site fidelity during the denning period but left the study area by late June, suggesting a potential reproduction failure.

MORPHOLOGICAL CHARACTERISTICS

We handled 33 coyotes in late summer 1994, 1995 and 1996 (19 pups and 14 adults; Figure 3). Effects of litter on body mass and size were minimized by sampling in different years. As we captured only one male pup and no adult female in the rural landscape, we restricted our statistical comparison of morphological measurements between landscapes to female pups and adult males. Date of capture coincided for rural and forest pups (rural:  $\bar{x} = 27$  August,  $n = 5$ , forest:  $\bar{x} = 31$  August,  $n = 6$ ,  $t_{(9)} = 1.32$ ,  $P = 0.22$ ). For adult males, the mean capture date occurred roughly one month

earlier in the forest than in the rural landscapes (rural:  $\bar{x} = 25$  August,  $n = 6$ , forest:  $\bar{x} = 26$  July,  $n = 4$ ,  $t_{(8)} = 3.70$ ,  $P = 0.006$ ). July and August both belongs to the same season (summer period: May to early September) as defined by Poulle, Crête & Huot (1995). Body mass and length of coyotes were significantly different between landscapes (mass:  $F_{(3, 14)} = 29.47$ ,  $P = 0.0001$ ; length:  $F_{(3, 14)} = 14.42$ ,  $P = 0.002$ ). Female pups weighed more in the rural landscape ( $9.0 \pm 1.4$  kg,  $n = 5$ ) than forest female pups ( $5.9 \pm 0.7$  kg,  $n = 6$ ;  $t_{(14)} = 3.35$ ,  $P = 0.002$ , Figure 3). Body length measured from the tip of the nose to the first caudal vertebra also differed significantly, being larger in the rural landscape (rural:  $0.77 \pm 0.05$  m,  $n = 5$ ; forest:  $0.68 \pm 0.02$  m,  $n = 5$ ;  $t_{(14)} = 1.99$ ,  $P = 0.03$ ). Rural adult males ( $n = 6$ ) tend to be 2 kg heavier than their forest counterparts, although this difference was not significant ( $15.5 \pm 2.3$  versus  $13.5 \pm 0.9$ ,  $n = 4$ ;  $t_{(14)} = 1.59$ ,  $P = 0.07$ ); body length of adult males averaged  $0.96 \pm 0.05$  m and  $0.91 \pm 0.05$  m in rural and forest landscapes, respectively ( $t_{(14)} = 1.21$ ,  $P = 0.12$ ).

Discussion

In our study area, rural and forest landscapes occur in close proximity, and coyotes were present in these two landscapes at low density. Our results show that foraging behaviour of coyotes varies between rural and forest landscapes throughout the growing season. Food habits differed between landscapes, as well as between periods especially with regard to woodchuck, white-tailed deer and fruit consumption. Rural coyotes exhibited a higher activity rate, particularly during daytime, and showed a higher movement rate during den attendance than forest coyotes; this trend reversed during the second part of the summer. Finally, rural coyotes tended to be heavier and taller than forest coyotes.

FOOD HABITS

Animal and plant components of coyote diet were quite similar in both landscapes during den attendance. However, prey species composition differed, especially for woodchuck and white-tailed deer. The higher consumption of white-tailed deer during den attendance in the forest landscape could have resulted from scavenging of carcasses following deer mortality during late winter and spring migration (A. Dumont, unpubl. data), or from predation on fawns later on (Harrison & Harrison, 1984; Messier & Barrette, 1982). A predominance of small mammals in the diet of coyotes living in agricultural and rural landscapes has also been observed in several food habit studies of eastern coyotes (Hilton, 1976; Lapierre, 1985; Harrison & Harrison, 1984; Person, 1988). During pup initiation, coyotes markedly increased their consumption of fruits in both landscapes. Elsewhere, berries seldom represent more than 20 to 30% of scat volume in coyotes (Hilton, 1976; Person, 1988), and in numerous studies they contributed less than 1% of the summer-fall diet (see Samson & Crête, 1997, for a review). For the overall summer, the volume of wildberries in scats of rural coyotes (12%; period May-October) was similar to the value reported from a mixed hardwood-coniferous forest located 200 km southwest of the study area (14%; period July-August; Messier, Barrette & Huot, 1986), whereas the

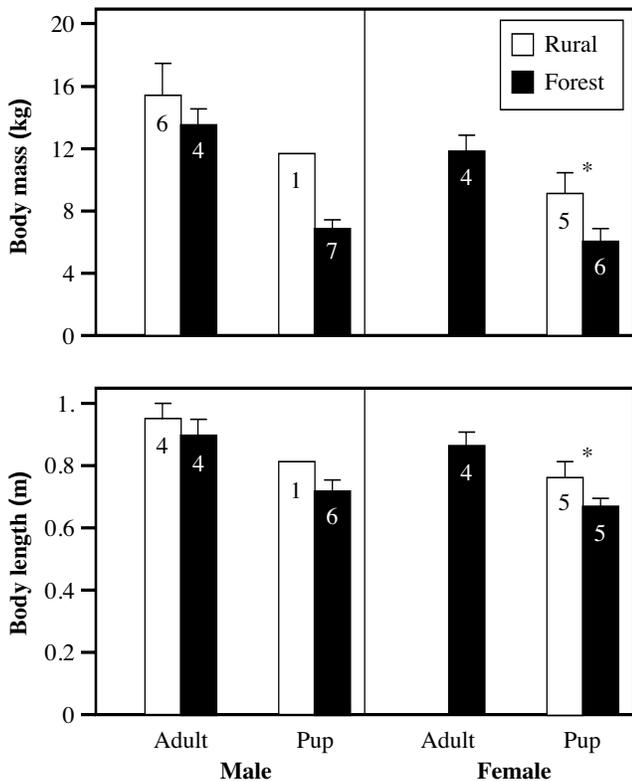


FIGURE 3. Morphological characteristics of rural and forest coyotes trapped in late summer 1994-1996 in southeastern Quebec. Body length was measured from the tip of the nose to the first caudal vertebra. Numbers in bars indicate sample size whereas asterisks show significant differences ( $P \leq 0.05$ ) between means.

volume observed for the forest landscape (30%) fell between that of rural coyote and the extreme volume (40%; period May-October) noted in the boreal forest of the Gaspé Peninsula (Samson & Crête, 1997), located 300 km north-east of our study area. It seems that, in forest landscapes of northeastern North America, wildberry consumption by coyotes increases with decreasing forest productivity.

Caturano (1983) and Person (1988) observed an increased consumption of wildberries in late summer for forest coyotes of Maine and Vermont, similar to what we have reported for southeastern Québec. They explained this shift as an optimal feeding strategy in time of food abundance. Other researchers considered animal prey as the preferred food source for coyotes, other items being consumed when those animal prey became scarce (Todd, Keith & Fischer, 1981; Barret, 1983; Cypher, Woolf & Yancy, 1993; Hernandez & Delibes, 1994). Data on food availability are necessary to determine if the high consumption of fruits during the second half of the summer is related to prey scarcity (Pouille, Crête & Huot, 1995; Crête & Lemieux, 1996; Samson & Crête, 1997) or to the energetic efficiency of exploiting concentrated fruit sources.

#### SPACE USE

Todd, Keith & Fischer (1981) as well as Gese, Rongstad & Mytton (1988) suggested an inverse relationship between prey availability, movement rate and activity. Rural coyotes moved at a higher rate and were more active during the day for the period of den attendance. Few studies have found that coyotes were more active during the day than at night (Gipson & Sealander, 1972; Camenzind, 1978; Andelt, 1985; Harrison, 1986), and most of them dealt with unexploited populations. Forest coyotes were less active and moved at a lower rate than their rural counterparts early in the growing season. Lower energetic requirements following the absence of reproduction or reproductive failure in monitored forest animals may explain these results.

During pup initiation, rural coyotes changed their activity pattern to become mostly nocturnal and reduced their movements, while forest coyotes modified their foraging strategies. The higher movement rate of forest coyotes at this time could be related to the patchy distribution of berry-producing areas, concentrated in clear-cuts. During the second half of the summer, forest coyotes also increased their daytime activity rate, which may have facilitated foraging on wildberries (Larivière, Huot & Samson, 1994). Even for canids, foraging on small wildberries might require good light in order to enhance contrast and discrimination of colors.

Movement and activity rates, averaged over the summer period, were similar in both landscapes. However, the sizes of home-ranges of forest coyotes exceeded by two to three times those of rural coyotes. Using the 95% minimum convex polygon method, home-range sizes of coyotes inhabiting hardwood forest habitats of Maine and New Brunswick were estimated at 43-46 km<sup>2</sup> (Caturano, 1983; Harrison, 1986; Major & Sherburne, 1987; Patterson, 1995). In rural Vermont, home-range averaged 16.5 km<sup>2</sup> (Person, 1988). Both estimates cover less than half the sizes of home-ranges we measured (forest: 101 km<sup>2</sup>, rural: 31 km<sup>2</sup>). Harrison (1992) reviewed home-range sizes of coyotes

within their historic range and in more recently colonized areas to find that coyotes in northeastern North America had larger home-ranges. This is explained by a lower productivity of food in eastern North America relative to that in the west (Harrison, 1992). We suggest that a lower productivity in forest landscape also explains the tendency toward larger home-ranges.

#### MORPHOLOGICAL CHARACTERISTICS

Integration of our results concerning space use and food habits suggests a lower productivity of the forest landscape as opposed to the rural one. Body mass and length tracked this difference between landscapes. In late summer, forest coyotes, especially pups, showed lower body mass and size than animals living in the rural landscape. One might argue that the difference we observed for adult males reflected an artifact resulting from the date of capture. However, Pouille, Crête & Huot (1995) observed relatively homogeneous body mass within a season, and noticed a major increase of body weight only in late October-November, at the beginning of the trapping season.

Pouille, Crête & Huot (1995) reported summer body mass of 12.5 kg and 11.1 kg for adult male and female forest coyotes, respectively, which is similar to the measurements we made for our forest animals (male: 13.5 kg, female: 11.8 kg). Rural male coyotes, the only sex for which we had data, averaged 15.5 kg. This is close to the average of 16 kg measured for adult males on the Gaspé Peninsula during winter, the season when fat reserves peaked (Pouille, Crête & Huot, 1995). The larger body mass of rural coyotes may reflect better physical condition. In contrast, the low body mass of forest pups compared to rural pups could be explained by the inability of their parents to provide sufficient food in an unproductive landscape. The slow body growth of forest pups may preclude reproduction by juvenile females, which may contribute to the low reproductive rate of forest coyotes reported by Pouille, Crête & Huot (1995). Gier (1968) mentioned that the proportion of females that breed in their first year was directly related to food supply. As the greatest variation in the number of breeding females results from the number of juvenile females that become sexually mature (Knowlton, 1972; Connolly, 1978; Kennelly, 1978), we conclude that the low productivity of the forest landscape curtails the demographic vigor of forest coyote populations.

#### SOURCE/SINK HYPOTHESIS

Hobbs & Hanley (1990) suggested that habitat evaluation should focus on mechanisms linking the performance of animal populations to resources in the habitats they use. The different foraging behaviours that we observed between rural and forest coyotes may cause a higher survival or fecundity rate in the former, creating possible source and sink dynamics. Validation of this hypothesis would require estimates of fecundity and survival; our results showed a possible mechanism by which source and sink dynamics could operate. The population dynamics of coyotes is further complicated by trapping, poaching and road kills that particularly affect rural coyotes. Based on the rate of scat collection along dirt roads, an index of coyote density (Knowlton & Stoddart, 1984, unpub. report), coyotes may

have been at a higher density in the rural (4.6 scats/km) than in the forest landscape (2.6 scats/km). However, density *per se* does not necessarily indicate whether source and sink populations exist. Source habitats with lower densities of animals have been reported elsewhere (Van Horne, 1983).

We suggest that forest landscapes are sub-optimal summer habitats for coyotes in southeastern Québec. The difference in foraging strategies reflected the lower quality of the forest landscape for coyotes, although energetic requirements of reproductive rural coyotes may have affected the relationship between foraging strategy and food availability. Coyotes can possibly maintain viable populations in northern forests, due to their high adaptability, their great mobility and the lower human presence (pseudo-sink; Watkinson & Sutherland, 1995). Long-term data on fecundity and survival of coyotes from contiguous rural and forest landscapes will be necessary to confirm that source and sink dynamics govern coyote numbers. However, our study suggests a process by which such a dynamics could operate.

### Acknowledgements

This study was funded by the Ministère de l'Environnement et de la Faune du Québec, a Natural Sciences and Engineering Research Council grant to J. Huot, the Fondation de la Faune du Québec and the Fondation Héritage Faune. We are grateful to N. Bergeron and R. Lemieux for their invaluable assistance in the field. M. Salaté greatly helped with laboratory work. G. Daigle of the Service de consultation statistique, Université Laval, supervised the statistical analysis. We also thank C. Barette, M. Festa-Bianchet, M. O'Donoghue and an anonymous referee for commenting on an earlier draft of this manuscript. J. P. Tremblay was supported by a NSERC scholarship.

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