Landscape Influence on *Canis* Morphological and Ecological Variation in a Coyote-Wolf *C. lupus* × *latrans* Hybrid Zone, Southeastern Ontario

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The ecology of Coyote-Wolf (*Canis latrans* × *C. lupus*) hybrids has never fully been typified. We studied morphological and ecological variation in *Canis* within a region of Coyote-Wolf hybridization in southeastern Ontario. We assessed *Canis* morphology from standard body measurements and ten skull measurements of adult specimens and found that *Canis* in this region are morphologically intermediate between Algonquin Provincial Park Wolves (*C. lupus lycaon*) and Coyotes, indicating a *latrans* × *lycaon* hybrid origin; however, there is a closer morphological affinity to *latrans* than *lycaon*. Analysis of 846 scats indicated dietary habits also intermediate between *lycaon* and Coyotes. We used a geographic information system (GIS) to assess spatial landscape features (road density, land cover and fragmentation) for six study sites representing three landscape types. We found noticeable variation in *Canis* morphology and diet in different landscape types. In general, canids from landscape type A (lowest road density, more total forest cover, less fragmentation) displayed more Wolf-like body morphology and consumed a greater proportion of larger prey (Beaver [*Castor canadensis*] and White-tailed Deer [*Odocoileus virginianus*]). In comparison, canids from landscape types B and C (higher road density and/or less total forest cover, more fragmentation) were generally more Coyote-like in body and skull morphology and made greater use of medium to small-sized prey (Groundhog [*Marmota monax*], Muskrat [*Ondatra zibethicus*] and lagomorphs). These landscape trends in *Canis* types suggest selection against Wolf-like traits in fragmented forests with high road density. The range of *lycaon* southeast of Algonquin Provincial Park appears to be limited primarily due to human access and consequent exploitation. We suggest that road density is the best landscape indicator of *Canis* types in this region of sympatric, hybridizing and unprotected *Canis* populations.

Key Words: Coyote, *Canis latrans*, Gray Wolf, *Canis lupus*, hybridization, road density, morphology, landscape influence, Ontario.

The objectives of this study were to assess potential relationships between landscape characteristics (e.g., road density, forest cover and fragmentation) and morphological and ecological variation in *Canis* in a Coyote-Wolf hybrid zone of southeastern Ontario. Coyote-Wolf (*Canis latrans* × *C. lupus*) hybridization (Lehman et al. 1991; Wilson et al. 1996) and intermediate-sized canids (Kolenosky and Standfield 1975; Nowak 1979; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987) have previously been described in eastern Ontario, an interface region between Wolf range in the north and Coyote range in the south (Kolenosky et al. 1978; Buss and de Almeida 1997). In parts of the Great Lakes region, spatial landscape features have been used to describe areas of favorable Wolf habitat (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), but not in relation to Coyote-Wolf hybridization.

Habitat and landscape conditions have been implicated in the extirpation of wild Red Wolves (*C. rufus*) prior to 1970, the shrinkage of the range of *C. lupus lycaon* and coyote colonization in eastern North America (Nowak 1978; Moore and Parker 1992), as well as extensive *latrans-lycaon* and *latrans-rufus* hybridization (Lehman et al. 1991; Wayne and Jenks 1991; Roy et al. 1994). The study area on the Frontenac Axis of southeastern Ontario is characterized by a forested matrix ranging from landscapes of continuous forest and low road density, potentially suitable Wolf habitat (Thiel 1985; Jensen et al. 1986, Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), to mixed forest-agricultural landscapes. It was hypothesized that *lycaon* would be found in continuously-forested landscapes similar to Algonquin Provincial Park to the north, and that Coyote-like animals would predominate in landscapes with less forest cover, more agricultural activity and higher road density.

This paper is relevant to the conservation of the adjacent Algonquin Provincial Park *lycaon* population. *Lycaon*, which has lost over half its historic range (Nowak 1995), is considered a subspecies of Gray Wolf (Nowak 1995), or more recently, a separate species, *C. lycaon*

(Wilson et al. 2000). Algonquin Provincial Park may represent one of few core *lycaon* populations remaining. The influence of hybridization on the Algonquin *lycaon* population (Wilson et al. 1996) is of concern; this study will describe conditions favoring hybridization.

Study Area

Regional Setting

The study was conducted from 1996 to 1998 in southeastern Ontario within a 10 000 km^2 region centered (45º15'N, 77ºW) approximately 80 km southeast of Algonquin Provincial Park (Figure 1). Topography varies from lowland flats of the Ottawa Valley to upland, rolling terrain of the Madawaska Highlands. Elevations range from approximately 150 m to 450 m. The area contains several large lakes and rivers, and wetlands are common. Mean daily July and January temperatures are about 19ºC and -11ºC, respectively. Mean annual precipitation ranges from 65 cm in the north to 90 cm in the southwest, and mean annual snowfall is 200 cm (Brown et al. 1968).

Most of the study area lies on the Frontenac Axis, or Frontenac Arch, part of the Precambrian rock of the Canadian Shield which extends from southeastern Ontario to upper New York State (Douglas 1976; Davidson 1988). Frontenac Axis physiography makes much of the study region unsuitable for agriculture; consequently, extensive portions remain forested and with low human population, although farms, communities and small towns are scattered throughout the region. The Axis is recognized as a link or corridor between the relatively undisturbed landscapes of Algonquin Provincial Park in Ontario and Adirondack State Park in New York (Keddy 1995). Highway 7, demarcating the lower third of the Ontario portion of the Axis, was used as the approximate southern boundary of the study region; south of the highway is much greater human settlement, higher road density and more agricultural activity. Approximately half of the study region has an all-season road density less than 0.6 km/km^2 (Buss and de Almeida 1997: Figure 4), and a considerable amount of the central Frontenac region is public land (Keddy 1995: Figure 7).

The study region is almost entirely within the Middle Ottawa section of the Great Lakes-St. Lawrence forest region (Rowe 1972). Common upland species include Sugar Maple (*Acer saccharum*), Beech (*Fagus grandifolia*), Yellow Birch (*Betula alleghaniensis*), Red Maple (*A. rubrum*), Eastern Hemlock (*Tsuga canadensis*), Eastern White Pine (*Pinus strobus*) and Red Pine (*P. resinosa*). Also occurring are White Spruce (*Picea glauca*), Balsam Fir (*Abies balsamea*), Trembling Aspen (*Populus tremuloides*), White Birch (*B. papyrifera*), Red Oak (*Quercus rubra*) and Basswood (*Tilia americana*). Common species in lowlands and wet areas include Eastern White Cedar (*Thuja occidentalis*), Tamarack (*Larix laricina*), Black Spruce (*Picea mariana*), Black Ash (*Fraxinus nigra*), Red Maple and White Elm (*Ulmus americana*).

When this research was conducted, *Canis* in this region were legally protected only in Algonquin Provincial Park (7571 km^2) and from December 15 to March 31 in three townships adjacent to the southeast corner of the Park. An estimated 150-200 Wolves in approximately 36-38 packs are found in Algonquin Park (J. Theberge, unpublished data). Canid densities are not known for the Frontenac region or most of the remainder of the province (Buss and de Almeida 1997). Wolves, Coyotes, and their hybrids are classed as furbearing animals in Ontario and can be hunted or trapped in the southern part of the province throughout the year with a small-game hunting license or trapping license, with no bag limits or quotas (Buss and de Almeida 1997).

Study Sites

Six landscapes (sites; Figure 1) averaging about 230 km^2 were selected to represent one of three *relative* landscape types: A (low road density, high percent forest cover, low fragmentation), B (moderate road density, moderate percent forest cover, moderate fragmentation), and C (high road density, low percent forest cover, high fragmentation; Table 2).

The Dacre and Grimsthorpe sites represented parts of the most continuously-forested areas on the Frontenac Axis. The Dacre site (Renfrew County), 180 km^2, is in the Madawaska Highlands, immediately east of highway 41 between the communities of Griffith and Dacre, and north of Centennial and Black Donald Lakes. The Grimsthorpe site (Hastings County and Lennox and Addington County), 246 km^2, is between highways 41 and 62, immediately west of Bon Echo Provincial Park and Skootamatta Lake and immediately north of Lingham Lake. The Dacre site has few permanent residences and Grimsthorpe has none, but both have several recreational or hunt camps. Most of the land in these two sites is public land with fairly extensive networks of logging roads.

The Millbridge site (Hastings County), 143 km^2, is located on highway 62 between the towns of Madoc and Bancroft. The Admaston site (Renfrew County), 196 km^2, is west of the town of Renfrew and south of highway 5. The Lanark site (Lanark County), 322 km^2, lies immediately east of highway 511 and north of the town of Lanark. The Lake Clear site (Renfrew County), 278 km^2, is between Lake Clear and Golden Lake, immediately east of highway 512 and west of the town of Eganville. Approximately 80 to 90% of the land in these four sites is privately owned, with quite extensive networks of regional and concession roads. Active and/ or abandoned farmlands are common.

Prey Base

Mammals found in the study area include White-tailed Deer (*Odocoileus virginianus*), Beaver (*Castor canadensis*), Muskrat (*Ondatra zibethicus*), Fisher

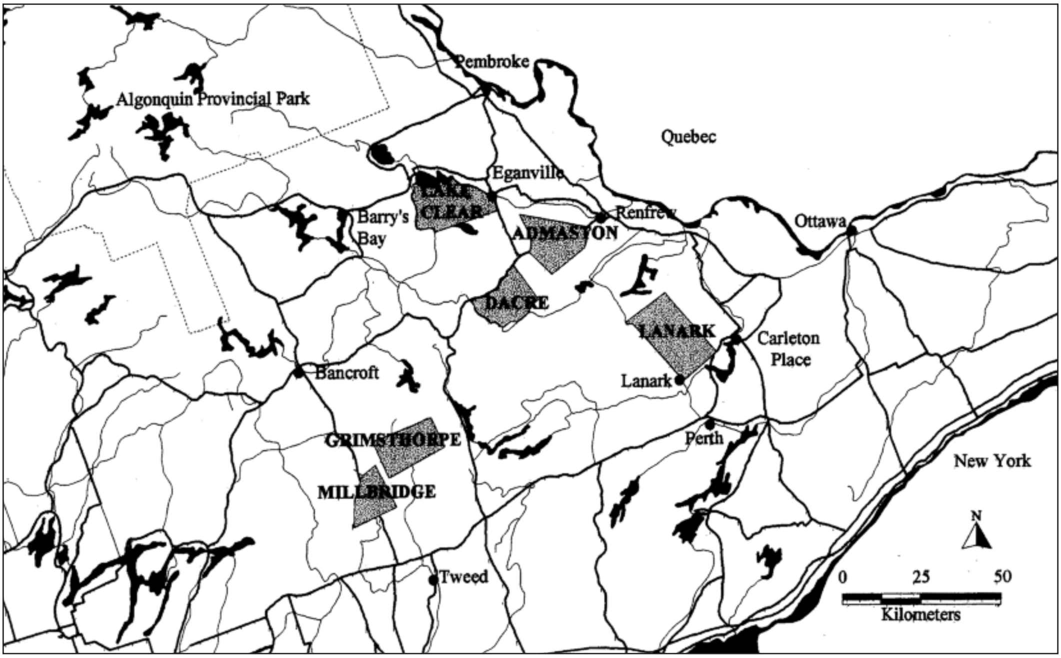

FIGURE 1. Six study sites (shaded polygons) in the Frontenac Axis region of southeastern Ontario.

(*Martes pennanti*), Marten (*Martes americana*), Raccoon (*Procyon lotor*), Groundhog (*Marmota monax*), Red Fox (*Vulpes vulpes*) and Black Bear (*Ursus americanus*), as well as smaller mammals including Snowshoe Hare (*Lepus americanus*), Eastern Cottontail (*Sylvilagus floridanus*), Mink (*Mustela vison*), Eastern Chipmunk (*Tamias striatus*) and numerous species of microtine rodents (Dobbyn 1994). Parts of the study region and individual sites are recognized as Deer wintering areas (Ontario Ministry of Natural Resources [OMNR] unpublished data). Moose (*Alces alces*), at the southern edge of their range in Ontario, occur at very low densities (≤ 0.03 – 0.05 Moose/km^2) in the study region (OMNR 1997; OMNR unpublished data, 1995-1996 and 1996-1997 aerial surveys) and are likely the only wild prey species not common in all sites. Domestic livestock are present in all sites except Dacre and Grimsthorpe; carcasses were used as bait for *Canis* by hunters in some other sites, making it difficult to use scat analysis to distinguish direct livestock predation from carrion or bait feeding.

Methods

Landscape Assessment

Roads were digitized from recent (1987 – 1996) Natural Resources Canada 1:50 000 topographic maps using ARC/INFO 7.2.1 (Environmental Systems Research Institute [ESRI], Redlands, California) and classed into two categories: (1) all-season roads including all public, paved and unpaved roads passable year-round by two-wheel-drive vehicle; and (2) seasonal roads and trails (not necessarily open to public use) including unpaved, unimproved roads, forestry roads, trails and rail-trails. Site area and linear road distance (i.e., sum of lengths of roads) were summarized using ARCVIEW 3.1 (ESRI, Redlands, California) and used to calculate two road densities for each site: (1) all-season roads, and (2) all-season roads, seasonal roads and trails. Seasonal roads were included in this study, unlike others (Thiel 1985; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995), as an indication of potential human access by four-wheel-drive vehicles, all-terrain vehicles and snowmobiles.

Land cover was determined for each site from remote sensing images (Landsat Thematic Mapper) at 25 m resolution from August 1996 (Lake Clear) and May 1996 (all other sites). Images were classified into 11 land cover classes (12 for Lake Clear; Table 1) using a minimum polygon size of 12 500 m^2. Due to considerable cloud cover over part of the Millbridge site, landscape assessment was based on a smaller, but typical area. Large cloud-shadow polygons in Lake Clear were excluded. Because a section of the Grimsthorpe site was affected by haze, making many forested areas appear as field and scrub vegetation, polygons there were manually re-classified to forest classes based on elevations: deciduous forest at higher elevations, wetlands or coniferous forest at lower elevations.

Landsat data were converted to ARC/INFO coverages, and FRAGSTATS*ARC 2.0.3 (Innovative GIS Solutions Inc., Fort Collins, Colorado) was used to summarize land cover classes and to calculate land-

TABLE 1. Comparison of standard body measurements of Frontenac *Canis* to Algonquin Park Wolves.

	Frontenac *Canis*		Algonquin Wolf	
Measurement	Mean ± SE	n	Mean ± SE	n
Male				
body mass (kg)	20.5 ± 0.6	27	30.3 ± 0.6	48
total length (cm)	139.3 ± 1.5	28	163.8 ± 1.4	47
foreleg length (cm)	36.9 ± 0.4	28	41.4 ± 0.4	42
hind foot length (cm)	21.5 ± 0.3	28	24.7 ± 0.3	47
Female				
body mass (kg)	17.5 ± 0.5	24	23.9 ± 0.6	40
total length (cm)	133.5 ± 1.7	26	154.3 ± 1.4	39
foreleg length (cm)	34.6 ± 0.5	24	39.0 ± 0.5	30
hind foot length (cm)	20.5 ± 0.3	24	23.3 ± 0.3	36

TABLE 2. Road density, land cover and landscape measures for two study sites for each of three landscape types in southeastern Ontario.

	Landscape Type A		Landscape Type B		Landscape Type C	
	Dacre	Grimsthorpe	Millbridge	Admaston	Lanark	Lake Clear
Road Density (km/km^2)						
All-season roads	0.01	0	0.33	0.50	0.64	0.65
Seasonal roads and trails	0.46	0.38	0.25	0.19	0.29	0.34
All roads and trails	0.47	0.38	0.58	0.69	0.93	0.99
Land Cover (% of landscape)						
Water	3.3	5.0	1.5	2.1	4.6	1.6
Wetland	1.1	4.1	3.2	1.6	3.2	3.2
Wetland, forested wetland	6.6	5.9	7.7	4.6	8.5	14.7
Lowland coniferous	50.4	19.4	20.1	24.3	16.9	27.2
Dense/mixed coniferous	22.9	31.8	24.7	30.9	18.3	18.9
Lowland/mixed deciduous	9.4	21.0	19.4	17.9	20.7	11.1
Upland deciduous	1.7	8.8	19.9	4.1	14.2	2.7
Scrub vegetation	1.8	2.4	1.4	3.6	3.8	5.5
Field	2.4	1.3	1.6	9.9	7.6	13.0
Road, rock, bare soil	0.3	0.3	0.4	0.8	1.2	2.0
Bare sandy soil	0.1	0.1	0.1	0.3	0.7	0.1
Quarry, surface mine	–	–	–	–	0.5	–
Landscape Measures						
Total area (ha)	17,361.8	23,397.1	13,469.0	18,553.4	30,566.4	26,015.3
Largest patch index (%)	35.7	3.3	3.6	2.6	2.3	2.6
Mean patch size (ha)	12.7	8.6	7.6	8.1	7.3	7.6
Patch density (#/100 ha)	7.9	11.6	13.2	12.3	13.7	13.1
Mean shape index	2.3	2.2	2.3	2.3	2.2	2.3
Area-weighted mean shape index	14.3	5.5	4.2	4.3	3.4	3.9
Simpson's diversity index	0.68	0.80	0.81	0.80	0.86	0.83

scape indices for each site. These indices were (1) total area of each site, (2) largest patch index (percentage of site occupied by largest patch), (3) mean patch size, (4) patch density (number of patches per 100 ha), (5) mean shape index (a measure of average perimeter-to-area ratio for all patches in the site), (6) area-weighted mean shape index (a measure of average perimeter-to-area ratio which gives more weight to large patches in the site by multiplying by the proportion of the site covered by each patch), and (7) Simpson's diversity index (a measure of the probability that any two randomly selected patches would be different land cover classes) (Table 2). These indices are described by McGarigal and Marks (1995).

The location of each Frontenac *Canis* specimen (see below) that did not fall within one of the six sites was assigned to one of the three landscape types based on a similar, but more general landscape assessment of a 250 km^2 (approximate) area centered on the known or approximate kill site. Road density and percent forested versus non-forested land were estimated for each of these kill areas through examination of topographic maps, OMNR district maps, classified land cover data and familiarity with the areas.

Body and Skull Morphology Assessments

Frontenac *Canis* body morphology was evaluated from carcasses of 51 adult specimens collected from trappers and hunters in the study region during winters (December to March) 1995-1996 through 1997-1998 and from six adult animals live-trapped during summer 1998. Carcass collection focused on the six sites; the location of all specimens was known within at least a few kilometres. Noted during necropsy of carcasses, or during examination of live-captures in the field, were sex, body mass, total body length (including tail), foreleg length (from the elbow, the obvious notch on the back side of the leg just below the chest, to the end of the foot pad on the longest toe [not including the nail], measured along the back side and following contours) and hind foot length. Frozen carcasses were thawed before measurements were taken. Unskinned body mass (BM) of skinned carcasses was estimated from their skinned body mass (SBM) using the regression BM = 0.97 SBM + 4.56 ($r^2 = 0.91$, n = 8 specimens for which both unskinned and skinned mass were known). The six live-captured animals were classed as more than 13 months old adult based on general tooth-wear patterns examined in the field (Bowen 1982; Landon et al. 1998). Other specimens were aged by Matson's Laboratory, Inc., Milltown, Montana, using cementum layer analysis of a lower canine tooth (Linhart and Knowlton 1967; Landon et al. 1998). Specimens at least one year old were considered adults; however, the actual minimum age was approximately 20 months since specimens were killed after December.

Body measurements were subjected to multivariate cluster analysis (SAS) to determine morphologically-similar groups (classes) of individuals which were then compared to landscape type. MANOVA (SAS) was used to determine if significant differences existed among the body size classes. Frontenac *Canis* body measurements were compared using a Student's t-test with existing data on live-trapped or hunter/trapper-killed adult Algonquin Park Wolves obtained between 1987 and 1997 (Theberge et al. 1996; J. Theberge, unpublished data). Frontenac *Canis* body morphology was also compared generally to Eastern Coyote morphology reported in the literature.

Skull measurements and analyses followed those of Nowak (1995). Ten skull measurements were taken with calipers and recorded to the nearest 0.5 mm: (1) greatest skull length, (2) zygomatic width, (3) alveolar length from P1 to M2, (4) maximum width across outer sides of P4, (5) palatal width between alveolar of P1, (6) width of frontal shield, (7) height from alveolar of M1 to most ventral point of orbit, (8) depth of jugal, (9) crown length of P4, and (10) crown width of M2. Linear discriminant analysis was used to determine possible trends in Frontenac skull morphology in relation to landscape type. Frontenac *Canis* skulls (26 male, 19 female) were considered "unknowns" and compared as individuals to three "known" groups of adult skulls: southwestern Ontario Coyotes (17 male, 23 female; OMNR collection 1958-1970), Adirondack Coyotes (9 male, 8 female; R. Chambers collection 1997 and 1998) and Algonquin Park Wolves (13 male, 12 female; 1989 to 1996; S. Stewart 1996*). Each Frontenac specimen was assigned to the group which it most resembled morphologically based on its statistical distance (Mahalanobis' distance, D^2) from the groups.

Because of incomplete carcasses and damaged skulls, Frontenac specimens used in multivariate body and skull analyses represented a sub-sample of all adult specimens collected during this study.

Diet Assessment

Frontenac *Canis* diet was assessed from 846 scats (479 summer, 367 winter) collected from May to August 1996 and throughout May 1997 and August 1997 along unpaved roads and trails throughout the six sites. Scats were classed by season (summer or winter) based on estimated age at date of collection. Old scats collected in May represented diet from the previous winter; scats deposited in May through August represented summer diet. Scats were heated in an autoclave at 120°C and 125 kPa for 20 minutes. Three hairs were randomly chosen from each scat and identified microscopically by scale patterns and pigment patterns of the medulla (Adorjan and Kolenosky 1969) and by comparison to a reference collection. Selection of a fourth hair results in an additional prey species in less than 3% of Algonquin Wolf scats (Swanson 1989), therefore three hairs were considered sufficient. Percent frequency of occurrence was considered as the number of occurrences of each mammalian prey type expressed as a percentage of the total number of hairs analyzed for each site and season. Percent frequency of occurrence was used to indicate relative amounts of prey consumed in various landscapes and to allow direct comparison to the Forbes and Theberge (1996) study which used the same analysis for Algonquin Wolf diet (three hairs per scat, percent frequency of occurrence). For each season, a chi-square analysis on a contingency table (using number of hairs rather than percent frequency of occurrence) was used to test the null hypothesis that there was no difference in mammalian prey consumed among sites. Some prey types were combined in the chi-square analysis to ensure that no more than 20% of the expected cell frequencies were less than five (Owen and Jones 1990); Moose and Cow were excluded since they were not available in all sites. Non-mammalian prey items were recorded on a presence/absence basis in each scat. Conclusions about food habits are limited in Lake Clear and Admaston because few scats were found (n = 30 and n = 51, respectively).

Results

Hybrid Position of Frontenac Canis

In general, Frontenac canids were intermediate between Algonquin Wolves and Coyotes in body morphology. On average, Frontenac canids were significantly smaller than Algonquin Wolves in all body measurements ($p < 0.001$ males, $p < 0.001$ females; Table 1). Frontenac *Canis* were considerably heavier than the average body mass reported for adult Eastern Coyotes throughout most of their range (males about 12.5 – 17 kg, females about 11 – 15 kg; e.g., Richens and Hugie 1974; Lorenz 1978; Moore and Millar 1986; Poulle et al. 1995). Coyotes from New Hampshire (males 20.3 kg, females 18.0 kg; Silver and Silver 1969) and Vermont (males 17.8 kg, females 16.4 kg; Person 1988) are closer in weight to Frontenac canids.

Description of Landscapes

Road densities and land cover summaries indicated increased human influence from type A to type C landscapes (Table 2). All-season road density was approximately 0 km/km^2 in landscape A, 0.33 and 0.50 km/km^2 in landscape B sites, and about 0.65 km/km^2 in landscape C. When all roads and trails were considered, density was considerably higher (0.38 – 0.99 km/km^2) in all landscape types. The highest proportions of forested land cover (coniferous and deciduous forest classes) were in landscape type A sites (Dacre 84.4%, Grimsthorpe 81.0%) and Millbridge (landscape type B, 84.1%); proportions were considerably lower in Admaston (landscape type B, 77.2%) and landscape type C sites (Lanark 70.1%, Lake Clear 59.9%). Millbridge was similar to landscape type A in total forest cover, but had a much higher road density.

Landscape indices revealed the expected trend of increased human disturbance (i.e., increased heterogeneity and fragmentation) from type A to type C (Table 2). Mean patch size was larger and patch density was lower in landscape A sites. Mean shape index values were similar for all sites. Area-weighted mean shape index values varied by landscape type, however, and indicated that large patches in all landscape types, but especially landscape type A sites, were more irregular (i.e., natural) in shape than small patches. The Simpson's diversity index values suggested greatest land-cover diversity in landscape type C sites.

Landscape Variation in Frontenac Canis

Five body size classes of Frontenac *Canis* were generated by multivariate cluster analysis for each sex (SAS; Table 3). Landscape type A was represented predominantly by canids with large body size (Figure 2a); 50% of 20 specimens from landscape type A were large-bodied specimens (size classes 4 and 5), although all male size classes and all except the smallest female size class were represented in landscape type A. Five (71%) of seven specimens from landscape type B were medium-sized specimens (classes 2 and 3), and all of the 21 specimens from landscape type C fit in small and medium body size classes (1, 2 and 3). The largest Frontenac specimens (size classes 4 and 5 combined) were significantly smaller (t-tests, $p < 0.05$) than Algonquin Wolves except in female foreleg length.

Frontenac *Canis* skull morphology was also more Wolf-like in landscape type A (Figure 2b) based on the linear discriminant analysis. Of 17 Frontenac *Canis* skulls from landscape type A, 9 (53%) most resembled Algonquin Wolves, 1 (6%) most resembled Adirondack Coyotes and 7 (41%) most resembled southwestern Ontario Coyotes. From landscape type B, 2 (15%) of the 13 Frontenac *Canis* specimens resembled Algonquin Wolves, 8 (62%) most resembled Adirondack Coyotes and 3 (23%) most resembled southwestern Ontario Coyotes. From landscape type C, 1 (6%) of the 15 Frontenac specimens was similar to Algonquin Wolves, 4 (27%) were most similar to Adirondack Coyotes and 10 (67%) were most similar to southwestern Ontario Coyotes.

Significant variation in diet was found among sites in both summer ($\chi^2 = 634.74$, df = 30, $p < 0.001$) and winter ($\chi^2 = 386.63$, df = 20, $p < 0.001$). Canids in landscape type A consumed large prey almost exclusively (Figure 3). Combined occurrences of Beaver and White-tailed Deer (adult and fawn) in scats from landscape A sites were 87.2% and 91.0% in summer and 82.6% and 86.3% in winter, considerably higher than landscape type B and C sites (34.4 – 50.0% in summer, 22.2 – 67.6% in winter). Fawn was a significant food item in all sites in summer and accounted for an average of 64% of all Deer occurrences in summer scats. In landscape types B and C, medium-sized prey (Groundhog, Muskrat and leporids) comprised a significant portion of the diet particularly in summer. Groundhog occurrence in summer scats corresponded closely to landscape type: < 2% in landscape A, 11.3 – 13.1% in landscape B and 23.0 – 27.8% in landscape C. Muskrat use was especially high in Millbridge (landscape B). Use of leporids and small mammals was low in most sites, but higher in landscapes B and C. Cow hair was found in scats from landscape types B and C; livestock and/or baiting was common in these sites. Non-mammalian prey items showed no obvious landscape trend, found in an average of 19.2% of summer scats (11.3 – 27.8% by site) and 4.6% of winter scats (2.7 – 8.7% by site). Fruit (*Rubus* spp., *Vaccinium* spp. and *Aralia* spp.) and grasses were the most common of these items. Insects, bird remains, garbage, eggshell, pine needles and buds occurred incidentally.

Discussion

Evidence of Intermediate Wolf/Coyote Characteristics

Frontenac *Canis* appear to hold an intermediate position between Eastern Coyotes and Algonquin Wolves in body size, skull morphology and diet, suggesting a *latrans-lycaon* hybrid origin. These results support previous morphological studies which described interme-

TABLE 3. Mean, minimum and maximum body measurements for five male (n = 26) and female (n = 22) classes of Frontenac *Canis* generated by multivariate cluster analysis (SAS).

		Body Mass (kg)			Total Length (cm)			Foreleg Length (cm)			Hind Foot Length (cm)		
Class [a]	n	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Male													
1	4	20.3	19.3	21.5	134.5	127.9	140.5	33.8	33.0	34.6	19.8	19.3	20.5
2	8	17.5	15.6	19.2	135.9	132.0	143.0	36.4	35.0	38.0	21.2	20.0	22.0
3	8	21.0	19.0	22.9	138.6	130.0	144.0	36.9	35.1	40.0	21.4	21.0	22.5
4	2	20.0	18.5	21.5	152.8	151.6	154.0	39.7	38.0	41.3	24.2	23.8	24.5
5	4	26.6	24.9	28.4	149.9	145.5	156.5	39.5	38.0	41.5	23.4	22.5	24.5
Female													
1	2	16.5	16.0	17.0	120.2	119.8	120.5	32.1	30.9	33.3	18.5	17.8	19.2
2	6	14.7	13.5	16.0	129.3	125.6	133.0	32.7	31.2	34.0	19.4	19.0	19.9
3	8	17.7	16.2	19.5	132.5	128.0	138.0	34.0	32.0	35.8	20.1	19.5	21.0
4	1	13.5	13.5	13.5	143.5	143.5	143.5	40.4	40.4	40.4	21.6	21.6	21.6
5	5	19.8	17.0	22.5	144.9	140.0	148.8	37.2	35.0	39.8	22.1	21.2	23.0

[a] Class 1 is smallest, 5 is largest (approximately); length measurements were given higher priority than body mass since it is subject to variation. These five classes accounted for 77% of the variation in male body size and 80% of the variation in female body size. Differences were significant among classes for both sexes (MANOVA, Wilk's Lambda Statistic, $p < 0.0001$).

diate-sized canids in southeastern Ontario and suggested a similar origin (Kolenosky and Standfield 1975; Nowak 1979; Schmitz and Kolenosky 1985). Our intermediate morphology and diet results are further supported by genetic analysis on the same Frontenac Axis specimens as were used for morphological analysis. Overall, allele frequencies of Frontenac *Canis* populations show them to be hybrids, but more similar to Coyotes in New Brunswick and New York State than to *lycaon* in Algonquin Provincial Park (A. Granacki, unpublished data).

The importance of White-tailed Deer in Frontenac *Canis* diet is consistent with the diet of both Wolves in the Great Lakes region (e.g., Pimlott et al. 1969; Van Ballenberghe et al. 1975; Voigt et al. 1976; Forbes and Theberge 1996) and Eastern Coyotes (e.g., Hilton 1976; Harrison and Harrison 1984; LaPierre 1985; Messier et al. 1986; Moore and Millar 1986; Parker 1986; Major and Sherburne 1987; Dibello et al. 1990; Samson and Crete 1997). However, the frequency of Groundhog, fruit and vegetation in Frontenac *Canis* summer scats is generally more characteristic of Eastern Coyotes (Hamilton 1974; Harrison and Harrison 1984; LaPierre 1985; Moore and Millar 1986; Parker 1986; Major and Sherburne 1987; Brundige 1993; Samson and Crete 1997) than Wolves in Algonquin Provincial Park and central Ontario (Pimlott et al. 1969; Voigt et al. 1976; Forbes and Theberge 1996). In contrast, the high use of Beaver by Frontenac *Canis* (excluding the Lake Clear site) is greater than Beaver use by Eastern Coyotes (Hilton 1976; Brundige 1993; Samson and Crete 1997) and similar to Wolf diet in the Algonquin region (Voigt et al. 1976; Forbes and Theberge 1996). Considerable use of Muskrat in Millbridge is uncharacteristic of *Canis* diet in northeastern North America.

Landscape Correlates of Canis *Types*

The most significant aspect of this study is in finding regional variation in *Canis* that correlates with landscape characteristics. In type A landscapes on the Frontenac Axis, the least influenced by humans, large body size, more Wolf-like skull morphology and high use of large prey indicate that canids remain the most *lycaon*-like. Similarly, but to an even greater degree, Algonquin Wolves retain morphological, behavioural and dietary traits typical of Wolves (Theberge et al. 1996) despite the introgression of Coyote mtDNA in the population (Lehman et al. 1991; Wilson et al. 1996), suggesting continued selection for Wolf-like characteristics in the Algonquin landscape. In contrast, in more disturbed Frontenac landscapes, smaller body size, more Coyote-like skull morphology and varied diet suggest selection for Coyote-like characteristics. The body morphology of small body size classes (Table 3) is comparable to measurements reported by Lorenz (1978) for New England Coyotes (average total lengths of 125.8 cm [range 112 – 137 cm] and 120.4 cm [110 – 151 cm], and hind foot lengths of 19.9 cm [17.8 – 21.6 cm] and 19.0 cm [17.8 – 22.2 cm] for males and females, respectively). The diverse diet with a greater proportion of medium to small prey in landscape types B and C is similar to Eastern Coyote diet in areas with farmland and/or non-forested land (Hilton 1976; Harrison and Harrison 1984; LaPierre 1985; Person 1988).

Preliminary genetic analyses of Frontenac *Canis* did not detect any distinct trend in genotypes in relation to landscape types (A. Granacki, unpublished data; S. Grewal, unpublished data). Landscape type A had the highest percentage of specimens with the most

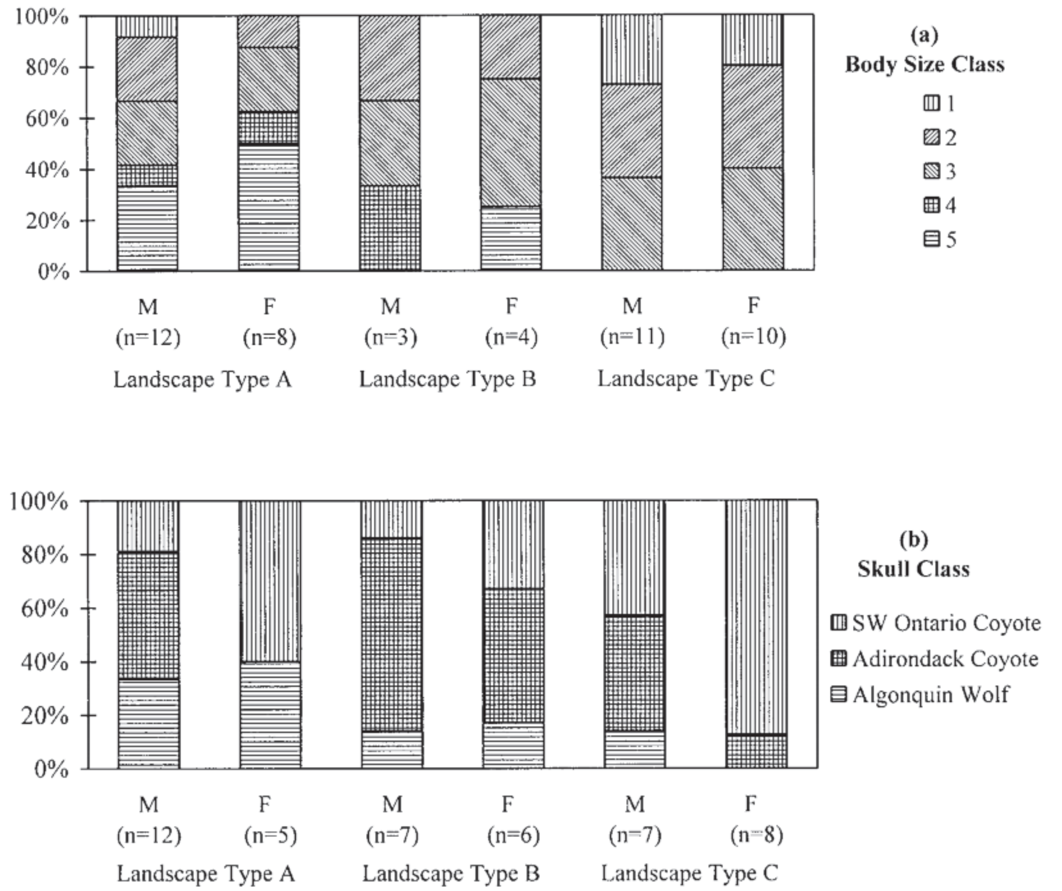

FIGURE 2 (a) Percent of male (M) and female (F) Frontenac *Canis* from each landscape type (A, B, C) in five body size classes (Class 1 is smallest, 5 is largest; see Table 3) based on cluster analysis, and (b) Percent of Frontenac *Canis* skulls from each landscape type that most resembled southwestern Ontario Coyotes, Adirondack Coyotes and Algonquin Wolves based on linear discriminant analysis. Frontenac *Canis* sample size for each landscape type is shown in parentheses.

lycaon-like genotypes (36% of 14 specimens) based on nuclear DNA analysis (A. Granacki 1998*). In landscape types B and C, 12% of 26 specimens and 26% of 39 specimens had *lycaon*-like genetic profiles, respectively. The percentages of Frontenac specimens from landscape types A, B and C with the most *latrans*-like genetic profiles were 29%, 35% and 28%, respectively.

Landscape differences in Frontenac *Canis* types suggest a hybridization scenario in southeastern Ontario similar to that involving *C. rufus* (Red Wolf) and *C. latrans* in the southeastern United States. As a result of human exploitation Red Wolves remained only in isolated areas of the southeastern United States (Gipson 1978). *Canis* with intermediate morphology (McCarley 1962; Riley and McBride 1975; Gipson 1978; Nowak 1979) and Coyote genotypes (Wayne and Jenks 1991; Roy et al. 1994) were documented when Red Wolves and Coyotes hybridized between about 1930 and the 1970s. The sequence of Red Wolf extirpation and occurrence of *rufus-latrans* hybrids indicated that hybridization between Red Wolves and Coyotes occurred last where habitat changes were least (Riley and McBride 1975; Nowak and Federoff 1996). The most Red Wolf-like skulls from Oklahoma, for example, were from areas last to be extensively influenced by human activities (McCarley 1962).

The variation in canid types described in southeastern Ontario landscapes could result from a selective influence of differences in forest conditions, differences in prey, or differences in degree of human exploitation. The data described here and results of other studies provide little evidence that variation is due to habitat selection for different forest conditions; i.e., habitat

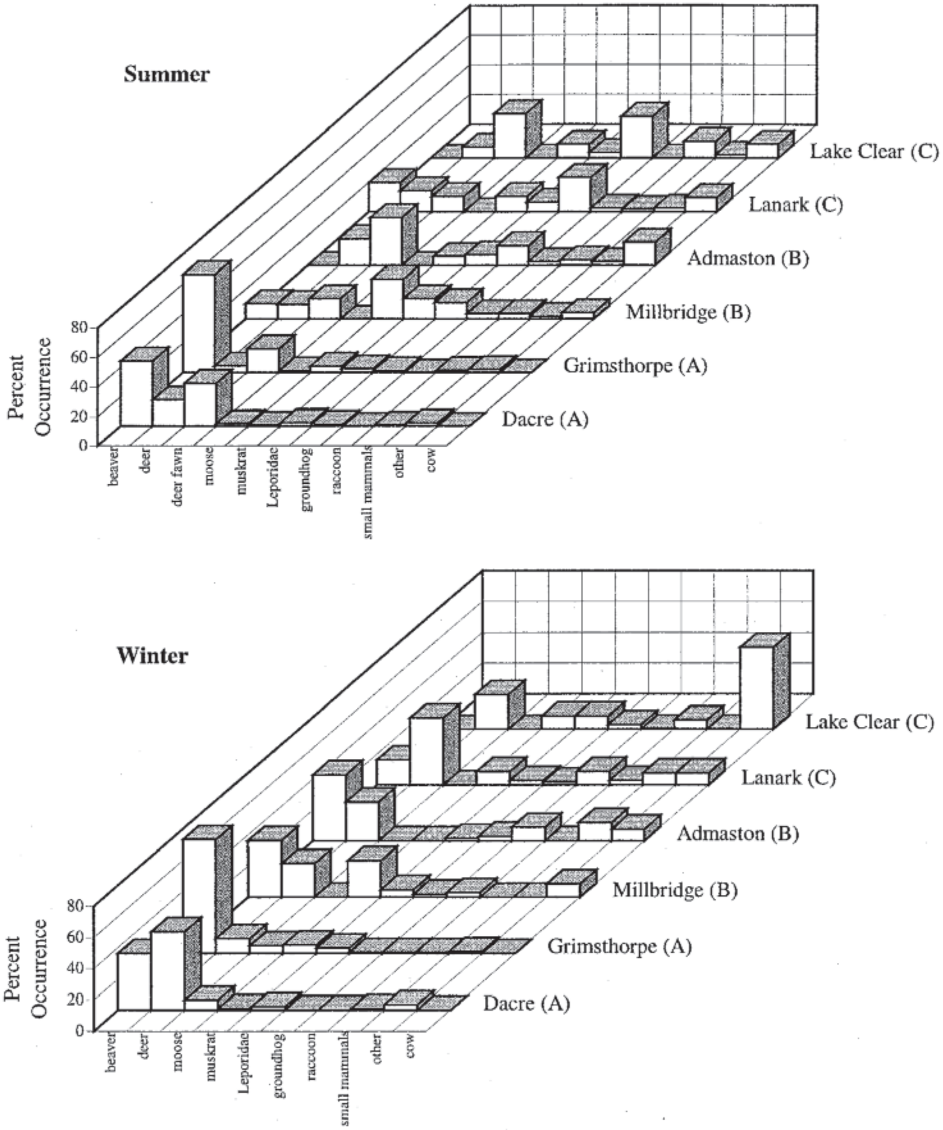

FIGURE 3. Variation in Frontenac *Canis* diet among six sites and three landscape types (A, B, C) in southeastern Ontario, based on percent frequency of occurrence of mammalian prey items in summer scats (Moose includes adult and calf) and winter scats.

choice by Wolf-like canids for more-forested habitat and by Coyote-like canids for less-forested habitat. Wolves can inhabit open and semi-wild landscapes (Mladenoff et al. 1995; Mladenoff et al. 1997) and, conversely, Eastern Coyotes occupy closed forests (Parker 1986; Major and Sherburne 1987; Samson and Crete 1997).

Natural selection could operate to favour larger Wolf-like canids where prey are larger, and smaller ones where prey are smaller, as suggested in previous studies of Ontario *Canis* (Kolenosky and Standfield 1975; Schmitz and Kolenosky 1985; Schmitz and Lavigne 1987). However, differences in Frontenac *Canis* body size (Table 3) seem too slight to be selected for by differences in prey size. Regarding use of large prey, Moose were almost absent from the diet in all three landscape types, whereas deer were used in all landscape types. Regarding use of smaller prey, small and medium-sized prey were utilized more in landscapes types B and C, but deer were also important in these landscapes (e.g., Lanark had a high proportion [43%] of deer in winter scats).

Road density, as an index of human activity, access and exploitation, might be the single-most useful indicator of *Canis* type where there are sympatric, hybridizing populations of *lycaon* and *latrans*. Higher Wolf mortality due to hunting and trapping has previously been reported in areas of higher road density where Wolves are not protected (Person et al. 1996). Our results suggest that the degree of human-caused selection through exploitation favors more Coyote-like canids. In landscape type C, where Coyote-like animals predominated, all-season road density was highest at approximately 0.65 km/km^2. In contrast, the most *lycaon*-like *Canis* were generally found in landscapes with lower all-season road density (i.e., approaching 0 km/km^2) and relatively low density of all roads and trails (i.e., about 0.4 km/km^2). In none of these sites are there any restrictions on the use of roads, like there are in Algonquin Provincial Park where *lycaon* exhibits predominantly Wolf-like morphology and behavioural characteristics (Theberge et al. 1996).

In eastern North America, Coyotes tended to expand into regions where Wolf populations declined (Gier 1975). Coyotes and hybrids have been found along the margins of the former range of *rufus* populations in the southeastern United States (Nowak and Federoff 1998) and along the southern edge of *lycaon* range in Ontario (Kolenosky and Standfield 1975; Schmitz and Kolenosky 1985). Exploitation produces conditions favoring *latrans-lycaon* hybridization within this region of sympatric, hybridizing and unprotected *Canis* populations in southeastern Ontario. In and near Algonquin Provincial Park, Coyotes appear to be progressively invading *lycaon* range by exploiting gaps in occupied range. The recent occurrence of some canids in Algonquin Provincial Park which are morphologically and genetically Coyote-like suggests that hybridization with Coyotes or hybrids is more likely in packs which have been fragmented, especially peripheral packs, primarily due to human-caused mortality (Theberge 1998: 256).

Conservation Implications

A road density of less than 0.6 km/km^2 has been described as necessary for wolf persistence in the Great Lakes region of the United States (Thiel 1985; Mech et al. 1988; Fuller et al. 1992; Mladenoff et al. 1995) where wolves are legally protected and populations are recovering (Mech 1995). This figure is not applicable as an indicator of *lycaon* distribution where wolves are not protected on the edge of their range in southeastern Ontario. Data from the Frontenac region suggest that the degree of human access through roads affects *Canis* types and that road densities even lower than 0.6 km/km^2 may limit persistence of *lycaon*. Although this study found little evidence of "pure" *lycaon* in the Frontenac region, presumably *lycaon* would be more likely to occur in landscapes similar to those described as type A in this study.

Management strategies for *Canis* where there is (or is potential for) Coyote-Wolf hybridization should consider low overall (i.e., all-season and seasonal) road density as the landscape feature most useful in predicting, and most critical in maintaining, the presence of Wolf-like canids or possibly Wolves. A road-density index lower than 0.6 km/km^2 appears to be particularly important where there is lack of protective status for canids and/or harvest seasons and bag limits. *Canis* management and *lycaon* conservation in southeastern Ontario should address the management and reduction of road access, for example through limiting construction of new roads, seasonally or permanently closing or gating roads, or rehabilitating seasonal roads after their primary function (e.g., forestry) is no longer required.

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Documents Cited (marked * in text)

Granacki, A. 1998. Microsatellite analysis of two Laurentian Highland canid populations outside of Algonquin Provincial Park. Undergraduate thesis, McMaster University, Hamilton, Ontario. 53 pages.

Stewart, S. 1996. Tooth and skull analysis of wolves (*Canis lupus*) from Algonquin Park, Ontario. Senior honours thesis, University of Waterloo, Waterloo, Ontario. 66 pages.

Literature Cited

Adorjan, A. S., and **G. B. Kolenosky.** 1969. A manual for the identification of hairs of selected Ontario mammals. Wildlife Resources Report Number 90, Research Branch, Ontario Department of Lands and Forests, Toronto, Ontario. 64 pages.

Bowen, D. W. 1982. Determining age of coyotes, *Canis latrans*, by tooth sections and tooth-wear patterns. Canadian Field-Naturalist 96: 339-341.

Brown, D. M., G. A. McKay, and **L. J. Chapman.** 1968. The climate of southern Ontario. Climatological Studies Number 5. Department of Transport, Meteorological Branch, Toronto, Ontario. 50 pages.

Brundige, G. C. 1993. Predation ecology of the eastern coyote, *Canis latrans* var., in the Adirondacks, New York. PhD thesis, State University of New York, Syracuse, New York.

Buss, M., and **M. de Almeida.** 1997. A review of wolf and coyote status and policies in Ontario. Ontario Ministry of Natural Resources. 88 pages.

Davidson, R. J. 1988. Foundations of the land – bedrock geology. Pages 36-47 *in* Legacy: the natural history of Ontario. *Edited by* J. B. Theberge. McClelland and Stewart Inc., Toronto, Ontario. 397 pages.

Dibello, F. J., S. M. Arthur, and **W. B. Krohn.** 1990. Food habits of sympatric coyotes, *Canis latrans*, red foxes, *Vulpes vulpes*, and bobcats, *Lynx rufus*, in Maine. Canadian Field-Naturalist 104: 403-408.

Dobbyn, J. (S.). 1994. Atlas of the mammals of Ontario. Federation of Ontario Naturalists, Don Mills, Ontario. 120 pages.

Douglas, R. J. W. 1976. Geology and Economic Minerals of Canada. Geological Survey of Canada, Department of Energy, Mines and Resources, Ottawa, Ontario.

Forbes, G. J., and **J. B. Theberge**. 1996. Response by wolves to prey variation in central Ontario. Canadian Journal of Zoology 74: 1511-1520.

Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and **G. B. Joselyn.** 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin 20: 42-55.

Gier, H. T. 1975. Ecology and social behavior of the coyote. Pages 247-262 *in* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand Reinhold Co., New York, New York. 508 pages.

Gipson, P. S. 1978. Coyotes and related *Canis* in the southeastern United States with a comment on Mexican and Central American *Canis*. Pages 191-208 *in* Coyotes: biology, behavior, and management. *Edited by* M. Bekoff. Academic Press, New York, New York. 384 pages.

Hamilton, W. J., Jr. 1974. Food habits of the coyote in the Adirondacks. New York Fish and Game Journal 21: 177-181.

Harrison, D. J., and **J. A. Harrison.** 1984. Foods of adult Maine coyotes and their known-aged pups. Journal of Wildlife Management 48: 922-926.

Hilton, H. 1976. The physical characteristics, taxonomic status and food habits of the eastern coyote in Maine. MSc thesis, University of Maine, Orono, Maine. 66 pages.

Jensen, W. F., T. K. Fuller, and **W. L. Robinson.** 1986. Wolf, *Canis lupus*, distribution on the Ontario-Michigan border near Sault Ste. Marie. Canadian Field-Naturalist 100: 363-366.

Keddy, C. 1995. The conservation potential of the Frontenac Axis: linking Algonquin Park to the Adirondacks. Canadian Parks and Wilderness Society, Ottawa, Ontario. 59 pages.

Kolenosky, G. B. 1983. Status and management of wolves in Ontario. Pages 35-40 *in* Wolves in Canada and Alaska: their status, biology and management. *Edited by* L. N. Carbyn. Canadian Wildlife Service, Report Series Number 45.

Kolenosky, G. B., and **R. O. Standfield.** 1975. Morphological and ecological variation among gray wolves (*Canis lupus*) of Ontario, Canada. Pages 62-72 *in* The wild canids: their systematics, behavioral ecology and evolution. *Edited by* M. W. Fox. Van Nostrand Reinhold Co., New York, New York. 508 pages.

Kolenosky, G. B., D. R. Voigt, and **R. O. Standfield.** 1978. Wolves and coyotes in Ontario. Ontario Ministry of Natural Resources, Wildlife Branch. 19 pages.

Landon, D. B., C. A. Waite, R. O. Peterson, and **L. D. Mech.** 1998. Evaluation of age determination techniques for gray wolves. Journal of Wildlife Management 62: 674-682.

LaPierre, L. E. 1985. Fall and winter food habits of the eastern coyote *Canis latrans* in southeastern New Brunswick. Proceedings of the Nova Scotia Institute of Science 35: 71-74.

Lehman, N., A. Eisenhawer, K. Hansen, L. D. Mech, R. O. Peterson, P. J. P. Gogan, and **R. K. Wayne.** 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution 45: 104-119.

Linhart, S. B., and **F. F. Knowlton.** 1967. Determining age of coyotes by tooth cementum layers. Journal of Wildlife Management 31: 362-365.

Lorenz, J. R. 1978. Physical characteristics, movement and population estimate of the eastern coyote in New England. MSc thesis, University of Massachusetts. 62 pages.

Major, J. T., and **J. A. Sherburne.** 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51: 606-616.

McCarley, H. 1962. The taxonomic status of wild *Canis* (Canidae) in the south central United States. The Southwestern Naturalist 7: 227-235.

McGarigal K., and **B. J. Marks.** 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General technical report PNW-GTR-351. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Mech. L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9: 270-278.

Mech, L. D., S. H. Fritts, G. L. Radde, and **W. J. Paul.** 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin 16: 85-87.

Messier, F., C. Barrette, and **J. Huot.** 1986. Coyote predation on a white-tailed deer population in southern Quebec. Canadian Journal of Zoology 64: 1134-1136.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and **A. P. Wydeven.** 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology 9: 279-294.

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and **A. P. Wydeven.** 1997. Causes and implications of species restoration in altered ecosystems: a spatial landscape projection of wolf population recovery. BioScience 47: 21-31.

Moore, G. C., and **J. S. Millar.** 1986. Food habits and average weights of a fall-winter sample of eastern coyotes, *Canis latrans*. Canadian Field-Naturalist 100: 105-106.

Moore, G. C., and **G. R. Parker.** 1992. Colonization by the eastern coyote (*Canis latrans*). Pages 23-37 *in* Ecology and management of the eastern coyote. *Edited by* A. H. Boer. Wildlife Research Unit, University of New Brunswick, Fredericton, New Brunswick. 194 pages.

Nowak, R. M. 1978. Evolution and taxonomy of coyotes and related *Canis*. Pages 3-16 *in* Coyotes: biology, behavior and management. *Edited by* M. Bekoff. Academic Press, New York, New York. 384 pages.

Nowak, R. M. 1979. North American Quaternary *Canis*. Monograph Number 6, Museum of Natural History, University of Kansas, Lawrence, Kansas. 154 pages.

Nowak, R. M. 1995. Another look at wolf taxonomy. Pages 375-397 *in* Ecology and conservation of wolves in a changing world. *Edited by* L. N. Carbyn, S. H. Fritts, and D. R. Seip. Canadian Circumpolar Institute, Occasional Paper Number 35. University of Alberta, Edmonton, Alberta. 642 pages.

Nowak, R. M., and **N. E. Federoff.** 1996. Systematics of wolves in eastern North America. Pages 187-203 *in* Wolves of America conference proceedings, November 12-14, 1996, Albany, New York. Defenders of Wildlife, Washington, D. C. 306 pages.