EASTERN COYOTE HOME RANGE, TERRITORIALITY, AND SOCIALITY ON URBANIZED CAPE COD

JONATHAN G. WAY,[1] University of Connecticut, Department of Natural Resources Management and Engineering, Box U-87, Storrs, CT 06269, USA
ISAAC M. ORTEGA, University of Connecticut, Department of Natural Resources Management and Engineering, Box U-87, Storrs, CT 06269, USA
PETER J. AUGER, Boston College, Biology Department, Higgins Hall, Chestnut Hill, MA 02467, USA

***Abstract*:** We studied home range size, spatial arrangements, territoriality, and sociality of 11 radio-tagged eastern coyotes, *Canis latrans*, inhabiting an urbanized area (Cape Cod, Massachusetts) between June 1998 and May 2000. Estimates of home range size depended on the method used. Average home range size for breeding adult coyotes, using the 95% minimum convex polygon vertex edited method, was 29.8 $\pm$ 5.3 km^2. Resident coyote groups showed limited overlap in home ranges. Juvenile coyotes had small home ranges ranging from 0.3–10.8 km^2. A transient and an associate coyote had the largest ranges (152.2 km^2 and 100.4 km^2, respectively). Home ranges of reproductive female coyotes were smaller than those of non-reproductive females during the denning season. Coyote social groups (or packs) consisted of 3-4 members and mean observed group size was 1.7 $\pm$ 0.1 (SE) coyotes. The density of resident coyotes on the study area was estimated at 0.07–0.15 coyotes/km^2 for the 95% vertex edited home range technique and 0.06–0.13 coyotes/km^2 for the more traditional 95% minimum convex polygon method.

Key words: *Canis latrans*, Cape Cod, eastern coyote, ecology, home range, Massachusetts, radiotelemetry, sociality, spatial avoidance, suburban wildlife, territoriality, urbanized.

Numerous studies have described home range (Gese et al. 1988, Holzman et al. 1992, Riley et al. 2003), sociality (Gese and Ruff 1997), or territoriality (Windberg et al. 1997, Knowlton et al. 1999, Sacks et al. 1999) of coyotes throughout North America, and, specifically in eastern North America (Harrison et al. 1989, Person and Hirth 1991, Brundige 1993, Patterson and Messier 2001). Reported home range sizes varied from 1 – >100 km^2. Most studies of coyotes have been conducted in non-urbanized areas (Bekoff and Wells 1980, Gese and Ruff 1997, Patterson and Messier 2001). Although there have been some studies of the effects of habitat fragmentation and human disturbance on coyotes existing in urbanized environments in the western United States (Bounds and Shaw 1997, Quinn 1997, McClennen et al. 2001, Tigas et al. 2002) our study provides the first description of

[1] Current address: Boston College, Environmental Studies Program, Higgins Hall, Chestnut Hill, MA 02467, USA. E-mail: wayjo@bc.edu

the ecology of coyotes residing in an urbanized area in eastern North America. Eastern coyotes, the largest of any extant coyote population (Silver and Silver 1969, Thurber and Peterson 1991, Wayne and Lehman 1992), may have different life history requirements than western coyotes (e.g., larger home ranges) which may potentially affect their ability to successfully inhabit urbanized areas.

There is considerable debate about the effects of anthropogenic influences on coyote home range use. Some studies have shown that coyotes inhabiting agricultural and developed (i.e., rural and urban) landscapes tend to have smaller home ranges than coyotes inhabiting more wooded areas (Atkinson and Shackleton 1991, Person and Hirth 1991, Riley et al. 2003). Increased ecosystem productivity and a greater availability of resources associated with agricultural and urbanized landscapes are believed to be the primary reasons why coyotes have smaller spatial requirements in these habitats. Conversely, Grinder and Krausman (2001) showed that urban coyotes in Tucson, Arizona maintained home ranges (12.6 km^2) typical of coyotes in other regions of the western United States. Additional information from urbanized environments may help elucidate coyote ecology under different environmental conditions.

Sociality is variable in coyotes, ranging from coyotes living in packs of 5-10 adults (Andelt 1985, Gese and Ruff 1997, Crabtree and Sheldon 1999, Way 2003), to groups of 3-4 animals (Person and Hirth 1991, Kamler and Gipson 2000, Patterson and Messier 2001) to a mated pair (Berg and Chesness 1978, Harrison 1992a,b). Little is known about sociality of coyotes in urbanized areas, especially in eastern North America (see Way 2003).

Coyotes arrived in western Massachusetts during 1957-58 and were first documented on Cape Cod during the late 1970s (Pringle 1960, J. Cardoza, Massachusetts Division of Fisheries and Wildlife, personal comm.). Home range, the area in which an animal normally lives (Burt 1943, Powell 2000), is an important measure of a species' natural history; coupled with territoriality and sociality information, knowledge of home range sizes can produce population estimates for coyotes in a general area. The purpose of this study was to gain baseline data on urbanized eastern coyotes on Cape Cod, Massachusetts for future hypothesis testing relating prey abundance and/or human activity to coyote space use and sociality in different regions of eastern North America. Our specific objectives were to examine: (1) home range sizes and spatial arrangements; (2) territoriality; and (3) sociality of eastern coyotes living in an urbanized environment.

STUDY AREA

Research was conducted within Barnstable County, Cape Cod, in southeastern Massachusetts (250 km^2; Fig. 1), with a concentration in the Town of Barnstable (155 km^2) between June 1998 and May 2000. The estimated human population density in the Town of Barnstable was 290 people/km^2, whereas entire Barnstable County averaged 203 people/km^2 (U.S. Census Bureau, 1998 estimates). The highest and lowest densities of people were found in Hyannis with 556 and West Barnstable with 89 people/km^2. Density of housing units varied from 328/km^2 in Hyannis to 39/km^2 in West Barnstable. Road density, defined as centerline km of roadway per km^2, was 4.7 for the town of Barnstable and 4.0 for Barnstable County (Cape Cod

Commission 1998).

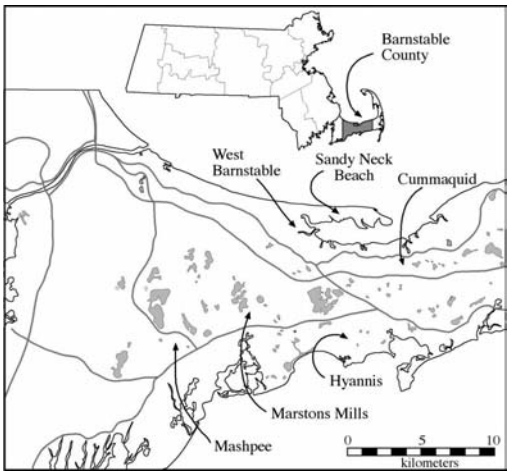

Fig. 1. Study area in Barnstable County, Cape Cod, Massachusetts showing principle locations and main roads. Inset shows location of Barnstable County and Cape Cod in Massachusetts.

Cape Cod (Barnstable County) is an artificial island (1,025 km^2) separated from the rest of Massachusetts by the Cape Cod Canal (<1 km wide x 15 km long). Two bridges, each approximately 1 km in length, enable access to Cape Cod. The Town of Barnstable is located within 15 km of the bridges on the west part of the peninsula. The region is classified as having a coastal temperate climate, and inland areas consist of maritime forests dominated by scrub oak (*Quercus ilicifolia*) and pitch pine (*Pinus rigida*) (Lazell 1976). Conservation areas ranging from 6–2,000 ha, cranberry bogs (2–50 ha) and golf courses (hereafter collectively defined as green or open areas) exist in scattered, patchy areas throughout the study site. They are not directly connected to other green areas (Meffe and Carroll 1994); rather, they are isolated fragments separated from other open areas by neighborhoods and roads.

Potential food sources for coyotes on Cape Cod include white-tailed deer (*Odocoileus virginianus*), gray squirrels (*Sciurus carolinensis*), woodchucks, (*Marmota monax*), cottontail rabbits (*Sylvilagus floridanus*), domestic cats (*Felis catus*), meadow voles (*Microtus pennsylvanicus*), muskrats (*Ondatra zibethicus*), red squirrels (*Tamiasciurus hudsonicus*), chipmunks (*Tamias striatus*), mice (*Peromyscus* sp.), opossum (*Didelphus virginianus*), Canada goose (*Branta canadensis*), ducks (*Anas* sp.), and along the coast, allochthonous food subsidies from the sea (Rose and Polis 1998). Potential competitors include red foxes (*Vulpes vulpes*), domestic cats, domestic dogs (*Canis familiaris*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), long-tailed weasels (*Mustela frenata*), American crows (*Corvus brachyrhynchos*), red-tailed hawks (*Buteo jamaicensis*), northern harriers (*Circus cyaneus*), great horned owls (*Bubo virginianus*), and turkey vultures (*Cathartes aura*).

METHODS

We captured coyotes in model 610B & 610C Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). Traps were checked twice daily. Non-target species were released immediately, whereas coyotes were given a hand-held intramuscular injection of 8 mg/kg of Telazol® (A. H. Robins Co., Richmond, Virginia, USA; Ballard et al. 1991, Sillero-Zubiri 1996) based on estimated body mass. Coyotes were then sexed, weighed, and measured. All animals $\geq$1 year of age (based on body size and dentition) were classified as adults (Bekoff and Jamieson 1975) and were fitted with radio-collars (MOD-225

and 335; Telonics Inc., Mesa, Arizona, USA) depending on the size of the animal. Pups of the year received either an implant radio-transmitter (IMP/300/L; Telonics Inc., Mesa, Arizona, USA) during summer or an adult sized radiocollar with foam taped inside to allow for growth if captured after 1 August. The capture and handling protocol was approved by the University of Connecticut's Institutional Animal Care and Use Committee (protocol YEE 0101), and by the Massachusetts Division of Fisheries and Wildlife (permit 038.98LP).

Coyotes were classified as breeding residents, resident associates, juveniles, or transients based on group affiliations and movements (Patterson and Messier 2001). Breeding residents were adult animals that had established home ranges and exhibited breeding behavior (i.e., pair bonding or denning [Person and Hirth 1991]). Resident associates were adults or subadults with home ranges that overlapped extensively with those of resident breeders and were observed interacting with breeding residents. A coyote that was captured between January and March and determined to be a probable pup of the previous year was classified as a subadult. Offspring of the year (pups) were classified as juveniles. Transient coyotes were adults that had large, poorly-defined home ranges (Person and Hirth 1991). We included transients in our analyses though there is debate whether such animals should be included because of their nomadic wanderings (Burt 1943, Powell 2000).

Telemetry techniques

Portable receivers (Custom Electronics, Urbana, Illinois, USA) and hand-held 3-element Yagi antennas were used to radio-track coyotes. Typically, an antenna was affixed to the outside of a moving vehicle's closed window until a signal was received. Once a signal was obtained, the bearing to the transmitter was determined using the loudest-signal homing method (Springer 1979). This process was repeated until the animal was pinpointed either on foot or by vehicle. Due to the urbanized environment and the associated high density of roads, controlled experiments determined that 95% of locations were <50 m from the known transmitter (Way 2000). We plotted each location on a standard road map then obtained Universal Transverse Mercator (UTM) coordinates for each location by clicking on the same area on a digitized mapping program (Terrain Navigator, Maptech, Greenland, New Hampshire, USA).

We attempted to locate each coyote daily throughout the study. Consistent efforts were made to locate coyotes approximately evenly throughout a 24-h period. From June 1998 to January 1999 we obtained daily fixes >6 hours apart to minimize autocorrelation between successive locations (Swihart and Slade 1985*a*,*b*; Harris et al. 1990; Person and Hirth 1991). However, from February 1999 to May 2000 we collected sequential data (Laundre and Keller 1984, Gese et al. 1990) to describe movement patterns and areas used by coyotes during a 24-h period (Andelt 1985). Roughly equal numbers of locations were taken throughout each 24-h observational period. A minimum of 15 min separated sequential locations. Individual coyotes were typically tracked for <4 hours and located 4–6 times per 24-h period. The maximum number of locations for an animal over the course of a 24-h period was 14. Throughout the study period, 19% of locations came from

sequential radio tracking sessions where ≤14 locations were obtained for each coyote in each 24-h block; 81% came from daily point samples.

Radiocollared coyotes and their companions were often sighted during night tracking. Occasionally, we parked vehicles in areas where we expected coyotes to travel (e.g., railroad tracks, power lines) and directly observed coyotes traveling. This technique was preferred when snow was on the ground because of the high albedo of the snow cover which permitted the use of binoculars for direct observations during the night. Binoculars, video-cameras, 15-45x spotting scopes, and night scopes were used to aid in direct observations and identification of individuals.

Spotlighting was the most common technique used to determine group size because most movements occurred at night. Areas were scanned for 4-8 seconds each time a coyote was believed to be close to our vehicles. Because coyotes ran away from spotlights on >90% of sightings, we kept the spotlights on for <8 seconds per session to reduce disturbance. If an individual or group was successfully sighted by spotlighting we typically left the area for >1 h to find a new group. Based on subsequent locations we believe that spotlighting usually only temporarily altered behavior. For example, subsequent locations of a previously-bedded coyote (i.e., before spotlighting) would usually be within 50–100 m of the bedding location.

Although we had no way of documenting the influence that our presence had on movements, we note that coyotes may have artificially increased the distance they traveled or altered their normal travel routes because of our actions.

Information was recorded on group size, and characteristics of each coyote (pelage coloration, pelage pattern, and physical characteristics such as body size), especially uncollared animals, to aid in identification of individuals. Using these data, we determined traveling group sizes (i.e., the mean number of coyotes observed during each sighting), and estimated pack sizes (i.e., the maximum number of individuals living within a territory for each social group [Patterson and Messier 2001]). Radiocollared coyotes were considered together if they were <300 m apart (Harrison and Gilbert 1985) and there were no roads separating them.

Home range analysis

We calculated home ranges using the minimum convex polygon (MCP; Mohr 1947) and the vertex edit methods in the Animal Movement Analysis Arc View extension program (Hooge and Eichenlaub 1997). Radiolocations were overlaid on a digitized topographical map (Terrain Navigator, Maptech, Greenland, New Hampshire, USA) that was imported and rectified into the program Animal Movement in Arc View. For each method, 100% and 95% of the most tightly clustered data points for each coyote were used to determine home range size. Harmonic mean outliers (Dixon and Chapman 1980, Hooge and Eichenlaub 1997) were used to calculate and delete the outer 5% of data for the 95% MCP and 95% vertex edited polygons. After each 100% and 95% MCP was displayed, we subjectively modified each polygon in the vertex edit mode to include only areas that were most likely used by each coyote. These alterations produced our 100% and 95%

vertex edited home ranges. Therefore, parts of the polygons that included major bodies of water (e.g., ocean, salt marsh), urban areas not used by coyotes, and any other similar areas were deleted. We believe that the vertex edited method was accurate in describing a coyote's normal home range for 3 reasons: (1) we routinely searched all portions of the study area equally (including those areas that we removed from vertex edited home ranges) when looking for radio-collared coyotes; (2) we had a high success rate (96.4%) in locating our collared animals; and (3) during instances when we did not find a coyote within its normal territory we increased our search pattern to include areas well beyond where we normally searched for a particular individual. When we could not find a coyote we concluded this happened for two reasons: (1) the frequency of the coyote's transmitter had shifted so we were unable to detect a signal; or (2) the coyote was off its territory.

We grouped animal locations into yearly home ranges and also compared the denning movements (Person and Hirth 1991) of a female coyote determined to be reproductive in 1999 with another female determined to be non-reproductive. April was selected as the denning month, because coyotes typically give birth in early April on Cape Cod (Way et al. 2001). We predicted that home range size would be smallest in April. Movements during the denning season were compared to yearly home ranges.

We used separate-variance *t*-tests to compare juvenile and adult, and male and female home range sizes (Ott 1993). Results were considered significant at $\alpha \leq 0.05$. Mean values and standard errors are reported. We calculated the estimated density of pre-whelping resident coyotes (transients excluded) in the study area by estimating the number of coyotes within family groups and dividing by the mean territory size of resident adults. This method is similar to those used to estimate wolf (Fuller and Snow 1988) and coyote (Kamler and Gipson 2000) densities in other studies, assuming contiguous and exclusive home ranges for residents.

RESULTS

Eleven coyotes (6 adults: 3 males and 3 females; 1 subadult male; 4 juveniles: 3 males and 1 female) were captured 16 times and monitored for 3,189 coyote-days (1 coyote day equals 1 day that an individual coyote was alive during the study). A total of 3,230 radio-locations was obtained between June 1998 and May 2000. Coyotes were followed for an average of 289 $\pm$ 60 (SE) days and an average of 294 $\pm$ 60 (SE) locations was obtained for each animal.

Home range analysis

Estimates of home range size depended on the method used (Table 1). Average home range size for breeding adult coyotes using the 95% MCP vertex edited method was 29.8 $\pm$ 5.3 (SE) km^2. Home ranges of resident males (39.1 $\pm$ 0.3 km^2) were larger than resident females (23.6 $\pm$ 6.7 km^2) (t = 7.83, 6 df, $P < 0.001$). Resident coyote groups showed limited overlap in home ranges after the outer 5% of relocations were deleted and polygons were adjusted to correlate with known movements and locations (95% MCP vertex edited method, Fig. 2).

The home range of a reproductive female (#9902) during the denning season (n = 39 locations, April 1999) was 16% of her yearly home range (2.0 km^2 *versus*

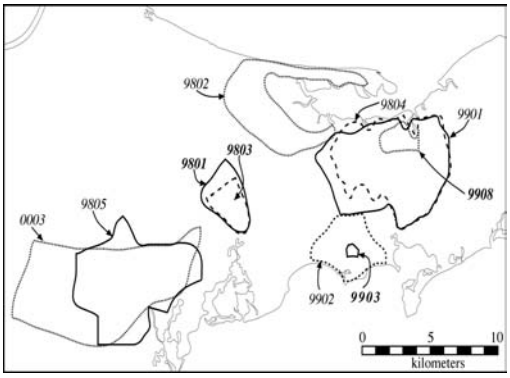

Fig. 2. 95% MCP vertex edited home ranges for eastern coyotes in Barnstable County, MA. Home ranges of male coyotes are in bold.

12.4 km^2 using the 95% MCP vertex edit method). Conversely, a non-reproductive resident coyote (#9802) maintained a yearly home range of 22.8 km^2 (95% vertex) and during the denning season (n = 31 locations) her range was 14.3 km^2, or 63% of her annual home range (Fig. 3).

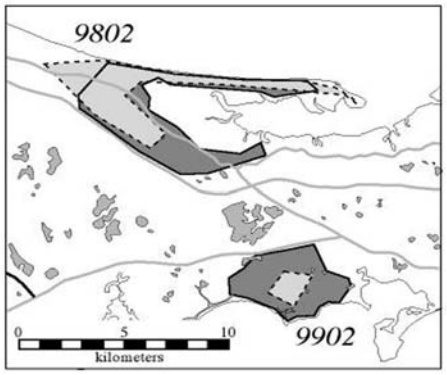

Fig. 3. Comparison of annual (dark shade) versus denning month (April) home range (light shade) for a non-reproductive (#9802) and reproductive female coyote (#9902) on Cape Cod, Massachusetts (95% MCP vertex edited).

Coyote #9902, which resided in the most urban part of Cape Cod (Hyannis), had the smallest home range of all the breeding coyotes (Table 1). She regularly traveled throughout this area but unlike most adult coyotes, #9902 was not observed making forays beyond her established home range.

Juvenile coyotes had small home ranges (0.3 – 10.8 km^2) depending on the method of data analysis used (Table 1, Fig. 2) despite being tracked until $\geq$5 months of age in September. These ranges were smaller than home ranges of resident adults (t = 4.7, 4 df, P < 0.005).

Conversely, 1 male transient (#0001) and 1 male associate (#0003) had the largest home ranges (152.2 km^2 and 100.4 km^2, respectively) in the study. Whereas the associate coyote #0003 made multiple excursions outside of his presumed natal area, coyote #0001 was nomadic with no discernable center of activity and traveled throughout the study area (Fig. 4).

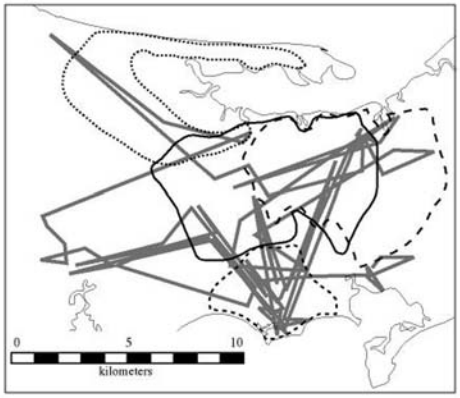

Fig. 4. Movements of transient coyote #0001 (shaded lines) overlaid on the 95% MCP vertex edited home ranges of adult coyotes on Cape Cod, Massachusetts.

Table 1. Home range sizes (km^2) of male and female eastern coyotes, Barnstable County, Cape Cod, Massachusetts, June 1998– May 2000 (*n* = 3230 radio-locations).

				Method used to estimate home ranges			
Social status	ID	Sex	# Radio-locations	100% MCP	100% Vertex	95% MCP	95% Vertex
Breeder	#9802	F	504	55.6	32.4	38.1	22.8
	#9804	F	562	59.3	49.6	40.1	35.5
	#9805	M	486	77.6	62.7	45.4	38.8
	#9902	F	503	16.6	14.6	13.5	12.4
	#9901	M	451	55.2	50.4	43.5	39.3
Mean ± SE	Breeders		501 ± 18	52.9 ± 10.0	41.9 ± 8.4	36.1 ± 5.8	29.8 ± 5.3
Associate	#0003	M	102	100.4	72.3	59.7	51.6
Juvenile	#9801	M	136	10.8	9.0	7.4	7.3
	#9803	M	103	6.0	5.7	5.4	4.8
	#9908	F	127	5.4	4.6	3.8	3.4
	#9903 [a]	M	124	0.4	0.3	0.4	0.38
Mean ± SE	Juveniles		123 ± 7	5.7 ± 1.8	4.9 ± 1.6	4.3 ± 1.3	4.0 ± 1.3
Transient	#0001	M	132	152.2	100.2	114.9	89.8

[a] Greatly expanded his home range on 3-20-00. He left the study area on 3-23-00.

Resident adult coyotes in our study were not affected adversely by the high density of roads. Many sightings involved coyotes crossing roads and neighborhoods to reach sections of their home ranges. Power lines, railroad tracks, golf courses, fire and dirt roads, secondary roads, and neighborhoods were the main travel routes used by radiocollared coyotes. Coyotes consistently bedded down during the day in all areas of their home ranges including within 50 m of houses, often using areas between houses in small, thickly vegetated patches of woods.

Territoriality

Besides the observed spatial segregation from adjacent groups (i.e., telemetry data) we observed 2 cases of territorial exclusion. In the first instance, on 29 December 1999, #9802 was located within the home range of the neighboring group (#9804, #9901, and 1 other member; Table 2, Fig. 2). At 2315 h, #9804 and #9901 were >5 km away from #9802. However, at 2345 h, #9804 and #9901 were located <200 m from #9802. At 2359 h, #9802 was observed running along the edge of a major road in an area illuminated by street lights. At 0053 h on 30 December 1999, #9802 was observed with a second coyote back in her home range approximately 7 km from the site of her encounter with #9804 and #9901.

The second incident took place on 9 February 2000 at 0740 h; this was one of the few daytime observations of coyotes we made during our study. Female coyote #9902 and 2 other coyotes that were regularly seen traveling with #9902 were in the center of their home range on a golf course. At 0750 h, the 3 coyotes separated. Transient coyote #0001, which was located near the initial sighting location of #9902, immediately chased and pinned one of #9902's companions (thought to be a female with which #0001 was attempting to mate). When the pinned coyote made a loud whining sound, #9902 and the remaining member of her group (assumed to be the breeding male) ran directly to her location. The presumed breeding male chased #0001 for >1 km. After the chase, #0001 left the golf course and crossed a major road during the daytime. The next day, #0001 was located at the edge of the home range of #9902's group. Transient coyote #0001 was sighted 3 days later and appeared to be uninjured.

Sociality

Sightings (excluding juveniles <6 months old; Andelt 1985) during the study period (n = 234) indicated that resident coyotes typically lived in groups of 3–4 adult members (Table 2). Mean observed traveling group size was 1.7 $\pm$ 0.1 (SE) coyotes, derived from the following data: 121 sightings involved 1 adult coyote, 68 involved 2, 39 involved 3, and 6 sightings involved 4 adult coyotes. It appeared that by late-fall (November) all juveniles that were not traveling with their natal group had either died or dispersed because tagged coyotes were believed to be traveling consistently with the same animals based on individual markings. Coyote #9802's group was the only group that did not consist of $\geq$3 members. However, she was never determined to be reproductive throughout 1998 and 1999, even though she did appear to be pair bonded and was seen with a second coyote on 21 occasions.

The estimated pre-whelping density of resident coyotes in the study area was 0.07–0.15/km^2 (90% CI) using the 95%

Table 2. Coyote social groups monitored in Barnstable County, Cape Cod, Massachusetts, June 1998–May 2000.

Social Group	Member(s)[a]	Adult Group Size	Successful Reproduction
Marstons Mills	9801, 9803	2-3	Yes (1998), 1999?, 2000?
West Barnstable	9802	2	No (1998 & 1999), 2000?
N. Centerville	9901[b]	2-3	Unknown
Cummaquid	9804, 9901[c]	3	Yes (1999 & 2000)
Mashpee	9805, 0003	3-4[d]	Yes (1999 & 2000)
Hyannis	9902	3-4[e]	Yes (1999 & 2000)

[a]Included at least 1 radio-collared adult coyote in each group.
[b]Regularly seen with 2 different adults, but was never found in a group of 3 while inhabiting Centerville.
[c]First documented with this group during December 1999. Membership of this group seemed to change (except for 9804) during fall 1999 but continued to consist of 3 members.
[d]Sighted with 4 adults on 1 occasion.
[e]Sighted with 4 adults on 4 occasions; 1 of these sightings included a possible 5th adult.

vertex edited data (Table 1 with an average of 3 coyotes per resident group). This estimate is the density of coyotes in areas that we considered to be coyote habitat (i.e., excluding oceans or tidal marshes). To compare our estimates with published estimates we also calculated the estimated density of coyotes using the more traditional 95% MCP technique. This estimate (0.06–0.13 coyotes per km^2; 90% CI) represented the entire geographic area encompassed by our study area.

DISCUSSION

Home range analysis

We believe that it was important to report unsuccessful attempts to obtain radio-fixes. Because automobiles were used to track coyotes (i.e., not airplanes), unsuccessful attempts to locate a coyote during a tracking bout could indicate that we underestimated home range sizes. It usually took $\geq$1 month of tracking to understand which areas individual coyotes were using. After this time, we developed appropriate search patterns to maximize our efficiency in locating study animals.

We recommend the vertex edited method to accurately map areas believed to have been used by coyotes in fragmented areas or areas where it is apparent that coyotes are not using part of a standard polygon's area, especially if there is a large number of radiolocations with which to modify MCP estimates. The 95% MCP vertex edited polygon produced the most accurate description of each coyote's regularly used home range. For example, the 100% (55.6 km^2) and 95% (32.4 km^2) MCPs of #9802's home range included a large salt marsh. However, she was never documented using that area during 504 locations. The resulting 100% (38.1 km^2) and 95 % (22.8 km^2) vertex-edited home ranges were smaller (and we believe more reflective of 9802's actual area of use) than the original MCP estimates (Table 1, Fig. 2).

Home ranges of juveniles were smaller than those of adults (Table 1; Fig. 2) despite monitoring all juveniles until at least the period of independence (September; Way et al. 2001). Similar results were reported by Harrison et al.

(1991) and Person and Hirth (1991). The juvenile that was located least often (#9908) dispersed in January during the study. Although Harrison (1992a) did not document any December-January coyote dispersals on his Maine study site, Person (1988) did document dispersal of 3 coyotes during January in Vermont. In our study, coyote juvenile #9908 used only 10% (95 MCP vector edited) of her probable mother's (#9804) home range before dispersing (Fig. 2). It is interesting that this juvenile used only a fraction of its parent's home range before dispersing. Messier and Barrette (1982) hypothesized that delayed dispersal ensures juveniles a safe place to forage and live. Further, we suggest that juvenile coyotes should generally delay dispersal at least long enough to learn (Andelt 1985, Patterson and Messier 2001) their parent's area of use.

The very small home range (0.3 km^2) of 1 juvenile coyote (#9903) was peculiar. This juvenile was infected with mange when originally captured and was rehabilitated in captivity for 6 weeks before being released. Perhaps the animal passed a critical stage in its learning and developmental process either when it was sick in the wild or while it was held in captivity. Following release, #9902 (#9903's presumed mother) and 2 other coyotes frequently passed through #9903's home range but #9903 was never observed traveling with them. Although #9903 did survive the winter living in a small woodlot bordered by houses and roads on all sides, his movement and space-use patterns were atypical of normal juvenile movements during winter (Harrison 1992a). As our study concluded, #9903 dispersed from the study area. Future research should investigate the success of releasing rehabilitated animals of all ages into the wild (Schultz et al. 1999).

Although males and females had different home range sizes on Cape Cod, this was likely an artifact of our sampling (Person and Hirth 1991). All resident adults used regular, well-defined home ranges and appeared to travel with the same group members. Because coyotes on Cape Cod were territorial, we believe that the 2 sexes use similar-sized home ranges. For this to be accurately determined, a higher sample size of each sex and 2-3 adults from each social group should be radiocollared and monitored simultaneously.

Person and Hirth (1991) documented that coyotes have smaller home ranges during the denning season. Furthermore, Mech et al. (1998) noted that non-reproductive wolves maintain their approximate annual home range during the denning season. Non-reproductive coyote 9802 used the majority of her annual home range, while 9902 (reproductive) used only a fragment of her yearly range during the month of parturition (Fig. 3).

Resident coyotes traveled extensively on power lines, golf courses, railroad tracks, dirt roads and trails, and occasionally along the edges of secondary and even primary roads. These green areas enabled coyotes to cross through, and reside near, highly developed areas (most houses on our study area did not have fences to impede coyote movements). Resident associate coyote #0003 often made excursions outside of his 95% MCP home range by traveling on these corridors. Associates and dispersing or transient coyotes may use these travel routes to familiarize themselves with the surrounding areas and look for vacant territories and breeding opportunities, and could easily follow these corridors back to

their natal home ranges (Kamler and Gipson 2000). Future research should determine the optimal or minimum patch size and the minimum required connectiveness of patches that allows coyotes to inhabit fragmented, urbanized landscapes (Meffe and Carroll 1994, Tigas et al. 2002).

Home range sizes of adult resident coyotes on Cape Cod were within the range of values reported for eastern coyotes (Table 3). These values are generally 100-200% larger than coyotes in western North America (Patterson and Messier 2001) and may reflect the eastern coyote's larger body size and questionable taxonomic status (Silver and Silver 1969, Wayne and Lehman 1992). Although Person and Hirth (1991) documented a 75% reduction of home range size in more urbanized areas of Vermont, all adult coyotes in our study maintained large ranges while inhabiting an urbanized environment, which is similar to other coyote studies in Tucson, Arizona (Grinder and Krausman 2001) and southern California (Tigas et al. 2002, Riley et al. 2003). It was surprising to document these large home ranges (and low densities) because food resources for coyotes seemed to be abundant on our study site. However, it was beyond the scope of our study to correlate food habits to home range size. Future research should attempt to document the feeding habits of coyotes and food availability to better understand spatial and social behaviors of coyotes that inhabit different environments. Additionally, ecological correlates of home range size and sociality might be elucidated through further analysis of human activity patterns in the area.

Territoriality

Coyote pack members on Cape Cod shared common home ranges and based on the presence of non-overlapping, adjacent home ranges, were territorial (Patterson and Messier 2001). This is consistent with the literature (Messier and Barrette 1982, Andelt 1985, Person and Hirth 1991, Sacks et al. 1999). Although transients (e.g., #0001) and even adults, trespassed through the home ranges of resident coyotes, they spent little time in these areas (maximum = 3 consecutive days in 1 home range) and adults never left their established home ranges for more than 1 night.

Although wolves have been documented to kill other wolves during territorial disputes (Mech et al. 1998), this behavior has rarely been documented for coyotes. Two cases occurred in northeastern North America (Okoniewski 1982, Patterson and Messier 2001). Perhaps direct chases such as the 2 observed during this study, coupled with howling (Lehner 1978) and scent marking (Gese and Ruff 1997) are sufficient to keep coyotes from neighboring groups from regularly meeting and possibly killing each other.

Sociality

The data in Table 2 include only adult coyotes from each group because observations of pups and juveniles would have over-inflated the estimates for resident group sizes. The 6 largest group sightings involved young juveniles (pups). One group seen on 31 May 2000 included 9 coyotes (3 adults and 6 pups), and the breeding female of the group was not present during the sighting. Four other groups involved 1 adult and 5 pups

Table 3. Sizes of home ranges (km^2) of adult eastern coyotes in eastern North America.

		Mean home range size			
Area	Environment	Males	Females	Method used	Source
Vermont	Rural/farm	18.7	17.1	Harmonic mean	Person and Hirth 1991
E. Maine	Forested	44.0	49.7	MCP[a] deleting outliers >3 km nearest point	Harrison and Gilbert 1985, Harrison et al. 1989
W. Maine	Mountainous	43.3		100% MCP	Major and Sherburne 1987
New York	Adirondacks	112.8		95% MCP	Brundige 1993
E. Nova Scotia	Forested	49.3		95% adaptive kernel	Patterson and Messier 2001
W. Nova Scotia	Forested	76.2		95% adaptive kernel	Patterson and Messier 2001
S. Quebec	Woodland	~30		95% MCP	Messier and Barrette 1982
Cape Cod, Mass.	Suburban	29.8[b]		95% MCP vertex edited	This study
Cape Cod	Suburban	52.9[b]		100% MCP	This study

[a]MCP = minimum convex polygon
[b]Resident adults only

(all during June), and another group involved 1 adult and 7 pups during July. Because dispersal and mortality of juveniles is high (Harrison 1991, J. Way unpublished data), group size estimates should focus on resident adult coyotes during the winter and spring when a coyote population is at its lowest density for a given year (Parker 1995).

Similar to descriptions by Messier and Barrette (1982) and Patterson and Messier (2001), the observed mean traveling size in our study was lower than our estimates for group size for each resident pack. It should be noted that the sighting data (i.e.., mean traveling group size) are highly biased to sightings of radio-tagged animals. Animals were located using radio telemetry, thus radio-transmitted animals were observed disproportionately. Although there were many sightings of single coyotes during the study, there is a good chance that these were animals associated with collared animals nearby that simply were not observed (85% of the sightings were made during the night). Furthermore, Crabtree and Sheldon (1999) noted that coyotes often traveled and hunted alone or in small groups even if they belonged to a pack.

Because only 1 adult died during our 2-year study, it seems probable that the same breeding pair may remain together over a period of years on Cape Cod. Our observations showed that coyotes form cohesive but relatively small packs. These trends are typical of coyotes from many regions of North America (Andelt 1985,

Person and Hirth 1991, Sacks et al. 1999, Kamler and Gipson 2000, Patterson and Messier 2001), yet are smaller than mean group sizes from many undisturbed areas of North America (e.g., National Parks - Bekoff and Wells 1980, Gese and Ruff 1997, Crabtree and Sheldon 1999). To form a pack of 3-4 in our study area, the mated pair is therefore accompanied by 1-2 other (associate) coyotes that are probably previous offspring of the pair (Patterson and Messier 2001).

We visually identified individual non-collared coyotes (Way 2000); and we suspected that the same unmarked adults were repeatedly seen with radio-collared coyotes. Coyotes #9804 and #9901 maintained separate home ranges before being located together (0 of 253 paired observations). However, from December 1999 to May 2000 they were located together on 87% of 126 paired observations (i.e., when both coyotes were located during a radio-tracking bout), and their new home range encompassed the majority of both of their previous ranges. They were pair bonded and successfully produced pups during the 2000 breeding season.

Coyotes #9805 and #0003 (breeder and associate, respectively) were located together on 67% of 90 paired observations from mid-January 2000 to May 2000. That they were not always located together might explain why there were many sightings of single, collared animals. This reinforces the idea that resident coyote groups consist of a breeding male and female and 1-2 resident associates that are probably pups of the previous year. Group members regularly separate and rejoin each other on a daily basis, thus the number of animals sighted in a group can vary greatly.

Dispersal and mortality are the two greatest contributors to small group sizes (Harrison 1992a). Breeding female #9804 and juvenile #9908 were located together 33% of the time between July and October 1999 (n = 90 paired observations). However, they were not documented together from November 1999 – January 2000 (n = 56), when #9908 dispersed. Additionally, 2 juveniles (#9801 and #9803) were located together 69% of the time (n = 100 observations) from June to August, but were only located together 50% (n = 10) of the time in September and appeared to be spending less time together until #9803 was killed by a car on 13 September 1998. These data indicate that some coyotes may be independent and ready to disperse during the fall of the year of birth, effectively precluding the possibility of extended family group formation (Bekoff 1977, Harrison 1992b).

The role of pack associates in coyote family groups is unclear (Kamler and Gipson 2000). Although Hatier (1995) found no evidence that associates participated in territorial defense, some associates did help with provisioning of the young. Other associate coyotes have not been observed to help care for young and have been termed ‘sloucher’ coyotes (Crabtree and Sheldon 1999:136); that is, coyotes which remain in their natal territory but do not assist in pup rearing. Kamler and Gipson (2000) found that associates did participate in territorial defense. In our study, we repeatedly observed 3-4 coyotes provisioning young. Although we have no quantifiable data (i.e., lack of adults radio-collared), there were 5 sightings where a radio-collared breeding coyote returned to a den site and within 10 minutes (usually at dusk or dawn—Way et al. 2001) an uncollared coyote left the den area, presumably to forage. These observations suggest that

associates protect or watch pups when breeding adults are away from den sites (Ryden 1979, Way et al. 2001). In addition, we made 6 nocturnal observations of 3 coyotes scent-marking areas within their home ranges. Gese and Ruff (1997) claimed that defending a territory was a primary reason for scent marking in coyotes. During 2 of these occasions an untagged associate coyote scent marked a bush and immediately afterwards the collared resident breeding male raise-leg urinated (Gese and Ruff 1997) over the associates' mark. These sightings suggest that associates may assist breeders in at least passively defending territories.

The emerging picture of eastern coyotes is that they have larger spatial requirements (and thus live at lower densities) than their western counterparts and typically live in groups of 3-4 animals. Research should continue to investigate group size dynamics and the sociality of eastern coyotes residing in urbanized areas. Focusing on juvenile coyote dispersal patterns will give additional insight into survival rates and the social organization of coyotes inhabiting Cape Cod and other areas.

ACKNOWLEDGMENTS

This study would not have been possible without the support of Dr. L. Venezia and his staff at the Hyannis Animal Hospital, funding from the International Fund for Animal Welfare, equipment grants from Boston College and Barnstable High School, in-kind donations from P. and G. Auger, T. and R. Way, and E. Strauss, and support from the Department of Natural Resources at the University of Connecticut, Storrs, Connecticut. We thank the people and town of Barnstable for allowing us to conduct research on their land. Special thanks are due to K. VondenDeale and her staff at WildCare. G. Auger and M. Norton assisted with fieldwork. S. Kachuba assisted with data entry. Two anonymous reviewers and B. Patterson provided helpful comments on an earlier draft of the manuscript.

LITERATURE CITED

Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 49:1-45.

Atkinson, K. T., and D. M. Shackleton. 1991. Coyote, *Canis latrans*, ecology in a rural-urban environment. Canadian Field-Naturalist 105:49-54.

Ballard, W. B., L. A. Ayres, K. E. Roney, and T. H. Spraker. 1991. Immobilization of gray wolves with a combination of tiletamine hydrochloride and zolazepan hydrochloride. Journal of Wildlife Management 55:71-74.

Bekoff, M. 1977. Mammalian dispersal and the ontogeny of individual behavioral phenotypes. American Naturalist 111:715-732.

_____, and R. Jamieson. 1975. Physical development in coyotes (*Canis latrans*) with a comparison to other canids. Journal of Mammalogy 56:685-692.

_____, and M. C. Wells. 1980. The social ecology of coyotes. Scientific American 242:130-148.

Berg, W. E., and R. A. Chesness. 1978. Ecology of coyotes in northern Minnesota. Pages 229-247 *in* M. Bekoff, editor. Coyotes: biology, behavior and management. Academic Press, New York, New York, USA.

Bounds, D. L., and W. W. Shaw. 1997. Movements of suburban and rural coyotes at Saguaro National Park, Arizona. Southwestern Naturalist 42:94-99.

Brundige, G. C. 1993. Predation ecology of the eastern coyote (*Canis latrans*) in the Adirondacks, New York. Dissertation, State University of New York, College of Environmental Science and Forestry, Syracuse, New York, USA.

Burt, W. H. 1943. Terrioriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346-352.

Cape Cod Commission. 1998. Cape trends: demographic and economic characteristics and trends. Cape Cod Commission, Barnstable, Massachusetts, USA.

Crabtree, R. L., and J. W. Sheldon. 1999. Coyotes and canid coexistence in Yellowstone. Pages 127-163 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040-1044.

Fuller, T. K., and W. J. Snow. 1988. Estimating wolf densities from radiotelemetry data. Wildlife Society Bulletin 16:367-370.

Gese, E. M., O. J. Rongstad, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management 52:640-646.

_____, D. E. Andersen, and O. J. Rongstad. 1990. Determining home-range size of resident coyotes from point and sequential locations. Journal of Wildlife Management 54:501-506.

_____, and R. L. Ruff. 1997. Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. Animal Behavior 54:1155-1166.

Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. Journal of Wildlife Management 65:887-898.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data – a review of the problems and techniques particularly as applied to the study of mammals. Mammal Review 20:97-123.

Harrison, D. J. 1992a. Dispersal characteristics of juvenile coyotes in Maine. Journal of WildlifeManagement 56:128-138.

_____. 1992b. Social ecology of coyotes in northeastern North America: Relationships to dispersal, food resources, and human exploitation. Pages 53-72 *in* A. H. Boer, editor. Ecology and management of the Eastern Coyote. Wildlife Research Unit, University of New Brunswick, Fredericton, Canada.

_____, and J. R. Gilbert. 1985. Denning ecology and movements of coyotes in Maine during pup rearing. Journal of Mammalogy 66:712-719.

_____, J. A. Bissonette, and J. A. Sherburne. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53:181-185.

_____, J. A. Harrison, and M. O'Donoghue. 1991. Predispersal movements of coyote pups in eastern Maine. Journal of Mammalogy 72:756-763.

Hatier, K. G. 1995. Effects of helping behaviors on coyote packs in Yellowstone National Park, Wyoming. Thesis, Montanta State University, Bozeman, Montana, USA.

Holzman, S., M. J. Conroy, and J. Pickering. 1992. Home range, movements, and habitat use of coyotes in south-central Georgia. Journal of Wildlife Management 56:39-46.

Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to arcview. Version Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Kamler, J. F., and P. S. Gipson. 2000. Space and habitat use by resident and transient coyotes. Canadian Journal of Zoology 78:2106-2111.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control:

an interface between biology and management. Journal of Range Management 52:398-412.

Laundre, J. W., and B. L. Keller. 1984. Home-range size of coyotes: a critical review. Journal of Wildlife Management 48:127-139.

Lazell, J. D., Jr. 1976. This broken archipelago: Cape Cod and the Islands, amphibians and reptiles. Demeter Press Book: Quadrangle, New York, New York, USA.

Lehner, P. N. 1978. Coyote vocalizations: a lexicon and comparisons with other canids. Animal Behavior 26:712-722.

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.

McClennen, N., R. R. Wigglesworth, S. H. Anderson, and D. G. Wachob. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). American Midland Naturalist 146:27-36.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota, USA.

Meffe, G. K., and C. R. Carroll. 1994. Principles of Conservation Biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Messier, F., and C. Barrette. 1982. The social system of the coyote (*Canis latrans*) in a forested habitat. Canadian Journal of Zoology 60:1743-1753.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Okoniewski, J. C. 1982. A fatal encounter between an adult coyote and three conspecifics. Journal of Mammalogy 63:679-680.

Ott, R. L. 1993. An introduction to statistical methods and data analysis. Duxbury Press, Belmont, California.

Parker, G. R. 1995. Eastern coyote: the story of its success. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Patterson, B. R., and F. Messier. 2001. Social organization and space use of coyotes in eastern Canada relative to prey distribution and abundance. Journal of Mammalogy 82:463-477.

Person, D. K. 1988. Home range, activity, habitat use, and food habits of eastern coyotes in the Champlain valley region of Vermont. M.S. Thesis, University of Vermont, Burlington, Vermont, USA.

_____, and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. Journal of Wildlife Management 55:433-441.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 *in* L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.

Pringle, L. P. 1960. Notes on coyotes in southern New England. Journal of Mammalogy 41:278.

Quinn, T. 1997. Coyote (*Canis latrans*) habitat selection in urban areas of western Washington via analysis of routine movements. Northwest Science 71:289-297.

Riley, S. P. D., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566-576.

Rose, M. D., and G. A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998-1007.

Ryden, H. 1979. God's Dog. Lyons & Burford, New York, New York, USA.

Sacks, B.N., M. M. Jaeger, J. C. C. Neale, and D. R. McCullough. 1999. Territoriality and breeding status of coyotes relative to sheep predation. Journal of Wildlife Management 63:593-605.

Schultz, R. N., A. P. Wydeven, and J. M. Stewart. 1999. Acceptance of a gray wolf, *Canis lupus*, pup by its natal pack after 53 days in captivity. Canadian Field-Naturalist 113:509-511.

Sillero-Zubiri, C. 1996. Field immobilization of Ethopian wolves. Journal of Wildlife Diseases 32:147-151.

Silver, H., and W. T. Silver. 1969. Growth and behavior of the coyote-like canid of northern New England with observations on canid hybrids. Wildlife Monographs 17.

Springer, J. T. 1979. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management 43:926-935.

_____. 1982. Movement patterns of coyotes in south central Washington. Journal of Wildlife Management 46:191-200.

Swihart, R. K., and N. A. Slade. 1985a. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019-1025.

_____ and _____. 1985b. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108:299-306.

Thurber, J. M., and R. O. Peterson. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). Journal of Mammalogy 72:750-755.

Way, J. G. 2000. Ecology of Cape Cod coyotes (*Canis latrans* var.). Thesis, University of Connecticut, Storrs, Connecticut, USA.

Way, J. G., P. J. Auger, I. M Ortega, and E. G. Strauss. 2001. Eastern coyote denning behavior in an anthropogenic environment. Northeast Wildlife 56:18-30.

Way, J. G., I. M. Ortega, P. J. Auger, and E. G. Strauss. 2002. Box-trapping eastern coyotes in southeastern Massachusetts. Wildlife Society Bulletin 50:695-702.

Way, J. G. 2003. Description and possible reasons for an abnormally large group size of adult eastern coyotes observed during summer. Northeastern Naturalist 10: in press.

Wayne, R. K., and N. Lehman. 1992. Mitochondrial DNA analysis of the eastern coyote: origins and hybridization. Pages 9-22 *in* A. H. Boer, editor. Ecology and management of the eastern coyote. Wildlife Research Unit, University of New Brunswick, Fredericton, New Brunswick, Canada. 194 pages.

Windberg, L. A., S. M. Ebbert, and B. T. Kelly. 1997. Population characteristics of coyotes (*Canis latrans*) in the northern Chihuahuan desert of New Mexico. American Midland Naturalist 138:197-207.