EASTERN COYOTE DENNING BEHAVIOR IN AN ANTHROPOGENIC ENVIRONMENT

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Abstract: We document coyote (*Canis latrans*) litter sizes and birth dates, characteristics of den and rendezvous sites, and associations of radiotagged adults (n = 9) and pups (n = 5) to den and rendezvous sites in an urbanized landscape in the northeastern United States (Cape Cod, Massachusetts) from 1994–2001. Size of 16 litters averaged 4.5 ± 1.15 (SD). Backdating of sightings indicated that pups were born between 21 March and 12 April. Mean den width at narrowest point was 28.9 ± 5.0 cm. Minimum den depth ranged from 2–>5 m. Dens >2 m long had roots that protruded from all sides of the tunnel suggesting that tree root systems were important structural components of dens in sandy soils. Aspect that dens faced varied from 2–303°; circular mean aspect was 246°, but there was no selection for direction of den entrance. Use of rendezvous sites began between late May and mid-June when pups were 8–10 weeks of age. Rendezvous sites had open areas bordered by densely vegetated woods that provided distant views in an otherwise forested environment. There was no difference between male and female attendance at den and rendezvous sites. Adults, commonly located at den and rendezvous sites during late-May–early-June, gradually decreased their frequency of den and rendezvous site attendance during the remainder of the summer. Wildlife managers in the northeast can use these data to identify potential den and rendezvous sites for coyotes, particularly in an urbanized environment.

Key words: anthropogenic environment, *Canis latrans*, Cape Cod, den sites, eastern coyote, Massachusetts, rendezvous sites, urbanization.

Most previous studies of coyotes in northeastern North America have occurred in forested areas of Maine and eastern Canada (Messier and Barrette 1982, Harrison and Gilbert 1985, Major and Sherburne 1987, Litvaitis and Harrison 1989, Harrison et al. 1991, Harrison 1992, Patterson et al. 1999, Patterson and Messier 2001). In addition to these studies, Tremblay et al. (1998) studied coyotes in a mixed agricultural and forested landscape in southeastern Québec, and Person and Hirth (1991) examined coyote ecology in an

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agricultural region of Vermont. Denning behavior and activities of adults and pups during pup rearing in the northeast were described by Harrison and Gilbert (1985), Parker and Maxwell (1989), Harrison et al. (1991), and Patterson et al. (1999). Only Harrison and Gilbert (1985) provided empirical data on den site characteristics and adult relationships to den sites in the northeast (but see Andelt et al. [1979] for similar data from Nebraska).

Despite the previous studies of coyote ecology in the northeast, the anthropogenic impact on coyote reproductive activities in urbanized ecosystems is largely unknown. The objective of our study was to describe coyote denning behavior in a suburban and human-dominated landscape in the northeast. Specifically, we describe litter sizes, estimated birth dates, characteristics of den and rendezvous sites, and associations of adult coyotes to den sites and rendezvous sites.

STUDY AREA

We studied coyotes in Barnstable County, Cape Cod, Massachusetts between June 1994 and December 2001 focusing on the town of Barnstable (land area 155.5 km^2; Fig. 1). In the town of Barnstable, human population density was 290 people/km^2, and in entire Barnstable County it averaged 203 people/km^2 (U. S. Census Bureau, 1998 estimates). The highest human density occurred in Hyannis with 556 people/km^2, whereas the lowest human density was in West Barnstable with 89 people/km^2. Density of housing units varied from 328.3/km^2 in Hyannis to 39.3/km^2 in West Barnstable (U.S. Census Bureau, 1998 estimates). Road density, defined as centerline km of roadway per km^2, was 4.66 for the town of Barnstable and 3.97 for Barnstable County (Cape Cod Commission, 1996, Barnstable, MA).

Cape Cod is an human-made 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 about 1 km long, enable access to Cape Cod. Barnstable is located within 15 km of the bridges on the west part of the peninsula. The region is classified as a coastal temperate climate dominated by a subclimax forest of scrub oak (*Quercus ilicifolia*) and pitch pine (*Pinus rigida*) (Lazell 1976).

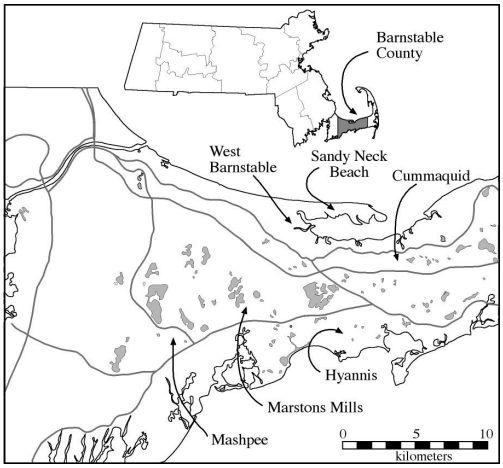

Fig. 1. Study area in Barnstable County, Cape Cod, Massachusetts. Inset shows location of Barnstable County and Cape Cod in Massachusetts.

METHODS

We captured coyotes in model 610B & 610C Tomahawk box traps (Tomahawk Live Trap Co., Tomahawk, Wis., USA). Animals ≥1 year of age based on body size and dentition were classified as adults. We further classified adult coyotes as either breeding residents or resident

associates (Andelt 1985). Breeding residents were adult coyotes that had established home ranges and exhibited breeding behavior such as 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.

We fitted adults with radiocollars (MOD-225 or 335, Telonics, Inc., Mesa, Arizona, USA). Pups received either an implant radiotransmitter (IMP/300/2, Telonics, Inc., Mesa, Arizona, USA), or an adult radiocollar with foam insert if captured > 1 Aug. We located study animals using portable receivers (Custom Electronics, Urbana, Illinois, USA) and hand-held 3-element Yagi antennas. Typically, an antenna was fixed to the window of a moving vehicle until a signal was detected. Animal locations were then determined by triangulation using a hand-held antenna and the loudest-signal method (Springer 1982). Due to the urbanized environment and the associated high density of roads, once a strong signal was obtained for an animal we were confident that successful radio-fixes were within 50 m of the animal's actual location. Controlled experiments (Way 2000) determined the mean errors for reference collars at known locations as 10 m (95% of errors were <50 m).

We monitored radiocollared coyotes daily during April and May to find den sites as recommended by Harrison and Gilbert (1985) and Parker (1995). When active den sites were found (defined by presence of fresh pup tracks or by sightings of pups) we recorded the following characteristics: location, number of openings, minimum den entrance width (cm), estimated den depth (m), soil type, aspect, and general habitat type. The circular mean aspect of den sites was calculated using simple circular statistics (Zar 1999). Rayleigh's test was used to determine if coyotes selected a particular den aspect (Zar 1999). We did not excavate dens; instead, we spotlighted through den entrances to estimate their depth. Because most dens were curved and we could not see the rear wall, den depth measurements were minimum estimates. Whenever possible, we determined minimum litter sizes from direct observations of litters. Age of pups was visually estimated based on body size (Parks 1979).

Abandonment of den sites was determined by the absence of tracks, sightings, and by monitoring of radio-tagged animals. Rendezvous sites are above ground resting sites that are frequently visited by pups and adults when dens are abandoned (Joslin 1967, Mech 1970, Messier and Barrette 1982, Harrison et al. 1991). Their use was determined by tracks, direct sightings, and activities of radio-tagged coyotes. In 1994, 1996, and 1997 den and rendezvous sites were located without the aid of radio-tagged coyotes by tracking, conducting howling surveys, and by opportunistic sightings (McCarley 1975, Gaines et al. 1995, Way 1996).

Attendance by adults at den and rendezvous sites was measured as the proportion of locations of radiotagged coyotes within a 300-m radius around den sites and the center of rendezvous sites (Harrison and Gilbert 1985). We monitored adults at den and rendezvous sites from April–August and defined this as the pup-rearing period. We defined the beginning of the pup-rearing period as when we first recorded breeding females or males localized at den sites. By

September, pups are self-sufficient and adults generally spend less time at rendezvous sites (Harrison 1992).

Approximately 50% of locations were taken during the dawn (0500 hr to 0900 hr) and dusk (1800 hr to 2100 hr) periods, which coincided with checking traps and making visual observations of coyote families. About 25% of remaining locations were obtained during each of the night (2100 hr to 0500 hr) and day (0900 hr to 1800 hr) periods. To ensure independence we used only those locations separated by >4.5 hr for analysis (Harrison and Gilbert 1985, Patterson and Messier 2001). Due to small sample sizes we pooled data and compared among breeding males, breeding females, and all coyotes combined.

We used a chi-square test of homogeneity (Ott 1993) to test for differences in attendance at den and rendezvous sites by 1) breeding males and females from April–August, 2) breeding males and females during the nursing (April–May) and weaned (June–August) periods, 3) male, female and all coyotes pooled together during each month, and 4) males, females and all coyotes pooled during the nursing and weaned periods. The expected probability of attendance at a den or rendezvous site was calculated by dividing the number of locations for a given period for one sex by the number of locations for both sexes for that period, then multiplying that by the total number of locations at den and rendezvous sites for both sexes for that period.

We used $\alpha = 0.05$ as the significance level in all analyses.

Care and use of coyotes was approved by the University of Connecticut Institutional Animal Care and Use Committee protocol #YEE 0101 (May 1998–June 2000), by Boston College's Institutional Animal Care and Use Committee Protocol Number 01-02 (May–August 2001) and by the Massachusetts Division of Fisheries and Wildlife permits # 038.98LP (May 1998–June 2000) and #046LP01 (May–August 2001).

RESULTS

We captured and radiocollared 9 adult coyotes (3 adult breeding males, 5 adult breeding females and 1 resident associate male) that were known to be attending pups during the study. One additional adult female (#9802) was monitored during the study but was not determined to be reproductive during 2 consecutive seasons (1998 and 1999). We also radiotagged 5 pups (4 with implant transmitters and 1 with an adult collar with foam insert). Radiocollared adults represented 6 distinct groups that occupied exclusive family territories (Way 2000, Way et al. 2002). Minimum litter size averaged 4.5 pups per litter (n = 16, SD = 1.15). Backdating of sightings indicated that pups were probably born between 21 March and 12 April (Table 1).

Den and rendezvous site characteristics

Mean den width at narrowest point was 28.9 cm (n = 17, SD = 5.0). Minimum den depth varied from 2–>5 m and averaged 2.5 m (n = 17, SD = 0.87). Dens >2 m long had roots protruding from all sides of the tunnel. The aspect dens faced varied from 2–303°. The circular mean aspect that den entrances faced was 246°, but there was no selection for a particular aspect for den entrances using Rayleigh's test (P = 0.78) (Zar 1999). All den sites were within 300 m of water ranging from vernal pools to streams to lakes, and with one exception were >300

Table 1. Estimated age and birth dates for 13 litters of coyote pups observed on Cape Cod, Massachusetts, 1994-2001.

Social Group	Date Observed	Estimated pup age	Estimated birth date
West Barnstable	9 Jun 1994	9-10 weeks	31 Mar-7 Apr
West Barnstable	30 May 1996	8 weeks	5 Apr
Marstons Mills	7 Jun 1997	9 weeks	6 Apr
Marstons Mills	8, 17 Jun 1998	10, 11 weeks	30 Mar
Hyannis	18 Apr 1999	20 days	30 Mar
Cummaquid	11 July 1999	3 months	11 Apr
Cummaquid	24 Apr 2000	12 days	12 Apr
Hyannis	23 May 2000	7 weeks	4 Apr
Mashpee	24 May 2000	6 weeks	11 Apr
Hyannis	21 Mar 2001	newborn[a]	21 Mar
Cummaquid	21 May 2001	6 weeks	8 Apr
N. Centerville	29 May 2001	7 weeks	9 Apr
Mashpee	30 Jul 2001	3.5 months	10 Apr

[a]coyote #9902 observed in den with newborn pup

m from the nearest house.

Den sites were devoid of prey remains and adult scats. A conspicuous pile of soil was located at the main entrance of all den sites. Of the 17 dens, 15 were dug into extensive root systems in sandy soil, 1 was dug under a rock in sandy soil, and 1 was dug into wet organic clay next to a salt marsh. All dens had 1 entrance. Sixteen were dug in well-drained areas, either on elevated mounds or at the top of small (10–15 m high) ridges or dunes and 1 den was dug under a fallen pine tree. Six dens were dug into the ridges of human-made bowls (10–20 m in diameter, 3–10 m high); most bowls were dug >20 years previously to supply soil for cranberry bogs. Six dens were dug into root systems in mixed pine–oak forests. Sixteen of 17 den sites were in open areas with little understory. These openings were 10–20 m^2 and were within 25 m of densely vegetated areas. One den was located in a dense brushy area.

The immediate area surrounding 8 of 17 den sites was later used as a rendezvous site. This occurred between late May and mid-June when the pups were an estimated 8-10 weeks of age.

Rendezvous sites were located in moderately to highly open areas such as swamps, abandoned cranberry bogs, pine forests, neighborhoods, shores of lakes and ponds, golf courses, and cultivated cranberry bogs. All rendezvous sites had densely vegetated woods surrounding them. All rendezvous sites were located within 0.4 km of water, and radiotagged animals were frequently documented in close proximity to water sources. Typically, these water sources were small ponds. However, based on tracks and sightings, lakes, rivers and streams, vernal pools and puddles, swamps, and cranberry bog ditches were also used by coyotes. Most rendezvous sites were located in wooded areas from 0.2 (Hyannis)–8.0 km (West Barnstable) from the nearest house despite all home ranges including a substantial amount of residential area

(Way 2000, Way et al. 2002). One rendezvous site was located closer to homes; however, this area was used by 3-month-old coyote pups that were beginning to forage independently.

Coyotes moved their pups to new den sites after every known human disturbance (n = 7) from April–May. Movements to new den sites ranged from 50 m to 1 km. It was difficult to determine whether adults moved their pups to new den sites, or if the pups were already using rendezvous sites during 3 disturbances in early June. Based on movements of adult coyote around localized, but not specific areas, it appeared that pups were already using rendezvous sites during these 3 occasions. The night (12 Jun 1998) following a disturbance by the senior author the Marstons Mills group moved to a new rendezvous site 4 km away.

Adult coyote relationships to den and rendezvous sites

There was no difference in attendance at den and rendezvous sites by breeding males and females during April (χ^2 = 2.115, df = 1, P = 0.15), May (χ^2 = 0.961, df = 1, P = 0.33), June (χ^2 = 0.997, df = 1, P = 0.32), July (χ^2 = 0.458, df = 1, P = 0.50), August (χ^2 = 0.34, df = 1, P = 0.56), or the weaned period (χ^2 = 0.163, df = 1, P = 0.69), but there was a marginally significant difference during the nursing period (April–May) when females were located at dens more than males (χ^2 = 3.286, df = 1, P = 0.07).

Breeding females were at den and rendezvous sites more than expected during April, May, and June and less than expected during July and August (χ^2 = 22.36, df = 4, P = 0.0001), and more than expected during the nursing period (χ^2 = 11.77, df = 1, P = 0.0006). A sharp change occurred between June and July when breeding female coyotes went from being at den and rendezvous sites during 73% of locations in June (n = 159) to 53% (n = 267) in July (Table 2). Breeding males showed no difference in den attendance from April through August (χ^2 = 0.938, df = 4, P = 0.92), or between the nursing and weaned periods (χ^2 = 0.230, df = 1, P = 0.63), averaging from 54–64% attendance every month (Table 2).

When data were pooled for all coyotes (including the 1 resident associate coyote), they were located at den and rendezvous sites more than expected during April–June and less during July–August (χ^2 = 14.815, df = 4, P = 0.005). Pooled data also indicated that coyotes were located at den and rendezvous sites more during the nursing than the weaned period (χ^2 = 6.929, df = 1, P = 0.008).

It was difficult to ascertain if adult coyotes were spending time with pups at rendezvous sites during September. All 5 radio-transmitted pups (including #9801 and #9803 who did not have an associated radiocollared adult) were mobile and four of the coyotes frequently moved between rendezvous sites (sometimes daily) during September and October (the 5th pup, #0101 stayed within a 1 km^2 farm and was not documented to leave until December 2001). In addition, the four coyotes also explored new areas outside of established rendezvous sites. Adult female #9804 was with female pup #9908 during 42% of observations (n = 55) in July and August 1999. During September and October 1999 they were located together on 35% (n = 17) and 6% (n = 17) of paired observations, respectively, but the pup was documented exploring previously unvisited areas within her parents' range and frequently moved between

Table 2. Frequency of locations (%) that adult coyotes were within 300 m of den and rendezvous sites April–August 1999, April–June 2000, and April–August 2001 on Cape Cod, Massachusetts. Sample sizes (No. locations) are given in parentheses. All coyotes were breeders except associate M0003. Blank spaces indicate that no data were collected from that coyote during a month.

Coyote	Year	April[a]	May	June	July	August
Cummaquid:						
F9804	1999	82 (33)	68 (31)	73 (30)	42 (38)	47 (32)
	2000	81 (21)	71 (14)	75 (16)		
	2001	83 (12)	77 (39)	81 (11)	48 (25)	24 (42)
M9901	2000	39 (18)	36 (14)	55 (11)		
Hyannis:						
F9902	1999	79 (38)	79 (24)	70 (30)	44 (41)	37 (38)
	2000	80 (44)	56 (27)	69 (29)		
	2001	79 (28)	71 (35)	67 (15)	63 (19)	63 (8)
	2001[b]	4 (28)	3 (35)	0 (15)	[c]	[c]
M0001	2001	55 (29)	15 (40)	31 (13)	17 (18)	[c]
	2001[b]	3 (29)	45 (40)	46 (13)	[c]	[c]
Mashpee:						
M9805	1999	100 (3)	41 (22)	54 (26)	61 (23)	38 (29)
	2000	81 (36)	86 (14)	54 (13)		
	2001	57 (14)	74 (34)	76 (17)	77 (43)	65 (43)
M0003	2000	36 (36)	64 (14)	46 (13)		
F0106	2001		62 (13)	88 (17)	60 (43)	64 (42)
Marstons Mills:						
F0110	2001			100 (5)[d]	59 (97)	47 (55)
N. Centerville:						
F0104	2001		67 (21)[e]	33 (6)[e]		
Totals for all breeders:						
Females		80 (176)	70 (204)	73 (159)	53 (267)	49 (199)
Males		64 (100)	60 (124)	63 (80)	60 (84)	54 (72)

[a]Data collection began when coyote first localized each year.
[b]Second den found in Hyannis home range but female unidentified
[c]Location of rendezvous site not known
[d]Captured 8 Jun 2001
[e]Captured 19 May 2001, killed by automobile 8 Jun 2001

rendezvous sites. These two coyotes were not documented together after October 1999 although #9908 did not disperse from her natal range until January 2000. Similarly, male pup #0101 was located with #9804 during 33% of 42 locations obtained during July and August 2001. During September and October they were not located together (n = 17) but #0101 was not documented leaving a 1 km^2 food

rich area—a farm where 2–3 dead chickens were thrown into the woods each day specifically for coyotes (Barnstable County Farm, personal communication). However, this coyote pup started to increase its range in December 2001 and was located with #9804 during 2 occasions in early December outside of the farm but within #9804's normal home range. Female pup #0112 was frequently located with at least one of her parents during September (74% of observations, n = 35) and October (60% of observations, n = 5) 2001 and also dramatically increased her movements during this time to encompass the majority of her parents' range. However, she was not located with either parent from October 2001 until she was killed by a vehicle in late November (n = 23 locations), though she did remain within her parent's home range during this time.

DISCUSSION

Our litter estimates were based on actual pup counts at dens in contrast to Knowlton (1972) who counted uterine scars of dead coyotes. We could not be positive if we witnessed entire litters during our observations. However, because we repeatedly observed the same pups (based on markings), and many sightings were made for >2 h we believe that our sightings represent whole litter sizes. Andelt (1985) suggested that some pups might die before initially leaving the den at about 5 weeks of age, thus becoming undetectable to observers. Though we made only 2 counts of litters inside dens, our observations suggest that most members of litters can survive past the period when they emerge from the den (5 of 5, 4–5 of 5–6). Average litter size in our study was slightly lower than others reported for the northeast (Parker 1995), though several reports were based on uterine scars and not live litters. Knowlton (1972) noted that average litter size varied inversely with density of coyotes. However, more recently, Crabtree and Sheldon (1999) suggested that litter survival and not litter size at birth is the major reproductive parameter that responds to human exploitation in a density-dependent manner because litter size varied little with prey abundance. Although litter sizes in our study were relatively high during July counts, our sample size of radiotagged pups is small. We need to monitor more pups to determine survival rates during the first year of a pup's life. Preliminary data suggest that 60% (n = 5) of radiotagged pups in our study have been hit and killed by cars. Of the remaining 2 pups, one survived to 1 year of age and the other dispersed and could not be found again — its fate is unknown (J. G. Way, Boston College, unpublished data).

The observation of male coyote #0001 tending 2 dens in the urban Hyannis area during 2001 (Table 2) is unusual because of the distance between dens. There are previous reports of tending more than 1 den by coyotes (Ortega 1988, Crabtree and Varley 1995, Parker 1995, Gese et al. 1996, Crabtree and Sheldon 1999) and wolves (*Canis lupus*)(Mech 1970, Mech et al. 1998). In these cases, dens of coyotes were all close together (~1 km), but #0001 tended 2 dens that were 2.8 km apart. Unfortunately, we were unable to monitor this group in late summer. Female #9902 abruptly abandoned her rendezvous site in July, and the rendezvous site for #0001's second litter was not located before #0001 was killed by a car on 20 August 2001. Female #9902 had a different mate (based on size and pelage characteristics) during

summer 2000 (#0001 was collared at the time and was occasionally in 9902's home range but did not travel with her). At least 2 associate coyotes, assumed to be from #9902's 1999 litter, assisted 9902 with pup rearing during 2000. During the 2001 breeding season (January–March) #0001 and #9902 were observed traveling with a third coyote on 11 occasions. Future genetic testing of additional captures in this group may reveal the kinship relationships among the members of this unusual pack.

In Maine, coyote pups were born from 19–25 April (Harrison et al. 1991). Our data indicate that coyotes on Cape Cod are born earlier. This perceived difference may be an artifact of low sample sizes in both studies or coyotes may actually be born earlier on Cape Cod, perhaps due to a warmer climate. Published birth dates for coyotes are lacking from much of northeastern North America (Harrison et al. 1991, Parker 1995). Consequently, researchers use data on pup birth dates from other studies (e.g., Harrison et al. 1991) to define biological seasons in their respective studies (Person and Hirth 1991, Patterson et al. 1999). Our data from Cape Cod provide additional empirical information on coyote denning behavior in the northeast.

Den and rendezvous site characteristics

That all but one den was dug into sandy soil was not surprising given the geology of the coastal environment on Cape Cod. Most areas on Cape Cod, except around marshes, have sand 15–30 cm below the ground surface. Therefore, it is likely significant that all dens dug into sandy soil were constructed into tree root systems which provided structural support so dens would not collapse. Despite the larger body size of eastern coyotes (Person 1988, Way 2000), den entrance widths in our study and in Maine (37 cm; Harrison and Gilbert 1985) were similar to those reported for western coyotes in Nebraska (32 cm; Althoff 1980).

Den sites were devoid of prey remains and adult scats, much like described by Harrison and Gilbert (1985). Although Harrison and Gilbert (1985) reported that coyote den sites were oriented towards the south (120-236°), in our study coyotes showed no preference for the direction that den entrances faced. Nevertheless, because most den sites were located in semi-open areas, solar warmth may indeed be an important factor in den site selection by coyotes on Cape Cod. As pups became bigger and explored outside of dens, the nearby brushy areas surrounding den sites provided escape cover.

Because of the correlation between coyotes moving pups from den sites and human disturbance, adult coyotes may have dug alternative dens before the move as proposed by Harrison and Gilbert (1985). This suggests that coyotes can recognize and remember previously excavated dens and can rapidly move their pups to those locations when necessary (Griffin 1984, Griffin 1992, Griffin 1998). O'Donoghue et al. (1998) reported that coyotes have a long-term spatial memory that enables them to remember the location of caches even after they have been covered by snow. Nevertheless, despite the suddenness of moves from den and rendezvous sites, the cause and effect relationship between disturbance and moving pups remains speculative because coyote groups commonly moved to different rendezvous sites during the course of our study.

Rendezvous sites were classic in appearance (Joslin 1967, Mech 1970, Messier and Barrette 1982). They offered views and open areas where adults could scan for danger and pups could play and forage. Nearby dense brushy areas enabled pups to rapidly retreat to safety if danger (mainly humans and domestic dogs [*Canis familiaris*] on Cape Cod) approached.

It was beyond the scope of this study to test whether coyotes preferred wooded areas to suburban areas in which to den. Nonetheless, a qualitative comparison is justified because standard methods were employed to record den site characteristics. Because coyotes were observed to forage freely at night in neighborhoods and other anthropogenic areas (Way 2000), it was apparent that coyotes did not always avoid built-up areas. It seemed that coyotes preferred to locate dens in wooded areas. Dens and rendezvous sites were also located near water. There are many apparently suitable areas on Cape Cod >1 km from freshwater; yet dens and rendezvous sites were always <0.4 km from water. Again, it was beyond the scope of this study to quantify these observations in terms of habitat selection.

Adult coyote relationships to den and rendezvous sites

Coyote pups are born in late March–early April on Cape Cod, so it is not surprising that females are in almost constant attendance of nursing pups during that time. Since females are frequently located near a den site when pups are young, there may be less need for males to attend dens during that period, except perhaps for short visits to bring food to the breeding female, or to guard the den from predators and conspecifics when the female is absent (Camenzind 1978). The small sample sizes in our study may have precluded detecting a significant difference between male and female attendance behavior at den sites during April and May. However, our data indicate that males (including the associate coyote) were regularly located at den sites providing strong evidence that both parents and associates cared for pups and shared in the duties of pup raising and protection, especially as summer progressed (Ryden 1975, Andelt et al. 1979, Andelt 1985, Harrison and Gilbert 1985, Crabtree and Sheldon 1999). We observed males and uncollared resident associate coyotes both bringing and regurgitating food to pups. Associate coyote #0003 was observed bringing a gray squirrel (*Sciurus carolinensis*) to the pups in his group. Future research should monitor several radiocollared coyotes in a group in order to determine more accurate den attendance patterns. This information could elucidate how different members of a coyote group (i.e., breeders vs. associates) contribute to pup-rearing, and might aid in determining the optimal number of adults that are necessary to successfully raise pups. Data on coyote den site selection and attendance patterns from different regions and ecosystems (e.g., rural vs. urbanized) would contribute to an emerging picture of coyote denning ecology.

Adult coyotes were commonly at den and rendezvous sites during late May–early June (Table 2) when coyotes are in transition from using den sites to using rendezvous sites. Our data provide evidence that adults spend extended amounts of time with pups during this time (overall 68%, $n = 252$). As Vila et al. (1995) noted for wolves in Iberia, pups

need to be protected from predators. In our study area potential predators include red foxes (*Vulpes vulpes*), domestic dogs, red-tailed hawks (*Buteo jamaicensis*) and great horned owls (*Bubo virginianus*). Coyote pups also have to be protected from potentially cannibalistic trespassing conspecifics from neighboring groups (Camenzind 1978, Brundige 1993, Patterson and Messier 2001). In addition, pups must learn how to hunt and be shown new areas (i.e., rendezvous sites) within the group's home range (Messier and Barrette 1982).

July is typically defined as the pup foraging and early independence period (Harrison and Gilbert 1985, Parker 1995). In our study, adult coyotes spent less time at rendezvous sites during the early pup independence period (late-July–August), which coincides when pups spend more and more time foraging on their own (Messier and Barrette 1982, Harrison et al. 1991).

Our data suggest that August is an appropriate time to stop monitoring adult coyote relationships to den and rendezvous sites. Similarly, Harrison and Gilbert (1985) found that by late September, <8% of locations of adults were at rendezvous sites. The increased movements and independence displayed by pups do not require adults to regularly attend rendezvous sites after August (Messier and Barrette 1982, Harrison and Gilbert 1985). Pups may even begin to disperse by late September of their first year (Harrison 1992). By fall, pups in our study greatly increased their home range but were rarely located with radiocollared adults. Messier and Barrette (1982) proposed that the separation between pup and adults at this time gives the adults more freedom until the pups acquire sufficient mobility or the necessary behavior required for hunting. They further suggested that juveniles can remain within the parental territory even without noticeable family bonds and benefit from access to a secure foraging area.

Our study documented den and rendezvous site characteristics, and adult and pup behavior at den and rendezvous sites during spring and summer in a coastal, anthropogenic environment. These data provide wildlife management agencies the information to identify coyote den and rendezvous sites in the northeast, and improve our understanding of coyote sociality in an urbanized environment.

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