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Coywolf, *Canis latrans* × *lycaon,* Pack Density Doubles Following the Death of a Resident Territorial Male

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We studied a subset of four radio-collared individuals that were a part of a larger study documenting Coywolf (*Canis latrans* × *lycaon*; Eastern Coyote) ecology in an urbanized landscape (Cape Cod, Massachusetts), and report on the territory of a typical sized pack that was subdivided roughly in half following the death of the breeding male from the original ("Centerville") pack. The original residents lived in a winter pack size (i.e., after pup/juvenile dispersal) of three or four individuals in a 19.66 km^2 territory and a density of 0.15–0.20 individuals/km^2, as determined by radio-tracking and direct observations, with their territory bordering that of other monitored packs. Following the death of the breeding male, two other radio-collared Coywolves (a young male from the original Centerville pack and a young female from a bordering pack) shifted their respective territories to overlap the majority of the original Centerville pack's territory. These two groups were the same size as the original pack (three or four individuals each) but occupied smaller territories (5.28 km^2 and 12.70 km^2) within the previous pack's territory. The combined density for the two new packs was estimated at 0.33–0.45 individuals/km^2 or 2.2 times greater than the former pack's density and was 2.5 times (0.38–0.50 individuals/km^2) greater when accounting for the slight (12%) overlap between the territories of the two new packs. Our results suggest that local Coyote/Coywolf density (i.e., at the pack level) may increase following the death of the breeding male of a given pack, probably because of the reduced (or lack of) protection of territorial boundaries. This finding has particular relevance to Coyote/Coywolf management programs aimed at reducing local densities via removal of individuals from these populations. Further implications exist for enriching our understanding of the trophic dynamics of urbanized habitats.

Key Words: Coywolf, Eastern Coyote, *Canis latrans* × *lycaon*, density, management, pack, population increase, territoriality.

Home range, or the area that an animal uses, is one of the most basic and critical life-history traits of wildlife species that we must understand in order to devise and implement effective conservation and/or management strategies (Powell 2000). As noted by Powell (2000: 74), "knowing animals' home ranges provides significant insights into mating patterns and reproduction, social organization and interactions, foraging and food choices, limiting resources, important components of habitat, and more" for those animals. Similarly, the territory is the portion of an animal's home range that is guarded by a group/individual and is a term often associated with carnivores (Clark et al. 1999; Mech and Boitani 2003a: 19-20). Depending on the species, a territory may be the animal's entire home range or it may be only part of it (Powell 2000).

A consistent theme of canid biology is that the majority of a wild dog's home range is guarded as its territory (MacDonald and Sillero-Zubiri 2004: 6). Coywolves (*Canis latrans* x *lycaon*; also called Eastern Coyote; Way et al. 2010) are similar to Coyotes (*C. latrans*) and Wolves (*C. lupus*) in that they live in territorial social groups (i.e., packs) consisting of a breeding pair, some of their full-grown offspring (termed beta- or pack-associates; usually one- or two-year-old individuals), and pups of the year (Gese et al. 1996b; Mech et al. 1998; Mech and Boitani 2003b; Patterson and Messier 2001; Way et al. 2002a; Way 2003). In our study area, previous research has documented that Coywolves live in territorial packs (i.e., most of their home range is guarded as a territory) typically consisting of three or four adult individuals (Way et al. 2002a), although larger packs of five or six individuals have been observed (Way 2003, 2007a). Because of these previous findings, we will hereafter refer to our findings as Coywolf territories and packs. In addition to territorial packs, lone individuals (termed nomads or transients) travel among resident packs and typically have much larger home ranges (see Parker 1995; Mech and Boitani 2003b; Way 2007b). Knowledge of a canid's territory and pack size (along with the number of transients in a population) can aid wildlife managers in more accurately estimating the size and density of local populations (Mech and Tracy 2004).

As top-order predators in many areas, Coyotes and Coywolves may have increased impacts on the trophic dynamics of urban habitats (Faeth et al. 2005). As such, it is critical that managers be able to make accurate estimations of their populations. In this paper we report on the territory of a normal-sized Coywolf pack (the Centerville pack) being used and partitioned between two packs following the death of two of the original pack's resident adults.

Methods

Fieldwork was conducted from 1998 to 2008 in the urbanized town of Barnstable (155 km^2), Cape Cod, Massachusetts, where human population density is 308 people/km^2 and housing density is 161/km^2 (Figure 1). Cape Cod (1024 km^2) is a residential area interspersed with numerous small (5–10 ha) and several large (100–500 ha) conservation areas. Areas of Cape Cod are rapidly urbanizing. Available habitat is fragmented, but it is connected via corridors such as powerlines, golf courses, railroad tracks, and even secondary roads. Most of the neighborhoods are not fenced, and Coywolves are readily able to travel through these areas to gain access to various portions of their territories (Way et al. 2004).

Coywolves were captured in box traps baited with supermarket meat scraps and road-killed Eastern Grey Squirrels (*Sciurus carolinensis*) (Way et al. 2002b). Following capture, Coywolves were fitted with a radio-collar (MOD 335 and MOD 400 collars; Telonics Inc., Mesa, Arizona, USA) for monitoring purposes. Radio-telemetry protocols are fully described by Way et al. (2002a) and Way et al. (2004). Portable receivers (Custom Electronics, Urbana, Illinois, USA) and hand-held 3-element Yagi antennas were used to radio-track both on foot and from a vehicle. Due to the abundance of roads present in the landscape we were working in, we mostly restricted our activities to cars, as Coywolves did not react to them as much as they did to people (e.g., by running away; J. Way, unpublished data). Occasionally we approached animals as close as possible on foot without disturbing them. Using a vehicle, we homed in on each individual's signal until its location had been pinpointed using the loudest-signal method (see Way et al. 2004). We used binoculars, spotting scopes, and video-cameras during daytime observations, and city street lights, night vision scopes, binoculars, and occasionally headlights during night-time observations (Way et al. 2002a, 2004). It is important to stress that we had minimal influence on Coywolf behavior despite obtaining highly accurate radio-locations. The majority of our sightings occurred with our car engine off, and observations (e.g., a Coywolf crossing a street near our research vehicle) indicated that we rarely altered a given individual's behavior (Way et al. 2002a). Radio-collared Coywolves were tracked throughout a 24-hour time period to ensure accurate representation of activity and movements, although 33% of radio-locations were collected during crepuscular hours, when Coywolves were most visible.

Radio-collared Coywolves were often seen with untagged companion(s), especially when at rendezvous sites (Way 2003, 2007a). A detailed description (e.g., size, coloration, distinguishing markings, and behavior) of the animals without radio-collars was made during every direct observation. In this manner, the unmarked individuals were identified based on appearance, as described by Way et al. (2002a). Overall, we identified as many individuals as possible from each study pack, as well as from other groups within the study area.

We classified Coywolves as adults or pups/juveniles. Adults were classified as all full-sized individuals, which likely included yearlings that remained on their natal territory. Behavior (e.g., submission to known adults) strongly implicated many of these helpers as offspring, and research suggests that it is usually yearlings who delay dispersal for a year to remain within their natal range (Patterson and Messier 2001; Way et al. 2002a). Pups were born around 1 April (Way et al. 2001) and were classified as such until October, when they approached full body size and became indistinguishable from adults/yearlings when observed in the field. Therefore, winter density estimates possibly include full-grown pups, as in other canid studies (Mech and Tracy 2004).

To estimate territory sizes, we used Home Range Tools for ArcGIS extension using ArcGIS Version 9.2 (Rogers et al. 2007). Territories were calculated using the 100% and 95% Minimum Convex Polygon (MCP) methods. We used the 95% MCP estimator for all ranges reported herein, except that we combined data from the two breeding resident Coywolves (#0104 and #0103) of the Centerville pack and used that 100% MCP estimator to describe the Centerville pack's territory (Figure 1) (subsequent tracking showed that this best approximated their territory size, i.e., the 100% MCP range bordered other territorial radio-collared packs not reported in this study) (J. Way, unpublished data; Figure 1).

Using Mech and Tracy's (2004) technique, we estimated pack density based on the observed territory and pack size for each of the three packs studied in this paper. Observed pack sizes were divided by their territory size (e.g., 4 Coyotes/2 km^2) and then converted to densities of individuals per km^2 (e.g., 2 Coyotes/km^2). A comparison of territory sizes in this paper is made at the pack level and does not incorporate our entire study area. While we acknowledge that there might have been additional individuals without radio-collars present, such as transients, the same animals without radio-collars were repeatedly observed traveling with radio-marked individuals (see Results). It is likely that any other Coywolves present in these study packs' territories were simply transients passing through the area. These individuals have much larger ranges than the local territory scale discussed in this paper (see Way 2007b). Furthermore, estimating density using this technique for territorial canids is standard in the literature, which typically acknowledges the presence of uncounted transients in a population (Mech and Boitani 2003a, 2003b; Mech and Tracy 2004).

Results

A total of 48 individual Coywolves (26 males, 22 females) consisting of 11 juveniles (7 males, 4 females), 12 yearlings (8 males, 4 females), and 27 adults (12 males, 15 females) was captured 65 times during our 10-year study. This paper focuses on four of those radio-collared individuals from 2001 to 2008: #0104, #0103, #0203, and #0204, all described in depth below.

Observations of the Centerville pack (Figure 1) began on 20 May 2001, when a thin, lactating, 15-kg female (ID #0104) was captured and radio-collared (see Way 2004 for more background on her). Coywolf #0104 and her probable mate (# 0103, an 18-kg adult male captured 22 December 2001) lived in a 19.66 km^2 territory located on both sides of Cape Cod's only major highway (Route 6). They lived in a winter pack size (i.e., after pup/juvenile dispersal) of three or four individuals: we consistently saw three individuals in that pack (20 observations) but made two observations of four individuals traveling together. The fourth individual, which was light-colored, was guessed to be a full-grown pup that was loosely affiliated with the pack and was also observed alone within the pack's territory on three occasions. Density was estimated at 0.15–0.20 individuals/km^2, with their territory bordering that of other radio-collared packs. We obtained 159 total telemetry fixes for #0104 and #0103 combined before each was hit and killed by cars on Route 6 (#0104 on 8 June 2001 and #0103 on 3 June 2002). Although we tracked #0104 for only one month, her movements encompassed #0103's territory, and previous research has shown that females with pups in our study area travel within their existing territory during the spring and summer (Way et al. 2001, 2002a). Therefore, we felt justified in combining data from Coyotes #0104 and #0103 into their territory estimate.

During summer 2001, the Centerville pack (led by male #0103 and an associate of #0104) raised a litter of four pups (see Way 2004) and we captured and radio-collared one of these pups (#0203, a 15.9 kg male) on 23 February 2002. Up through the month #0103 was killed (i.e., June 2002), #0203 lived in a 10.46 km^2 area located entirely within the boundaries of the Centerville pack's (i.e., his parent's) territory (Table 1) and was a pack associate/helper. He and male #0103 were frequently located together (see Way 2004) until #0103 was hit and killed by a car in June 2002. Coywolf #0203 was observed acting submissively to his putative father, #0103, as they tended pups in spring 2002. During that same time period, a 13.6-kg yearling female (#0204), captured 6 March 2002 in Cummaquid, was living immediately to the east of the Centerville pack. Coywolf #0204 gave birth to an observed four or five pups during that time period and traveled with one other adult. Up through June 2002, #0204's pack lived in a 12.36 km^2 (95% MCP) territory which had very limited overlap with the Centerville pack's territory (Table 1; Figure 1).

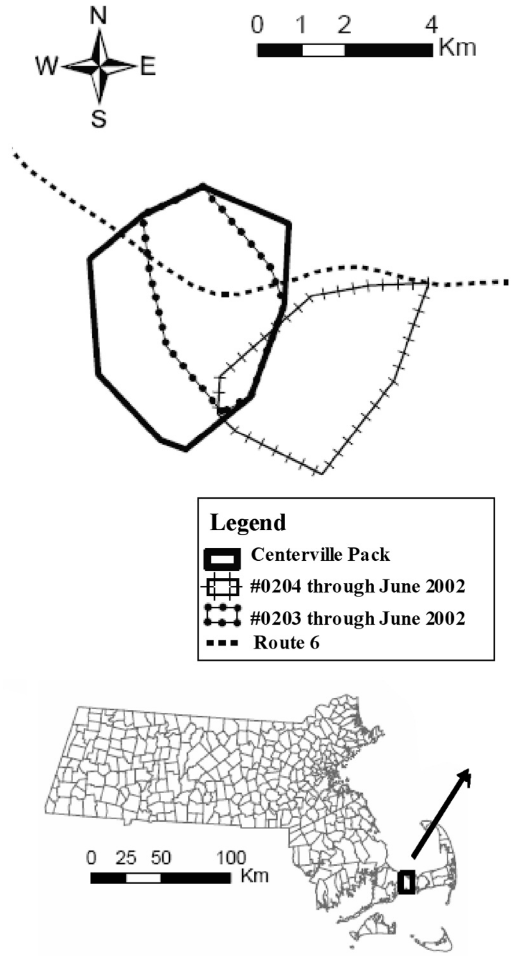

FIGURE 1. Territories for Coywolves on Cape Cod, Massachusetts, through June 2002, when #0103 (part of the Centerville pack) died.

TABLE 1. Proportion of overlap of Coywolf territories in Centerville, Massachusetts. For example, the value 0.0812 (row 2, column 3) should be interpreted as 8.12% of #0204's territory through June 2002 was overlapped by #0203's territory through June 2002. Or the value 0.8569 (row 5, column 3) should be interpreted as 85.69% of #0203's territory after June 2002 was overlapped by #0203's territory through June 2002.

	Centerville Pack	#0204 through June 2002	#0203 through June 2002	#0204 after June 2002	#0203 after June 2002
Centerville Pack	—	0.0548	0.5321	0.5413	0.2684
#0204 through June 2002	0.0872	—	0.0812	0.0585	x
#0203 through June 2002	1.0000	0.0960	—	x	0.4325
#0204 after June 2002	0.8380	0.0570	x	—	0.0488
#0203 after June 2002	0.9994	x	0.8569	0.1174	—

Following the death of #0103 during June 2002, #0203 and #0204 readjusted their territories (Figure 2). Coywolf #0203 decreased the size of his territory almost exactly in half (from 10.46 km^2 to 5.28 km^2) after #0103's death and stayed mostly north of Route 6, while #0204 maintained virtually the same territory size as before #0103's death (from 12.36 km^2 to 12.70 km^2), although she shifted her range westward using the southern portion of the Centerville pack's former territory (Figure 2).

Approximately 86% of #0203's new territory (i.e., post-June 2002) overlapped his former one (i.e., through June 2002), whereas only ~6% of #0204's new territory overlapped her former one (Table 1). The new territories of #0203 and #0204 displayed little overlap (~12%), and they essentially subdivided the Centerville pack's former territory in two with #0203 (and his pack) using the northern section and #0204 (and her pack) using the southern section. Specifically, 99.9% and 83.8% of #0203's and #0204's new ranges, respectively, overlapped with the Centerville pack's former territory, and 88% of #0203's and #0204's combined new (i.e., post-June 2002) territories overlapped the Centerville pack's former territory (Table 1).

Coywolves #0203 and #0204 lived as a breeding male and female in each of their respective packs, reproduced in April of each year they were radio-tracked, and lived in a pack size of three or four full-sized individuals. We directly observed both tending pups (and observed #0204 lactating), knew their respective mates by sight (i.e., physical characteristics), and consistently observed both individuals traveling as part of a small pack of three Coywolves on 40 occasions for #0204's pack and 22 times for #0203's pack (a fourth individual in each pack was only occasionally observed; #0203's pack = 4 sightings; #0204's pack = 6).

We estimated a winter density of 0.57–0.76 individuals/km^2 and 0.24–0.32 individuals/km^2 for #0203's and #0204's packs, respectively. The combined density for the two packs post-June 2002 was 0.33–0.45 individuals/km^2, ~2.2 times greater than the estimate for the Centerville pack. When accounting for the 12% overlap in the outer edge of each pack's territories (i.e., removing that area from one of the pack's territory sizes; Table 1), Coywolf densities were 0.38–0.50 individuals/km^2 or ~2.5 times greater than the Centerville pack's estimated density.

Coywolf #0203's and #0204's post-June 2002 territories remained consistent for over two and a half years (Figure 2). Coywolf #0203 was located 103 times until his death (gunshot) on 28 February 2005 on his territory, while #0204 was located 1422 times through August 2008 (including two recaptures: 6 May 2006, 16.8 kg; 3 May 2008, 18 kg) on her territory. Coywolf #0204 was still alive (and was still being radio-tracked) as of the completion of this study.

Discussion

This study documents a more than two-fold increase in local Coywolf pack density in the Centerville area of the town of Barnstable, Massachusetts, following the death of a resident pair of breeding Coywolves. Following the death of the original resident pair, that pack's territory was roughly divided in two; the northern portion was annexed by a beta male member (and his pack associates) of the original Centerville pack and the southern portion was occupied by a pack whose territory formerly bordered, with minimal overlap, on the Centerville pack's territory to the east. While it is difficult to understand the process of how and why these Coywolves subdivided the original territory approximately in half, the data clearly show the multilane highway (Route 6) as the approximate divider. The 12% overlap of the two pack's ranges involved both groups infrequently exploring the other side of the highway (Figure 2).

In order for the density (and, in turn, the population size) of a territorial species such as a Coyote, Coywolf, or Wolf to increase, at least one of the following scenarios must occur: (1) average pack territory size decreases (e.g., Person and Hirth 1991; Mech and Boitani 2003b); (2) average pack size increases (e.g., Way 2003); (3) the number of transient individuals in a population increases (see Way 2007b and sources within); or (4) packs become less territorial, allowing for overlap among territories of neighboring packs (Forbes and Theberge 1995; Mech and Boitani 2003b). The first two scenarios (and possibly the fourth) occur at a local, resident pack(s) scale in canids, depending largely on the availability of food (e.g., Gese et al. 1996a; Crabtree and Sheldon 1999), while the third scenario occurs over a much greater spatial scale, as the result of the long-distance movements often exhibited by transient canids. Observations detailed in our study support an increase in canid density under scenario 1, where the new packs subdivided the Centerville pack's original territory roughly in half, yet each pack lived at a normal pack size (i.e., three or four individuals) within each small territory.

Gese (1998) documented a similar shift in the territories of resident Coyote packs following the death of an alpha male in Yellowstone National Park (Wyoming, USA), although no increase in Coyote density was observed. One potential explanation for the original territory in our study being divided is the following: subsequent to the death of the breeding male of the Centerville pack (#0103), there was no dominant male remaining to ward off non-pack members (e.g., see Gese 2001), thereby allowing an influx of Coywolves into the area. Similarly, researchers studying Cougars (*Puma concolor*) and Black Bears (*Ursus americanus*) have demonstrated that, in certain instances, killing adult territorial males can cause an influx and hence greater population density of both of these species in a local area (Sargeant and Ruff 2001; Hornocker and Negri 2010: 138, 236, 239).

While not quantified in this paper, the increase in density did not appear to be the result of a change in food availability, as rodents and rabbits comprised the majority of food during both periods (i.e., prior to and following the death of the original resident pair), and there was no noticeable change in the availability of these or other food sources (e.g., anthropogenic sources, domestic cats) in the study area (J. Way, unpublished data). However, more rigorous studies need to better correlate food resources with Coyote/Coywolf density.

This research highlights the need to study carnivores in a diversity of landscape settings over broad temporal scales to elucidate factors causing variability in territory and group sizes. Coyotes and Coywolves are territorial, and this effectively limits their density (Gese et al. 1996a, 1996b; Patterson and Messier 2001; Way et al. 2002a). Therefore, it is likely that there are many factors other than food availability that can influence territory size and population density in a given locale. For instance, there may be a behavioral mechanism whereby transients (either as individuals or in pairs) settle into any vacant territory they can find, even if it is smaller than a typical territory used by a (former) pack or is of suboptimal quality.

Additionally, it is plausible that social factors may serve to reduce dispersal rates in populations suffering above-average mortality rates (Frank and Woodroffe 2001). For example, the social gaps caused by the loss of dominant pack members as the result of control programs or trapping may enable lower ranking animals, which would otherwise disperse (e.g., Gese

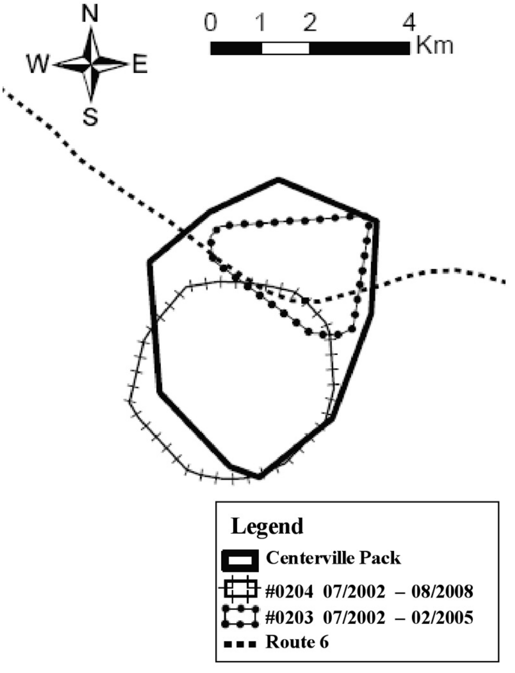

FIGURE 2. Territory of the original Centerville pack (Coywolves #0104 and #0103) until the death of #0103 in June 2002, and territories for #0203 and #0204 after June 2002 on Cape Cod, Massachusetts. Note: #0203 acted as a pack associate (using most of the original range of the Centerville pack) until his putative father, #0103, died.

et al. 1996b), to remain on their natal territory (Frank and Woodroffe 2001; Gittleman et al. 2001). This may be the case with Coyote #0203 in our current study where, after #0203's putative parents (#0104 and #0103; Way 2004) were killed, he was able to remain on a portion of his natal territory as a dominant breeding male.

Future research should monitor the long-term stability of these territories, as was done in this study. For example, if there were a short-term decrease in territory sizes and then an expansion back to one pack in the original territory, the findings of a reduction in the size of the territory would be inconclusive. It is notable in this study, however, that both territories remained small for more than two years after the original pack's dominant male died.

Management Implications

In areas of low to moderate natural and human-caused mortality, where there is a theoretical abundance of transient Coyotes/Coywolves that have the potential to move into a vacant territory, an unanticipated consequence of control/reduction programs may be a subsequent increase in the density of Coyotes or Coywolves (at least locally, at the pack scale) following the removal of a breeding male. Under this scenario, there is the possibility that newly colonizing individuals may use smaller areas than the original pack(s), thereby increasing local canid density. Though the mechanisms underlying such shifts to smaller territories are still poorly understood, the occurrence of these shifts in itself is noteworthy, albeit at the small scale (i.e., one pack forming two) observed in this study. There is considerable documentation of transients quickly filling territories left vacant following the death and/or range shift of resident Coyotes and Coywolves (Harrison 1992; Gese 1998; Knowlton et al. 1999; Way 2007b).

If this observed pattern is robust across human-dominated habitats, the potential increased Coyote or Coywolf density that follows territory loss may have significant top-down impacts. Such patterns were observed in Phoenix, Arizona, USA, where the presence of Coyotes increased the foraging activity of songbirds, likely as a result of top-down impacts on feral cats (Adley and Warren, unpublished data). Research similar to ours conducted at larger spatial and temporal scales may provide improved insight into Coyote/Coywolf space-use dynamics and allow for a better understanding of why control programs have historically been inefficient and ineffective (Parker 1995) as well as potentially inhumane and unethical, given the social, intelligent, playful nature of Coywolves (Way 2007a).

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