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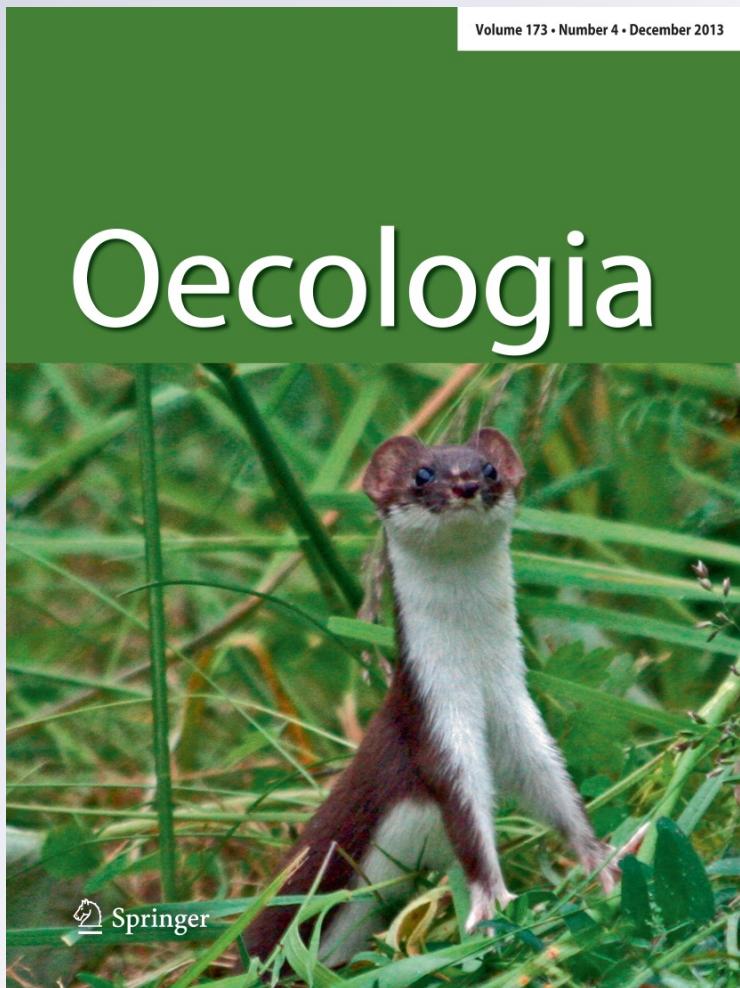
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Inter-specific territoriality in a *Canis* hybrid zone: spatial segregation between wolves, coyotes, and hybrids

John F. Benson · Brent R. Patterson

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Abstract Gray wolves (*Canis lupus*) and coyotes (*Canis latrans*) generally exhibit intraspecific territoriality manifesting in spatial segregation between adjacent packs. However, previous studies have found a high degree of interspecific spatial overlap between sympatric wolves and coyotes. Eastern wolves (*Canis lycaon*) are the most common wolf in and around Algonquin Provincial Park (APP), Ontario, Canada and hybridize with sympatric gray wolves and coyotes. We hypothesized that all *Canis* types (wolves, coyotes, and hybrids) exhibit a high degree of spatial segregation due to greater genetic, morphologic, and ecological similarities between wolves and coyotes in this hybrid system compared with western North American ecosystems. We used global positioning system telemetry and probabilistic measures of spatial overlap to investigate spatial segregation between adjacent *Canis* packs. Our hypothesis was supported as: (1) the probability of locating wolves, coyotes, and hybrids within home ranges ($\bar{x} = 0.05$) or core areas ($\bar{x} < 0.01$) of adjacent packs was low; and (2) the amount of shared space use was negligible. Spatial segregation did not vary substantially in relation to genotypes of adjacent packs or local environmental conditions (i.e., harvest regulations or road densities). We provide the first telemetry-based demonstration of spatial segregation between wolves and coyotes, highlighting the novel relationships between *Canis* types

in the Ontario hybrid zone relative to areas where wolves and coyotes are reproductively isolated. Territoriality among *Canis* may increase the likelihood of eastern wolves joining coyote and hybrid packs, facilitate hybridization, and could play a role in limiting expansion of the genetically distinct APP eastern wolf population.

Keywords *Canis lycaon* · Home range · Hybridization · Overlap · Utilization distribution

Introduction

Territoriality has been defined in numerous ways by ecologists, but a common definition refers to defense of home ranges that are spatially segregated from other individuals or social groups (Burt 1943; Maher and Lott 1995; Gordon 1997). Territoriality allows animals to retain relatively exclusive use of space and access to the resources therein, usually food, dens or nests, and/or mates (Gese 2001). In addition to ensuring access to limited resources, spatial segregation among territorial animals may also serve to minimize encounters and direct conflict between individuals or social groups that depend on the same or similar resources for survival and reproduction (Wilson 1975).

Territoriality is most often used to describe behavior among individuals of the same species (Burt 1943; Gese 2001), as morphological and ecological similarities between conspecifics often lead to strong intraspecific competition for resources (Begon et al. 1996). However, territoriality also sometimes occurs between individuals of different species, often among congeners or within guilds when competition for shared resources is strong (Hoi et al. 1991; Begon et al. 1996; Tynkkynen et al. 2006). Logically, interspecific territoriality and spatial segregation might be

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predicted between parental types of hybridizing species that also exhibit intraspecific territoriality because hybridization involves closely related species that often share morphological and ecological traits, and have similar resource requirements. Additionally, hybrid individuals often exhibit morphology intermediate to parental types (Wolf and Mort 1986; Grant and Grant 1994) which may further intensify competition between individuals within hybrid zones.

Wolves (*Canis* spp.) and coyotes (*Canis latrans*) both exhibit intraspecific territoriality, which manifests in a high degree of spatial segregation between social units (Gese 2001; Mech and Boitani 2003). However, as noted by Berger and Gese (2007), no telemetry-based studies have documented a high degree of interspecific spatial segregation between wolves and coyotes. Fuller and Keith (1981) suggested that wolves and coyotes had non-overlapping home ranges in northeastern Alberta, in a study based on movements of one radio-collared coyote and capture location of four others in relation to wolf territories. Subsequent research with larger sample sizes has invariably found a high degree of overlap between sympatric wolves and coyotes. For example, coyotes in Riding Mountain National Park, Manitoba overlapped spatially and temporally with wolves and were attracted to areas of wolf activity, likely to locate wolf-killed ungulates for scavenging (Paquet 1991). Thurber et al. (1992) found that home ranges of all coyotes they studied overlapped with those of wolves in Alaska. Arjo and Pletscher (1999) showed that annual coyote home ranges overlapped with those of wolves more than seasonal home ranges, but overlap was considerable for both periods (median overlap = 100 % annually, 60 % seasonally). Berger and Gese (2007) documented a high degree of spatial overlap between home ranges and, in some cases, core areas of wolves and coyotes in Wyoming where coyote home ranges were completely subsumed within those of wolves in areas of highest wolf density. In areas with substantial spatial overlap between coyote and wolf home ranges and core areas, coyotes apparently reduce risk of interspecific aggression from wolves by modifying resource selection within these shared ranges in response to escalated risk of encountering wolves (Atwood and Gese 2010). Thus, virtually all studies have found that coyotes and wolves do not exhibit spatial segregation, and it appears that coyotes must balance the risks of wolf aggression with the rewards gained by scavenging from wolf-kills (Paquet 1991; Arjo and Pletscher 1999; Berger and Gese 2007; Atwood and Gese 2008, 2010).

Most previous investigations of spatial relationships between wolves and coyotes have involved populations of gray wolves (*Canis lupus*) and coyotes in western North America, where the species are reproductively isolated (García-Moreno et al. 1996; Pilgrim et al. 1998; Kyle et al. 2006). In these western ecosystems, wolf and

coyote interactions tend to be characterized by aggression from wolves towards coyotes and scavenging of wolf food resources by coyotes (Paquet 1991; Berger and Gese 2007; Atwood and Gese 2010). In portions of eastern North America inhabited by intermediate-sized wolves, eastern (*Canis lycaon*, Ontario) or red (*Canis rufus*, North Carolina) wolves, we predict different relationships between wolves and coyotes and a higher degree of spatial segregation for several reasons. First, eastern and red wolves share genetic similarities with coyotes, either because they share a recent common ancestor with coyotes (Wilson et al. 2000) or because they represent the outcome of past hybridization between gray wolves and coyotes (von Holdt et al. 2011). Regardless, eastern and red wolves are intermediate in size between gray wolves and coyotes (Phillips and Henry 1992; Benson et al. 2012), which likely increases competition for food and other resources with coyotes. Furthermore, eastern and red wolves have both hybridized extensively with coyotes where they are sympatric, hybridization appears to be ongoing, and backcrossing of hybrids with wolves and coyotes has been documented (Wayne and Jenks 1991; Adams et al. 2007; Rutledge et al. 2010a; Benson et al. 2012). This means that eastern/red wolves, coyotes, and hybrids all represent potential mating opportunities for one another, suggesting potential competition for mates as well as food.

We studied wolves, coyotes, and hybrids in a hybrid zone central Ontario in and adjacent to Algonquin Provincial Park to investigate spatial segregation among sympatric *Canis* types. We hypothesized that, in contrast to sympatric wolves and coyotes in western North America, packs of all *Canis* types in our study area would exhibit a high degree of both intra- and inter-specific spatial segregation of home ranges and core areas. Additionally, we conducted research in three separate study units that were characterized by differences in genetic composition of the resident packs, habitat fragmentation (i.e., by roads), and harvest regulations. Therefore, we also investigated whether variation in these factors influenced spatial segregation between adjacent packs and resulted in differences in spatial overlap across the three study units. Our results provide novel documentation of interspecific spatial relationships between wolves and coyotes in an area where hybridization occurs and clarify potential differences with previously studied systems in western North America where wolves and coyotes are reproductively isolated.

Materials and methods

Study area

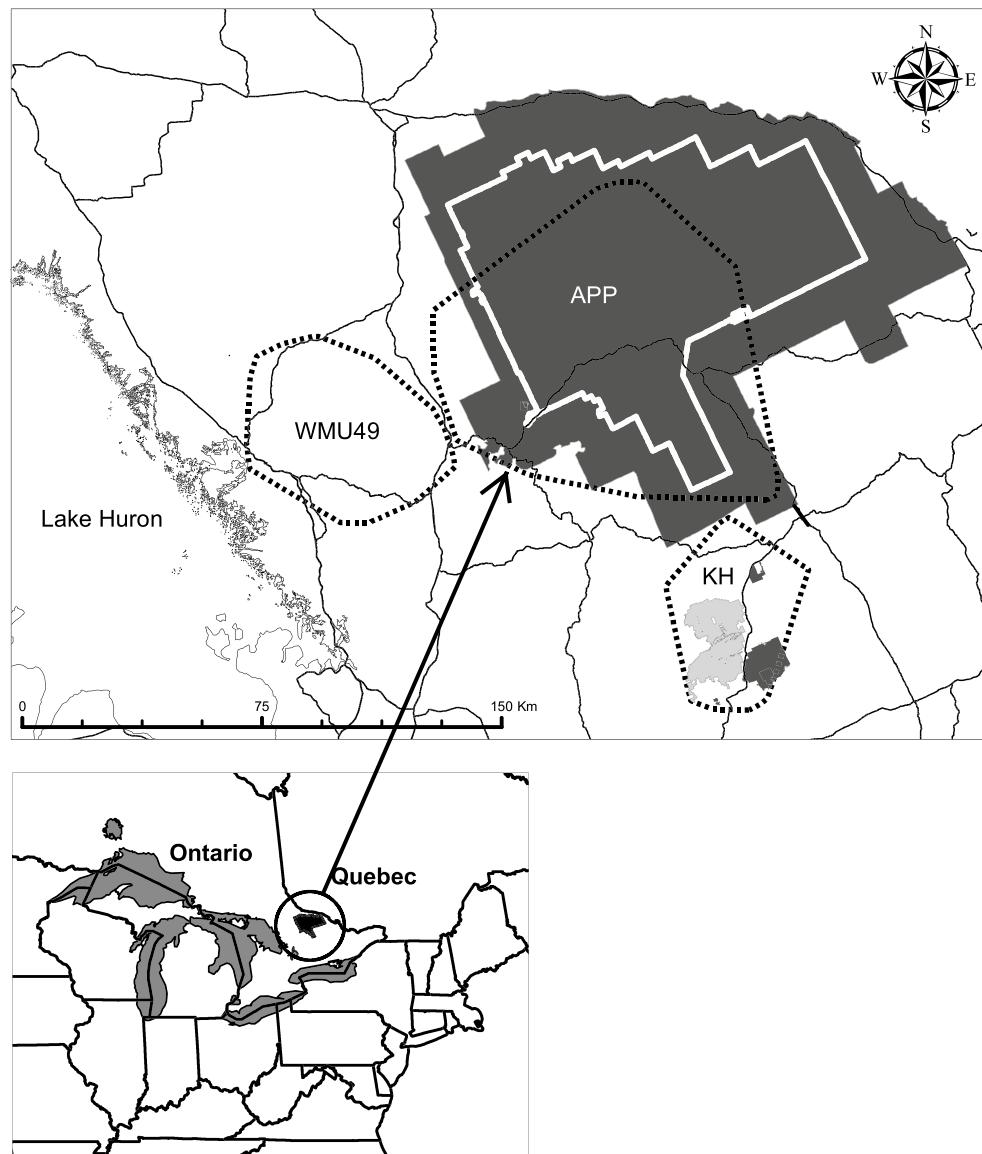
We studied wolves and coyotes in a hybrid zone with three distinct *Canis* types (eastern wolves, eastern coyotes, and

gray wolves; Benson et al. 2012) in central Ontario from 2007 to 2011 in three study units within an approximately 16,000-km² study area in and around Algonquin Provincial Park: (1) western Algonquin Provincial Park (APP), (2) Kawartha Highlands (KH), and (3) Wildlife Management Unit 49 (WMU49; Fig. 1). In APP, we monitored animals mostly in the western portion of the 7,715-km² Provincial Park. Except for small portions of home ranges of two packs, the ranges of APP animals were within the Provincial Park and the surrounding harvest ban area (park + ban area = 15,623 km²) where wolf and coyote harvest has been illegal since December 2001 (Fig. 1). Wolf and coyote harvest by trapping and hunting was allowed, on a seasonal or year-round basis, in WMU49 and KH, except for several smaller protected areas within KH. Wolf and coyote hunting was illegal, but trapping was allowed, in

Kawartha Highlands Signature Site (375 km²), whereas hunting and trapping were both illegal in the Peterborough Game Reserve (155 km) and in four smaller ($16 \text{ km}^2 < 1 \text{ km}^2$) protected areas in KH (Fig. 1). However, we note that all study animals in KH were at risk of harvest mortality despite these smaller protected areas, as home ranges and movements of all radio-collared wolves, coyotes, and hybrids in KH overlapped with harvested areas.

Density of primary (1°) and secondary (2°) roads in the home ranges of wolves, coyotes, and hybrids were lowest in APP (1° = 0.02, 2° = 0.09 km/km²), intermediate in KH (1° = 0.05, 2° = 0.34 km/km²), and highest in WMU49 (1° = 0.09, 2° = 0.57 km/km²; road densities from Benson et al. 2012). Primary roads were paved roads with relatively high traffic volume classified as freeways, expressways or highways. Secondary roads were mostly paved and

Fig. 1 Three study units [Wildlife Management Unit 49 (WMU49), Algonquin Provincial Park (APP), Kawartha Highlands (KH)] in central Ontario, Canada where spatial overlap of wolves, coyotes and hybrids was studied, 2007–2011. Study units are denoted by minimum convex polygons (dashed borders) created using telemetry data from study animals. White line denotes APP park boundary and black lines are major roads. Dark gray shading indicates areas where wolves and coyotes are fully protected from harvest, whereas light gray shading indicates areas where trapping (but not hunting) was allowed



were classified as arterial, local/street, or collector roads, except for a few major gravel forest access roads in APP that received relatively high traffic volume and allowed speeds of >50 km/h. Therefore, we studied wolves, coyotes, and hybrids in three study units representing a gradient of human disturbance: APP (full protection for wolves/coyotes, lowest road density); KH (partial protection for wolves/coyotes, intermediate road density); and WMU49 (no protection for wolves/coyotes, highest road density).

As discussed in Benson et al. (2012) eastern wolves, gray wolves, and coyotes in central Ontario have experienced varying and uncertain histories of hybridization. Thus, we do not suggest that the eastern wolves, gray wolves, and eastern coyotes we studied are necessarily “pure” representations of the ancestral genomes of these species. We also acknowledge controversy regarding the origin of the eastern wolf (e.g., Wilson et al. 2000; Kyle et al. 2006; von Holdt et al. 2011). Nonetheless, the *Canis* types in our study area were genetically and morphologically distinct (Benson et al. 2012), and we refer to them as “eastern wolves,” “gray wolves,” and “coyotes” for simplicity. Resident canids in western APP were primarily eastern wolves (63 %) with smaller numbers of gray wolf-eastern wolf hybrids (18 %), or eastern or gray wolf × coyote hybrids (15 %; Benson et al. 2012). Resident canids in KH were a more balanced mix of eastern wolves (38 %), coyotes (33 %), and eastern wolf × coyote hybrids (19 %; Benson et al. 2012). Resident canids in WMU49 were mostly coyotes (64 %) or coyote-eastern wolf hybrids (24 %), with fewer wolves (7 %; Benson et al. 2012). Therefore, eastern wolves were the dominant canid in APP, KH was inhabited by a relatively balanced combination of eastern wolves, coyotes, and hybrids, and coyotes and hybrids were the dominant canids in WMU49.

Field methods

We captured wolves, coyotes, and hybrids using padded foothold traps, modified neck snares, and with net-guns fired from helicopters. We immobilized animals captured in traps and snares, whereas animals captured with net-guns were restrained manually without immobilizing agents. All capture and handling of animals was done in accordance with, and was approved by, Trent University (protocol no. 08039) and Ontario Ministry of Natural Resources (permit nos. 04–75 through 11–75) Animal Care Committees. We deployed mortality-sensitive global positioning system (GPS; Lotek Wireless, Newmarket, ON) or very high frequency (VHF; Lotek Wireless; Telonics, Mesa, AZ; SirTrack, Havelock North, New Zealand) radio-collars on captured animals to monitor movements and survival. GPS collars were programmed to remain on the animals for approximately 1 year and collect approximately 4,000

locations. We monitored collared animals at least once per week using aerial and ground telemetry for survival and to determine/verify pack associations for the duration of the study.

Home range estimation and spatial overlap analysis

We estimated fixed kernel (Worton 1989; Börger et al. 2006) home ranges (95 %) and core areas (60 %) using the plug-in estimator to determine optimal bandwidth (Sheather and Jones 1991) for focal packs using GPS telemetry data. We used 95 and 60 % for home ranges and core areas, respectively, for consistency with previous studies investigating spatial segregation between wolves and coyotes (Arjo and Pletscher 1999; Berger and Gese 2007; Atwood and Gese 2010). Our telemetry-fix schedules were variable within and across some months for some collars such that areas used during intensive fix periods would have been over-represented if we had used all of the data. Therefore, we systematically subsampled data from collars with variable fix schedules so that the data used to estimate each home range were collected at regular intervals throughout the year (i.e., a fix every 1.5, 2, 4, 5 or 6 h depending on the collar). We estimated home ranges using concurrent data (i.e., from identical date ranges) for both packs in each dyad to ensure that we were comparing space use during periods when both packs were occupying their home ranges. We used data from 58–365 days to estimate home ranges for each dyad ($\bar{x} = 165$ days, SE = 20, $n = 26$ dyads), beginning with the first day that concurrent data were collected for a given dyad. As noted by Börger et al. (2006) it is critical to use data sampled from an equal number of days when comparing kernel home ranges, but inferences from such comparisons are robust to variation in the number of fixes. After subsampling, we used all data to estimate home ranges in most cases ($\bar{x} = 729$ locations, SE = 46, $n = 52$ home ranges); however, we excluded locations from one long-range (>84 km) movement by one pack outside of their normal area of use during winter to visit a known deer yard. Some resident wolves migrate from their home ranges within APP to exploit abundant prey in deer yards in areas adjacent to APP (Forbes and Theberge 1996; Cook et al. 1999). Given that our objective was to compare space use of adjacent packs while they were occupying their home range, excluding extra-territorial locations from such packs was appropriate. For packs that we monitored over multiple years, we calculated separate annual home ranges for each year, thus, in two cases, we estimated two sets of annual home ranges and core areas for a given dyad. We included these home ranges as separate data points given that annual differences in resource availability or pack membership may have influenced the degree of overlap between adjacent packs in different years. In total, we

estimated 52 home ranges and core areas for 26 pack dyads (nine from APP, six from KH, 11 from WMU49) comprising 28 different packs of wolves, coyotes, and hybrids.

To investigate spatial segregation, we estimated home ranges for pack dyads occupying adjacent 95 % home ranges. We considered home ranges to be adjacent if two 95 % home ranges either: (1) overlapped to some extent (89 % of dyads); or (2) were separated by <1.5 km at their closest boundaries ($n = 3$, 1.15, 0.5, 0.06 km). Fieberg and Kochanny (2005) reviewed methods to evaluate spatial segregation and overlap and concluded that methods using the utilization distribution (UD) (Worton 1989) were superior to earlier, simplistic comparisons of home range overlap. Accordingly, we compared overlap of home ranges and core areas using two probabilistic methods utilizing UDs of neighboring animals to investigate spatial segregation. We used the probability of home range overlap (PHR) to estimate the probability of an individual from pack j being in pack i 's home range or core area ($\text{PHR}_{i,j}$) and vice versa ($\text{PHR}_{j,i}$) using the formula proposed by Fieberg and Kochanny (2005):

$$\text{PHR}_{i,j} = \iint_{A_i} \hat{\text{UD}}_j(x, y) dx dy \quad (1)$$

where $\hat{\text{UD}}_j$ is the estimated UD for canid pack j and A_i is the area of overlap of pack i 's home range with pack j 's, x and y represent estimates of the UD at a set of grid points, and $dx dy$ are the area of each grid cell. PHR should be superior to a similar, commonly used method:

$$\begin{aligned} \text{Proportion of overlap} &= \\ &\text{Area of overlap}_{i,j} / \text{area of home range}_i, \end{aligned} \quad (2)$$

which simply determines the proportion of an individual's home range that is overlapped by another individual because the PHR accounts for differences in the relative probability of space-use by utilizing the UD (Fieberg and Kochanny 2005). However, because PHR is similar in principle to the proportional measure of area of overlap (Eq. 2), it should be useful for coarse comparisons with previous studies that did not estimate UDs. Next, we estimated the utilization overlap index (UDOI):

$$\text{UDOI} = A_{i,j} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \hat{\text{UD}}_i(x, y) \times \hat{\text{UD}}_j(x, y) dx dy, \quad (3)$$

which provides a joint measure of overlap between two neighboring individuals or packs. A value of 0 indicates no overlap and a value of 1 indicates complete overlap and uniform space use (Fieberg and Kochanny 2005). UDOI values >1 are also possible if two UDs are non-uniformly distributed and have a high degree of overlap (Fieberg

and Kochanny 2005). UDOI is likely the most appropriate technique for quantifying overlap in terms of shared space-use, particularly for studies using UD-based estimates of home range (e.g., kernels) and GPS telemetry (Fieberg and Kochanny 2005). We calculated home ranges, utilization distributions, PHR, and UDOI in R Statistical software 2.13.1 using the Adehabitat package and code obtained from the lead author of Fieberg and Kochanny (2005).

Genetic ancestry

We extracted DNA from blood or hair samples obtained from study animals at capture and amplified and scored 12 microsatellite loci as described in Benson et al. (2012). We determined genetic ancestry of all captured and radio-collared animals with genetic analyses described in detail by Benson et al. (2012). Animals of known genetic ancestry in most (82 %) of the packs included in our spatial overlap analyses were eastern wolves, coyotes, or eastern wolf × coyote hybrids. However, there were animals from five packs (three in APP, one in KH, one in WMU49) that were eastern wolf × gray wolf hybrids ($n = 3$ packs), coyote × gray wolf hybrids ($n = 1$ pack), or eastern wolf × gray wolf × coyote hybrids ($n = 1$ pack). For simplicity, hereafter we refer to all animals of wolf origin (eastern wolves and eastern wolf × gray wolf hybrids) as "wolves" and all animals of mixed wolf and coyote ancestry (eastern wolf × coyote, coyote × gray wolf, or eastern wolf × gray wolf × coyote) as "hybrids." Packs in which individuals of known ancestry were either all wolves or all coyotes were classified as "wolf" and "coyote" packs, respectively. However, not all packs were composed of individuals from a single *Canis* type. Any pack that contained at least one hybrid, or contained both wolves and coyotes, was considered to be a hybrid pack. We knew the genetic identity of both breeding animals in 75 % of the packs included in our overlap analyses, through genetic analysis or by inferring the genotype of an unknown breeder from the genotypes of a known breeder and their direct offspring (Benson et al. 2012; Table 1). For packs where both breeders were known, we suspect that most other pack members that were not sampled were offspring of the breeding pairs because *Canis* packs in the APP region are family-based and are generally composed of a breeding pair and their direct offspring (Rutledge et al. 2010b; Benson et al. 2012). Offspring that were not sampled would not have changed our pack-genotype classifications because their genotypes would reflect those of their parents. Therefore, although our knowledge of genetic ancestry for all pack members of all focal packs was incomplete, we believe our data allowed us to reliably classify packs as wolf, coyote, or hybrid for the purposes of our analyses.

Table 1 Genotypes of breeding pairs in *Canis* packs included in analyses of spatial overlap between adjacent pack dyads in central Ontario 2007–2011

Breeding pair	n
Wolf–wolf	7 ^{a,b}
Coyote–coyote	5 ^{c,d}
Coyote–hybrid	5
Wolf–unknown	4
Hybrid–hybrid	2
Coyote–unknown	2
Coyote–wolf	1 ^e
Wolf–hybrid	1
Unknown	1 ^f

All breeding relationships were determined via genetic pedigree analysis from Benson et al. (2012) unless otherwise noted

^a Two breeding genotypes inferred from wolf parent and direct wolf offspring in pack

^b One breeding relationship inferred because only two adults (both wolves, male and female) in pack

^c Two breeding genotypes inferred from coyote parent and direct coyote offspring in pack

^d One breeding relationship inferred because only two adults (both coyotes; male and female) in pack

^e Breeding genotype inferred from one wolf parent and 50–50 % (approximately) wolf-coyote hybrid offspring in pack

^f Adult male coyote only captured animal in pack, breeding status unknown

Observational data

As noted by Gese (2001), territoriality among wolves and coyotes is readily accepted, but the actual mechanisms are rarely observed. As in our study, territoriality is often inferred via indirect means such as spatial segregation of home ranges or through evidence of scent-marking, as direct observation of territorial defense is rare for elusive carnivores (Gese 2001). We describe three observations from the field that provided more direct (though limited by sample size) information regarding inter- and intraspecific territoriality among wolves, coyotes, and hybrids in our study area.

Results

Across our study area, there was a high degree of spatial segregation between wolves, coyotes, and hybrids (Figs. 2, 3, 4; Tables 2, 3, 4). For all animals, the probability of being located within the 95 % home range of a specific adjacent pack was <0.22 ($\bar{x} \text{ PHR}_{95\%} = 0.052, \text{SE} = 0.007, n = 52$). For all animals, the probability of being located within the 60 % core area of a specific neighbor was <0.08 and for 65 % of animals the probability was 0

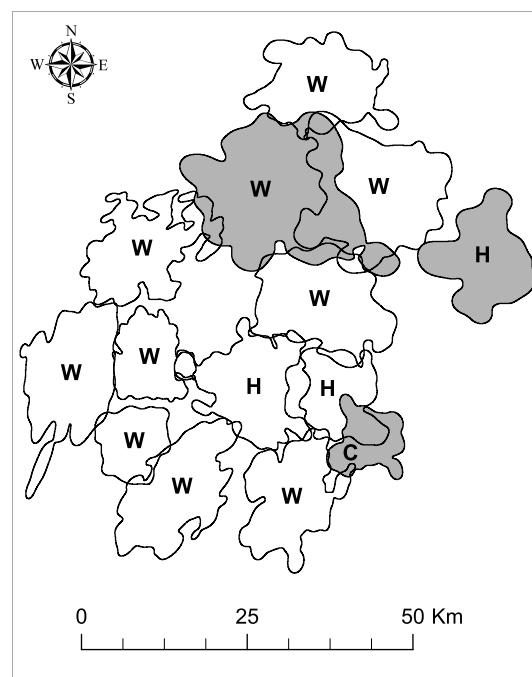


Fig. 2 Annual 95 % fixed kernel home ranges of wolf (W), coyote (C), and hybrid (H) packs in Algonquin Provincial Park, Ontario, Canada, 2007–2011. Home ranges shown here differ slightly from those used in overlap analyses because: (1) analyses were restricted to concurrent data for all dyads; (2) small, non-contiguous portions of home ranges were removed for clarity; and (3) not all packs shown were included in overlap analyses because we restricted analyses to concurrent dyads. Packs not included in analyses are shown in gray shading

($\bar{x} \text{ PHR}_{60\%} = 0.009, \text{SE} = 0.002, n = 52$). The UDOI also indicated that wolves, coyotes, and hybrids were spatially segregated as all dyads exhibited low overlap of 95 % home ranges ($\bar{x} = 0.004, \text{SE} = 0.001, n = 26$) and 60 % core areas ($\bar{x} < 0.001, \text{SE} < 0.001, n = 26$) relative to uniform space use. All UDOI values for 95 % home ranges were <0.03 and all UDOI values for 60 % core areas were <0.002.

Overlap between both home ranges and core areas was negligible and appeared to be similar between adjacent wolf–wolf, wolf–coyote, wolf–hybrid, coyote–hybrid, and hybrid–hybrid pack dyads (Tables 2, 3). There also were not substantial differences in home range or core area overlap among the three study units (Table 4). Given the consistently negligible degree of overlap of 95 % home ranges and near complete spatial segregation of 60 % core areas in relation to genetic ancestry of adjacent packs and across study units, statistical comparison of overlap estimates did not seem appropriate or necessary to evaluate our hypothesis, or to investigate potential differences across study units. Wolves, coyotes, and hybrids were clearly spatially segregated and the degree of spatial segregation did not

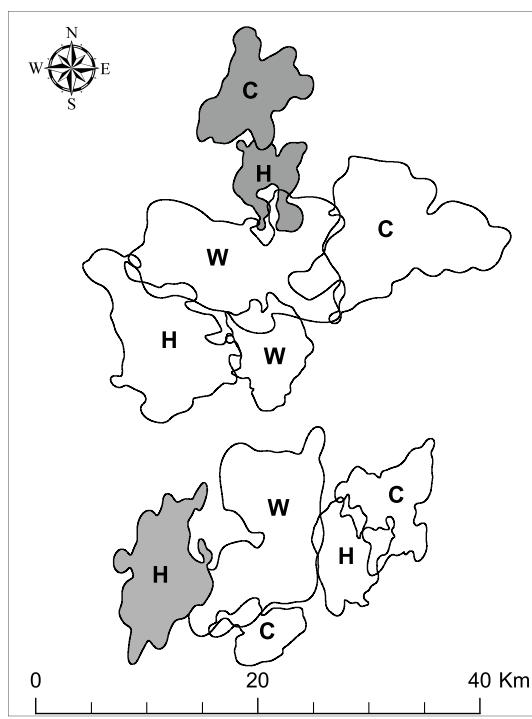


Fig. 3 Annual 95 % fixed kernel home ranges of W, C, and H packs in Kawartha Highlands, Ontario, Canada, 2009–2010. Home ranges shown here differ slightly from those used in overlap analyses because: (1) analyses were restricted to concurrent data for all dyads; (2) small, non-contiguous portions of home ranges were removed for clarity; and (3) not all packs shown were included in overlap analyses because we restricted analyses to concurrent dyads. Packs not included in analyses are shown in gray shading. For abbreviations, see Fig. 2

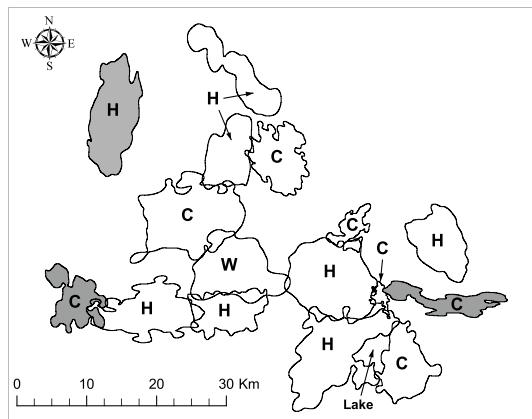


Fig. 4 Annual 95 % fixed kernel home ranges of W, C, and H packs in Wildlife Management Unit 49, Ontario, Canada, 2007–2011. Home ranges shown here differ slightly from those used in overlap analyses because: (1) analyses were restricted to concurrent data for all dyads; (2) small, non-contiguous portions of home ranges were removed for clarity; and (3) not all packs shown were included in overlap analyses because we restricted analyses to concurrent dyads. Packs not included in analyses are shown in gray shading. A large lake that occupied an area between adjacent home ranges is also shown. For abbreviations, see Fig. 2

Table 2 Mean probability of a pack of a given genotype being located in the 95 % home range ($PHR_{95\%}$) and 60 % core area ($PHR_{60\%}$) of an adjacent pack of a given genotype in central Ontario, Canada 2007–2011

	$PHR_{95\%}$	SE	<i>n</i>	$PHR_{60\%}$	SE	<i>n</i>
Wolf in wolf	0.039	0.016	12	0.011	0.007	12
Hybrid in hybrid	0.073	0.020	6	0.010	0.007	6
Wolf in coyote	0.084	0.044	3	0.018	0.017	3
Coyote in wolf	0.065	0.006	3	0.008	0.007	3
Wolf in hybrid	0.020	0.010	7	0.003	0.003	7
Hybrid in wolf	0.042	0.020	7	0.007	0.007	7
Coyote in hybrid	0.075	0.049	7	0.011	0.007	7
Hybrid in coyote	0.055	0.028	7	0.008	0.008	7
Overall	0.052	0.008	52	0.009	0.002	52

Also shown are SEs and number of packs (*n*)

appear to be strongly influenced by the genetic composition of adjacent packs or by differences in environmental conditions across study units (Tables 2, 3, 4; Figs. 2, 3, 4).

Observations of aggressive encounters between canids

First, we documented the killing of a hybrid (coyote × eastern wolf) breeding adult male in WMU49, whose mate was a coyote, by a neighboring pack of wolves (gray wolf × eastern wolf). Field evidence and necropsy of the carcass conclusively attributed cause of death to be aggression from wolves. We documented a GPS-collared wolf from the adjacent pack at the mortality site concurrent with the estimated time of death and we found beds of wolves in the snow near the carcass (<100 m). We also established that a second wolf from the suspected aggressor pack was present at the mortality site through genetic identification of a hair sample collected from one of the beds. This mortality occurred in an area of home range overlap between the two packs (included as a dyad in our analysis) approximately 0.7 and 1.6 km from the closest border of the hybrid and wolf packs' home range, respectively.

Second, while tracking a hybrid breeding female (her mate was a coyote) in a focal pack in WMU49 during a helicopter flight, we observed the radio-collared hybrid female running from two larger uncollared canids across an open sand pit. After being cornered against a pond by the larger animals, the collared female turned to face the aggressors and the three canids fought intensely for approximately 20 s. The attacking animals appeared to be uncomfortable with the hovering helicopter, turning to look at it several times during the encounter before abandoning the fight and running in the direction from which they came. The hybrid female limped away in the other direction, but survived the incident and was alive at the

Table 3 Mean overlap, as estimated by the utilization distribution overlap index (UDOI), of 95 % home ranges ($UDOI_{95\%}$) and 60 % core areas ($UDOI_{60\%}$) between neighboring dyads of wolf, coyote, and hybrid packs

Pack 1	Pack 2	$UDOI_{95\%}$	SE	n	$UDOI_{60\%}$	SE	n
Wolf	Wolf	0.002	0.002	6	<0.001	<0.000	6
Wolf	Coyote	0.006	0.003	3	<0.001	0.001	3
Wolf	Hybrid	0.002	0.001	7	<0.001	<0.000	7
Coyote	Hybrid	0.006	0.004	7	<0.001	<0.000	7
Hybrid	Hybrid	0.007	0.008	3	<0.001	<0.000	3

Also shown are SEs, and number of pack dyads (n) for each mean in central Ontario, 2007–2011

Table 4 Mean (\bar{x}) PHR_{95 %}, UDOI_{95 %}, PHR_{60 %} and UDOI_{60 %} of adjacent *Canis* packs in three study units in (Algonquin Provincial Park; APP) and adjacent to [(Kawartha Highlands (KH), Wildlife

Management Unit 49 (WMU49)] APP and the surrounding buffer area where *Canis* harvest is banned in central Ontario, Canada, 2007–2011

	PHR _{95 %}			PHR _{60 %}			UDOI _{95 %}			UDOI _{60 %}		
	\bar{x}	SE	n^a	\bar{x}	SE	n^a	\bar{x}	n^b	SE	\bar{x}	SE	n^b
APP	0.042	0.012	18	0.009	0.003	18	0.003	9	0.002	<0.000	<0.000	9
KH	0.072	0.018	12	0.014	0.005	12	0.005	6	0.002	<0.000	<0.000	6
WMU49	0.049	0.011	22	0.006	0.004	22	0.004	11	0.003	<0.000	<0.000	11

We also show SEs and samples sizes (n) for each mean overlap index. For other abbreviations, see Tables 2 and 3

^a Number of packs in dyads of adjacent packs

^b Number of dyads of adjacent packs

end of the study >1 year later. This observation occurred approximately 1 km from the closest border to her home range. Given the disparity in size between the attacking animals and the hybrid female, we suspected the two attacking animals were wolves, but their genetic identity was unknown.

Third, we heard aggressive barking, howling, and fighting noises originating from across a lake (<100 m from our location) outside of our field station. We immediately confirmed that two radio-collared coyotes [a resident breeding male (within its home range) and a resident pup (approximately 7 months old, just outside its pack's home range)] from two different, adjacent packs were present at the location of the encounter. We tracked the pup as it moved quickly to the east, across a road and back to its territory following the apparent fight. Based on ground telemetry, the resident breeding male did not appear to continue the chase beyond the border of its territory. We investigated the site the next day and found the remains of a deer at the approximate location where the aggressive vocalizations were heard. This encounter occurred on the periphery of one pack's home range (approximately 150 m from the closest boundary) and just outside the second pack's range (<200 m from closest boundary). We suspect the pup from the adjacent pack was attracted by the deer carcass and was attacked and chased off by the breeding male of the resident pack.

Discussion

Our hypothesis was supported as wolves, coyotes, and hybrids exhibited a high degree of spatial segregation with neighboring packs, regardless of genotype. However, we found no evidence that differences across study units in harvest regulations, fragmentation by roads, or genetic structure of the local *Canis* populations influenced spatial overlap. Spatial segregation between adjacent packs was high throughout the study area, such that any differences in relation to these environmental conditions were inconsequential. Thus, wolves, coyotes, and hybrids in the central Ontario hybrid zone appear to be territorial with each other, regardless of the genotypic composition of adjacent packs. Our results highlight the novelty of the relationships between genetically distinct *Canis* types present in this eastern wolf-eastern coyote-gray wolf hybrid zone relative to previous studies of gray wolves and coyotes.

It is generally accepted that wolves are highly territorial and that a high degree of spatial segregation exists between adjacent wolf packs (reviewed by Mech and Boitani 2003). Coyote territoriality is also well established in the literature (e.g., Carmenzind 1978; Barrette and Messier 1980; Gese and Ruff 1997; Gese 2001). Differences in methodology between our study and many earlier studies in terms of home range estimators (minimum convex polygon vs. kernel UD), overlap indices (proportion of overlap vs.

UD-based measures), and telemetry (VHF vs. GPS) makes comparing results of overlap analyses across studies difficult. Furthermore, although many studies have conducted telemetry-based studies of wolves in North America, few, if any, have quantified the actual proportion or probability of overlap between adjacent packs. Many previous studies have provided convincing visual representations of the degree of overlap by plotting adjacent home ranges (e.g., Van Ballenberghe et al. 1975; Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987; Fuller 1989; Theberge and Theberge 2004), but did not report results of spatial overlap analyses. Methodological differences notwithstanding, mean proportion of overlap of home ranges between adjacent packs of wolves in Poland appeared to be similar to the overlap we documented between *Canis* packs in Ontario (Jędrzejewski et al. 2007). We suggest that wolves, coyotes, and hybrids in the Ontario hybrid zone we studied exhibit spatial segregation comparable to that observed among wolf packs studied elsewhere, even though direct comparisons of the exact degree of overlap were problematic.

Studies in the Greater Yellowstone Ecosystem in Wyoming and Montana quantified spatial overlap of wolf and coyote home ranges and core areas using the simple, proportional overlap metric described above (Eq. 2; Arjo and Pletscher 1999; Berger and Gese 2007; Atwood and Gese 2010). This metric is similar, but not equivalent, to the UD-based PHR_{ij} that we used. Atwood and Gese (2010) reported a high degree of 95 % home range ($\bar{x} = 0.78$) and 60 % core area overlap ($\bar{x} = 0.82$) for coyotes in wolf home ranges in southwest Montana. In northwestern Montana, overlap of annual male and female coyote 94 % home ranges was high ($\bar{x} = 0.74\text{--}1.00$ across years and sexes, whereas 62 % core area overlap was more variable (range: 0–1.00; Arjo and Pletscher 1999). In Grand Teton National Park, Wyoming four coyote 95 % home ranges were completely subsumed within wolf home ranges ($\bar{x} = 1.00$), whereas 60 % core area overlap was more variable with two coyotes exhibiting close to complete overlap with wolf core areas (0.96 and 0.97) and two coyotes showing no overlap of core areas (Berger and Gese 2007). Thus, although different methods were used for estimating overlap, the differences in overlap between studies of western gray wolves and coyotes, and the spatially segregated wolves and coyotes in our study (95 % home ranges, $\bar{x} = 0.065$; 60 % core areas, $\bar{x} = 0.008$; Table 2), were sufficient to establish that interspecific relationships between wolves and coyotes are drastically different between the two systems.

Berger and Gese (2007) also calculated the UDOI for wolves and coyotes, facilitating more direct comparisons. UDOI for wolves and coyotes in Grand Teton National Park ranged from 0.03–0.23 for 95 % home ranges ($\bar{x} = 0.13$) and 0–0.17 for 60 % core areas ($\bar{x} = 0.08$; Berger and Gese

2007). The mean UDOI for wolf-coyote dyads in our study was 0.006 for 95 % home ranges and <0.001 for 60 % core areas (Table 3), which are both more than an order of magnitude lower than mean UDOI values documented in Wyoming. Although the samples sizes of wolf-coyote dyads were low for both studies ($n = 3$, our study; $n = 4$, Berger and Gese 2007), four other dyads in our analyses contained wolves and coyotes in adjacent packs and were spatially segregated ($\bar{x} \text{ PHR}_{95\%} = 0.03$, SE = 0.04, $n = 4$; $\bar{x} \text{ UDOI}_{95\%} < 0.001$, SE < 0.001, $n = 4$). These dyads were classified as wolf-hybrid because the packs with coyotes each contained one hybrid animal. Regardless, when compared with previous work, our results clearly illustrate differences between western wolf-coyote systems and indicate that wolves, coyotes, and hybrids are spatially segregated in the APP region, regardless of genetic ancestry of individuals of adjacent packs.

Variation in the density of ungulate (moose and deer) prey across central Ontario clearly influences the distribution of wolves, coyotes, and hybrids across the landscape. Indeed, coyote ancestry in resident canids was negatively associated with moose density in and adjacent to APP as wolves tend to establish ranges in areas of highest moose densities (Benson et al. 2012). However, Benson et al. (2012) noted that there were exceptions to the general trend as several coyote packs had established home ranges in areas of high moose density and few roads that seemed suitable for wolves. Our current results may be relevant as interspecific territoriality may modify selection of home ranges at the landscape level. Eastern wolves are the dominant canid in APP and appear to have resisted hybridization more effectively within the park than in adjacent areas (Rutledge et al. 2010a; Benson et al. 2012). Spatial exclusion of coyotes from home ranges within APP may be one mechanism by which eastern wolves have minimized hybridization and retained their genetic distinctiveness. However, territorial aggression of resident coyotes and hybrids in response to dispersing wolves adjacent to APP where coyotes are abundant (e.g., WMU49) may also make it difficult for eastern wolves to become established outside of the park. Displacement of hybrids and coyotes by pairs of endangered red wolves in North Carolina was identified as the most important parameter influencing quasi-extinction and persistence probabilities of red wolves in population viability analysis (Fredrickson and Hedrick 2006). However, to our knowledge, aggression by resident coyotes and hybrids towards dispersing eastern or red wolves has not been considered as a mechanism limiting population expansion for hybridizing wolves of conservation concern in Ontario or North Carolina. A recent sampling effort adjacent to the population core of reintroduced red wolves in coastal North Carolina failed to detect any red wolves outside of the experimental population area, as

the canids detected were coyotes and hybrids (Bohling and Waits 2011). Harvest mortality of red wolves in these adjacent areas likely plays a significant role in reducing dispersal success into unprotected landscapes (Bohling and Waits 2011), as it appears to with eastern wolves outside of APP (Benson et al. 2013). Dispersing red and eastern wolves that are able to avoid harvest mortality may still have difficulty establishing breeding ranges beyond their core populations due to territorial aggression from resident coyotes and hybrids. Eastern wolves are larger than both coyotes and hybrids, but the differences are subtle (Benson et al. 2012). Wolves generally disperse individually (Mech and Boitani 2003), and would be unlikely to successfully displace a pack of resident coyotes or hybrids. Eastern wolves dispersing into areas saturated with coyote and hybrid territories such as WMU49, probably have limited options for territory establishment and instead may join packs and establish breeding unions with coyotes or hybrids when possible. Thus, territoriality among *Canis* types in areas adjacent to APP may play significant roles in reducing eastern wolf dispersal success, facilitating hybridization, and limiting the expansion of the genetically distinct APP eastern wolf population.

Rich et al. (2012) found that human-caused mortality influenced territoriality of wolves and suggested conflict with humans can increase the cost of territoriality by reducing the number of pack members available for defense and/or by causing wolves to avoid areas rich in resources where harvest risk was high. Rutledge et al. (2010b) suggested that harvest mortality increases the occurrence of unrelated animals in wolf packs, which could decrease pack cohesion. Thus, territoriality and spatial segregation between canid packs might be predicted to be greatest in unharvested areas that are relatively free of human disturbance. However, although our study area represented a gradient of human disturbance and harvest regulations (see “Study Area”), these differences did not appear to influence territoriality between wolves, coyotes, and hybrids. Spatial segregation was consistently high across all study units (Table 4; Figs. 2, 3, 4).

Obviously we did not capture every canid in our study area; however, we are confident that the degree of spatial segregation we documented was not due to missing entire packs that overlapped with the packs we monitored. Our capture efforts were intensive within each study unit during the years of the study (APP and WMU49 2007–2010, KH 2009–2010), we captured >150 canids, and the configuration of their home ranges closely resembles the mosaic pattern of territorial canids found by other studies (e.g., Van Ballenberghe et al. 1975; Fritts and Mech 1981; Peterson et al. 1984; Ballard et al. 1987; Fuller 1989; Theberge and Theberge 2004; Figs. 2, 3, 4). There were a few noticeable gaps in this mosaic of packs (Figs. 2, 3, 4), which were due

to difficulty in establishing traplines in these areas because of poor road access or private land. We often captured multiple animals on the same trapline, or within the same home range of a focal pack, and animals captured within a given area always belonged to the same pack except when: (1) they were transient or dispersing (non-pack) animals, or (2) we were trapping near home range boundaries and captured animals from adjacent home ranges. Therefore, we are confident that our capture and telemetry data accurately reflect the spatial relationships between wolves, coyotes, and hybrids within our study area in the hybrid zone in and adjacent to APP.

Gese (2001) noted that direct observations of wild canid territorial defense are difficult to obtain due to the elusive nature of wolves and coyotes, and that few researchers have been fortunate enough to document such behavior. Although our direct field observations represented a small number of occurrences, they are consistent with reports of wolf–wolf and coyote–coyote territoriality (e.g., Mech 1994; Gese 2001) and provide useful information supporting the conclusion that wolves, coyotes, and hybrids are territorial with each other in the central Ontario *Canis* hybrid zone. Most cases of intraspecific killing among wolves occur in areas of overlap between adjacent packs and close to home range boundaries (Mech 1994), as in the first two observations reported above. Our first two observations and supporting data are notable, because: (1) they were interactions between animals known or suspected to be of different genetic types; and (2) they were consistent with previous descriptions of aggressive, intraspecific wolf territorial interactions in terms of their position relative to known home range boundaries. In contrast, previous descriptions of aggressive encounters between wolves and coyotes have generally involved coyotes scavenging at wolf kills (e.g., Gese 2001; Atwood and Gese 2008). Furthermore, Atwood and Gese (2008) reported that all intraspecific mortalities of coyotes attributed to wolves were <200 m from a wolf-killed carcass. We visited all clusters of GPS locations for the hybrid packs (i.e., the recipients of aggression) involved in the first two observations described above as part of a predation study to locate all ungulate kills. However, we failed to find any evidence of a carcass within 5 km of the aggressive encounters. Thus, the first two observations appear more consistent with reports of wolf–wolf territorial aggression, rather than wolf–coyote competition for carcasses. The third observation, likely involved a carcass, but was also consistent with previous descriptions of intraspecific territorial behavior between coyotes. Gese (2001) observed 112 instances of intraspecific territorial defense by coyotes and noted that the alpha male (i.e., breeding male) was most likely to confront intruding animals, that residents in their home range were usually successful at repelling the intruders, that they abandoned the chase near the home range

boundary, and that fights did not end in mortality (but see Okoniewski 1982; Patterson and Messier 2001). All of these characteristics are consistent with our observation and have also been described by other researchers (Bekoff and Wells 1986; Carmenzind 1978). Thus, we conclude that our third observation likely represented both a competitive interaction over a carcass and active territorial defense between a resident and intruding coyote.

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