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Space use and social ecology of coyotes (*Canis latrans*) in a high-elevation ecosystem: relative stability in a changing environment

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Abstract Coyote (*Canis latrans*) spatial and social ecology are variable, but have been little studied in high-elevation environments. In these temperate ecosystems, large ungulates are prevalent and coyote pack size may be large in order for them to scavenge and defend ungulate carcasses from conspecifics in neighboring packs. We initiated a study to understand the spatial and social ecology of coyotes on the Valles Caldera National Preserve, a high-elevation (2450–3400 m) protected area in northern New Mexico. Our objectives were to (1) describe the home range size and habitat use of coyotes in the preserve, (2) describe coyote movements within and outside of packs, and (3) to evaluate the relationship between coyote social cohesion and the amount of elk (*Cervus elaphus*) in the coyote diet. We acquired global positioning system and telemetry locations from 33 coyotes from August 2005 to July 2009. We classified 23 coyotes (70 % of individuals) as residents (i.e., territorial) during at least part of the study and ten coyotes (30 %) as transients. Overall mean home range size of resident packs was 10.6 ± 2.2 (SD) km². Home range size varied between packs, but did not vary by season or year. Coyotes used dry and wet meadow habitats as expected based on availability; coyotes used riparian habitat more than

expected, and forests less than expected. Social cohesion did not vary among biological seasons. Alpha coyotes were more socially cohesive with each other than with other pack members, and a transient exhibited temporal–spatial avoidance of pack members while inside the pack’s territory followed by integration into the pack. Contrary to expectations, we found no relationship between coyote social cohesion and the proportion of elk in coyote diets. We concluded that coyote space use and sociality on the preserve were relatively stable year-round despite changes in biological needs, snow depth, and utilization of variously sized prey.

Keywords Habitat use · Social cohesion · Home range · Resident · Transient

Introduction

There have been numerous studies of coyote (*Canis latrans*) social and spatial ecology throughout North America (e.g., Messier and Barrette 1982; Andelt 1985; Mills and Knowlton 1991), but few studies have been conducted on coyotes at high elevations (e.g., Bekoff and Wells 1980; Bowen 1982; Gese et al. 1996a; Dowd et al. 2014). A general consensus of studies indicates coyote space use can be stable through time (Kitchen et al. 2000a; Young et al. 2006), but varies by geographic location. In addition, home range size of resident packs can be influenced by resources or habitat types (Gese et al. 1988a). In terms of social ecology, coyote populations can be divided into resident and transient individuals (e.g., Camenzind 1978; Bowen 1982; Bekoff and Wells 1986), but social organization differs among populations, and the way in which an individual transitions into or out of resident packs also varies (Andelt 1985; Gese 2001). Previous studies

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evaluating coyote social ecology have examined seasonal group size with most of these studies having found the largest coyote group sizes in winter, coinciding with a shift in diet from rodents to ungulates (Camenzind 1978; Bekoff and Wells 1980; Bowen 1981; Andelt 1985; Gese et al. 1988b). Gese et al. (1988b) concluded that larger winter group sizes were primarily due to increased sociality during the breeding season, and these larger groups were then able to forage for larger prey, as well as defend ungulate carcasses from conspecifics (Bekoff and Wells 1980, 1986; Gese 2004). In contrast, Bowyer (1987) found a higher percentage of coyotes in groups during June up to and including November, but the amount of mule deer (*Odocoileus hemionus*) in scats did not vary seasonally.

Our study provides insight into a high-elevation ecosystem with a predator–prey environment in which no anthropogenic predator removal is permitted, similar to studies on coyotes in several national parks (Murie 1940; Bekoff and Wells 1980; Gese et al. 1996a). The Valles Caldera National Preserve (VCNP) was federally purchased in 2000 as a “unique land mass, with significant scientific, cultural, historic, recreational, ecological, wildlife, fisheries, and productive values” with the specifics of management to be determined by a trust and board of trustees (Valles Caldera Preservation Act 2000). In 2014, the US Congress put the management of the preserve under the National Park Service. Management of coyotes or other predators has not occurred on the VCNP while under federal management, but remains a contentious issue. The VCNP is also a critical calving area for Rocky Mountain elk (*Cervus elaphus nelsoni*).

Similar to in most national parks, coyotes are valuable as watchable wildlife for the general public on the VCNP, but they also carry a stigma, particularly among some elk hunters, livestock operators, and neighboring landowners as having negative impacts on livestock and the elk population via predation on elk calves. Low elk calf:cow ratios coincided with the cessation of persecution of coyotes when the federal government purchased the land and established the preserve. Increased visibility of coyotes and anecdotal observations of coyote predation on elk calves, and a perception of larger coyote group sizes during the elk calving season, further implicated coyotes by some members of the public. Additionally, neighboring land managers have cited the need to maintain elk populations at levels that reduce impacts on other natural resources including aspen (*Populus tremuloides*) and riparian areas (Rupp et al. 2001; Neff et al. 2007). Many of the elk that calve and summer on the VCNP migrate eastward to more human-populated areas during winter (Biggs et al. 2010) where there are different concerns, such as elk-vehicle collisions and impacts on private land. While separate studies were initiated to evaluate movements of adult elk and cause-specific mortality of elk calves on the VCNP (Biggs et al. 2010; Bernal 2013), the focus of this

study was to describe the spatial and social ecology of coyotes to increase our understanding of coyotes in high-elevation environments and inform managers about the elk-coyote dynamic on the VCNP. Our objectives were to:

1. Describe the home range size and habitat use of VCNP coyotes.
2. Describe coyote movements within and outside of packs.
3. Evaluate the relationship between coyote social cohesion and the amount of elk in the coyote diet.

Materials and methods

Study area

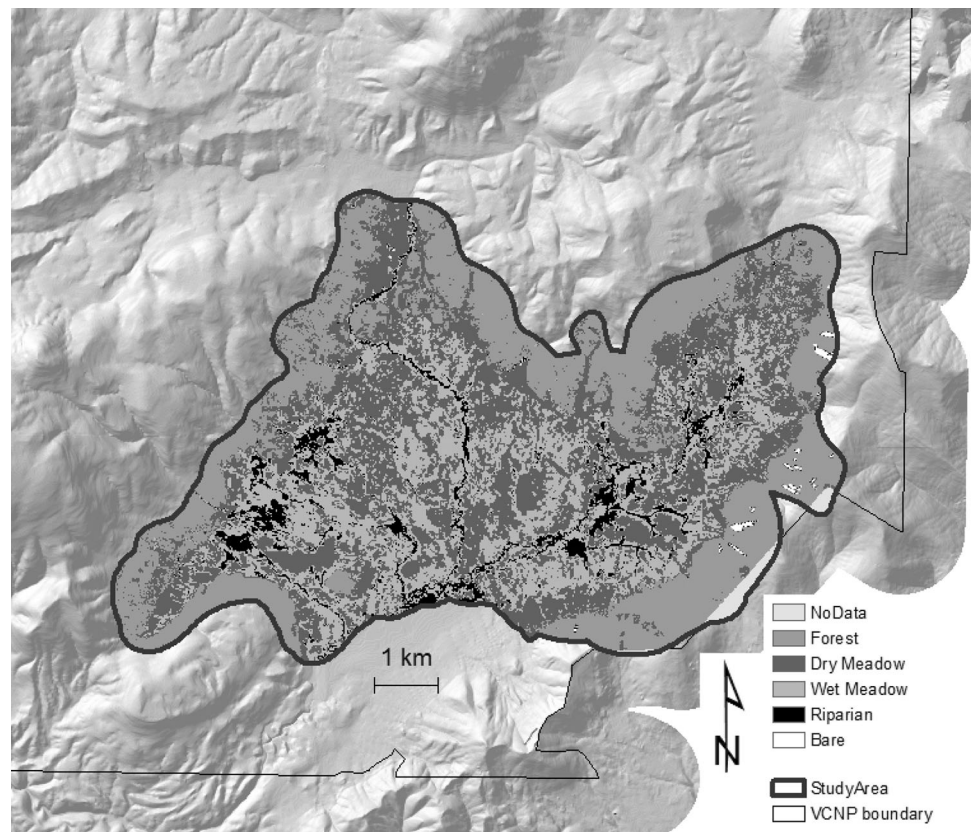
The 360-km² VCNP is located in the Jemez Mountains in north-central New Mexico. The landscape is characterized by forested mountains (2700- to 3400-m elevation) and large, grassland meadow valleys (2450- to 2700-m elevation). Our study took place in the vicinity of the Valle Grande, a large grassland meadow in the southeastern portion of the VCNP (Fig. 1). Mean annual precipitation was 640 mm ± 9.7 (SD), predominantly in the form of monsoon rains (July and August) and winter snow (November up to and including March; Valles Caldera Trust, unpublished data). Mean July maximum and minimum temperatures were 25.5 and 5.5 °C, respectively; mean January maximum and minimum temperatures were 4.6 and −16.5 °C, respectively (Valles Caldera Trust, unpublished data). Average snow depths for winters (November–March) 2005–2006 up to and including 2008–2009 were 65.5, 5.0, 52.4 and 43.2 cm, respectively (Natural Resources Conservation Service SNOTEL, unpublished data). There was light traffic on designated unpaved roads from limited recreation, administration, and research purposes. Elk hunting was permitted on the edges of the study area and the remainder of the VCNP, but did not occur on the Valle Grande. Predators, in addition to coyotes, included cougars (*Puma concolor*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and badgers (*Taxidea taxus*). Coyote prey included montane voles (*Microtus montanus*), elk, cottontail rabbits (*Silvilagus nuttallii*), beetles (Coleoptera) and grasshoppers (Orthoptera) (Gifford 2013).

The vegetation communities of the VCNP were described by Muldavin and Tonne (2003) and Muldavin et al. (2006) and included 20 vegetation classes. We grouped their categories as follows.

Forest

Ponderosa pine (*Pinus ponderosa*) and blue spruce (*Picea pungens*) forests bordered the grassland valleys. Mixed

Fig. 1 Study area boundary and habitat types within the study area on the Valles Caldera National Preserve (VCNP), New Mexico



conifer forests, comprising Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce, southwestern whitepine (*Pinus strobiformis*), limber pine (*Pinus flexilis*), and ponderosa pine, covered mountain slopes up to about 3050-m elevation, with spruce-fir forests dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*), at the highest elevations. Sites heavily impacted by past burning or logging were populated by aspen (*Populus tremuloides*) or Gambel oak (*Quercus gambelii*) on warmer sites, though oak was rare.

Dry meadow

Montane grasslands were highly diverse with >125 species of grasses and forbs (Muldavin and Tonne 2003) and were dominated by pine dropseed (*Blepharoneuron tricholepis*), Parry's oatgrass (*Danthonia parryi*), Arizona fescue (*Festuca arizonica*), Thurber's fescue (*Festuca thurberi*), and Kentucky bluegrass (*Poa pratensis*) alliances.

Wet meadow

Wet meadows and riparian/wetland communities occurred on areas subject to periodic flooding, with soils becoming saturated at least briefly during most years. They were

dominated by facultative and obligate wetland grasses, sedges and rushes, including tufted hairgrass (*Deschampsia caespitosa*), wooly cinquefoil (*Potentilla hippiana*), Baltic rush (*Juncus balticus*), Kentucky bluegrass (*Poa pratensis*), and common dandelion (*Taraxacum officinale*).

Riparian

Riparian communities comprised Northwest Territory sedge (*Carex utriculata*), smallwing sedge (*Carex microptera*), wooly sedge (*Carex lanuginosa*), and common spikerush (*Eleocharis palustris*). During summers, sedges in the riparian areas grew much taller than the meadow grasses. Perennial woody species such as willows (*Salix* spp.), alders, and birch were notably absent from the riparian areas and it was unknown if this was due to hydrological or soil characteristics, or historically heavy grazing (Muldavin and Tonne 2003).

Animal capture

We captured coyotes using padded-foot-hold traps and anesthetized them for handling. We also captured coyotes with a net-gun fired from a helicopter (Barrett et al. 1982; Gese et al. 1987); coyotes captured via helicopter were processed without chemical immobilization. We measured

body length and weight, determined sex, and estimated age based on tooth wear (Gier 1968). We fitted each coyote with a global positioning system (GPS) collar (Lotek Wireless, Newmarket, ON) plus an independent lightweight secondary very high frequency (VHF) radio collar (Advanced Telemetry Systems, Isanti, MN), or a VHF radio collar alone (Lotek Wireless). We evaluated GPS collar accuracy by calculating the mean distance between stationary test collar fixes and high-resolution GPS locations, and found a 17.4-m (median) and 34.2-m (mean) GPS collar location error based on 1003 test fixes; the fix acquisition rate from our test collars was 98.7 %. Capture and handling protocols were approved by the Institutional Animal Care and Use Committees at Utah State University (no. 1338) and the National Wildlife Research Center (QA-1492).

Home range size determination

Animals were classed as either transient individuals, or members of a resident social unit (i.e., pack) based upon space use (Gese et al. 1988a, 1990). Social units (i.e., packs) were evident based on individuals' locations overlapping almost completely in definable areas which were nearly exclusive of adjacent social units (Windberg and Knowlton 1988) with the exception of extra-territorial movements by individuals or occasionally by pairs of animals. Social units (packs) were confirmed by behavioral observations; pack members were considered to be the "resident" coyotes. We removed locations from long extra-territorial movements, defined as four or more sequential locations ≥ 2 -km outside of the area used by the pack, prior to calculating home ranges.

We divided locations into three biological seasons: breeding/gestation (1 December–31 March), pup rearing (1 April–31 July), and dispersal (1 August–30 November). For all analyses, the pack was defined as the individuals occupying a space together during one or more biological seasons. We sub-sampled location data to every 4 h to standardize location sampling across the duration of the study (Gese et al. 1990; White and Garrott 1990). The 4-h sampling scheme also reduced temporal autocorrelation (Swihart and Slade 1985a, b), though temporally autocorrelated data may provide better estimates of home range sizes and other movement measures (Aebischer et al. 1993; de Solla et al. 1999; Fieberg 2007) when the animal is the sample unit rather than individual observations (Kenward 1992; Otis and White 1999). Because coyote pack members used nearly identical areas, we defined the sample unit as a coyote pack to avoid pseudoreplication.

We used the 95 % fixed kernel density estimation (Worton 1989; ESRI ArcGIS; Hawth's Analysis Tools) to calculate home range size for each pack during each biological season. Because resident coyotes are territorial

(Camenzind 1978; Bekoff and Wells 1986; Andelt 1985; Gese 2001), it was biologically justified to calculate territories as a single, continuous polygon. Further, visual inspection of GPS collar data indicated that a single, continuous polygon was an appropriate generalization of space use of coyote packs. An ad hoc bandwidth (h) selection method was adapted (Kie 2013), starting with $h = 1000$ and incrementally reducing by 10 % until the smallest h was reached to calculate a single continuous 95 % kernel polygon (also see Berger and Gese 2007; Jacques et al. 2009; Kie et al. 2010). We chose these methods of home range calculation and bandwidth selection because of their reported robustness for large data sets (Seaman et al. 1999). To check the reliability of the home range estimation method with our data, we evaluated the relationship between home range size and the number of locations and the number of coyote individuals used in the calculation using correlation analysis. We compared home range sizes by ANOVA based on year, biological season, and pack. For each biological season, we also calculated the percent home range overlap of each pack when data were available for adjacent packs. Home range overlap was determined by measuring the amount of overlap between a pack's home range and each neighboring adjacent home range separately (i.e., paired overlap assessment).

Habitat use and availability

We used a vegetation map created by Muldavin et al. (2006) for delineating the habitat types within the VCNP. Muldavin et al. (2006) originally identified 20 vegetation classes and we reduced the number of vegetation classes into five habitat types described above in "Study area" to increase map accuracy and provide ecologically meaningful habitats for coyote space use: forest, dry meadow, wet meadow, riparian, and bare ground (Fig. 1). Streams bisected the study area and were lined by riparian areas on both sides; therefore, we included water in the riparian habitat type. We eliminated the bare ground category from analysis since it comprised < 0.5 % of seasonal home ranges. We did not have vegetation data for small portions of three seasonal pack home ranges (East and Rincon packs) when they extended outside of the VCNP (Fig. 1). We excluded these "no data" areas from analysis because they were negligible within observed home ranges (< 2.4 % in all cases) and observed use (< 1.3 % in all cases). We defined the study area by the extent of the home range boundaries of observed coyote packs.

We compiled locations by pack and then calculated habitat use as the proportion of resident coyote locations inside the pack home range within each habitat type during each biological season [i.e., 3rd order resource selection (Johnson 1980)]. We evaluated the variation in habitat use by seasons and by packs using contingency table analysis. We

calculated habitat availability as the proportion of raster cells of each habitat type within the pack's home range during each season [3rd order resource selection (Johnson 1980)]. We evaluated the differences in habitat use and availability by pack using contingency table analysis. We compared habitat use to habitat availability within the home range for each pack during each biological season using independent χ^2 -tests and Bonferroni confidence intervals (Neu et al. 1974; Byers et al. 1984). Because the coyotes did not use diverse terrain (i.e., the valley is relatively flat), we were primarily interested in habitat use based on vegetation types, so the information added by using a resource selection function would have been superfluous.

Social ecology

We used GPS location data to investigate social cohesion between coyote pack members and to evaluate the relationship between social cohesion and the frequency of elk in the diet. Whereas previous studies measured cohesiveness by observations of coyote group size (Camenzind 1978; Bowyer 1987; Gese et al. 1988a), we calculated the distance between simultaneous (within 1 min) GPS locations of paired pack members while both were within the pack home range (White et al. 1994; Kitchen et al. 1999), and we calculated a mean distance for each pair for each month. For comparison, we calculated a separation distance expected due to chance by averaging distances between non-simultaneous locations for each pair at random times >6 h apart (adapted from Kitchen et al. 1999). We used Student's *t*-test to compare distances between simultaneous-paired locations to distances expected due to chance for each pair of coyotes occupying a shared home range (Kitchen et al. 1999). We compared the monthly mean distance between pairs of pack members using Student's *t*-test. To evaluate whether social cohesion changed through the year, we compared social cohesion between biological seasons using ANOVA. We analyzed food habits of coyotes on VCNP concurrently with the location data presented here (Gifford 2013). We predicted coyotes would be more socially cohesive (i.e., smaller mean distance between individuals) when consuming larger prey. Therefore, we used regression analysis to evaluate the relationship between social cohesion and the monthly frequency of elk (calf, adult, and total) in coyote scats [see Gifford (2013) for details on coyote diet analysis].

Results

We captured 36 coyotes and fitted them with radio collars, which yielded GPS locations from 21 individuals and triangulation locations from 12 additional individuals during

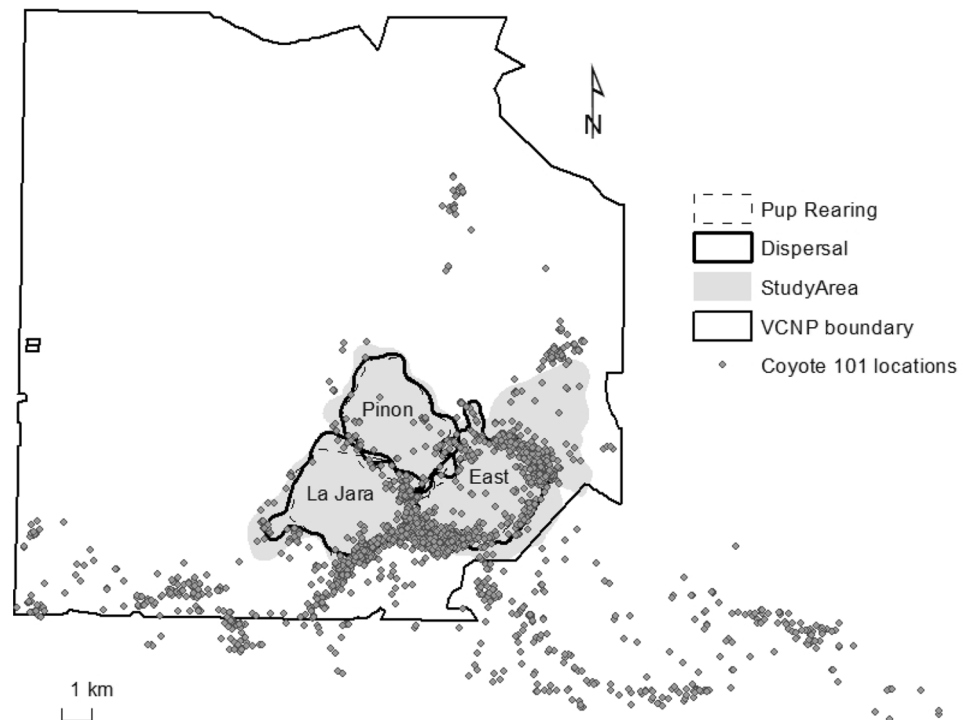
August 2005 up to and including July 2009; we excluded three individuals from analysis due to the failure of GPS collars or drop-off mechanisms and insufficient triangulation locations. Locations of territorial individuals were concentrated in a single area during one or more biological season; transient individuals had less fidelity to specific areas and often traveled around the edges of the areas occupied by the resident packs (Fig. 2). We identified two types of transient movements. All coyotes which were transient when we initially captured them remained transient for as long as we were able to track them (up to 34 consecutive months). Most coyotes, which were initially members of a pack and then became transient, later joined another pack during the study; these "displaced residents" often used a small area around the pack home range boundaries and home range overlap areas. We classified 23 coyotes (70 % of individuals) as residents during at least part of the study and ten coyotes (30 %) as transients. Four of the resident coyotes also exhibited transient movements during ≥ 1 month of our study.

We identified four packs using the Valle Grande (Fig. 3). For all analyses, the pack was defined as the individuals occupying a space together during one or more biological seasons. Therefore, four individuals were used in calculations for more than one pack during the study. During the breeding/gestation season of 2007, a social disruption occurred wherein several radio-collared individuals changed packs (three coyotes moved from the La Jara pack to the Piñon pack, one coyote moved from the Piñon pack to the La Jara pack) or became transients (two coyotes from the Piñon pack became transients; one joined the La Jara pack 1.5 years later and the other coyote joined the La Jara pack 2.5 years later). While the cause of this social disruption was unknown, the death of an alpha individual can bring about a reshuffling of the pack hierarchy and precipitate movement or exchange of individuals (Gese 1998).

Home range size

We used 16,411 GPS locations from 17 resident individuals in four packs spanning August 2005 up to and including July 2009 (covering 11 biological seasons) to determine home range size and habitat use. Overall mean home range size was 10.6 ± 2.2 (SD) km^2 ($n = 23$ seasonal pack home ranges), and varied significantly between packs ($F = 3.19$, $df = 3, 19$, $P = 0.047$; Table 1). We found no effect of year ($F_{4,6} = 1.15$, $P = 0.42$) or season ($F_{2,8} = 0.27$, $P = 0.77$) on home range size of resident coyotes. Home range size averaged 11.7 ± 0.5 , 11.0 ± 2.8 , 12.2 ± 1.8 , and 7.4 ± 2.3 km^2 for the La Jara, Piñon, East, and Rincon packs, respectively. Given the mean pack home range size of 10.6 km^2 , and observed

Fig. 2 Boundaries of resident coyote pack home ranges and locations for transient coyote C101 during 2006 on the VCNP, New Mexico



pack sizes of from five to six adults with transients comprising an additional 30 % of the population, we estimated the population density to be 0.61–0.73 coyotes/km² in the study area. We found no relationship between home range size ($n = 23$ seasonal pack home ranges) and the number of locations used in the home range size calculation (range 57–2392, $r = 0.22$, $P = 0.30$), nor between seasonal pack home range size and the number of coyote individuals used to calculate the seasonal pack home range (range 1–4, $r = -0.005$, $P = 0.98$). Adjacent home ranges overlapped an average of 6.1 % ($n = 14$ seasonal pack home ranges; Table 1).

Habitat use and availability

Each pack had all four habitat types available within its home range: forest, dry meadow, wet meadow, and riparian. For the study area, dry meadow was the predominant habitat type (39.8 %) followed by forest (34.1 %), wet meadow (20.8 %), and riparian (4.1 %). Dry meadow was most often the largest component of seasonal pack home ranges (22 of 23 seasonal pack home ranges, 48.3 % mean availability), and riparian was most often the smallest component (22 of 23 seasonal pack home ranges, 4.1 % mean availability). During each of the biological seasons for which two or more packs were observed, availability varied significantly between packs ($n = 8$ biological seasons, $P < 0.001$ in all cases). Of the four habitat types, each pack used dry meadow most frequently during every

biological season (46.4 % mean use, $n = 23$ pack biological seasons). Riparian or forest was the habitat type least used by each pack during each biological season (14 and nine pack biological seasons, respectively; $n = 23$ pack biological seasons). Habitat use varied significantly between packs within seasons ($P \leq 0.001$ in all cases), and pack use varied significantly between seasons ($P < 0.001$ in all cases).

Coyote packs used riparian habitat more than expected based on availability, and forests less than expected (Table 2). They most often used wet and dry meadows in proportion to availability. Use varied significantly from availability for each pack within each biological season ($P \leq 0.034$ in 22 cases, $\alpha = 0.05$) except for the Rincon pack during the breeding/gestation season of 2008 ($P = 0.074$). Availability of riparian habitat averaged 4.4 % of the home ranges, but was used on average 12 % of the time. In contrast, availability of forest habitat averaged 22.9 % of the home ranges and was used 16 % of the time.

Sociality

We collected simultaneous GPS locations from individuals in two packs. In the La Jara pack, we measured social cohesion between five individuals (up to three at a time) during 12 months. Each pair had ≥ 54 simultaneous locations within the pack home range during each month (mean $n = 111$ simultaneous location pairs). In the Piñon pack,

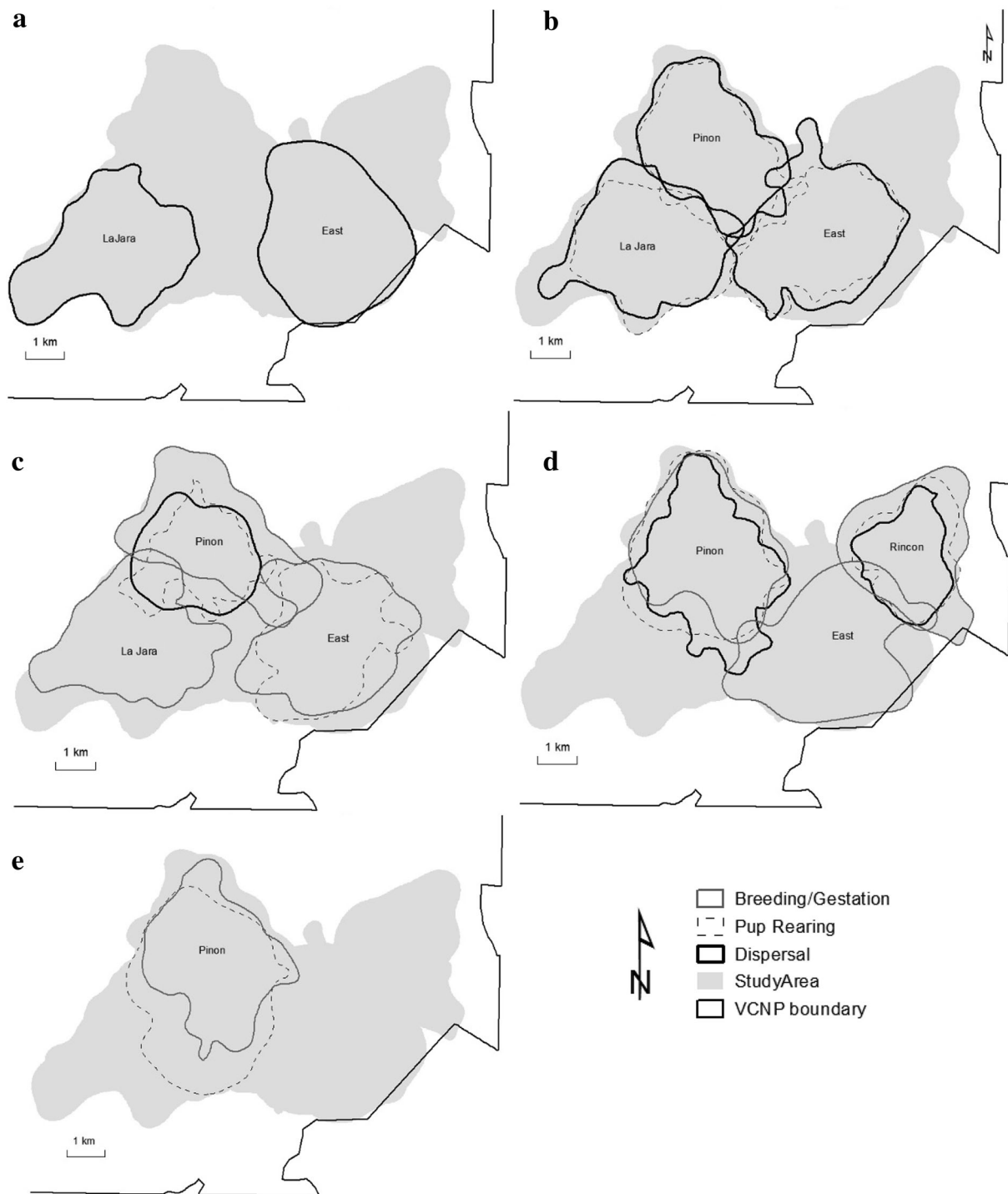


Fig. 3 Boundaries of four resident coyote territories for three biological seasons during **a** 2005, **b** 2006, **c** 2007, **d** 2008, and **e** 2009, VCNP, New Mexico. All four packs were present in all years, but a radio-collared coyote was not available for tracking in that pack during certain years

we measured social cohesion between seven individuals (up to four at a time) during 22 months, including the alpha pair during 13 months. Each pair had ≥ 41 simultaneous locations within the pack home range during each month (mean $n = 113$ simultaneous location pairs). Social cohesion was not correlated with home range size ($r^2 = 0.035$).

As predicted, the simultaneous locations of paired pack members were closer than expected due to chance (calculated as locations paired at random times ≥ 6 h apart; $P < 0.001$ for all pairs). The Piñon alpha pair was more cohesive with each other than each was with the third Piñon pack member ($P < 0.001$). Differences in social

Table 1 Home range size and overlap (km²) of resident coyote packs during three biological seasons on the Valles Caldera National Preserve, New Mexico, 2005–2009

Years	Biological season	Pack	Home range size			Home range overlap		
			<i>n</i> (individuals)	<i>n</i> (locations)	Area (km ²)	No. adjacent packs observed	Area (km ²)	Overlap (%)
2005	Dispersal	East	1	258	14.0			
		La Jara	3	732	11.9			
2006	Pup rearing	East	1	418	10.1	2	0.06	0.6
		La Jara	2	825	11.0	2	0.63	5.7
		Piñon	4	1321	11.0	2	0.61	5.5
	Dispersal	East	1	508	12.8	2	0.49	3.8
		La Jara	2	1248	12.1	2	0.63	5.2
		Piñon	3	1389	10.5	2	0.94	8.9
2007	Breeding/gestation	East	1	287	12.3	1	1.38	11.2
		Piñon	3	381	11.7	1	0.29	2.4
		La Jara	2	664	11.7	2	1.67	14.2
	Pup rearing	East	2	187	10.1	1	0	0
		Piñon	2	357	6.5	1	0	0
		Dispersal	Piñon	1	196	7.5		
2008	Breeding/gestation	East	1	57	14.0	2	1.61	11.5
		Rincon	1	81	10.0	1	0.24	2.6
		Piñon	3	308	9.2	1	1.37	13.7
	Pup rearing	Rincon	2	181	6.7			
		Piñon	3	1821	13.6			
	Dispersal	Rincon	1	601	5.5			
Piñon		4	2392	12.3				
2009	Breeding/gestation	Piñon	3	1641	11.6			
	Pup rearing	Piñon	1	558	16.1			

cohesion between biological seasons were not significant (Piñon pack, $P = 0.896$; La Jara pack, $P = 0.289$). We found no statistically significant relationships between social cohesion of the Piñon and La Jara packs and the amount of adult elk ($r^2 = 0.075$, $F = 2.11$, $P = 0.079$), calf elk ($r^2 = 0.005$, $F = 0.12$, $P = 0.363$) or total elk ($r^2 = 0.084$, $F = 2.38$, $P = 0.067$) in their diet. While the P -values approached significance for two of these correlations ($P = 0.079$ and $P = 0.067$), the correlation coefficients explained <9 % of the variance and therefore were not biologically meaningful.

One male coyote (C26) had been a member of the La Jara pack (May 2006–January 2007) and then joined the Piñon pack following the social disruption during the breeding/gestation season of 2007, after a period of transient movements and a period of time back and forth between the La Jara and Piñon pack territories. During March 2008, he transitioned from using all of the Piñon home range to only using part of it; it was unclear whether to consider C26 a Piñon pack member while he used only part of their territory. During March up to and

including August 2008, the distance between C26 and the resident pack members while inside the pack home range was significantly greater than the distances between the simultaneous locations of Piñon pack member pairs ($P < 0.001$), and the distances between C26 and Piñon pack members were greater than locations of Piñon pack members paired at random times ≥ 6 h apart ($P = 0.007$), indicating avoidance of the pack members. During August up to and including October, C26's mean distance from the resident coyotes declined; during September up to and including December his cohesion with pack members was similar to that of the non-alpha pack-member pairs ($P = 0.31$), and significantly less than the distances expected due to chance ($P = 0.015$), and he resumed using the entire Piñon pack home range. Beginning in January 2009 he established a home range outside of the VCNP and no longer used the Piñon home range enough for comparison (he had only eight, four, and two locations within the Piñon home range during January, February and March 2009, respectively).

Table 2 Coyote habitat use compared with availability of forest, dry meadow, wet meadow, and riparian habitats, during three biological seasons [breeding/gestation (*B/G*), pup rearing (*PR*), dispersal (*D*)] on the Valles Caldera National Preserve, New Mexico, 2005–2009

	B/G	PR	D
Forest			
2005			–o
2006		–oo	–
2007	oo+	–	–
2008	–o	–	–
2009	–	–	
Dry meadow			
2005			oo
2006		–o	oo+
2007	–o+	–o	o
2008	ooo	–o	–o
2009	–	–	
Wet meadow			
2005			o+
2006		oo+	ooo
2007	–o	oo	o
2008	ooo	o+	++
2009	+	+	
Riparian			
2005			++
2006		+++	+++
2007	o++	o+	+
2008	oo+	o+	o+
2009	+	+	

Habitat preference (*plus symbol*), habitat avoidance (*minus symbol*), or neutral use (*zero*), for a coyote pack during each season and year monitored; the *number of symbols* equals the number of packs

Discussion

Pack home range boundaries remained relatively stable despite changes in individual pack members. The size of resident pack home ranges on the VCNP was similar to values reported in similar habitats and elevations in the west. In Grand Teton National Park, Wyoming, Berger and Gese (2007) reported annual coyote home ranges averaged $13.12 \pm 1.59 \text{ km}^2$ in the portions of their study area which were free of wolf. Winter home ranges of coyotes in southwestern Montana (1300- to 2500-m elevation) were $11.02 \text{ km}^2 \pm 1.03$ (SE), and were calculated using a 95 % fixed kernel (Atwood and Gese 2010). In Yellowstone, Gese et al. (1996a) reported territory sizes ranged from 8.8 to 14.3 km^2 (mean 10.3 ± 0.42 SE) in the Lamar Valley.

The size of resident pack territories of the VCNP did not vary significantly by season or year, consistent with

previous studies (Camenzind 1978; Bowen 1982; Andelt 1985), though differences have been found between seasons in other studies (e.g., Gese et al. 1988a). The observed stability in home range size over the study period was likely influenced by calculating home range sizes by social unit (i.e., pack) rather than by individual coyotes. For example, the effect of a breeding female traveling less during whelping (Andelt 1985) would be dampened by movements of additional pack members or compensated for by other pack members foraging more extensively to provision pups. In addition, even as individual coyotes may have changed pack alliances, the “pack” home range remained relatively stable. The diverse food base utilized by coyotes in the study area during the study period (Gifford 2013) also likely contributed to the spatial stability of home ranges. Andelt (1985) speculated that seasonal constancy in home range size resulted from resident groups continuously occupying nearly all available habitats, related to maintenance of year-round pair bonds (Kleiman 1977; Kleiman and Brady 1978; Andelt and Gipson 1979; Andelt 1985). This was consistent with our observations: pack home ranges were nearly adjacent or slightly overlapping during each time step when coyotes from neighboring territories were observed.

Coyotes on our study area used dry and wet meadows as expected, forests less than expected, and riparian areas more than expected. Foraging was unlikely to be more productive in the riparian areas due to the height and density of vegetation. Similarly, Gese et al. (1996b) documented low rates of small mammal detection and capture by coyotes in riparian habitat in Yellowstone National Park relative to upland meadow and grassland habitats. On several occasions we located and flushed radio-collared individuals which seemed to have been resting under the canopy of tall sedges in the riparian areas. Riparian areas also contained open water for drinking. The sedges offered cover and shade not available in the wet meadow and dry meadow habitat types. Though the forests also offered shade, there was little ground cover. Predation by cougars was the most frequent known cause of mortality for radio-collared coyotes (unpublished data), and all cougar-cached coyote carcasses were found in forest habitat. We interpret the use of riparian areas more than expected and forests less than expected as risk-avoidance behavior.

We inferred that coyotes generally limited their use of forests across the VCNP. The resident packs we studied filled the grassland valleys and sometimes used the forest edges. If additional coyote territories were adjacent to our study area, those territories would predominantly comprise forested mountains; we found no evidence of packs occupying the forested areas. We set traps in meadows and forests, but trapping in forest habitat was unsuccessful. Similarly, we found coyote scats on forest transects

(Gifford 2013), but only when and where Valle Grande coyote pack home ranges extended into forests. Further, use of forests was limited even by wide-ranging transients. Transients used spaces on the edges, overlap areas, and between known resident home ranges (Fig. 2). They had similar patterns of locations in the VCNP grassland valleys outside of our study area where resident packs were observed but were not radio-collared. In the case of C26, a transient coyote used meadow habitat within a pack home range while avoiding the pack members for a period of months. In contrast to Kamler and Gipson's (2000) conclusion that transient coyotes were pushed to sub-optimal habitats not occupied by resident coyotes, on the VCNP it seems that both resident and transient coyotes limited their use of forests.

Though territory boundaries were relatively stable, we documented several changes in the individuals occupying the territories. Coyote individuals changing from resident to transient or transient coyotes joining packs have been documented in previous studies (Gese et al. 1988a; Kamler and Gipson 2000). While coyotes in our study area generally followed two behavior modes (resident and transient), we observed differences in movements among transients. While some transients exhibited long movements consistently, other transients used a small space on edges or overlap areas of resident coyote home ranges. The transients with more localized movements had been recently displaced from a pack and eventually either joined a pack or greatly increased their home ranges. Bekoff and Wells (1986) coined the term "roamers" to describe non-dispersing yearlings using the periphery of their natal territory while rarely interacting with the pack. We documented space use on the periphery of a territory by adult coyotes leading to acceptance or rejection by a pack. As evidenced by C26's movements, designation as a pack member depends on when a coyote is using an area in relation to the resident pack, in addition to overlapping spatially during a period of time. Camenzind (1978) described aggressive behavior of resident coyotes to transients, and Kamler and Gipson (2000) inferred transient avoidance of residents based on differences in habitat use between resident and transient coyotes. The lengthy tenure of some individuals as transient coyotes was likely due to the lack of turnover among resident breeding animals and territories reflecting the low level of human exploitation (i.e., coyotes were not persecuted within the study area).

In contrast to previous studies which measured social cohesion in terms of group size, we found that social cohesion did not vary by coyote biological seasons. By measuring social cohesion using simultaneous locations of established individuals within packs, we eliminated the confusion caused by variation in timing of juvenile dispersals (Gese et al. 1988b) and temporary aggregations of

coyotes at carcasses (Murie 1940; Camenzind 1978; Bowen 1981; Gese et al. 1988b). Our analysis was not affected by individuals joining or dispersing from packs and instead focused on the movements within packs.

Contrary to our expectation, we found no relationship between social cohesion and the proportion of elk in coyote diets. We expected that feeding on and defending carcasses would result in greater social cohesion (smaller distances between individuals) during times when coyotes had higher proportions of adult elk in their diet. If cooperative hunting affected coyote movements during elk calving we expected an increase in social cohesion coincident with the amount of elk calves in coyote diets. We concluded that coyote sociality on VCNP was relatively stable year-round despite changes in biological needs and prey size. Similarly, Young et al. (2008) determined that short-term changes in carcass availability did not result in space-use changes when population conditions were relatively stable.

Previous studies indicated coyote predation on ungulates was related to ungulate vulnerability due to snow, separation from the herd, or compromised health (Gese and Grothe 1995). Elk captured in the Jemez Mountains had >50 % of locations in Ponderosa pine and mixed conifer during calving (May–June) and summer (July–August) seasons (Biggs et al. 2001), when calves are most vulnerable to predation. In western Wyoming, cow elk sought habitat with cover (deciduous, shrubland or conifer) for parturition (Barbknecht et al. 2011). During the pup-rearing season (April–July) we observed 12 % of coyote locations in forest and 88 % in open habitats (dry meadow, wet meadow and riparian). Bernal (2013) reported most coyote-killed elk calves on VCNP were found in meadow or forest edge habitats, and bear mortalities in forest or forest edge. Given these relationships between elk habitat use and predation, discussion is warranted pertaining to the management of meadow-forest edges.

In terms of predator–prey interactions, Bernal (2013) showed black bears killed more elk calves than coyotes (40.6 % of mortality versus 35.9 %), though observations of bear predation attempts on elk calves were rare. The perception of many members of the public is that coyotes are the principal predator of elk calves, since the public has observed coyotes killing elk calves. To better understand the discrepancy between our findings and public perception, future research needs to quantify human habitat use and activity patterns on VCNP with those of coyotes, elk and bears. We expect humans would overlap with coyotes the most, with diurnal activity patterns and frequent use of open meadow landscapes, thereby allowing increased observations of coyotes killing elk calves, while black bear predation of elk calves goes largely unobserved. Increased coyote activity during daylight hours may also reinforce public perceptions of increased coyote numbers on the

study area. Kitchen et al. (2000b) documented that coyotes shifted to more diurnal activity pattern following 8 years of reduced coyote persecution by humans. Similarly, McClennen et al. (2001) found higher mean diurnal activity in coyotes with less human disturbance. If the perception that more coyotes were seen on the VCNP following federal purchase and cessation of persecution was correct, the change may be due in part to an increase in visibility following a shift to more diurnal activity patterns and not an increase in the overall coyote population size.

In national parks where hunting of predators also does not occur, the ecosystem dynamics of elk are varied. In Rocky Mountain National Park, Colorado, declines of willow and aspen have been documented and attributed to high ungulate populations (Olmsted 1979; Baker et al. 1997; Peinetti et al. 2002). Lubow et al. (2002) concluded that the park population was food-limited density dependent, likely at a higher population level than achieved under natural regulation with top predators. In addition to vegetation impacts inside Rocky Mountain National Park, the large elk population also impacted residential areas of the nearby town of Estes Park (Schultz and Bailey 1978). In Yellowstone National Park, Wyoming, following wolf (*Canis lupus*) reintroduction and grizzly bear (*Ursus arctos horribilis*) recovery alongside a severe climate and increased harvest, elk populations have declined (Vucetich et al. 2005) and elk movements and habitat use have changed (Fortin et al. 2005; Mao et al. 2005). Associated trophic cascades have been documented, including recovery of riparian vegetation (Beyer et al. 2007) and aspen (Ripple and Beschta 2007). The greater reproductive impact of cow elk hunting relative to wolf predation (Wright et al. 2006) suggested adjusting hunting pressure was a more powerful management tool than predation for regulating elk population size. Whether coyotes on our study area are capable of filling a similar niche to wolves in Yellowstone is doubtful. Body size of coyotes generally limits them to killing small and medium-sized prey. While efficient predators of elk calves, coyote predation on mature, prime-aged elk is very rare and limited to circumstances where the elk is either very old or very young, plus being nutritionally compromised, and snow conditions limit elk access to forage (Gese and Grothe 1995). Coyote predation is generally limited to elk calves in the summer, whereas wolf predation on elk occurs year-round and can include all sex and age classes, thereby having a more overall influence on ecosystem dynamics both directly and indirectly (Christianson and Creel 2010; Creel et al. 2011; Eisenberg et al. 2015).

On the VCNP, we found the territories of the resident coyote packs to be relatively stable both seasonally and annually, similar to other studies in high-elevation environments (Gese et al. 1996a; Dowd et al. 2014). Even when

availability of various sized prey changed seasonally and annually (Gifford 2013), space use and social ecology of the coyote packs remained unchanged. Plasticity in their social ecology and land-tenure system are well-known traits of coyotes (Bekoff and Wells 1986), and their ability to adapt to changing prey and snow depth in high-elevation environments reinforces our understanding of their adaptability to changing environmental conditions.

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Compliance with ethical standards

Conflict of interest We have no potential conflicts of interest. Our research involved animals. Capture and handling protocols were approved by the Institutional Animal Care and Use Committees of Utah State University (no. 1338) and the National Wildlife Research Center (QA-1492).

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