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Ecology of Coyotes on the Valles Caldera National Preserve, New Mexico: Implications for Elk Calf Recruitment

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ECOLOGY OF COYOTES ON THE VALLES CALDERA NATIONAL PRESERVE,

NEW MEXICO: IMPLICATIONS FOR ELK CALF RECRUITMENT

by

Suzanne J. Gifford

A thesis submitted in partial fulfillment
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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Ecology of Coyotes on the Valles Caldera National Preserve,

New Mexico: Implications for Elk Calf Recruitment

by

Suzanne J. Gifford, Master of Science

Utah State University, 2013

Major Professor: Dr. Eric M. Gese
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An understanding of coyote (*Canis latrans*) ecology was critical to developing

management plans on the nascent Valles Caldera National Preserve (VCNP) in northern

New Mexico. Managers concerned about low elk (*Cervus elaphus*) recruitment also

observed a concomitant increase in sightings of coyotes and observations of coyote

predation on elk calves. The goals of this study were to describe food habits and spatial

and social ecology of coyotes on VCNP, particularly as related to ecological interactions

with elk. Our objectives were to identify, quantify, and assess the temporal variation in

coyote diet, to describe coyote home-range size and habitat use, to describe coyote

movements within and outside of packs, and to evaluate the relationship between coyote

social cohesion and the amount of elk in the coyote diet. We examined coyote food

habits via monthly scat analysis (n = 1,385 scats). The most frequent taxa were rodents

(predominantly *Microtus* spp. and *Thomomys talpoides*), elk (adult and calf), insects (Orthoptera and Coleoptera), lagomorph (*Sylvilagus nuttallii*), and plants. Most food types varied significantly seasonally and annually. Variation in climatic variables and relative abundance or vulnerability of food items may explain the diet variation of coyotes observed. We examined global positioning system (GPS) and triangulation location data from 33 coyotes. We classified 23 coyotes (70%) as residents during at least part of the study and 10 coyotes (30%) as consistently transient. Mean home-range size was 11.0 ± 2.6 (SD) km^2 and varied significantly between packs but did not vary by season or year. Coyotes used dry and wet meadow habitats in proportion to availability; coyotes used riparian habitat more than expected and forests less than expected. Social cohesion did not vary by biological season. Alpha coyotes were more socially cohesive with each other than with their pack associate, and a transient exhibited temporal-spatial avoidance of pack members while inside the pack's home range followed by integration into the pack. We found no relationship between coyote social cohesion and the proportion of elk in coyote diets. We concluded that coyote sociality on the VCNP was relatively stable year-round despite changes in biological needs and prey size.

(116 pages)

PUBLIC ABSTRACT

Ecology of Coyotes on the Valles Caldera National Preserve,

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Valles Caldera National Preserve (VCNP) managers were concerned about low elk recruitment observed at the same time as an apparent increase in sightings of coyotes and observations of coyote predation on elk calves. The goal of this study was to describe coyotes' ecological interactions with elk, particularly coyote diet and movements on the Valle Grande, a large grassland meadow in the southeastern portion of the VCNP.

We examined coyote diet by quantifying undigested remains of food items in coyote scats (feces). The most frequent taxa were rodents (montane voles and pocket gophers), elk (adult and calf), insects (grasshoppers and beetles), mountain cottontail rabbits, and plants. Most food types varied significantly seasonally and annually, likely due to climatic variation and the relative availability or vulnerability of food items. In particular, an increase in calf elk consumed during summer 2006 followed a dry winter when elk may have been in a lower nutritional state.

We analyzed locations of 33 coyotes, obtained via global positioning system (GPS) collars and radio-tracking. We classified 23 coyotes as residents, living with a social group in a defined area (11.0 km^2 mean), and 10 coyotes as transient, with less fidelity to specific areas and often travelling around the edges of the areas occupied by the four resident packs. Coyotes spent most of their time in dry meadow habitat. Coyotes spent more time in riparian habitat than expected based on its availability within home range and less time in forests. We found no relationship between coyote social cohesion (proximity of pack members to each other) and the proportion of elk in coyote diets. We concluded that coyote sociality on VCNP was relatively stable year-round despite changes in biological needs and prey size.

ACKNOWLEDGMENTS

PREFACE

Chapter 2, Food habits of coyotes (*Canis latrans*) in the Valles Caldera National Preserve, New Mexico, and Chapter 3, Spatial and social ecology of coyotes (*Canis latrans*) on the Valles Caldera National Preserve, New Mexico, will be submitted to the Journal of Wildlife Management. Coauthors will be Eric Gese and Robert Parmenter.

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CHAPTER 1

INTRODUCTION

Coyotes (*Canis latrans*) play many ecosystem roles due to their generalist nature and mesocarnivore status – predator, scavenger, primary consumer, prey – with their impacts on the ecosystem dependent on many ecological, climatic, and anthropogenic factors. Despite a substantial body of literature on coyote ecology and management, concerns and questions persist as to how coyotes impact or regulate various prey populations. Historic coyote management has generally focused on removal or population reduction of coyotes to reduce predation on domestic livestock or big game species. Current management plans for many areas now take into account wildlife viewing opportunities as well as the ecological role of the coyote.

The Valles Caldera National Preserve (VCNP) in the Jemez Mountains of New Mexico was federally purchased in 2000 for its aesthetic, ecological, cultural, productive, and recreational values. The northern New Mexico public advocated strongly for the federal purchase of the property and has remained vocal and involved in planning and management efforts on the VCNP. The Valles Caldera Trust (VCT) was established to manage the VCNP as an experiment in public land management; the VCT was to manage the Preserve as a working ranch, implementing science-based management, while protecting the ecosystem of the Preserve and surrounding area and providing for public recreation, with the aim of eventually becoming financially self-sustaining.

In addition to its large grassland valleys and forested mountains, the VCNP may be best known for its visible high-density elk herd. The New Mexico Department of

Game and Fish (NMDGF) released the Rocky Mountain subspecies (*Cervus elaphus nelsoni*) in the Jemez Mountains in the 1940s and 1960s to replace the extirpated Merriam's elk (*Cervus elaphus merriami*). Estimates for the Jemez Mountains elk population in 2005 were 2,700 – 4,200 animals, of which approximately 3,000 resided on the VCNP (NMDGF, unpublished data). A lottery for elk hunt permits presented the most promising opportunity for the VCT to generate revenue. During 2000-2007 the elk hunt was the only VCT program to generate a profit; through 2012 it has continued to be the most profitable program run by the VCT (Valles Caldera Trust 2012). Portions of the VCNP are critical elk calving areas for the Jemez Mountains herd, and the entire VCNP serves as summer range as well as occasional winter range during low-snow years for a large portion of the elk population. Given the financial reliance of the VCT on the elk herd, managers were concerned over low calf:cow ratios observed during 2003 through 2006, which were the lowest estimated ratios in the state of New Mexico, and lower than those estimated in the Jemez Mountains in the preceding decades (NMDGF, unpublished data).

The decline in calf:cow ratios coincided with increased traffic and recreation on the VCNP, cessation of persecution of coyotes, elimination of bear (*Ursus americanus*) and cougar (*Puma concolor*) hunts, and severe drought. Coyote predation on elk calves was observed on the VCNP, and some observers were eager to attribute the low elk recruitment to coyote predation alone. Some community members publicly called for the VCT to implement control of predators to increase elk calf recruitment rates.

Concomitantly, discussion over the desirable size of the Jemez elk herd and the carrying capacity of the region transpired among regional biologists and other stakeholders. Concern increased over the impact elk might be having on browse species such as aspen *(Populus tremuloides)*, Gambel's oak (*Quercus gambelii*), and New Mexican locust (*Robinia neomexicana*; Krantz 2001). Biologists considered whether degraded riparian zones might recover with lower densities of elk.

A location-specific study was needed on the ecology of coyotes and their potential role in elk calf mortality on the VCNP to make informed decisions regarding management of coyotes and elk. 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 our study was to describe the ecology of coyotes on the VCNP to better inform managers on the elk-coyote relationship.

Previous food habit analyses have shown coyote diets to be influenced by the abundance of prey both spatially and temporally (e.g., Bowyer et al. 1983, Hamlin et al. 1984, Richer et al. 2002, Prugh 2005). In certain ecosystems, predation by coyotes has been shown to be a major cause of mortality of neonatal ungulates (e.g., Barrett 1984, Smith and Anderson 1996, Ballard et al. 2001). Occurrence of ungulates in coyote diets may be related to coyote social status (Gese et al. 1996*a*), coyote group size (Bowen 1981, Bowyer 1987, Gese et al. 1988*a*), alternate prey availability (e.g., Hamlin et al. 1984, Lingle 2000), nutritional status of ungulates relative to the time of year (Gese and Grothe 1995, Kunkel and Pletscher 1999), and availability of carrion.

There have been numerous studies of coyote social and spatial ecology (e.g., Messier and Barrette 1982, Andelt 1985, Mills and Knowlton 1991) but few studies at high elevations (e.g., Bekoff and Wells 1980, Bowen 1982, Gese et al. 1996*b*).   A general consensus of studies indicates that coyote space use can be stable through time (Kitchen et al. 2000, Young et al. 2006), but habitat use and coyote response to disturbance vary by geographic location. In addition, home-range size of resident packs can be influenced by resources or habitat types (Gese et al. 1988*b*). In terms of social ecology, a coyote population can be divided into resident and transient individuals (e.g., Camenzind 1978, Bowen 1978, Bekoff and Wells 1986) but proportions of resident and transient individuals and the way in which individuals transition into or out of resident packs vary among populations (Andelt 1985, Kamler and Gipson 2000, Gese 2001).

Previous studies 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. 1988*a*). Gese et al. (1988*a*) 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. In contrast, Bowyer (1987) found a higher percentage of coyotes in groups during June through November, but the amount of mule deer (*Odocoileus hemionus*) in scats did not vary seasonally. Comparison of the observations at different sites is confounded by whether young of the year or groups at carcasses are included in counts, or by use of an arbitrary distance designating when coyotes were considered "together."

The objective of our study was to describe the ecological role of the coyote on the VCNP in terms of food habits, space use and social organization. First, we identified coyote diet components and assessed the temporal variation in coyote diet. Second, we described the spatial and social ecology of coyotes in terms of home-range size, habitat use, and coyote movements within and outside of packs. Finally, we evaluated the relationship between coyote social cohesion and the amount of elk in the coyote diet.

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CHAPTER 2

FOOD HABITS OF COYOTES (*CANIS LATRANS*) IN THE VALLES CALDERA

NATIONAL PRESERVE, NEW MEXICO

ABSTRACT – An understanding of coyote (*Canis latrans*) ecology was critical to developing management plans on the nascent Valles Caldera National Preserve (VCNP) in northern New Mexico. Managers concerned about low elk (*Cervus elaphus*) recruitment have also observed a concomitant increase in sightings of coyotes and observations of coyote predation on elk calves. The goal of this study was to identify and quantify coyote diet and assess the temporal variation in coyote diet on the VCNP, particularly as related to elk calf consumption. We examined coyote food habits via monthly scat analysis (n = 1,385 scats) with scat collections from May 2005 to November 2008. The most frequent taxa were rodents (predominantly *Microtus* spp. and *Thomomys talpoides*), elk (adult and calf), insects (Orthoptera and Coleoptera), lagomorph (*Sylvilagus nuttallii*), and plants (grass and conifer needles or cone). Additional minor scat components were present in ≤7% of scats analyzed. Contingency table analysis showed significant seasonal variation of all food types within all years, with the exception of lagomorph consumption within 2006, 2007, and 2008. Contingency table analysis showed significant annual variation of most food types by season, except elk and lagomorph consumption between summers, and elk, lagomorph, and insect consumption between winters. Variation in climatic variables and relative abundance or vulnerability of food items may explain the diet variation of coyotes observed during the study.

Winter snow appeared to influence the vulnerability of the main prey species through detection and capture probability or nutritional influences.

INTRODUCTION

Predators' role in regulating prey populations depends on a broad range of ecological and environmental factors (e.g., Menge and Olson 1990, Sinclair and Pech 1996). Coyotes (*Canis latrans*) are known to be a generalist and opportunistic predator and scavenger (Murie 1940). Use of a particular prey species will depend on prey availability, climatic variables (temperature, precipitation, snow depth), nutritional status of prey, age structure of the prey population, and prevalence of conspecific and intra-guild competition for prey items (e.g., Mech et al. 1991, Murray et al. 1997, Phillips and White 2003). Previous food habit analyses have shown coyote diets to be influenced by the abundance of prey both spatially and temporally (e.g., Bowyer et al. 1983, Hamlin et al. 1984, Richer et al. 2002, Prugh 2005). In certain ecosystems, predation by coyotes has been shown to be a major cause of mortality of neonatal ungulates (e.g., Barrett 1984, Smith and Anderson 1996, Ballard et al. 2001). Occurrence of ungulates in coyote diets may be related to coyote social status (Gese et al. 1996*a*), coyote group size (Bowen 1981, Bowyer 1987, Gese et al. 1988), alternate prey availability (e.g., Hamlin et al. 1984, Lingle 2000), nutritional status of ungulates relative to the time of year (Gese and Grothe 1995, Kunkel and Pletscher 1999), and availability of carrion, including gut piles left by elk hunters.

Our objective was to quantify coyote diet and assess the temporal variation in coyote diet, particularly as related to elk calf consumption, on the Valles Caldera National Preserve (VCNP), New Mexico. The VCNP is a newly designated federal preserve with long-term natural resources management being largely undetermined; therefore, a location-specific study was essential for informing future management plans. Management plans on the VCNP required information on the ecology of coyotes as related to elk population (*Cervus elaphus*), as revenues from elk hunts were critical to the financial sustainability of the VCNP. Managers were concerned about the sustainability of the elk population in light of calf:cow ratios estimated as the lowest in the state of New Mexico in 2004 (New Mexico Department of Game and Fish, unpublished data; Valles Caldera Trust, unpublished data) which coincided with increased visibility of coyotes and observed coyote predation events on elk calves. Scat analysis is a reliable noninvasive method for determining the diet components of coyotes (e.g., Murie 1951, Ortega 1987, Brillhart and Kaufman 1995, Alvarez-Castaneda and Gonzalez-Quintero 2005). Due to their relative availability as prey items on the study area, expected diet components were predicted to include elk, rodents (particularly *Microtus* sp., *Peromyscus* sp., and *Cynomys gunnisoni*), and insects (primarily Coleoptera and Orthoptera.)

Study Area

The VCNP is a 360 km^2 volcanic caldera in north-central New Mexico (Fig. 2-1), characterized by large, grassland meadow valleys (approximately 2600-2800 m elevation), and forested mountains (approximately 2800-3400 m elevation). Meadows

were dominated by Parry's Oatgrass (*Danthonia parryi*), Thurber fescue (*Festuca thurberi*), Arizona fescue (*Festuca arizonica*), pine dropseed (*Blepharoneuron tricholepis*) and Kentucky bluegrass (*Poa pratensis*) alliances, with a diversity of sedges (*Carex* spp.) and rushes (*Juncus* spp.) in the wet meadow and riparian areas (Muldavin and Tonne 2003). Our study focused on the vicinity of the Valle Grande—a large grassland meadow in the southeastern portion of the VCNP (Fig. 2-1). Mean annual precipitation was 640 mm ± 9.7 (SD), predominantly in the form of monsoon rains (July and August) and winter snow (November through March; Valles Caldera Trust, unpublished data). Mean July daily maximum and minimum temperatures were 25.5 and 5.5ºC, respectively; mean January daily maximum and minimum temperatures were 4.6 and -16.5ºC, respectively (Valles Caldera Trust, unpublished data). 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.

METHODS

We collected coyote scats weekly or bi-weekly during 43 months from May 2005 to November 2008 on 25-40 km of transects on lightly traveled gravel roads (Fig. 2-1). When snow conditions prevented collection from roads, we collected scats from cross-country ski and snowshoe trails. We cleared all scats from transects during each survey ensuring scats collected would have been deposited since the previous collection. Scat samples were frozen until the time of analysis.

We divided scats by collection month for analysis and randomly selected 30-40 scats for analysis for months when >40 scats were collected. We dried scats at 60-70ºC for a minimum of 24 hours to kill parasites and bacteria, including *Echinococcus* spp. (Colli and Williams 1972). We transferred scats to a double layer of fine-mesh nylon bags, soaked in warm water for ≥48 hours (Kelly 1991), rinsed thoroughly, and washed and dried in a clothes washer/dryer (Johnson and Hansen 1979, Springer and Smith 1981).

We identified diet items from scats by visual inspection and comparison to published keys (Glass 1981, Jones and Manning 1992, Moore et al. 1997, Martin et al. 2000), reference texts (Adjoran and Koenosky 1969, Gilbert et al. 1981, Gilbert 2003, Elbroch 2006), and reference collections (mammalian hair and skeleton specimens courtesy of University of New Mexico Museum of Southwestern Biology, Albuquerque, New Mexico; insect, reptile, plant, seed, and additional mammal specimens courtesy of Valles Caldera Trust Research Inventory and Monitoring Program, Jemez Springs, New Mexico), or consultation with experts. We identified mammal remains to genus or species level. We identified birds and insects to class and order levels, respectively.

For each scat, we estimated the percent volume of diet items to the nearest 20% to reduce the bias toward over-reporting the volume of small prey items (Martin et al. 1946, Weaver and Hoffman 1979) which have higher surface-to-volume ratios than large prey and therefore have more indigestible hair relative to digestible flesh. We compiled results to calculate relative volume for each month; volume totaled 100% across all prey types for each month. We calculated the relative frequency of each prey item as the

proportion of scats each month containing ≥10% of each item; each prey type could be present in up to 100% of scats.

For statistical comparisons, we used monthly relative frequency rather than volume (Ciucci et al. 1996). We compared the frequency of diet items between seasons within years and between years by season using contingency table analysis (SPSS for Windows). We compiled diet items into 5 predominant groups: rodents, elk, insects, lagomorphs, and plants (birds and reptiles were too infrequent to be considered predominant groups), and we compiled monthly scat calculations into 4 seasons per year. We defined seasons based on expected climactic, phenological, and food availability patterns: Spring (March – May, characterized by snow melt, wind, and typically dry weather), Summer (June – August, characterized by the availability of insects and elk calves, the highest temperatures, and the onset of the monsoon rains), Fall (September – November, characterized by elk hunting season and therefore the availability of elk carcass remains left by hunters), and Winter (December – February, characterized by the coldest temperatures and deep snow). We did not compare diets between packs because all pack home ranges were comprised of the same four habitat types (Chapter 3), so presumably the packs had access to the same prey within their respective territories.

RESULTS

We analyzed a total of 1,385 coyote scats from 15 phenological seasons spanning 43 months. The most frequent taxa were rodents (predominantly *Microtus* spp. and *Thomomys talpoides*), elk (adult and calf), insects (Orthoptera and Coleoptera),

lagomorph (*Sylvilagus nuttallii*), and plants (grass and conifer needles or cone; Table 2-1); the same taxa also comprised most of the volume of scats (Fig. 2-2). We observed 40 additional taxa each present in ≤7% of scats (Appendix 2-1). Diet components identified were entirely naturally-occurring items, despite a significant and growing human presence on the VCNP (Valles Caldera Trust 2009).

Elk remains were present in coyote scats during all months of the study. Elk calf hairs could be distinguished from adult elk hairs until calves were 5-months-old, during October or November each year. The general trend was two peaks of elk consumption per year, one in spring or early summer (June most years) which was principally calf elk, and another in winter (peaked during November-January; Fig. 2-3). Variation of calf in scats was significant between summer seasons (P = 0.0986). Elk calf consumption followed the same pattern during 2005, 2007 and 2008 with a peak in June which declined through summer, followed by a lesser peak in September. During 2006, however, calf consumption generally climbed through the summer with the peak for the year in September. The low points of elk consumption during the study period occurred in April and November 2008. The frequency of elk varied seasonally during all years of the study, and variation during spring and fall seasons were significant between years (Tables 2-2, 2-3).

Rodent remains often comprised ≥30% of the volume of scats (Fig. 2-4). Rodent taxa included 11 genera within 5 families, predominated by genus *Microtus* (Fig. 2-4, Appendix 2-1). *Microtus* remains were present in coyote scats during 42 of the 43 months of the study period; 64.3% of monthly occurences of Rodentia were Cricetids,

and 80.3% of monthly ocurrences of Cricetids were *Microtus*. Gophers (Geomyidae; *Thomomys talpoides*) were consistently present in smaller proportions (20.2% of monthly occurences of Rodentia). Sciurid mammals were present only during warmer months (8.9% of monthly occurences of Rodentia). Rodent occurrence varied significantly between all seasons and years (Tables 2-2, 2-3). Rodents occurred in scats more frequently during the low-snow 2005-2006 winter (63.8% of scats) than during the 2006-2007 and 2007-2008 deep snow winters (28.4 and 31.0% occurrence). Prairie dog (*C. gunnisoni*) remains were found in small amounts during all summers of the study (Appendix 2-1).

Lagomorph remains were nearly entirely *Sylvilagus nuttallii*; out of 184 lagomorph occurrences, 183 were *S. nuttallii* and 1 was *Lepus californicus*. During winter 2005-2006 we noted a prey shift when *Microtus* consumption sharply declined and *Sylvilagus* consumption reached its peak for the study period. Seasonal variation in lagomorph occurrence was only significant during one year of the study; annual variation was significant between spring and fall seasons but not between summers and winters (Tables 2-2, 2-3).

Pulses of insect consumption during the summer months were apparent (Fig. 2-5). Coyotes on the VCNP consumed insects almost exclusively from two orders, Coleoptera (beetles) and Orthoptera (grasshoppers and crickets), with the peak of Coleopteran consumption occurring just prior to the peak of consumption of Orthopterans during all four summers (Fig. 2-5). The overall volume of insects in the diet appeared similar for all summers (2005-2007), with insects occurring during 6 to 9 months per year.

However, the composition between Coleoptera and Orthoptera varies. During the summers of 2005 and 2007, Orthoptera greatly dominated insect remains (99.6% and 77.4%), but was only 56.3% of insect occurrences during 2006, with Coleoptera consumption comprising nearly all of the remaining percentage. We observed a smaller and briefer pulse of insect consumption during the summer of 2008 than during summers 2005-2007, with insects only occurring during 4 months of 2008 (Fig. 2-5). Very few Orthopterans were recorded, and the pulse of Coleoptera consumption was later than the three preceding summers, peaking in July compared with May/June for 2005-07 (Fig. 2-5). Frequency of insects in scats varied seasonally for all years of the study and varied annually for all seasons when insects were available (Tables 2-2, 2-3).

DISCUSSION

Elk was an important diet item for VCNP coyotes, and was the only taxon present in coyote scats during all months of the study. The overall trend was a brief pulse in June each year (calves) and a broad peak in winter months. Coyote consumption of calves represented a combination of predation and scavenging. Coyote predation on elk calves and coyote scavenging of calves killed by other predators (eagle, bear and cougar) have been observed on VCNP. Coyotes were also observed scavenging calves which died of causes other than predation (e.g., still-born, caught in fence, bacterial infection). We expected a high presence of calf remains in coyote scats collected during June and July. By mid-July, calves would have survived the neonatal stage and would be much less vulnerable to predation (Smith and Anderson 1996, Bernal 2013). Therefore we expected

the presence of calf hair to diminish by August of each year. However, calves occurred in coyote scats through August of each year suggesting that either the VCNP elk calves were vulnerable to coyote predation past the neonatal stage, or that coyotes scavenged calves killed by other predators or other causes during late summer.

The volume of calf hair in scats was greater in September each year than during the preceding months. Calves were expected to be stronger and faster in September than in preceding months, so it is unlikely that direct coyote predation increased. Bull elk hunts began on VCNP in early September. Though calves and their dams were not hunted until October each year, we observed that the presence of human predators in September immediately increased elk vigilance and decreased the amount of time elk spent in the open meadows. With adult and calf elk spending more time in the hiding cover of forests, we expected them to be more susceptible to cougar (*Puma concolor*) predation. Likewise, we observed a shift in coyote habitat use from the meadows to the forest edge with the onset of the elk hunts (Chapter 3). Subsequently, Bernal (2013) found during 2009-2011 the mean age of radio-tagged elk calves on VCNP killed by cougars was 127.3 days (range 5-244), whereas calves killed by coyotes or bears averaged 8.0 and 9.7 days, respectively. Coyote scavenging of cougar-killed elk calves may therefore explain the increase of elk calf hair in the September diets. The amount of elk calf hair in scats was low or absent by October which likely represented a real decline in consumption of elk calves; however, the distinction between calf and adult elk hair was less clear in October and not reliable by November.

The variation of elk calf in coyote scats was significant between summer seasons. During summers 2005, 2007, and 2008, there was a large spike in calf consumption in June which quickly declined. During 2006, however, the amount of elk in the coyote diet generally increased through the summer, comprising 20-30% of the volume during July, August and September (Fig. 2-3). Bernal's (2013) latest documented coyote-caused mortality of a tagged elk calf on VCNP during 2009-2011 was a 31-day-old calf; given the median birth dates he reported for calves, coyote-caused mortality would have ceased by early July, similar to Smith and Anderson's (1996) finding that all neonatal elk mortality occurred by 15 July in northwest Wyoming. Bernal's (2013) study occurred during years of average precipitation on VCNP, including average snow depths preceding and during the study (Natural Resource Conservation Service data). In contrast, during our study, summer 2006 followed an extreme low-snow year on VCNP (Natural Resource Conservation Service data; Fig. 2-6). Elk on VCNP were consistently in very good to excellent body condition going into winters per examination of organ fat of hunter-harvested elk (Valles Caldera Trust, unpublished data). During winters with average snowfall, VCNP elk migrated to adjacent lower-elevation winter range (Biggs 2007). However, during low-snow winters, most of the elk herd stayed on VCNP where less desirable winter forage may have compromised elk nutritional status (Biggs 2007). The January crude protein in VCNP grasses was measured to be 2.4-4.2% during 2004 (R. Parmenter, unpublished data), which is insufficient for elk to maintain their body mass through the winter (Cook 2002). Weber et al. (1984) reported that according to body weight and blood serum indicators, elk using the lower elevation winter range were

on a higher dietary level than elk wintering on VCNP were, and they suggested that the observed difference in body weights of cow elk based on wintering sites could affect calf survival. Thorne et al. (1976) reported that cow elk which lost weight during winter months produced lower birth-weight calves than cows that did not lose weight, and that chances of calf survival declined substantially as birth weight declined. We suggest that the dry 2005-2006 winter negatively influenced the health and vulnerability of the elk calves born the subsequent spring, with compromised nutrition as a result of failure to migrate to lower-elevation winter range as a possible mechanism. Whether the vulnerability of calves was more specifically due to cow health during gestation or lactation, the timing of parturition, or the nutritional quality of summer forage for calves, and whether additional stressors such as human or predator disturbances occur on VCNP during winter bears further study.

The total volume of elk in coyote scats increased through the fall months, as expected based on observations of coyotes scavenging gut piles from hunter-harvested elk and carcasses of hunter-wounded elk. Elk hunts ceased by the end of November each year. Elk hair was present in winter scats at a consistently high amount, contrary to our expectation of reduced availability of elk to coyotes during winters and despite the large differences in the severity of the winters during the study period (Fig. 2-6). Some elk remained on the Preserve even during winters of average or above average snow depth (J. R. Biggs, unpublished data). The high volume and frequency of elk in winter scats suggested there may be winter-killed elk despite the relatively low severity of VCNP winters compared with the northern portion of elk distribution and despite the relatively

close proximity of lower elevation winter range. The source of elk in coyote diets could be coyote predation on winter-impaired elk, persistence of remains of hunter-harvested and hunter-wounded elk through winter months, or scavenging of elk killed by cougars, vehicles, or other causes. Coyote predation on adult elk, even by groups of coyotes, was likely rare, and previous impairments of the elk (e.g. by snow, injury, fences, poor nutritional condition, or separation from the herd) must be considered (Murie 1951, Gese and Grothe 1995). Carrion may be over-represented in canid scats relative to fresh carcasses because of the additional hide and hair consumed (O'Gara 1986) or low collectability of a high proportion of the first scats produced after feeding on a large carcass (Floyd et al. 1978).

Voles were a predominant year-round food of coyotes on the VCNP during the entire study period. Voles are a reliable prey source since they are active near the ground surface nocturnally and diurnally year-round. Identification between Cricetid species was difficult and relied on teeth; as a result, some of the prey identified as *Microtus* may have belonged to the similar but less frequent *Myodes* genus. *Microtus montanus* was common on the VCNP; *M. longicaudus* and *Myodes gapperi* also occurred but were less common. Cricetid populations have an irruptive nature. *M. montanus* reproduction can be highly facultative depending on the availability of vegetation (Negus et al. 1977). Cricetids were more frequent in scats during the 2005-2006 low-snow winter than during the two deep-snow winters, consistent with previous studies of the influence of snow depth on coyote predation on small mammals. Wells and Bekoff (1982) found longer coyote predatory sequences on voles when snow was deep and greater coyote capture

success in shallow snow. Gese et al. (1996*b*) found a clear advantage to coyotes at low (5 to 15 cm) snow depth rather than no snow, with decreased small mammal detection rates and capture attempts as snow depth increased >15 cm. Hamlin et al. (1984) concluded that in north-central Montana, continuous 30 cm snow depth for at least part of winter was important for microtine biology independent of coyote predation, since voles benefited from deeper snow for winter breeding and insulation from severe cold temperatures. Likewise, coyote consumption of voles on the VCNP was highest during spring and fall 2008, following two consecutive snowy winters (Fig. 2-6). It was possible that the vole population on the VCNP was higher during 2008 than the other years of the study. Other rodent families occurred much less frequently in coyote diets. Prey from the family Sciuridae were not available to coyotes during winter months since the Sciurid species on the VCNP hibernate.

Lagomorph species identified in scats reflected live species observations on the VCNP. While *S. nuttallii* was commonly observed, there was only one documented observation of *Lepus californicus* on the VCNP during 2003-2013 (R. R. Parmenter, Valles Caldera Trust, personal communication). The frequency of lagomorph (*S. nuttallii*) consumption did not vary significantly between most seasons or years (Table 2-2). A fairly consistent, low level of cottontails was found in the coyote scats, only twice exceeding 30% of the volume for a single month, and only dropping to zero when insect consumption was at or near peak in August 2005 and July 2006, and when elk consumption was at its peak in December 2006. A noteworthy peak in lagomorph consumption occurred in winter 2006-2007 when in January 2007, *S. nuttallii* was present

in 50% of scats. A large storm covered the ground with deep snow which ostensibly made cottontails easier for coyotes to catch; at the same time, rodent consumption was at its lowest frequency of the 43-month study.

The frequency of prey in the family Soricidae is likely underestimated. Due to their small size, the bones and teeth were more likely to have been digested in the coyotes' stomach acids or missed during lab analysis. Weaver and Hoffman (1979) also noted a bias of detection of larger prey species more often than smaller species in coyote scats.

The annual variation of insects in coyote scats by spring, summer and fall seasons (Table 2-3) was presumably associated with the timing and intensity of insect population irruptions. In summer 2008, the pulse of insect consumption was noticeably smaller than the other summers during the study by both volume (Fig. 2-5) and frequency measures; rodents increased to their highest volume and frequency in scats during this time. Possible mechanisms were a low insect (particularly Orthopteran) population, or an increase in the vole population during 2008.

Mule deer (*Odocoileus hemionus*) was found in surprisingly few of the scats (2 out of 1,385), despite a consistent, very small mule deer population fawning in the study area, suggesting negligible coyote predation or scavenging on adult or juvenile mule deer during the study period. Analysis of cougar scats currently underway preliminarily suggests a greater presence of deer remains in cougar scats and confirmed our ability to distinguish between mule deer and elk hair.

Cattle remains were also conspicuously missing from coyote scats. The grazing season began in June due to the high elevation, so most calves were a few months old before they were transported to the VCNP. To date, wild predator killing of domestic cattle has not been observed on the VCNP (R. R. Parmenter, personal communication).

We identified plant remains in coyote scats during all months of the study period except one (December 2007; Fig. 2-2). Plants were generally ≤15% of the relative volume (Fig. 2-1). Plant remains were predominantly grasses (83.3% of monthly plant occurences were grass), with fewer conifer needles or cones, and occassional seeds or leaves (Table 2-1, Appendix 2-1).

MANAGEMENT IMPLICATIONS

The Valles Caldera ecosystem was dynamic in terms of climate and vegetative phenology, with coyote diet fluctuating across seasons and years presumably tracking changes in prey availability and vulnerability, as well as changes in coyote biological needs. Despite the presence of numerous minor diet items, coyotes' diet was consistently comprised of the same five predominant groups. Winter snow appeared to influence the vulnerability of the main prey species through detection and capture probability or nutritional influences.

Smith (1998) determined that weather conditions while bull elk were in utero and timing of spring green-up during a bull elk's birth year were among the best predictors of antler size throughout his life. Conversely, bull elk born following unfavorable conditions are less likely to ever be among the largest bulls. The increased predation we

observed would serve to reduce recruitment during these low-productivity years,

potentially improving forage and habitat availability for successful bulls born during

years of average or above average winter and spring moisture. Increased hiding cover

and higher alternate prey populations also as a result of increased moisture may

additionally protect these cohorts from predation. These natural influences should serve

to support management for a trophy elk herd.

Prescribed fire has improved the nutritional content of the grass forage on VCNP

(R. Parmenter, unpublished data), though grass forage quality improvements following

fire may be short-lived (Dills 1970). With large wildfires on VCNP during 2011 and

2013 also changing the composition of the forest plant communities, including increases

in browse species (Valles Caldera Trust unpublished data), the detrimental nutritional

effect of dry winters may be partially or completely mitigated.

We observed coyote mortalities from apparent starvation during late winter and

early spring on VCNP (unpublished data), apparently due to low availability of food

combined with the energetic cost of locomotion through snow (Crête and Larivière

2003). Though VCNP coyotes have a diverse diet, availability of food may have a role in

regulating the VCNP coyote population.

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Table 2-1. Total and relative occurrence of major food items in coyote scats, Valles Caldera National Preserve, New Mexico, 2005-2008. All other food items comprised ≤7% of coyote diet.

Taxon	Total occurrence (%)
Rodentia	
Cricetidae	
Microtus spp.	602 (43)
Geomyidae	
Thomomys talpoides	214 (15)
Elk *Cervus elaphus*	
Adult	541 (39)
Calf	315 (23)
Insects	
Orhthoptera	288 (21)
Coleoptera	186 (13)
Lagomorpha	
Sylvilagus nuttallii	183 (13)
Plants	
Grass	796 (57)
Conifer (needles, cone)	200 (14)

Table 2-2. Contingency table analysis of seasonal variation in coyote diet within years, Valles Caldera National Preserve, New Mexico, 2005-2008.

	Rodent	Elk	Insect	Lagomorph	Plant
2005	P = 0.012	P = 0.043	P < 0.001	P = 0.001	P < 0.001
2006	P < 0.001	P < 0.001	P < 0.001	P = 0.491	P = 0.066
2007	P < 0.001	P = 0.001	P < 0.001	P = 0.263	P = 0.686
2008	P < 0.001	P < 0.001	P < 0.001	P = 0.307	P < 0.001

Table 2-3. Contingency table analysis of annual variation in coyote diet by season, Valles

Caldera National Preserve, New Mexico, 2005-2008.

	Rodent	Elk	Insect	Lagomorph	Plant
Spring	$P = 0.008$	$P < 0.001$	$P < 0.001$	$P = 0.018$	$P < 0.001$
Summer	$P < 0.001$	$P = 0.088$	$P < 0.001$	$P = 0.115$	$P = 0.001$
Fall	$P < 0.001$	$P < 0.001$	$P = 0.001$	$P = 0.007$	$P = 0.001$
Winter	$P < 0.001$	$P = 0.637$	$P = 0.179$	$P = 0.594$	$P = 0.045$
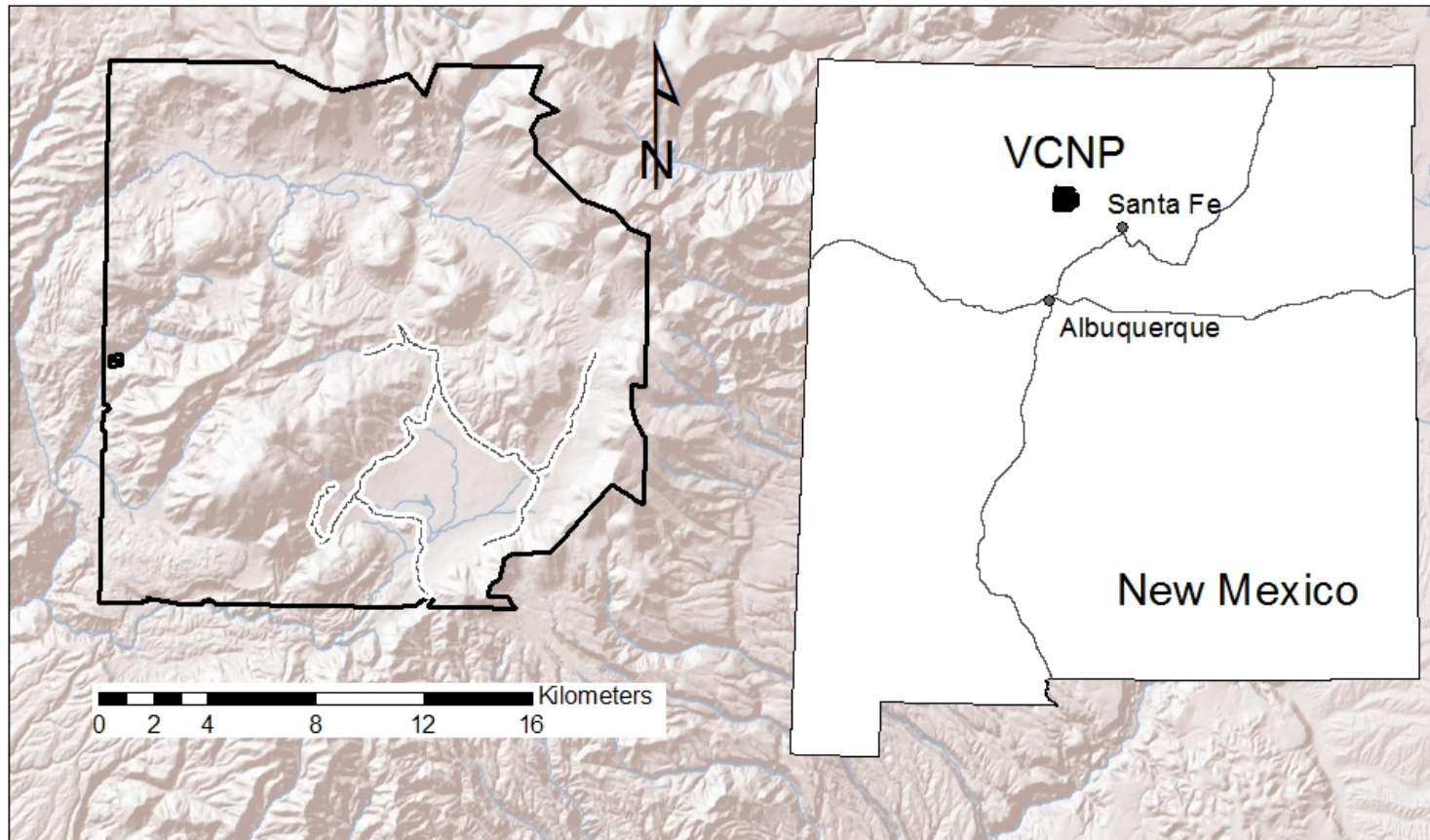
Figure 2-1. Roads surveyed for coyote scats on the study area, Valles Caldera, National Preserve, New Mexico, 2005 – 2008.

Figure 2-2. Monthly relative volume of major components in coyote scats (n = 1,385), Valles Caldera National

Preserve, New Mexico, 2005-2008. Monthly sample size of scat examined indicated above each month.
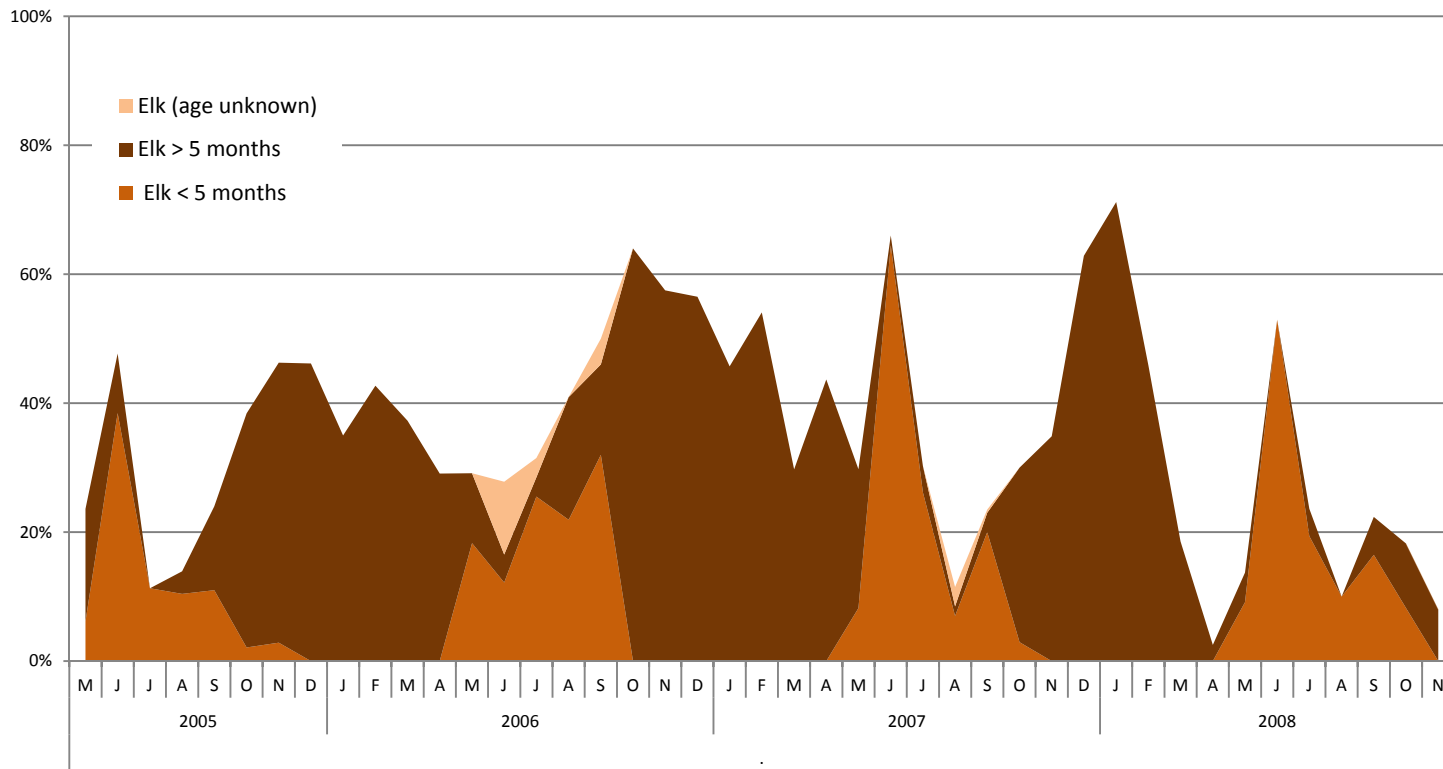
Figure 2-3. Monthly relative volume of elk in coyote scats (n = 1,385) by age class, Valles Caldera National Preserve, New Mexico, 2005-2008.
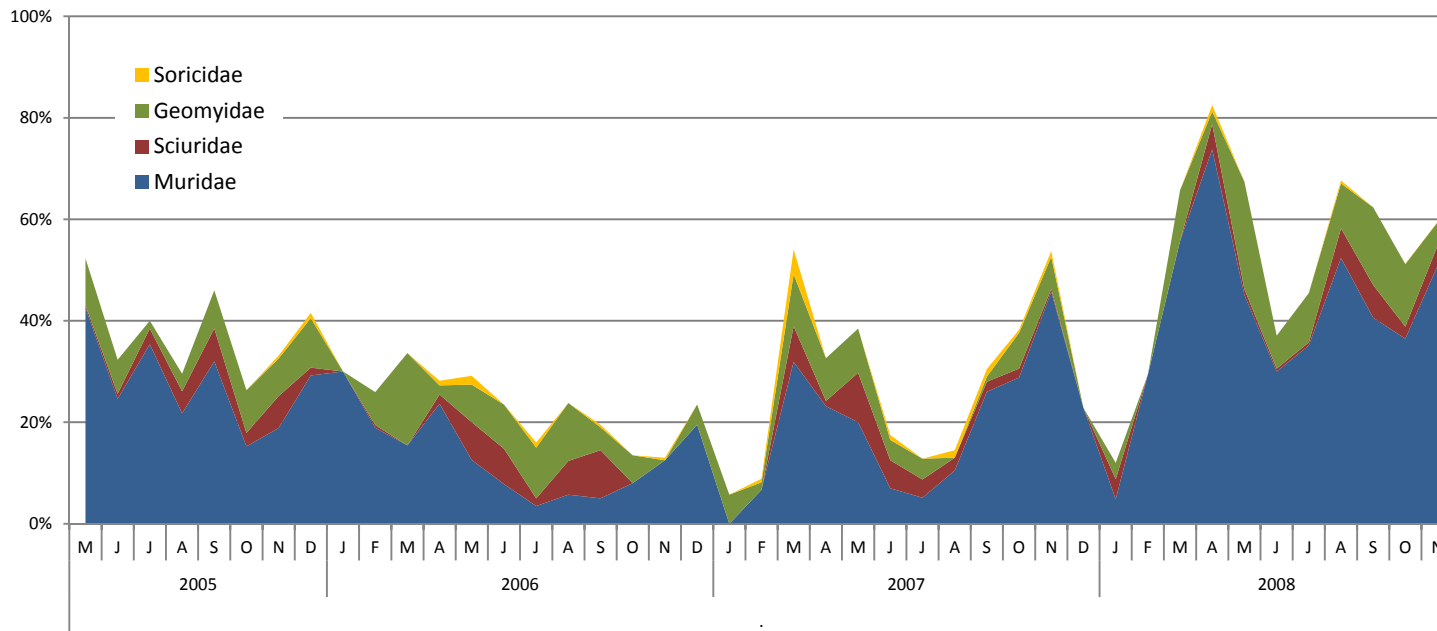
Figure 2-4. Monthly relative volume of Rodentia and Soricomorpha in coyote scats (n = 1,385) by family, Valles Caldera

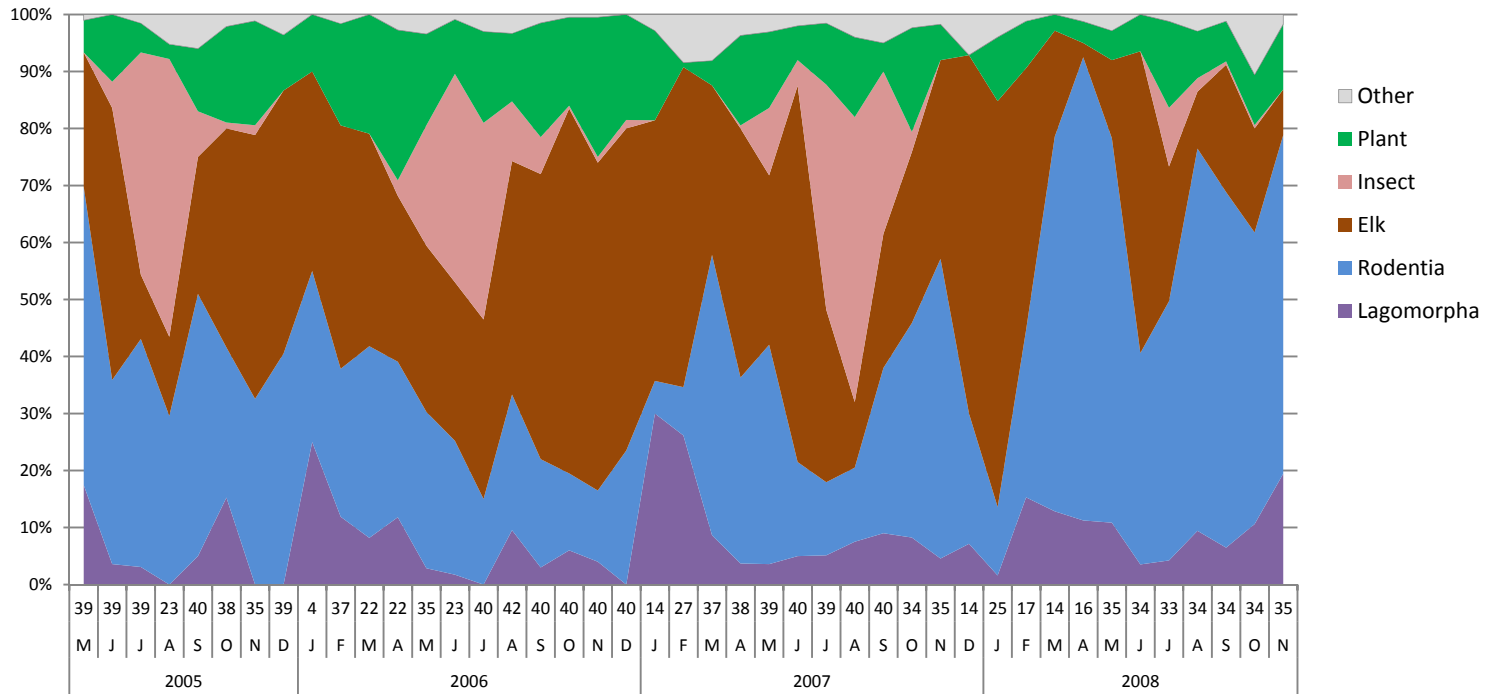National Preserve, New Mexico, 2005-2008.
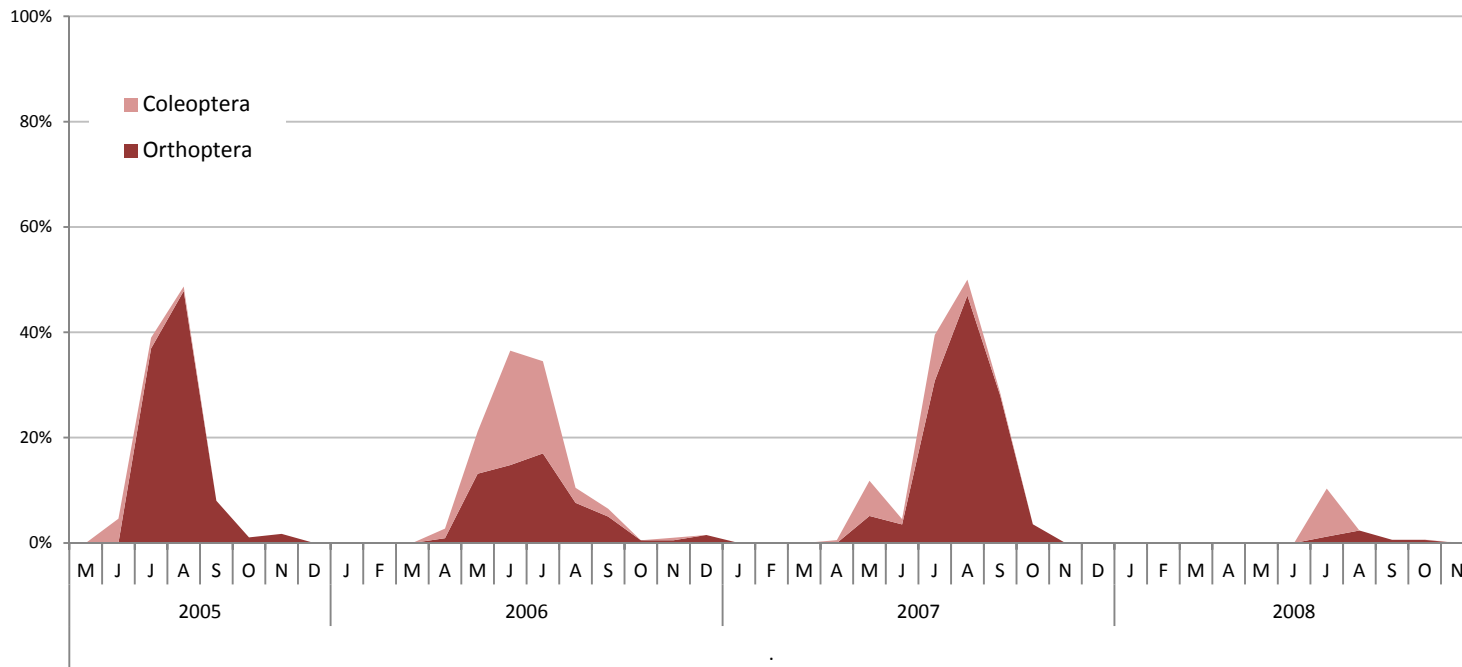
Figure 2-5. Monthly relative volume of insects in coyote scats (n = 1,385) by order, Valles Caldera National Preserve, New Mexico, 2005-2008.
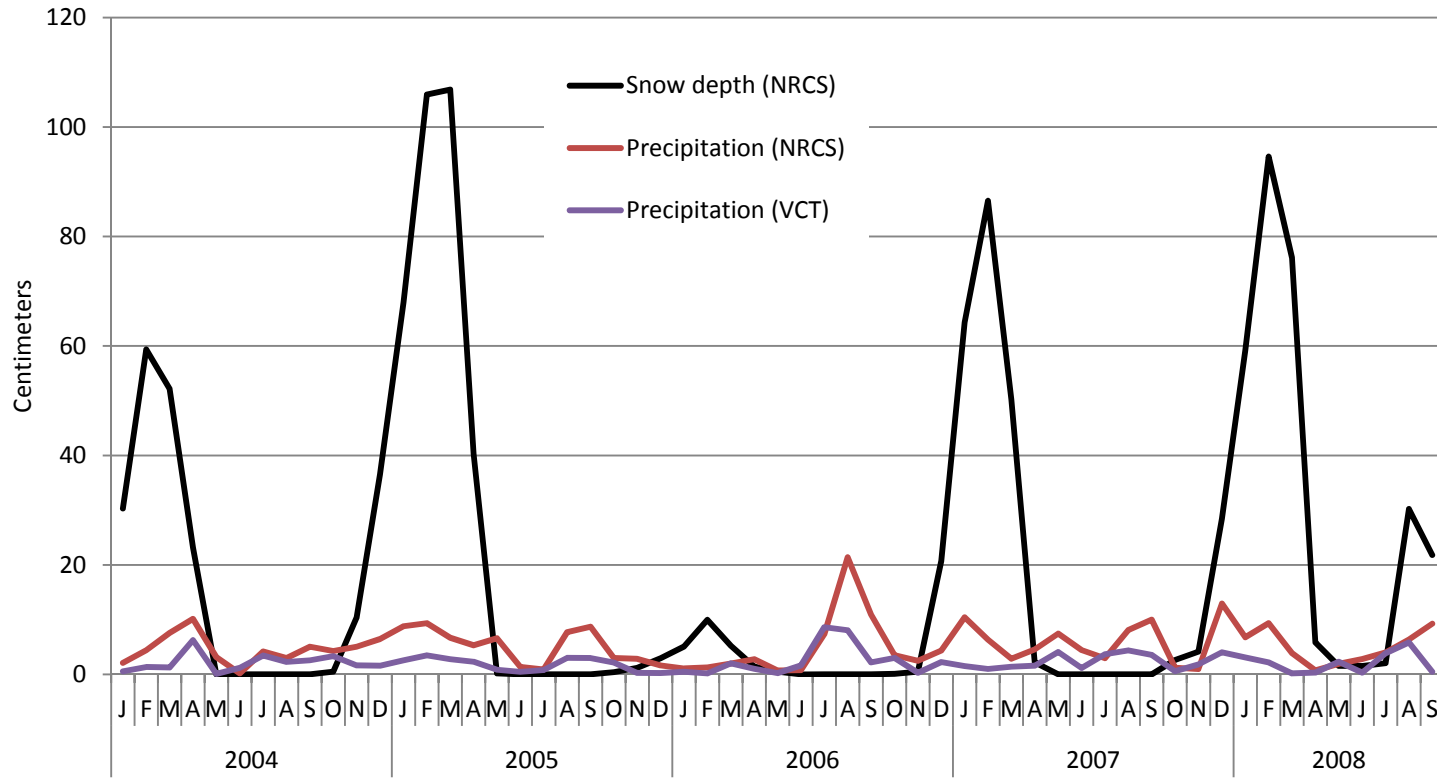
Figure 2-6. Monthly precipitation and average daily snow depth in the Jemez Mountains, New Mexico, 2004-2008. Data were collected by Natural Resources Conservation Service (NRCS) and the Valles Caldera Trust (VCT).

Appendix 2-1. Comprehensive list of taxa identified from coyote scats, Valles

Caldera National Preserve, New Mexico, 2005-2008.

TAXON	Total occurrence (%)
Elk *Cervus elaphus*	
Adult	541 (39)
Calf	315 (23)
Age unknown	16 (1)
Rodentia	
Cricetidae	
Microtus spp.	602 (43)
Peromyscus spp.	94 (7)
Ondatra zibethicus	25 (2)
Myodes gapperi	13 (1)
Neotoma spp.	12 (1)
Geomyidae	
Thomomys talpoides	214 (15)
Sciuridae	
Callospermophilus lateralis	36 (3)
Sciurus aberti	36 (3)
Cynomys gunnisoni	30 (2)
Neotamias spp.	20 (1)
Tamiasciurus hudsonicus	4 (0.3)
Unidentifiable	13 (1)
Soricomorpha	
Soricidae	
Sorex spp.	35 (3)
Lagomorpha	
Sylvilagus nuttallii	183 (13)
Lepus sp.	1 (0.07)
Insects	
Orhthoptera	288 (21)
Coleoptera	186 (13)
Plants	
Grass	796 (57)

Conifer (needles, cone)	200 (14)
Seeds	9 (0.6)
Leaf/ Forb	7 (0.5)
Nuts	4 (0.3)
Wood	3 (0.2)
Ribes sp.	2 (0.1)
Tree bud	1 (0.07)
Birds (feathers, shells)	99 (7)
Other mammals	
Bobcat (*Lynx rufus*)	6 (0.4)
Black bear (*Ursus americanus*)	4 (0.3)
Unknown mammal	4 (0.3)
Long-tailed weasel (*Mustela frenata*)	3 (0.2)
Badger (*Taxidea taxus*)	1 (0.1)
Western spotted skunk (*Spilogale gracilis*)	1 (0.1)
Mule deer (*Odocoileus hemionus*)	2 (0.1)
Grey fox (*Urocyon cinereoargenteus*)	2 (0.1)
Raccoon (*Procyon lotor*)	1 (0.1)
Cougar (*Puma concolor*)	1 (0.1)
Coyote (*Canis latrans*)	1 (0.1)
Other insects	
Hymenoptera; Formicidae (ants)	2 (0.1)
Diptera (flies)	2 (0.1)
Lepidoptera (butterfly)	1 (0.1)
Snake	6 (0.4)
Other / Unidentifiable	32 (2)

CHAPTER 3

SPATIAL AND SOCIAL ECOLOGY OF COYOTES (*CANIS LATRANS*) ON THE

VALLES CALDERA NATIONAL PRESERVE, NEW MEXICO

ABSTRACT – An understanding of coyote (*Canis latrans*) ecology was critical to developing management plans on the nascent Valles Caldera National Preserve (VCNP) in northern New Mexico. Coyote spatial and social ecology can be variable and little is known about high elevation populations. Our objectives were to describe the home-range size and habitat use of VCNP coyotes, to describe coyote movements within and outside of packs, and to evaluate the relationship between coyote social cohesion and the amount of elk (*Cervus elaphus*) in the coyote diet. We examined global positioning system (GPS) and triangulation location data from 33 coyotes during August 2005 through July 2009. We classified 23 coyotes (70% of individuals) as residents during at least part of the study and 10 coyotes (30%) as consistently transient. Overall mean home-range size of resident coyote packs was 11.0 ± 2.6 (SD) km^2. Home-range size varied significantly 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 by biological season. Alpha coyotes were more socially cohesive with each other than with their pack associate, and a transient exhibited temporal-spatial avoidance of pack members while inside the pack's home range followed by integration into the pack. Contrary to our expectation, we found no relationship between coyote social cohesion and the proportion

of elk in coyote diets. We concluded that coyote sociality on the VCNP was relatively stable year-round despite changes in biological needs and prey size.

INTRODUCTION

There have been numerous studies of coyote social and spatial ecology (e.g., Messier and Barrette 1982, Andelt 1985, Mills and Knowlton 1991) but few studies at high elevations (e.g., Bekoff and Wells 1980, Bowen 1982, Gese et al. 1996*a*). A general consensus of studies indicates that coyote space use can be stable through time (Kitchen et al. 2000, 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. 1988*a*). In terms of social ecology, coyote populations can be divided into resident and transient individuals (e.g., Camenzind 1978, Bowen 1978, Bekoff and Wells 1986) but social organization differs among populations, and the way in which individuals transition into or out of resident packs also varies (Andelt 1985, Kamler and Gipson 2000, Gese 2001). Previous studies 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. 1988*b*). Gese et al. (1988*b*) 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. In contrast, Bowyer (1987) found a higher percentage of coyotes in groups during June through November, but the amount of mule deer (*Odocoileus hemionus*) in scats did

not vary seasonally. Comparison of observations at different sites is confounded by whether young of the year or groups at carcasses are included in counts, or by use of an arbitrary distance designating when coyotes were considered "together."

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 some national parks (Murie 1940, Bekoff and Wells 1980, Gese et al. 1996*a*). 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" to allow "continued operation as a working ranch under a unique management regime which would protect the land and resource values of the property and surrounding ecosystem while allowing and providing for the ranch to eventually become financially self-sustaining" with the specifics of management to be determined by a Trust and Board of Trustees (Valles Caldera Preservation Act 2000). Management or hunting of coyotes (*Canis latrans*) or other predators has not occurred on the VCNP while under federal management, but remains a contentious issue. VCNP is also a critical calving area for Rocky Mountain elk (*Cervus elaphus nelsoni*).

Similar to 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 to livestock and the elk population via predation on elk calves. In contrast to national parks, revenue from elk hunts is critical to the financial sustainability of the VCNP as it is the

most profitable public activity on the Preserve (Valles Caldera Trust 2012). Low elk

calf:cow ratios (New Mexico Department of Game and Fish unpublished data 2003,

2005) coincided with the cessation of persecution of coyotes when the federal

government purchased the land and established the Preserve. Anecdotal increased

visibility of coyotes and 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 to other natural resources

including aspen (*Populus tremuloides*), riparian areas, archaeological resources and

livestock grazing areas outside of the VCNP (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 different concerns are present,

such as elk-vehicle collisions and impacts to private lands.

A location-specific study was needed for making informed decisions regarding

management of coyotes, elk and livestock on the VCNP. 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 our study was to describe the

spatial and social ecology of coyotes to inform mangers about the elk- coyote dynamic on

the VCNP. Our objectives were to describe the home-range size and habitat use of

VCNP coyotes, to describe coyote movements within and outside of packs, and to

evaluate the relationship between coyote social cohesion and the amount of elk in the

coyote diet.

Study Area

The 360-km^2 Valles Caldera National Preserve (VCNP) was located in the Jemez

Mountains in north-central New Mexico, and was managed by the Valles Caldera Trust.

The landscape was characterized by forested mountains (2700-3400 m elevation) and

large, grassland meadow valleys (2450-2700 m elevation). Our study focused on the

vicinity of the Valle Grande, a large grassland meadow in the southeastern portion of the

VCNP which is dissected by the East Fork of the Jemez River and its associated riparian

areas (Fig. 3-1). The study area ranged from 2600 to 3100 m in elevation. Mean annual

precipitation was 640 mm ± 9.7 (SD), predominantly in the form of monsoon rains (July

and August) and winter snow (November through March; Valles Caldera Trust,

unpublished data). Mean July maximum and minimum temperatures were 25.5 and

5.5ºC, respectively; mean January maximum and minimum temperatures were 4.6 and -

16.5ºC, respectively (Valles Caldera Trust, unpublished data). Average snow depths for

winters (November through March) 2004-05 through 2008-09 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.

Mammalian 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*), and Coleopteran and Orthopteran insects (Chapter 2).

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

Forests and Woodlands (forest) – Ponderosa pine (Pinus ponderosa) and blue spruce (Picea pungens) forests bordered the grassland valleys. Mixed conifer forests, comprised of Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), blue spruce (*Picea pungens*), southwestern whitepine (*Pinus strobiformis*), limber pine (*Pinus flexilis*), and ponderosa pine (*Pinus ponderosa*), 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 coverage was rare within our study area. Stand structure and species composition of forests throughout the Jemez Mountains show departure from historic conditions due to fire suppression (Touchan et al. 1996).

Montane grassland/ Dry meadow (dry meadow) – Montane grasslands were highly diverse with more than 125 species of grasses and forbs recorded (Muldavin and Tonne 2003). They were dominated by upland grasses and forbs: pine dropseed (*Blepharoneuron tricholepis*), Parry's oatgrass (*Danthonia parryi*), Arizona fescue (*Festuca arizonica*), Thurber's fescue (*Festuca thurberi*), and Kentucky bluegrass (*Poa pratensis*) alliances.

Montane wet meadow (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. Plant species of wet meadows primarily included tufted hairgrass (*Deschampsia caespitosa*), wooly cinquefoil (*Potentilla hippiana*), Baltic rush (*Juncus balticus*), Kentucky bluegrass (*Poa pratensis*), and common dandelion (*Taraxacum officinale*).

Riparian / Wetland (riparian) – Riparian plant communities were comprised of 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 are notably absent from the riparian areas and it is unknown if this is due to hydrological or soil characteristics or historically heavy grazing (Muldavin and Tonne 2003).

METHODS

We captured coyotes using padded-foothold traps (Livestock Protection Company, Alpine, TX; or Oneida Victor, Eucild, OH) and anesthetized them for handling with 10 mg/kg tiletamine hydrochloride and zolazepam hydrochloride (Kreeger 1999). 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 size and weight, collected hair and blood samples,

determined sex, and estimated age based on tooth wear (Gier 1968). We fitted coyotes with global positioning system (GPS) collars (Lotek Wireless, Inc., New Market, Ontario) with secondary very high frequency (VHF) transmitters (Advanced Telemetry Systems, Isanti, MN), or VHF transmitters alone (Lotek Wireless, Inc., New Market, Ontario). We evaluated GPS collar accuracy by calculating the mean distance between stationary test collar fixes and high-resolution GPS locations.

Home-Range Size

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 long (2 to >100km) 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 4 or more sequential locations ≥2-km outside of the area used by the pack, prior to calculating home ranges.

We divided locations into seasons corresponding with the biology of territorial coyotes (modified from Smith et al. 1981): breeding/ gestation (1 Dec – 31 Mar), pup rearing (1 Apr – 31 Jul), and dispersal (1 Aug – 31 Nov). Since the breeding/gestation season crossed calendar years, we included December data in the breeding/gestation season labeled with the succeeding year for simplicity (e.g., breeding/gestation 2007

included 1 Dec 2006 – 31 Mar 2007). For all analyses, the pack was defined as the individuals occupying a space together during ≥1 biological season.

We eliminated locations within 24 hours post-release to reduce bias from capture and subsequent recovery. We sub-sampled locational data to every 4-hours to standardize locational sampling across the duration of the study (Gese et al. 1990, White and Garrott 1990). The 4-hour sampling scheme also reduced temporal autocorrelation (Swihart and Slade *1985a,b*), though more highly temporally autocorrelated data may provide better estimates of home range sizes and other movement measures (Reynolds and Laundré 1990, Aebischer et al. 1993, de Solla et al. 1999, Fieberg 2007) when the animal is the sample unit rather than the individual observations (Kenward 1992, Otis and White 1999). Since coyote pack associates 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. Since resident coyotes are territorial (Camenzind 1978, Bekoff and Wells 1986, Andelt 1985, Allen et al. 1999, Gese 2001), it was biologically justified to calculate home ranges as a single, continuous polygon. Further, visual inspection of GPS collar data indicated that a single, continuous polygons was an appropriate generalization of space use of coyote packs. An *ad hoc* bandwidth (h) selection method was adapted (J. G. Kie, unpublished data), 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; J.G. Kie, unpublished data). Seaman

et al. (1999) reported home range size from kernel density estimates are more reliable

using a minimum of 30 to 50 observations per home range, based on simulated locations.

J. G. Kie (unpublished data) reported no influence of degree of autocorrelation on bias

when using $h_{ad\ hoc}$ as described above. We used 57 to 2392 locations to calculate each

seasonal pack home range. 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 single 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.

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) identified 20 vegetation classes to

produce a 2 m x 2 m cell size raster map generated through a combination of ground

plots, aerial photography, satellite image processing and band ratioing; model validation

was conducted but a final accuracy assessment was not calculated. We reduced the

number of vegetation classes by combining the original 20 classes into the following 5

habitat types to increase map accuracy and provide ecologically meaningful habitats for

coyote space use: forest, dry meadow, wet meadow, riparian, and bare ground (Fig. 3-2,

Appendix 3-1). Streams bisected the study area and were lined by riparian areas on both

sides. Stream widths were smaller than our observed GPS collar error and coyotes were

unlikely to spend time in open water. Therefore, we included water in the riparian habitat

type. Since road widths were also smaller than our observed GPS collar error, we

interpolated the raster map so cells classified as road or were changed to match the

adjacent habitat type. We eliminated the bare ground category from analysis since it

comprised <0.5% of seasonal home ranges in all except two cases (<2.6% in all cases)

and ≤1.2% of use in all cases. 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. 3-2). 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 greatest 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 by pack using contingency table analysis; we

also used contingency table analysis to evaluate the differences in habitat availability by

pack. We compared habitat use to habitat availability within the home range for each

pack during each biological season using independent Chi square tests and Bonferroni confidence intervals (Neu et al. 1974, Byers et al. 1984). Since the coyotes did not use diverse terrain 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 associates and to evaluate the relationship between pack 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. 1988*a*), we found that group size observations were biased by length of observation, vantage point, and time of day. Instead, to evaluate social cohesion, we calculated the distance between simultaneous (within 1 minute) 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 hours 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 associates 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 (Chapter 2). We predicted that 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.

RESULTS

We captured and radio-collared 36 coyotes which yielded GPS locations from 21 individuals and triangulation locations from 12 additional individuals during August 2005 through July 2009; we excluded three individuals from analysis due to failure of GPS collars or drop-off mechanisms and insufficient triangulation locations. Seven coyotes were re-captured and re-collared during the study. Locations of territorial individuals were concentrated in a single area during ≥1 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. 3-3). We identified two types of transient movements. All coyotes which were transient when we initially captured them remained transient as long as we were able to track them (up to 34 consecutive months); these individuals all showed the wide-ranging transient movements previously described in the literature (Camenzind 1978, Kamler and Gipson 2000). 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 10 coyotes (30%) as consistently transient. Four of the resident coyotes also exhibited transient movements during ≥1 month of our study.

We calculated 17.4 m (median) and 34.2 m (mean) GPS collar location error based on 1003 test fixes from 12 test locations. The fix acquisition rate from our test collars was 98.7%. Biggs et al. (2001) found that neither vegetation cover nor slope were significant predictors of GPS collar position acquisition rates in the Jemez Mountains. However, S. R. Rupp (unpublished data) determined that land cover type, slope, aspect and elevation can affect DOP on GPS collars in the Jemez Mountains. Eliminating points based on DOP values could have biased our habitat use results. Therefore, we did not censor coyote locations based on recorded fix variables (Dilution of Precision [DOP], number of satellites, or fix type [2-D or 3-D]). When we plotted test collar locations on the vegetation map, 90.9% of the fixes were classified in the correct vegetation category.

We identified 4 packs using the Valle Grande (Fig. 3-4). For all analyses, the pack was defined as the individuals occupying a space together during ≥1 biological season. 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 (3 coyotes moved from the La Jara pack to the Pinon pack, 1 coyote moved from the Pinon pack to the La Jara pack) or became transients (2 coyotes from the Pinon pack became transient; one

joined the La Jara pack 1.5 years later and the other coyote joined the La Jara pack 2.5 years later).

Home-Range Size

We used 16,411 GPS locations from 17 resident individuals in 4 packs spanning August 2005 through July 2009 (covering 11 biological seasons) for determining home range size and habitat use. Overall mean home-range size was 11.0 ± 2.6 (SD) km^2 (n = 23 seasonal pack home ranges), and varied significantly between packs (F = 3.19, df = 3, 19, P = 0.047; Table 3-1). We found no effect of year (F = 1.15, df = 4, 6, P = 0.42) or season (F = 0.27, df = 2, 8, 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, Pinon, East, and Rincon packs, respectively (Fig. 3-4). Given the mean pack home range size of 11.0km^2, and observed pack sizes of 5 to 6 adults with transients comprising an additional 30% of the population, we estimated the population density to be 0.59 to 0.71 coyotes per km^2 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 to 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 to 4, r = -0.005, P = 0.98). Adjacent home ranges overlapped an average of 6.1% (n = 14 seasonal pack home ranges; Table 3-1).

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 2 or more packs were observed, availability varied significantly between packs (n = 8 biological seasons, P < 0.001 in all cases; Figs. 3-5, 3-6, 3-7).

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 9 pack biological seasons, respectively; n = 23 pack biological seasons). Habitat use varied significantly between packs within seasons (P ≤ 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 3-2). 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 ≤ 0.034 in 22 cases, α = 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.

Social Ecology

We collected simultaneous GPS locations from individuals within two packs. In

the La Jara pack, we measured social cohesion between 5 individuals (up to 3 at a time)

during 12 months. Each pair had $\geq$ 54 simultaneous locations within the pack home

range during each month (mean n = 111 simultaneous location pairs). In the Pinon pack,

we measured social cohesion between 7 individuals (up to 4 at a time) during 22 months,

including the alpha pair during 13 months. Each pair had $\geq$ 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 $\geq$ 6 hours apart; P

< 0.001 for all pairs). The Pinon alpha pair was more cohesive with each other than each

was with the third Pinon pack associate (P < 0.001; Fig. 3-8a, b). Differences in social

cohesion between biological seasons were not significant (Pinon pack: P = 0.896, La Jara

pack: P = 0.289). We found no relationship between social cohesion of the Pinon and La

Jara packs and the amount of adult (r^2 = 0.075, F = 2.113, P = 0.079), calf (r^2 = 0.005, F =

0.126, P = 0.363) or total (r^2 = 0.084, F = 2.386, P = 0.067) elk in their diet (Fig. 3-10).

One male coyote (C26) had been a member of the La Jara pack (May 2006 –

January 2007) and then joined the Pinon 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 Pinon pack territories. During March 2008,

he transitioned from using all of the Pinon home range to only using part; it was unclear

whether to consider C26 a Pinon pack associate while he used only part of the territory.

During March through 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 Pinon pack associate pairs ($P < 0.001$), and the

distances between C26 and Pinon pack associates were greater than locations of Pinon

pack associates paired at random times ≥ 6 hours apart ($P = 0.007$), indicating avoidance

of the pack members (Fig. 3-9). During August through October, C26's mean distance

from the resident coyotes declined; during September through December his cohesion

with pack members was similar to 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 Pinon pack home range. Beginning in January 2009 he established a

home range outside of the VCNP and no longer used the Pinon home range enough for

comparison (he had only 8, 4, and 2 locations within the Pinon home range during

January, February and March 2009, respectively).

DISCUSSION

Home-Range Size

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 the literature for 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 ± 1.59 km^2 in the portions of their study area which were wolf-free; they used fixed-kernel density home range calculation and bandwidth selection criteria similar to our analysis. Winter home ranges of coyotes in southwestern Montana (1300 – 2500 m elevation) were 11.02 km$^2 \pm 1.03$ (SE), and were calculated using a 95% fixed kernel with least-squares cross validation (Atwood and Gese 2010). In Yellowstone, Gese et al. (1996a) reported territory sizes ranging from 8.8 to 14.3 km^2 (mean 10.3 ± 0.42 SE) in the Lamar Valley, based on visual locations and observations of coyote behavior.

The size of resident pack home ranges of the VCNP did not vary significantly by season or year, consistent with some previous studies (Camenzind 1978, Bowen 1978, Andelt 1985), though differences have been found between seasons in other previously published analyses of individual space use (e.g. Althoff 1978, Springer 1982, Laundré and Keller 1984, 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 (Laundré and Keller 1984, 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 (Chapter 2) also likely contributed to the spatial stability of home ranges. Andelt (1985) speculated that seasonal constancy in home range size on his sites resulted from resident groups continuously occupying nearly all available habitats, likely 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.

Habitat Use and Availability

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. (1996*b*) 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. 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 be predominantly comprised of 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 (Chapter 2), 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. 3-3). 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 (personal observation). 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.

Social Ecology

Though home range boundaries were relatively stable, we documented several changes in the individuals occupying the home ranges. Coyote individuals changing from resident to transient or transient coyotes joining packs have been documented in previous studies (Gese et al. 1988*a*, Kamler and Gipson 2000). While coyotes in our

study area generally followed 2 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 to or rejection from a pack.

As evidenced by C26's movements, designation as a pack associate 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.

To our knowledge, avoidance of resident coyotes by transients had not previously been

measured.

In contrast to previous studies which measured coyote cohesion in terms of group

size, we found that cohesion did not vary by coyote biological seasons. By measuring

cohesion using simultaneous locations of established individuals within packs, we

eliminated the confusion caused by variation in timing of juvenile dispersals (Gese et al.

1988*b*) and temporary aggregations of coyotes at carcasses (Murie 1940, Camenzind

1978, Bowen 1981, Gese et al. 1988*b*). 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 coyote cohesion

and the proportion of elk in coyote diets. We expected that feeding on and defending

carcasses would result in greater 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

cohesion coincident with the amount of elk calves in coyote diets. We conclude that

coyote sociality on VCNP is 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.

MANAGEMENT IMPLICATIONS

Previous studies have indicated that coyote predation on ungulates is related to

ungulate vulnerability due to snow, separation from the herd or compromised health

(Gese and Grothe 1995). Elk captured in the eastern 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 the western Wyoming area of the Greater Yellowstone Ecosystem, 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 12.4% of coyote

locations in forest and 88.0% in open habitats (dry meadow, wet meadow and riparian).

Bernal (2013) reported that 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, further discussion is warranted

pertaining to the management of meadow-forest transition and edge areas. If an increase

in elk recruitment is desired, these areas could be managed to increase protection of elk

calves. The specific temporal-spatial vulnerability of elk calves to coyote and bear

predation bears further study, including the proximity of calf mortality sites to livestock

fencing.

Fire suppression has been one of the most important anthropogenic disturbances

in the Jemez Mountains, resulting in forest species composition and stand structure

conditions outside of the historic range (Touchan et al. 1996). During 2011 and 2013,

large-scale fires burning at moderate and high severities changed the forests bordering the

Valle Grande. Further study will elucidate whether coyotes expand into the newly non-

forested areas, and whether habitat use of other predators (bears and cougars) changes.

Regrowth of understory vegetation may provide improved nutrition for elk (R. R.

Parmenter, unpublished data) and improved hiding cover for calves.

Bernal (2013) showed that bears kill more elk calves than coyotes (40.6% of

mortality versus 35.9%), though human observations of bear predation attempts on elk

calves were rare. To better understand the discrepancy between our findings and

perception, future research could quantify and compare human habitat use and activity

patterns on VCNP with those of coyotes, elk and bears. We expect that humans would

overlap with coyotes the most, with diurnal activity patterns and frequent use of open meadow landscapes. Kitchen et al. (2000) documented that coyotes shifted to more diurnal activity pattern following 8 years of reduced coyote persecution by humans. Similarly, McClennan 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 was likely due at least in part to an increase in visibility following a shift to more diurnal activity patterns.

In national parks where hunting of predators also does not occur, the ecosystem dynamics of elk are varied. In Rocky Mountain National Park, decline of willow and aspen have been documented and attributed to high ungulate populations (Olmstead 1979, Baker et al. 1997, Peinetti et al. 2002). Lubow et al. (2002) conclude that the park population is 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 impacts residential areas of the nearby town of Estes Park (Schultz and Bailey 1978). In Yellowstone National Park, following wolf (*Canis lupus*) reintroduction and grizzly bear (*Ursus arctos horribilis*) recovery alongside 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) suggests adjusting hunting pressure is a more powerful management tool than predation for regulating elk population size.

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Table 3-1. Home range size and overlap (km^2) of resident coyote packs during 3 biological seasons on the Valles Caldera National Preserve, New Mexico, 2005-2009.

Year	Biological season	Pack	Home range size			Home range overlap		
			N (individuals)	N (locations)	Area (km^2)	# adjacent packs observed	Area (km^2)	% Overlap
2005	Dispersal	East	1	258	14			
		LaJara	3	732	11.9			
2006	Pup Rearing	East	1	418	10.1	2	0.06	0.6%
		LaJara	2	825	11	2	0.63	5.7%
		Pinon	4	1321	11	2	0.61	5.5%
	Dispersal	East	1	508	12.8	2	0.49	3.8%
		LaJara	2	1248	12.1	2	0.63	5.2%
		Pinon	3	1389	10.5	2	0.94	8.9%
2007	Breeding/Gestation	East	1	287	12.3	1	1.38	11.2%
		Pinon	3	381	11.7	1	0.29	2.4%
		LaJara	2	664	11.7	2	1.67	14.2%
	Pup Rearing	East	2	187	10.1	1	0	0%
		Pinon	2	357	6.5	1	0	0%
	Dispersal	Pinon	1	196	7.5			

2008	Breeding/Gestation	East	1	57	14	2	1.61	11.5%
		Rincon	1	81	10	1	0.24	2.6%
		Pinon	3	308	9.2	1	1.37	13.7%
	Pup Rearing	Rincon	2	181	6.7			
		Pinon	3	1821	13.6			
	Dispersal	Rincon	1	601	5.5			
		Pinon	4	2392	12.3			
2009	Breeding/Gestation	Pinon	3	1641	11.6			
	Pup Rearing	Pinon	1	558	16.1			

Table 3-2. Coyote habitat use compared with availability for (A) forest, (B) dry meadow, (C) wet meadow, and (D) riparian habitats during 3 biological seasons (B/G: breeding/gestation; PR: pup rearing; D: dispersal) on the Valles Caldera National Preserve, New Mexico 2005-2009. A "+" indicates use was significantly greater than available for one pack based on Bonferroni confidence interval calculation; a "–" denotes use was significantly less than available for one pack; differences which were not statistically significant are indicated by "o."

A. Forest	B/G	PR	D
2005			-o
2006		-oo	---
2007	oo+	--	-
2008	--o	--	--
2009	-	-	

B. Dry Meadow	B/G	PR	D
2005			oo
2006		--o	oo+
2007	-o+	-o	o
2008	ooo	-o	-o
2009	-	-	

C. Wet Meadow	B/G	PR	D
2005			o+
2006		oo+	ooo
2007	--o	oo	o
2008	ooo	o+	++
2009	+	+	

D. Riparian	B/G	PR	D
2005			++
2006		+++	+++
2007	o++	o+	+
2008	oo+	o+	o+
2009	+	+	
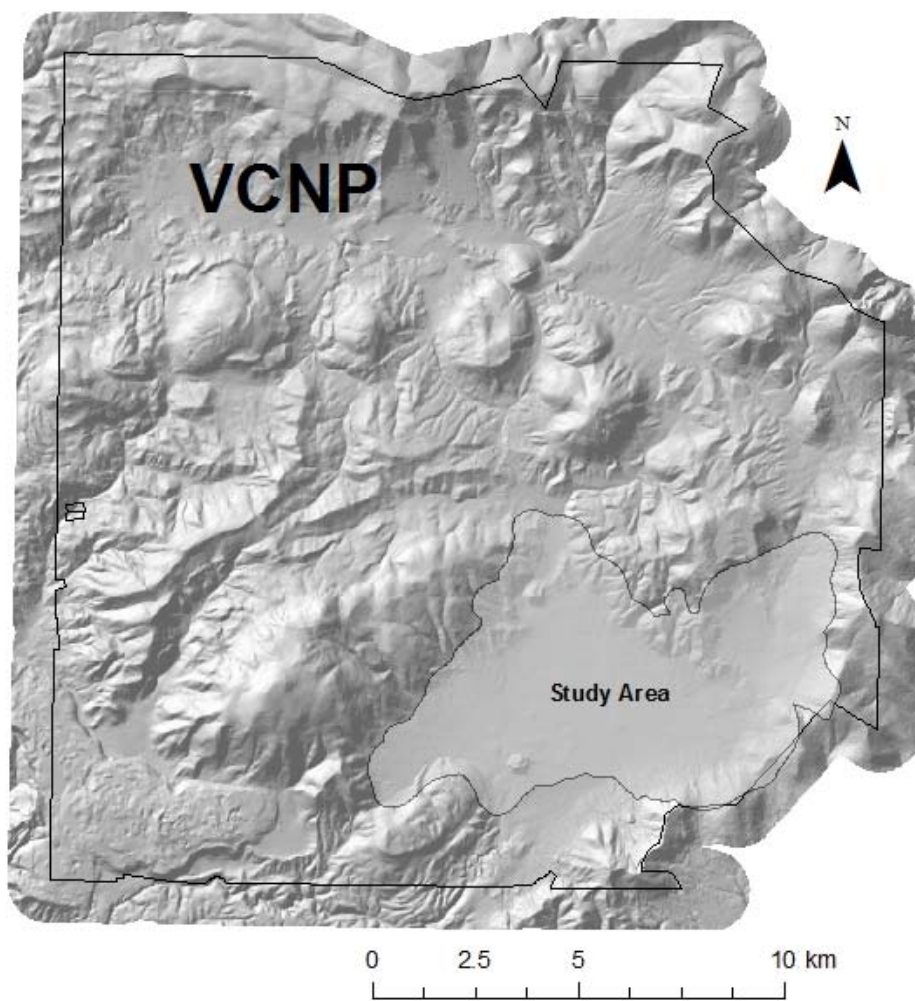
Figure 3-1. Delineation of the study area in the Valles Caldera National Preserve (VCNP), New Mexico.
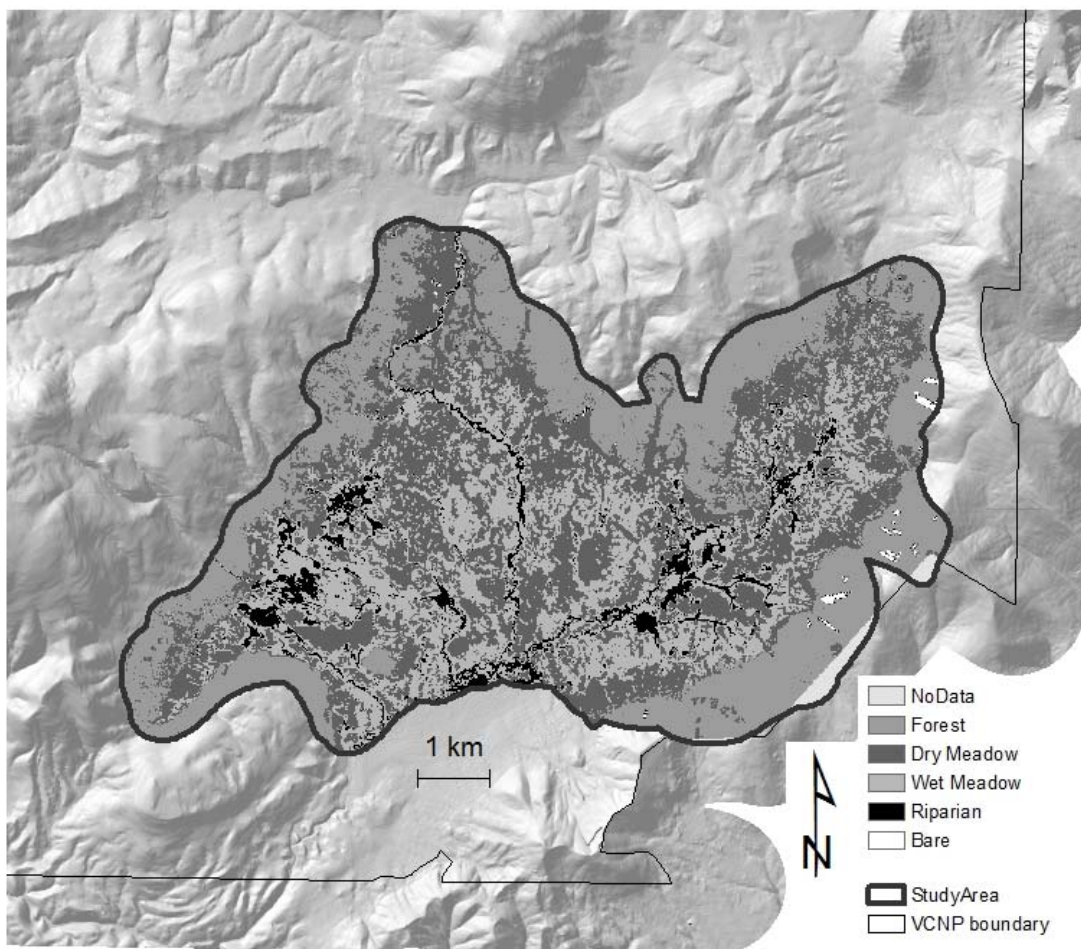
Figure 3-2. Habitat types within the study area on the Valles Caldera National Preserve

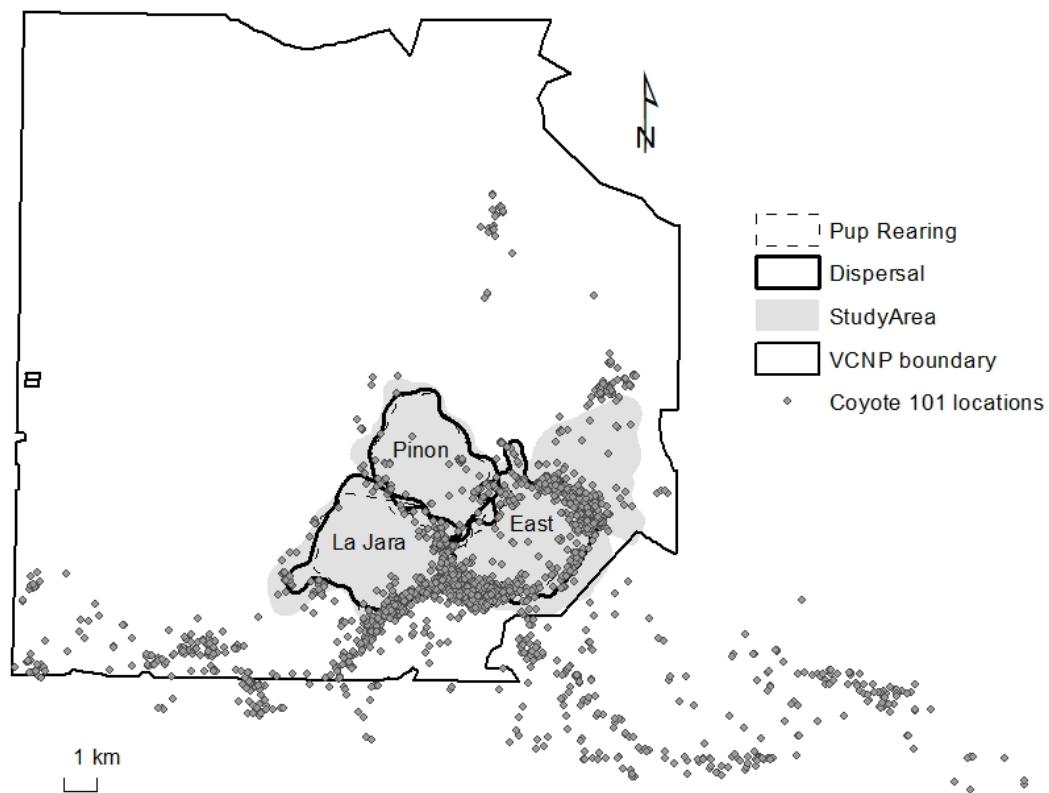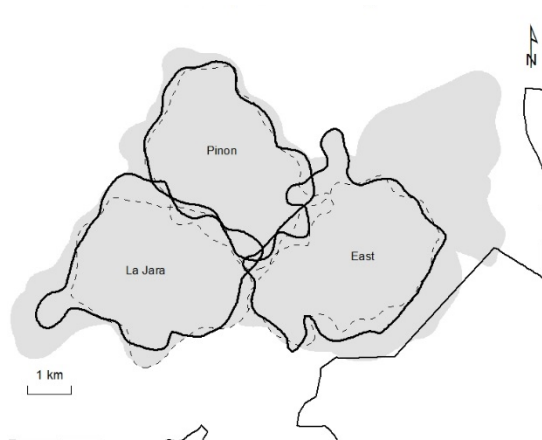(VCNP), New Mexico, adapted from a vegetation map created by Muldavin et al. (2006).

Figure 3-3. Boundaries of resident coyote pack home ranges and locations for transient coyote C101 during 2006 on the Valles Caldera National Preserve (VCNP), New Mexico.
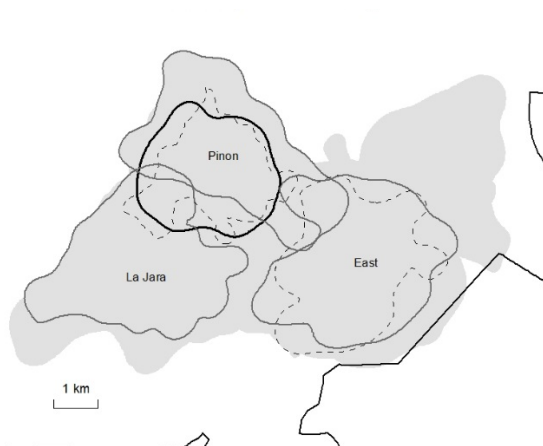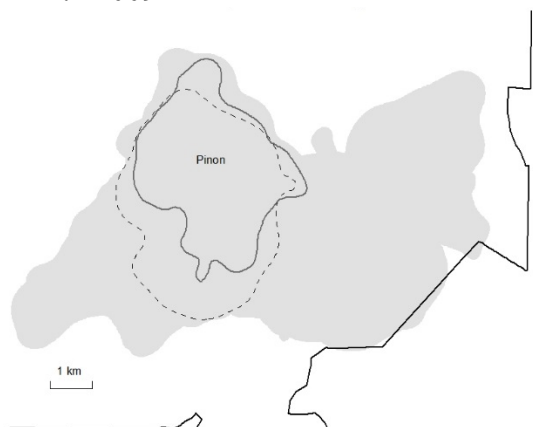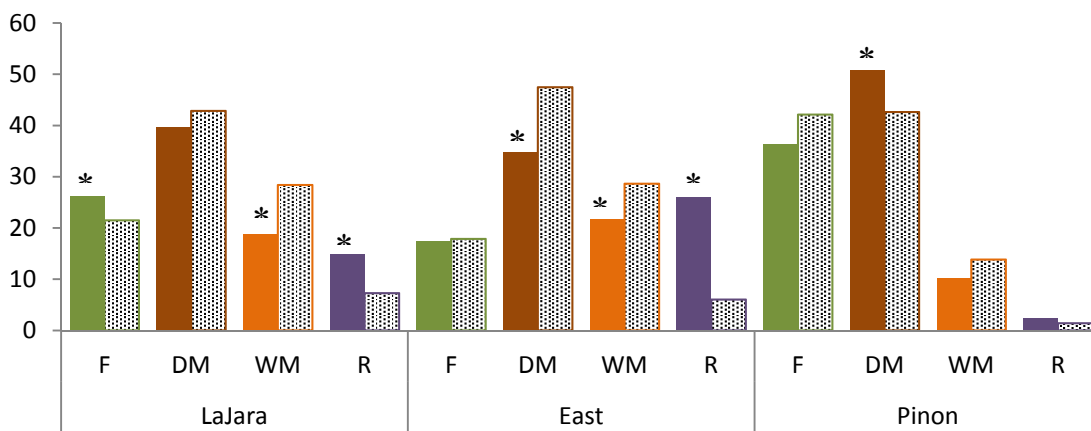
A. 2005

B. 2006

C. 2007

D. 2008

E. 2009

Breeding/Gestation
Pup Rearing
Dispersal
StudyArea
VCNP boundary

Figure 3-4. Boundaries of resident coyote pack home ranges on the Valles Caldera

National Preserve (VCNP), New Mexico during (A) 2005, (B) 2006, (C) 2007, (D) 2008,
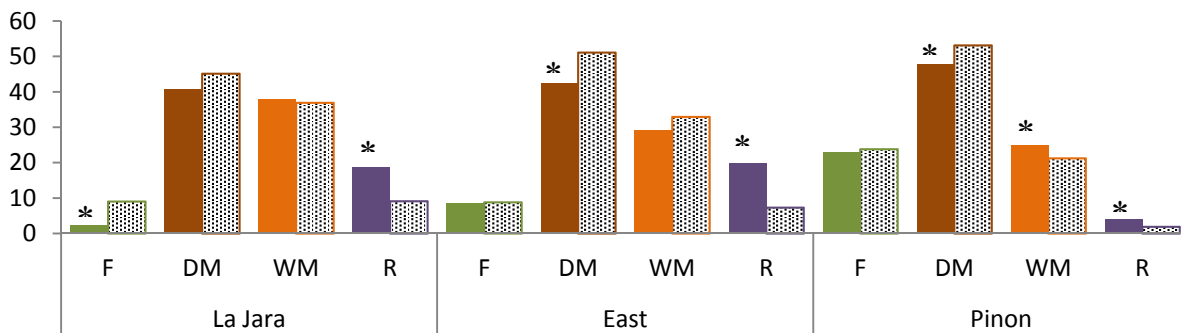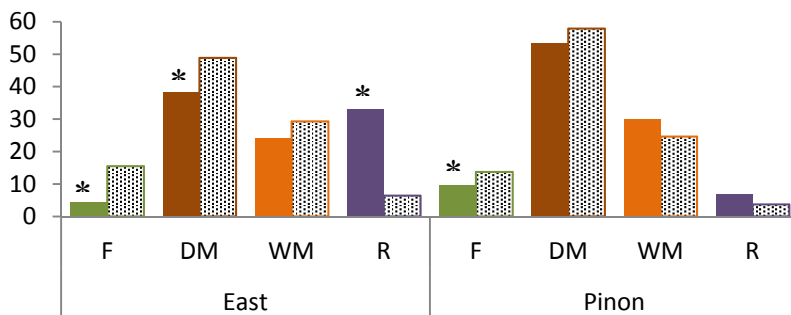
and (E) 2009.

A. 2007

B. 2008

C. 2009

Forest Used — Forest Available
Dry Meadow Used — Dry Meadow Available
Wet Meadow Used — Wet Meadow Available
Riparian Used — Riparian Available
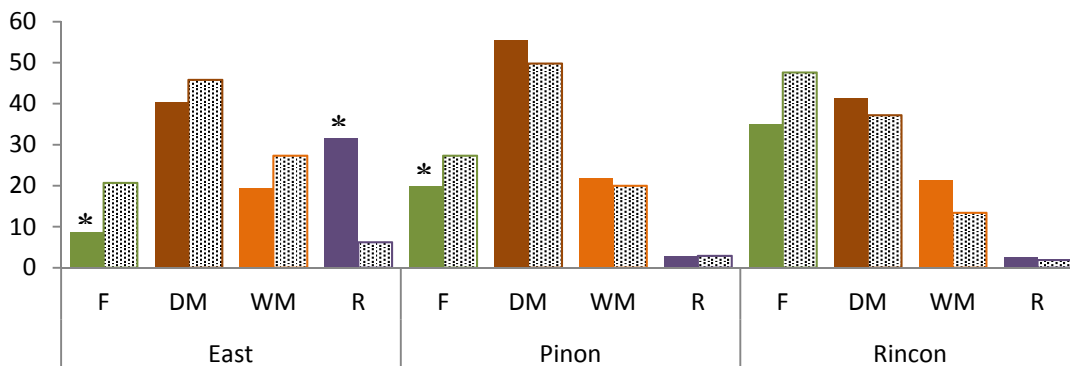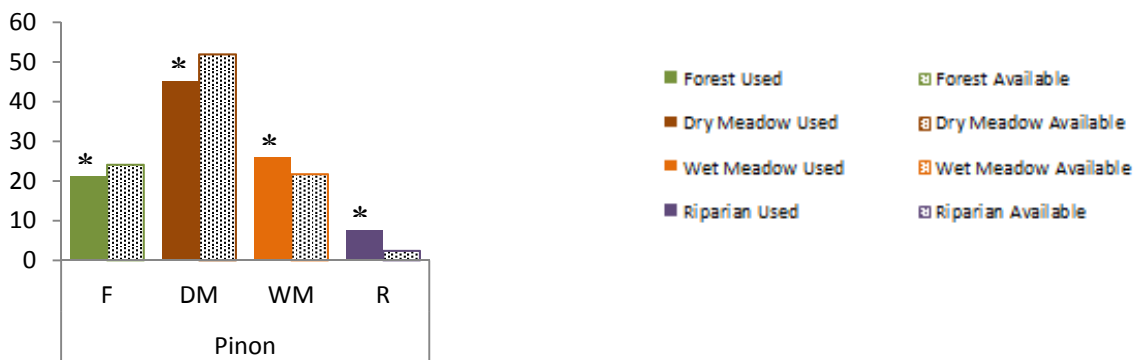
Figure 3-5. Habitat use versus availability for resident coyote packs in the Valles Caldera

National Preserve, New Mexico, during the breeding /gestation season for (A) 2007, (B)

2008, and (C) 2009. * indicates a significant difference between use and availability ($\alpha =$
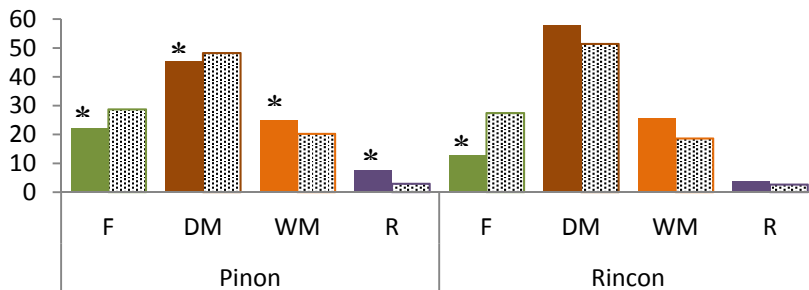
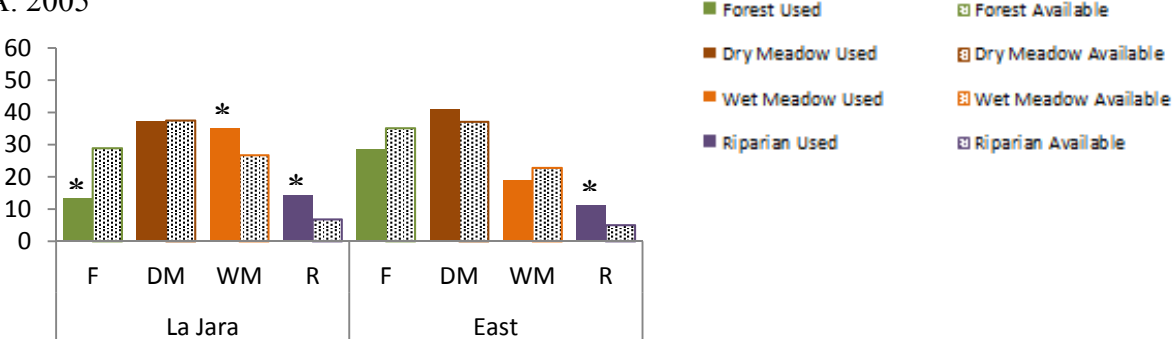0.05, based upon Bonferroni confidence intervals).

A. 2006

B. 2007

C. 2008

D. 2009

Forest Used   Forest Available

Dry Meadow Used   Dry Meadow Available

Wet Meadow Used   Wet Meadow Available
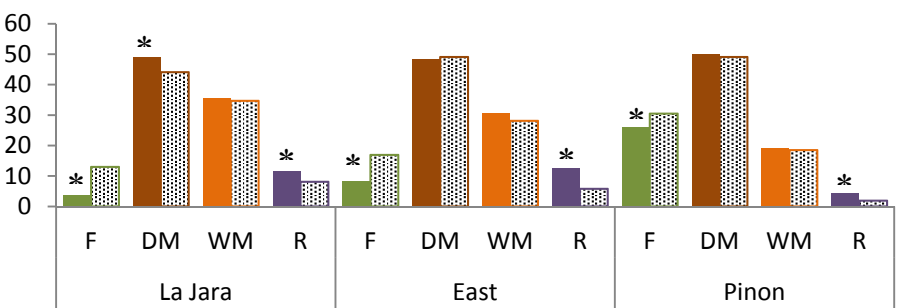
Riparian Used   Riparian Available

Figure 3-6. Habitat use versus availability for resident coyote packs in the Valles Caldera

National Preserve, New Mexico, during the pup rearing season for (A) 2006, (B) 2007,

(C) 2008, and (D) 2009. * indicates a significant difference between use and availability

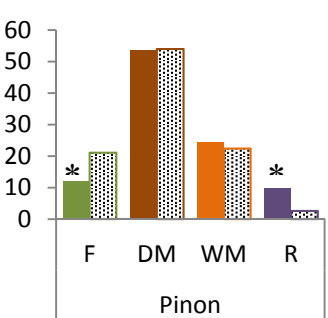($\alpha = 0.05$, based upon Bonferroni confidence intervals).

A. 2005

B. 2006

C. 2007

D. 2008

Legend:
- Forest Used
- Forest Available
- Dry Meadow Used
- Dry Meadow Available
- Wet Meadow Used
- Wet Meadow Available
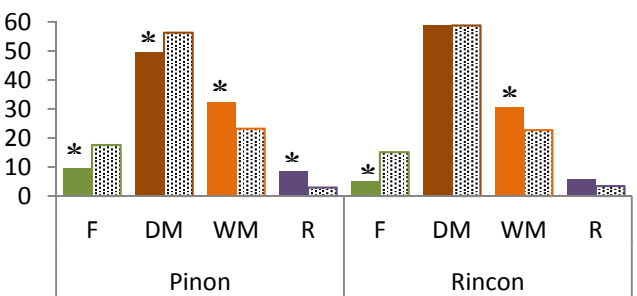- Riparian Used
- Riparian Available

Figure 3-7. Habitat use versus availability for resident coyote packs in the Valles Caldera National Preserve, New Mexico, during the dispersal season for (A) 2005, (B) 2006, (C) 2007, and (D) 2008. * indicates a significant difference (P < 0.05, based upon Bonferroni confidence intervals).
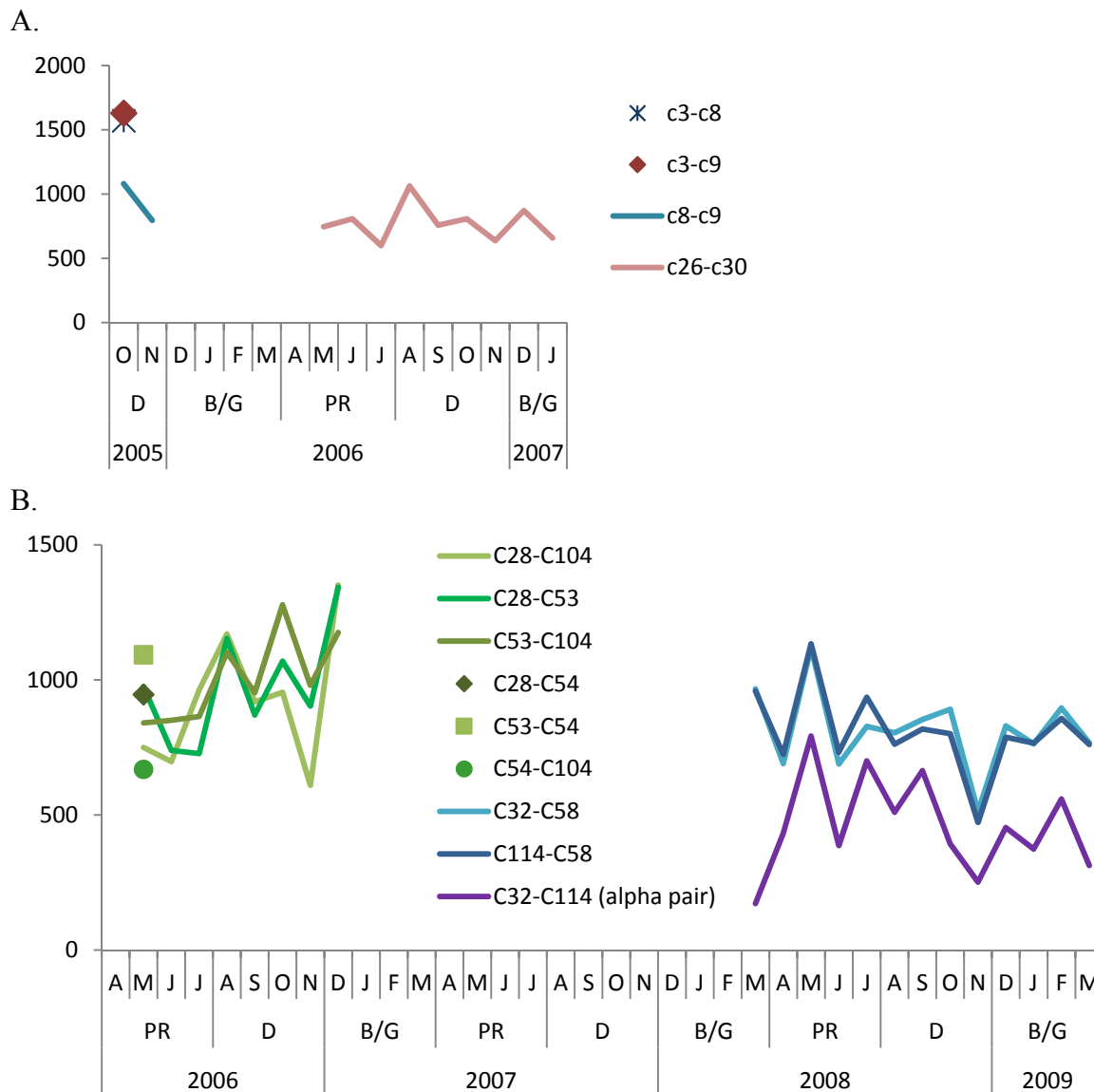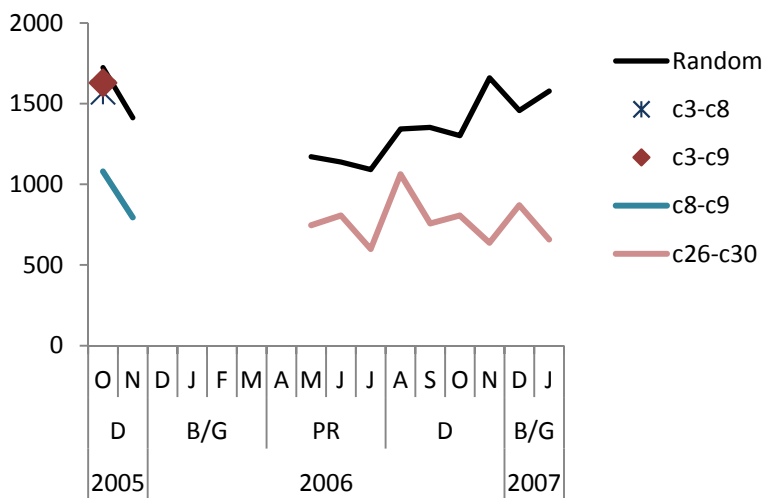
A.

B.

Figure 3-8. Social cohesion as measured by the average distance (m) between simultaneous locations of paired pack associates for each month for the (A) La Jara pack, and (B) Pinon pack, on the Valles Caldera National Preserve, New Mexico, 2005-2009. Biological seasons (B/G: breeding/gestation; PR: pup rearing; D: dispersal) are labeled.
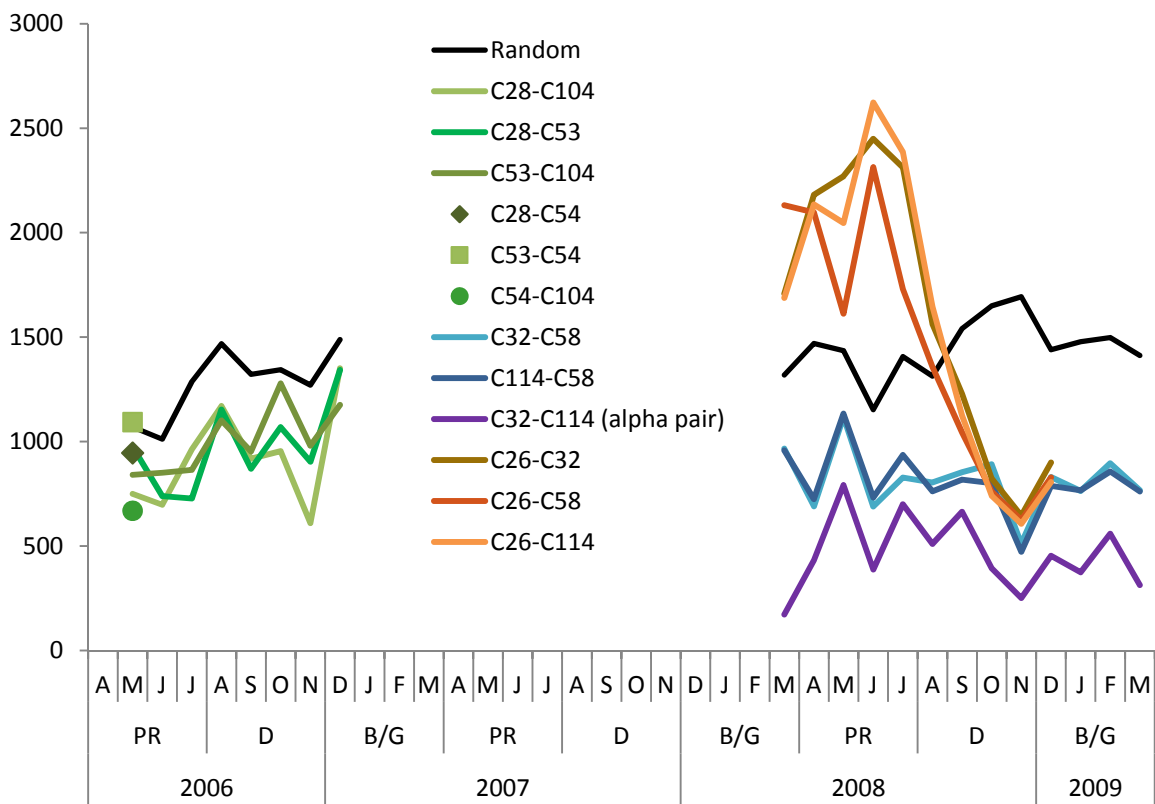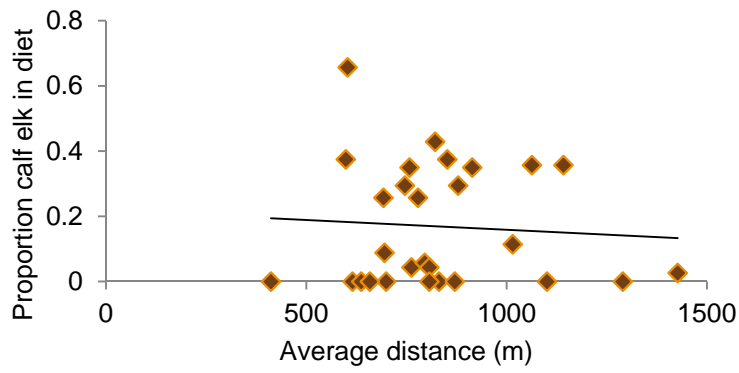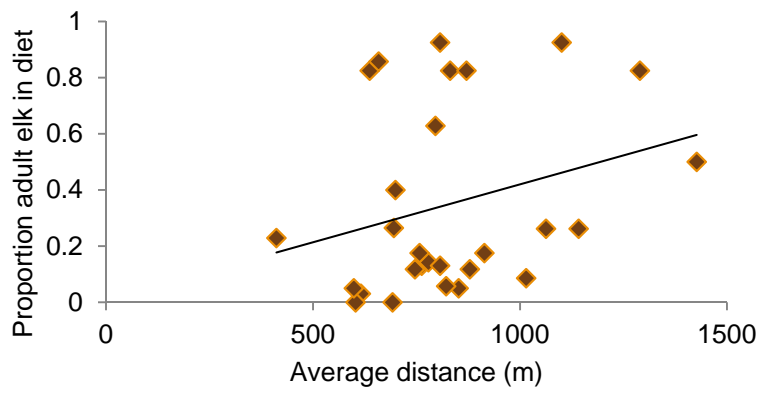
A.

B.

Figure 3-9. Social cohesion as measured by the average distance (m) between

simultaneous locations of paired pack associates for the A. La Jara pack and B. Pinon

pack and Pinon pack member interactions with coyote C26 on the Valles Caldera

National Preserve, New Mexico, 2005-2009. The solid black line represents the

separation distance expected due to chance calculated by averaged paired points at

random times > 6 hours. Biological seasons (B/G: breeding/gestation; PR: pup rearing;

D: dispersal) are labeled.

A. Calf elk

B. Adult elk

C. Total elk
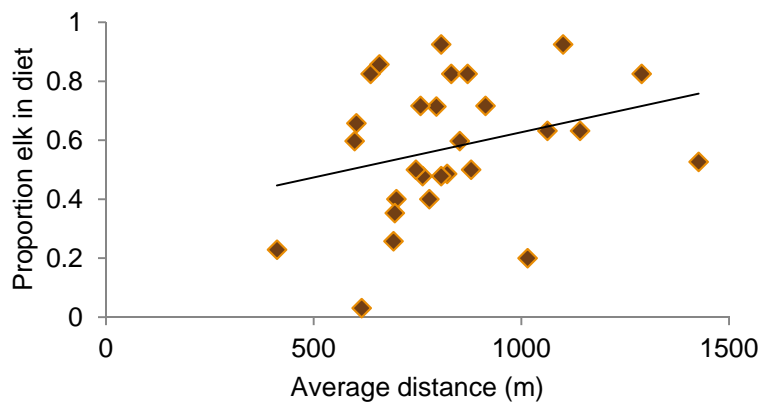
Figure 3-10. Non-significant relationships between social cohesion as measured by the average distance (m) between simultaneous locations of paired pack associates for the Pinon pack and the proportion of A. calf elk ($R^2 = 0.005$, $F = 0.126$, $P = 0.363$), B. adult elk ($R^2 = 0.0753$, $F = 2.113$, $P = 0.079$), and C. total elk ($R^2 = 0.0843$, $F = 2.386$, $P = 0.067$) in coyote diet on the Valles Caldera National Preserve, New Mexico, 2006-2009.

Appendix 3-1. Grouped vegetation types used in coyote habitat use and availability

evaluations on Valles Caldera National Preserve, New Mexico 2005-2009.

Habitat type (this analysis)	Vegetation type described in Muldavin et al. 2006
Forest	Aspen forest and woodland (dry mesic)
	Aspen forest and woodland (moist mesic)
	Blue spruce fringe forest
	Mixed conifer forest and woodland (dry mesic)
	Mixed conifer forest and woodland (moist mesic)
	Ponderosa pine forest
	Spruce-fir forest and woodland (dry mesic)
	Spruce-fir forest and woodland (moist mesic)
	Gambel oak - mixed montane shrubland
Dry meadow	Lower montane grassland
	Upper montane grassland
	Forest meadow
Wet meadow	Wet meadow
Riparian	Wetland
	Open water
	Montane riparian shrubland
Bare ground	Felsenmeer rock field
	Sparsely vegetated rock outcrop
	Post-fire bare ground
Excluded from analysis	Roads - disturbed ground

CHAPTER 4

SUMMARY

We investigated the ecological role of the coyote (*Canis latrans*) on the Valles

Caldera National Preserve (VCNP), in the Jemez Mountains, New Mexico, during 2005 –

2009. Our objectives were to quantify and assess the temporal variation in coyote diet,

particularly as related to elk (*Cervus elaphus nelsoni*) calf consumption, and to describe

the spatial and social ecology of coyotes in terms of home-range size, habitat use, and

social cohesion, and finally to evaluate the relationship between coyote social cohesion

and the amount of elk in the coyote diet.

We collected and analyzed 1,385 coyote scats for dietary analysis. The coyote

diet was comprised of rodents (primarily montane voles, *Microtus montanus*), elk (adult

and calf), insects (orders Coleoptera and Orthoptera), lagomorphs (*Sylvilagus nuttallii*),

and plants. Elk and voles were the primary year-round foods for coyotes, and snow

seemed to be an important driver of coyote prey selection. Voles were a reliable prey

source since they were active near the ground surface nocturnally and diurnally year-

round. Voles were less frequent in the coyote diet during the 2005-2006 low-snow

winter than during the two deeper-snow winters. This concurs with findings by Wells

and Bekoff (1982) and Gese et al. (1996*a*) that coyotes gain an advantage at hunting

voles in shallow snow, but snow >15 cm deep reduces capture rates of voles. Adult elk,

ostensibly primarily available as carrion, was consumed during almost every month of

our study, but predominantly during and following fall elk hunts on VCNP. During three

spring seasons which followed average winters, coyotes consumed elk calves primarily during June each year. Similarly, Bernal (2013) found coyote-caused mortality of elk calves occurred primarily in June during 2009-2011 on the VCNP; these were years of average precipitation and snow (Natural Resource Conservation Service data). However, following the 2005-2006 low-snow winter, coyote consumption of calves continued through the summer months. We infer that the dry winter increased the vulnerability of the elk calves born the subsequent spring, with a possible mechanism being compromised nutrition of dams as a result of failure to migrate to lower-elevation winter range. Whether the vulnerability of calves was more specifically due to cow health during gestation or lactation, timing of parturition, or nutritional quality of summer forage for calves, and whether additional stressors such as human or predator disturbances on VCNP played a role requires further study. Managers tracking elk recruitment need to consider climactic influences and annual variability as part of long-term population planning.

We captured and radio-collared 36 coyotes. Coyotes were organized in 4 packs occupying the Valle Grande. 70% of the coyotes we radio-tracked were residents during at least part of the study and 30% were consistently transient. Coyote home range boundaries and sizes 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 the literature for similar habitats and elevations in the west, including Grand Teton National Park, Wyoming (Berger and Gese 2007), southwestern Montana (Atwood and Gese 2010) and Yellowstone National Park, Wyoming (Gese et al. 1996*b*). Coyotes

used dry and wet meadows as expected, forests less than expected, and riparian areas more than expected based on availability within pack home ranges. We interpret the use of riparian areas more than expected and forests less than expected as risk avoidance behavior, since predation by cougars (*Puma concolor*) 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. 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. The sedges offered cover and shade not available in the wet meadow and dry meadow habitat types, and hiding cover not available in forests.

Contrary to our expectation, we found no relationship between coyote social cohesion and the proportion of elk in coyote diets. We expected that feeding on and defending carcasses would result in greater social cohesion 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 cohesion coincident with the amount of elk calves in coyote diets. Coyote social cohesion also did not vary by biological season. We concluded that coyote sociality on the VCNP is relatively stable year-round despite changes in biological needs and prey size.

In addition to widely-ranging transient coyotes, we also documented transient coyotes with localized movements in the small spaces on edges or overlap areas of resident coyote 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 this space use pattern by adult coyotes leading

to acceptance to or rejection from the pack. One individual used part of a territory while avoiding the resident pack; to our knowledge, avoidance of resident coyotes by transients had not previously been measured.

Fire suppression has been one of the most important anthropogenic disturbances in the Jemez Mountains, resulting in forest species composition and stand structure conditions outside of the historic range (Touchan et al. 1996). Large-scale wildfires burning at mixed intensity on the VCNP during 2011 and 2013 may change the space use dynamics of coyotes and elk and may improve the nutrition of elk forage and increase hiding cover. Prescribed fire has improved the nutritional content of the grass forage on VCNP (R. Parmenter, unpublished data), though grass forage quality improvements following fire may be short-lived (Dills 1970). These more intense fires may result in increases in browse species over several years. Further study would be needed to elucidate whether coyotes expand into the newly non-forested areas, and whether habitat use of other predators (bears [*Ursus americanus*] and cougars) changes in response to fire.

To further investigate the role of climatic variation in elk recruitment, studies of the elk population age structure could evaluate whether small or missing cohorts in the adult elk population correspond with particular climatic conditions, specifically dry winters. Future studies of coyote space use may consider their activity patterns and habitat use in relation to those of humans, considering how this overlap influences human perceptions of coyotes and whether the human-coyote dynamic changes with increased human traffic or changes in activities (i.e., hunting).

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