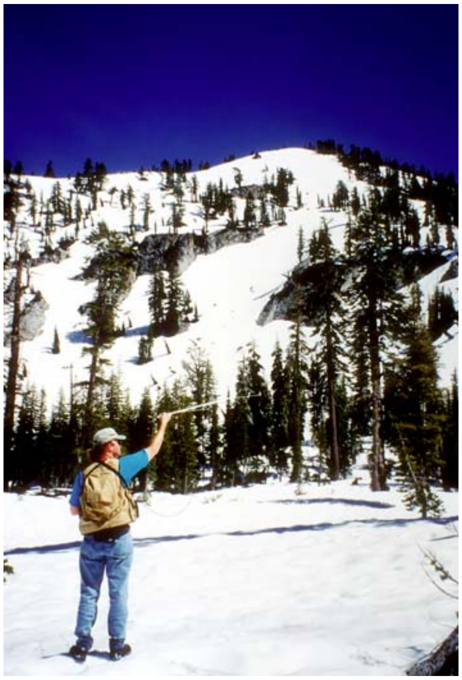

Ecology of Red Fox (*Vulpes vulpes*) in the Lassen Peak Region of California, USA

by

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Department of Environmental Science, Policy and Management
University of California, Berkeley
Fall 2005

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by

John Dixon Perrine III

B.S. (Vanderbilt University) 1991
M.S. (Miami University) 1995

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Committee in charge:

Professor Reginald H. Barrett, Chair
Professor Stephen R. Beissinger
Professor James L. Patton

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Abstract

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Professor Reginald H. Barrett, Chair

The red fox population inhabiting California's Cascade and Sierra Nevada mountains (*Vulpes vulpes necator*) is listed as a State Threatened species, but its management has been hindered by a lack of basic ecological information. I conducted a comprehensive study of the red foxes in the Lassen Peak region to quantify their local distribution, resource utilization, activity patterns, niche overlap with likely competitors and genetic affinity with other red fox populations. The population was restricted to the region's highest elevations, occurring >1300 m and primarily within the western half of Lassen Volcanic National Park. Red fox detections at camera traps in summer were positively correlated with elevation, highway density and the detection of coyotes, and were negatively correlated with shrub and herbaceous cover; in winter, detections were positively correlated with elevation, highway density and mature closed-canopy forest cover. Their diet was predominantly mammals, especially rodents and mule deer (*Odocoileus hemionus*), supplemented by birds, insects and manzanita (*Arctostaphylos nevadensis*) berries as seasonally available. Lagomorphs were virtually absent from the fox diet. Collared red foxes (n = 5) had large seasonal home ranges (95% MCP; mean = 2,564 ha in summer and 3,255 ha in winter). On average, summer locations were 479 m higher than winter locations. Their summer range is likely unsuitable in winter due to deep soft snow and the lack of lagomorphs, a critical winter food for many other red fox populations, and these factors may limit the Lassen red fox population. Marten (*Martes americana*) used the same habitat as the foxes but preyed upon smaller rodents and were more diurnal. Coyotes (*Canis latrans*) were nocturnal like the foxes but were generally at lower elevations and ate larger prey. The Lassen foxes all had the same mtDNA haplotype, which was the most common haplotype among historic *V. v. necator* specimens and was rare in the exotic fox populations from California's lowlands. Ecological and genetic evidence indicates that the Lassen red foxes are the native, threatened *V. v. necator*, not exotic foxes dispersed from the lowlands. Additional research is necessary to locate additional mountain red fox populations in California and to identify the factors preventing their dispersal to the lowlands and vice versa.

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including extracting, amplifying and sequencing. Ben Sacks at UC Davis identified the fecal parasites and provided a lot of helpful comments on the genetic analysis.

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OK Shannon, it's done. Now let's go have an adventure!

Dedicated to the memory of Gary Polis.

Have you ever really had a teacher?

One who saw you as a raw but precious thing, a jewel that,
with wisdom, could be polished to a proud shine?

If you are lucky enough to find your way to such teachers,
you will always find your way back.

Mitch Albom, 1997
"Tuesdays with Morrie"

INTRODUCTION

The red fox (*Vulpes vulpes*) is a small canid (4-7 kg) with an elongated snout, large pointed ears, slender legs and body, and a large bushy tail with a white tip (Lariviere and Pasitschniak-Arts 1996). The red fox has the most extensive natural distribution of any terrestrial carnivore, inhabiting much of North America, Europe, Asia, and the northern extremes of Africa (Voigt 1987, Nowak 1999). Additionally, the red fox was introduced to Australia around 1865, where it has flourished (Lloyd 1980). This broad geographic range is largely a product of the unspecialized nature of the red fox and its broad tolerances for many types of habitats and foods (Lloyd 1980). A total of 10 red fox subspecies are recognized in North America (Figure 1) (Hall 1981), although it is questionable whether all 10 are valid subspecies (Roest 1979). The vast majority of the ecological research on North America red foxes has been conducted on populations in the eastern and central regions. There is virtually no published ecological research on the red foxes that inhabit the mountain regions of western North America (Aubry 1983, 1997).

California's Sierra Nevada and southern Cascade Mountains are inhabited by *V. v. necator*, the Sierra Nevada red fox. Historically, *V. v. necator* occurred at high elevations throughout the Sierra Nevada from Tulare County northward to Sierra County, as well as in the vicinities of Mt. Shasta and Lassen Peak (Grinnell et al. 1937) (Figure 2). Within these areas, the red foxes were restricted to high-elevation forests and the subalpine areas near treeline. Ingles (1965) described their habitat as the red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*) forests and the alpine fell-fields of the subalpine zone. Even within favorable areas, population density was likely >1 individual per square mile (260 ha) (Grinnell et al. 1937). No ecological studies have been conducted on this subspecies, presumably due to their low population density and the ruggedness of their habitat. Information on their distribution, population density, habitat associations, reproduction, diet and other ecological characteristics is based almost entirely upon trappers' reports summarized by Grinnell et al. (1937). But even these data are sparse: from the 1920s through the 1950s, the annual trapping harvest was usually <25 mountain red foxes statewide (Grinnell et al. 1937, Gould 1980).

In 1974, the state legislature prohibited trapping and other non-scientific take of red fox in California due to apparent population declines of the Sierra Nevada red fox (Gould 1980). It was listed as a State Threatened species in 1980. Although not federally listed, it is a US Forest Service "sensitive species." The California Department of Fish and Game has classified *V. v. necator* as "extremely endangered," with <6 viable occurrences, or <1000 individuals, or <2000 acres (810 hectares) of occupied habitat (CDFG 2004). Its current distribution, population size, and demographic trend are unknown. A recent assessment concluded that the *V. v. necator* "remains one of the few State-listed animals for which there is no information on current status other than periodic sightings filed mostly by inexperienced observers" (CDFG 1996: 17). The lack of ecological information upon which to base management planning has itself been cited as a threat to the subspecies' survival (CDFG 1987).

In addition to the threatened native Sierra Nevada red fox, California also has populations of non-native red foxes (Grinnell et al. 1937, Gould 1980, Lewis et al. 1999). These animals were first documented in the northern Sacramento Valley, from Sutter to Shasta Counties, at elevations below 105 m (350 ft) (Grinnell et al. 1937). Grinnell et al.

(1937) believed that these foxes had been introduced in the late 1880s, but the source populations were unknown. Morphological analysis, particularly skull measurements, indicated that these "Sacramento foxes" were most similar to the red fox of the northern Great Plains, *V. v. regalis* (Roest 1977). However, the variability among subspecies was too great to confidently classify any individual fox to any particular group. The lowland red foxes were not assigned to any subspecies and the recommendation was made simply to refer to them as "Valley foxes" (Roest 1977).

Grinnell et al. (1937: 385) expressed no concern about the possible negative impacts upon the native Sierra Nevada red fox, as the exotic red fox population was "very restricted, evidently wholly cut off from the population of the Sierra Nevada." Unfortunately, the range of the exotic red foxes increased dramatically in the following decades. By the early 1990s, "Valley" red foxes inhabited at least 36 counties in California (Lewis et al. 1999). In addition to the Sacramento Valley, their range included virtually the entire area between Los Angeles and the San Francisco Bay region, extending eastward through the San Joaquin Valley to the Sierra Nevada foothills (Figure 2). Red foxes escaping from commercial fur farms may have contributed to this sudden expansion. From the 1920s through the 1940s, nearly 125 fur farms were operational throughout California, primarily along the northern coast, the mid-state and near Los Angeles (Lewis et al. 1999). Although most fur farms were at lower elevations, several were within the historic range of the Sierra Nevada red fox. Other exotic red fox populations, introduced for rodent control or sport hunting, were within the known dispersal distance from the range of the native mountain foxes (Lewis et al. 1995). It is unclear to what extent exotic "lowland" red foxes may have extended into the mountains, hybridizing with the threatened native red foxes or displacing them entirely (Lewis et al. 1995, Lewis et al. 1999).

In March 1993, a red fox was detected on the Eagle Lake District of the Lassen National Forest by an automatic camera trap established as part of a statewide wolverine (*Gulo gulo*) survey (Kucera 1995). The Lassen National Forest and the adjacent Lassen Volcanic National Park are within the historic range of the Sierra Nevada red fox (Figure 2), and have been where most recent sightings have occurred (Grinnell et al. 1937, Schempf and White 1977). The camera traps suggested that a red fox population remained in the area, but the photographs could not reveal whether the animals were native, exotic or hybrids (Kucera 1995). Additional camera traps and sighting reports confirmed the presence of several individuals in the area. Two foxes were captured and radio-collared just south of Lassen Park in the spring of 1997 (Kucera 1999). Pilot projects conducted in the summers of 1998 and 1999 suggested that a thorough ecological investigation of the local red fox population was feasible and also necessary to determine the proper management of the population.

RESEARCH GOALS AND OBJECTIVES

The primary goals of this research project were:

a) To quantify the distribution and resource utilization of the red fox population in the Lassen Peak region. Specific objectives included documenting diet, daily and seasonal activity patterns, home range size and characteristics, and habitat utilization for denning and foraging. Demographic patterns such as reproductive rates and mortality factors would also be documented. Ascertaining the distribution, resource utilization, and population trend of the local red fox population is fundamental to effective management whether the foxes themselves are native, exotic or hybrids.

b) To quantify the extent of niche overlap among the Lassen red foxes and two potential competitor, coyote (*Canis latrans*) and marten (*Martes americana*), with particular emphasis upon diet, habitat use and activity patterns (Schoener 1974). Interspecific competition is a major factor in many mesocarnivore communities (Buskirk 1999). Agonistic interactions between red fox and coyote have been well-documented in the eastern and central United States, with the larger-bodied coyote the dominant competitor (Johnson et al. 1996). However, none of these studies have been conducted in the mountainous habitat typical of the Sierra Nevada red fox. If the Lassen red fox were the threatened native subspecies, reducing antagonistic interactions with sympatric coyotes could be an important step in their conservation. Marten are also common in the Lassen Peak region (Grinnell et al. 1937, Schempf and White 1977), although they are also considered a “sensitive species” by the US Forest Service (CDFG 2004). Competitive interactions between red fox and marten have been poorly studied in North America, but have been the subject of several studies in northern Europe (*M. martes*) (Lindstrom 1989, Storch et al. 1990, Overskaug 2000). Red foxes occasionally kill marten, and avoidance of red fox has been hypothesized as a factor contributing to marten habitat use (Drew and Bissonette 1997). If the Lassen red foxes were the invasive exotic subspecies, they might have important impacts upon the ecology and conservation of the local marten population.

c) To use genetic techniques to determine whether the red fox population currently inhabiting the Lassen region is more similar to those red foxes that historically occupied the mountainous regions (the native Sierra Nevada red fox) or to those red foxes that are currently inhabiting the lowland regions (the exotic Valley red fox). Genetic analysis is necessary because traditional morphological techniques cannot reliably conclude whether individual animals are from mountain or valley populations (Roest 1977). Quantifying the Lassen population’s genetic affinity with the historic mountain red foxes and the current lowland red foxes will be critical to the Lassen foxes’ effective management, and will provide context for the ecological information obtained in this study.

STUDY AREA

The “Lassen Peak region” is comprised of Lassen Volcanic National Park and the surrounding Lassen National Forest in northeastern California (Figure 2). Lassen Volcanic National Park is a 430 km^2 reserve that contains the highest elevations in the area (1600 to 3200 m), including Lassen Peak, a dormant volcano that is the southernmost peak in the Cascade Range (Figure 3). The rugged topography of Lassen Park is dominated by several types of conifer communities, including mountain hemlock (*Tsuga mertensiana*) and whitebark pine (*Pinus albicaulis*) above 2400 m, red fir (*Abies magnifica*) and lodgepole pine (*P. contorta*) from 2400 to 2000 m, and white fir (*A. concolor*) and Jeffrey pine (*P. jeffreyi*) below 2000 m (Figure 4). Shrub (predominantly *Arctostaphylos nevadensis*) and wet alpine meadow communities are also common, as are talus slopes at higher elevations (Taylor 1990, Parker 1991, White et al. 1995).

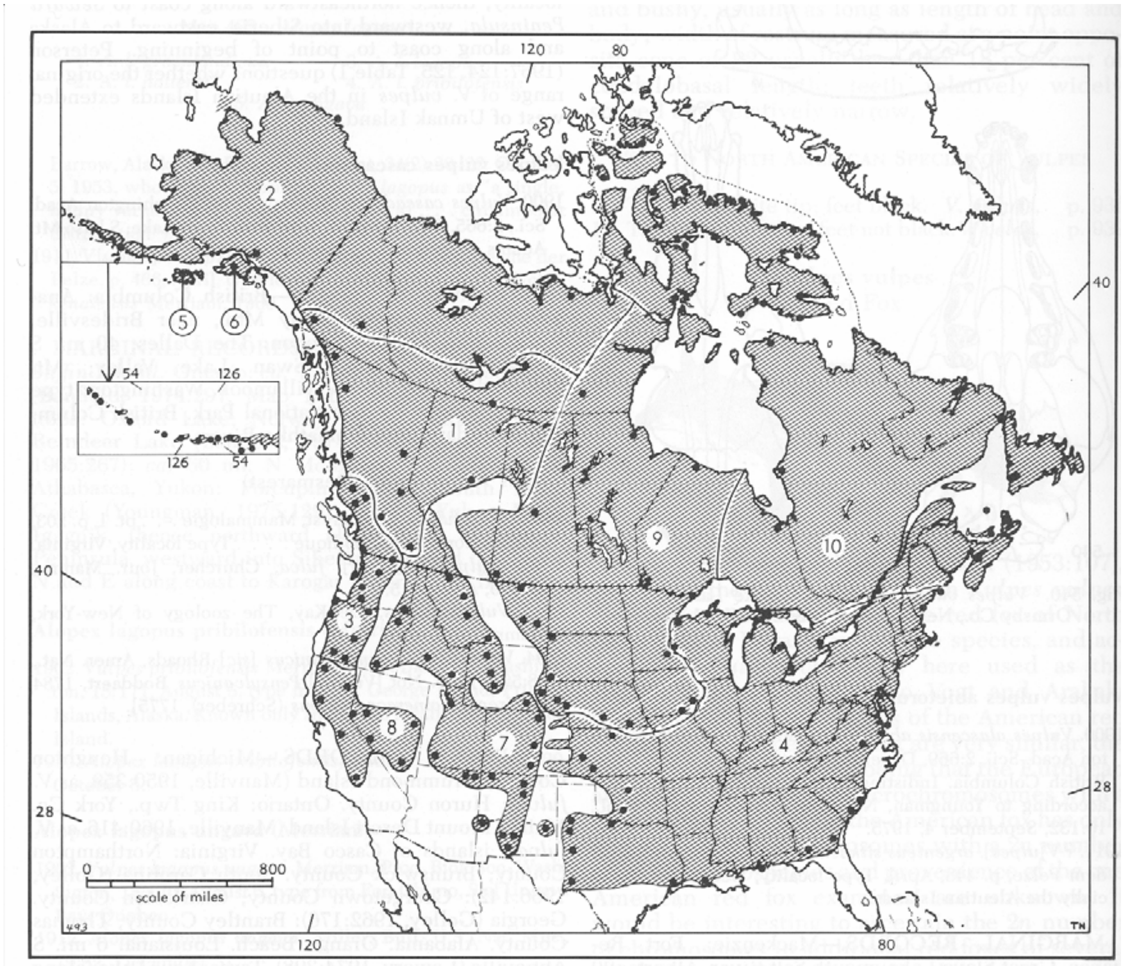
Approximately 75% of the Park is federally-designated wilderness, and most of the remaining area is managed as such (LVNP 2001).

Surrounding the Park is the 4,860 km^2 Lassen National Forest. Elevations on the forest are generally lower than the park, down to 100 m in the western foothills, but extend up to 3000 m on several peaks (Figure 3). Like the park, Lassen Forest is also dominated by conifers (Figure 4), predominantly lodgepole, Jeffrey, Ponderosa and sugar pine (*P. lambertiana*); red and white fir; Douglas fir (*Pseudotsuga menziesii*) and incense cedar (*Calocedrus decurrens*). Approximately 8% of the Lassen Forest area is chaparral, principally greenleaf manzanita (*Arctostaphylos patula*) above 1000 m and wedgeleaf ceanothus (*Ceanothus cuneatus*) below 1000 m (LNF 1992). An additional 4% is sagebrush, primarily big sage (*Artemesia tridentata*) and bitterbrush (*Purshia tridentata*), which occur in the flatter northern and northeastern portions of the Forest. Hardwoods, mostly blue oak (*Quercus douglasii*) and black oak (*Q. kelloggi*), are restricted to the western foothills below 1000 m and comprise about 5% of the Lassen Forest area. Much of the forest is actively managed for commercial timber production, but approximately 8% of the area is within the Caribou Wilderness (8,300 ha) east of Lassen Park, the Thousand Lakes Wilderness (6,600 ha) northwest of the Park and the Ishi Wilderness (16,600 ha) in the foothills to the west (LNF 1992). The administrative boundary of the Lassen National Forest also includes numerous campgrounds and snowmobile recreation areas, and several villages such as Mineral and Mill Creek (Figure 5).

The Lassen region has a Mediterranean climate with warm dry summers and cold wet winters. Mean monthly temperature in Mineral (1478 m) ranges from -0.8°C in

January to 17.2°C in July (Beaty and Taylor 2001). Most of the annual precipitation occurs as snow from November through April (Parker 1991, Beaty and Taylor 2001). From December through March, average monthly snowfall is typically >50 cm (Krohn et al. 1997). At high elevations, snowpacks may exceed 5 m in depth (Figure 6) and may persist well into the summer months.

Figure 1: Red fox subspecies in North America (from Hall 1981).



1. *Vulpes vulpes abietorum*
2. *V. v. alascensis*
3. *V. v. cascadensis*
4. *V. v. fulva*
5. *V. v. harrimani*
6. *V. v. kenaiensis*
7. *V. v. macroura*
8. *V. v. necator*
9. *V. v. regalis*
10. *V. v. rubricosa*

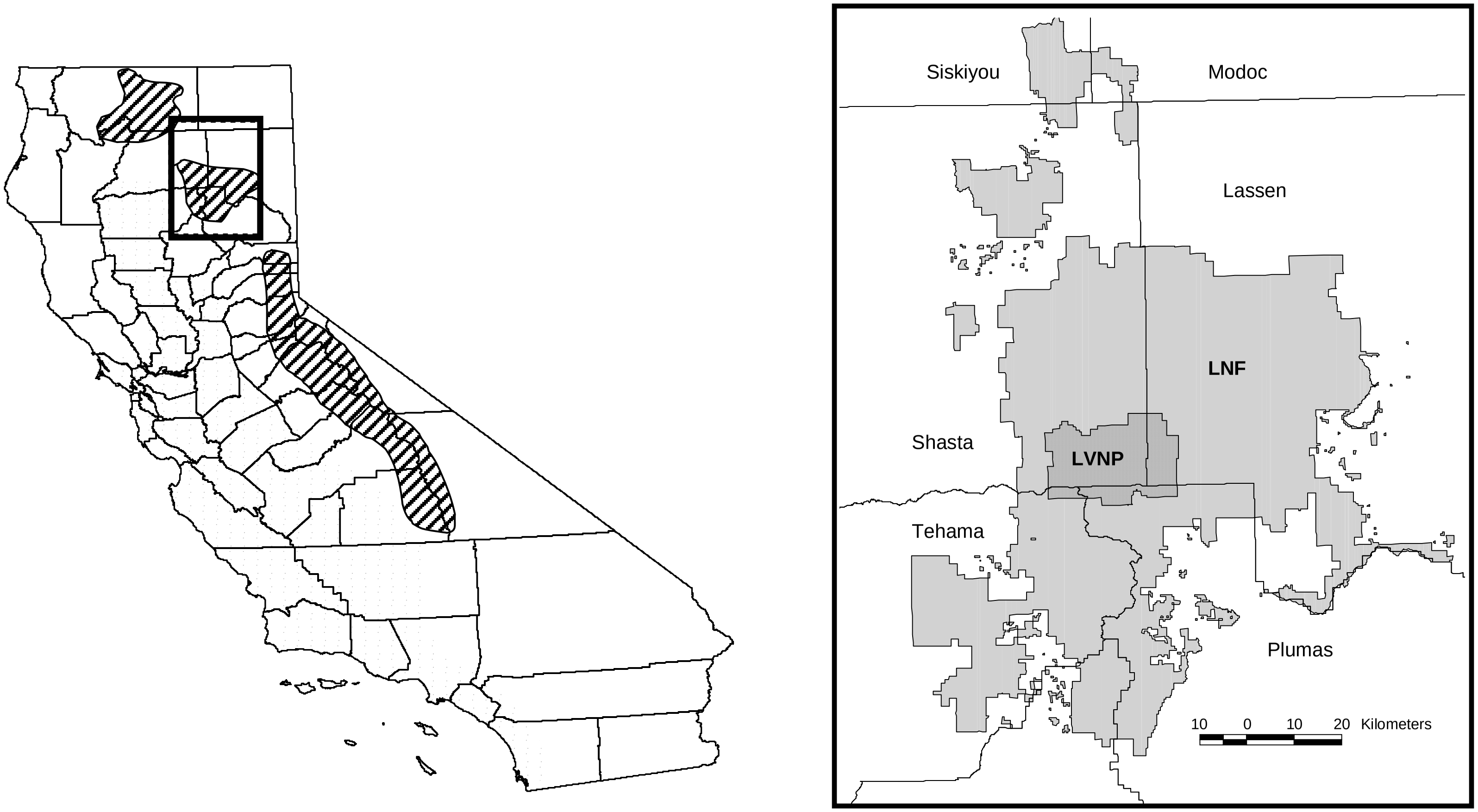


Figure 2: Study area relative to native and exotic red fox range in California. The Lassen Region (box) is centered upon one of the three historic population centers for the native Sierra Nevada red fox (striped areas). Exotic “valley” red fox currently inhabit much of the lowland areas to the west and south (shaded area). Range maps based upon Grinnell et al. 1937 and Lewis et al. 1999. “LNF” = Lassen National Forest; “LVNP” = Lassen Volcanic National Park.

Figure 3: Major vegetation types in the Lassen Peak region.

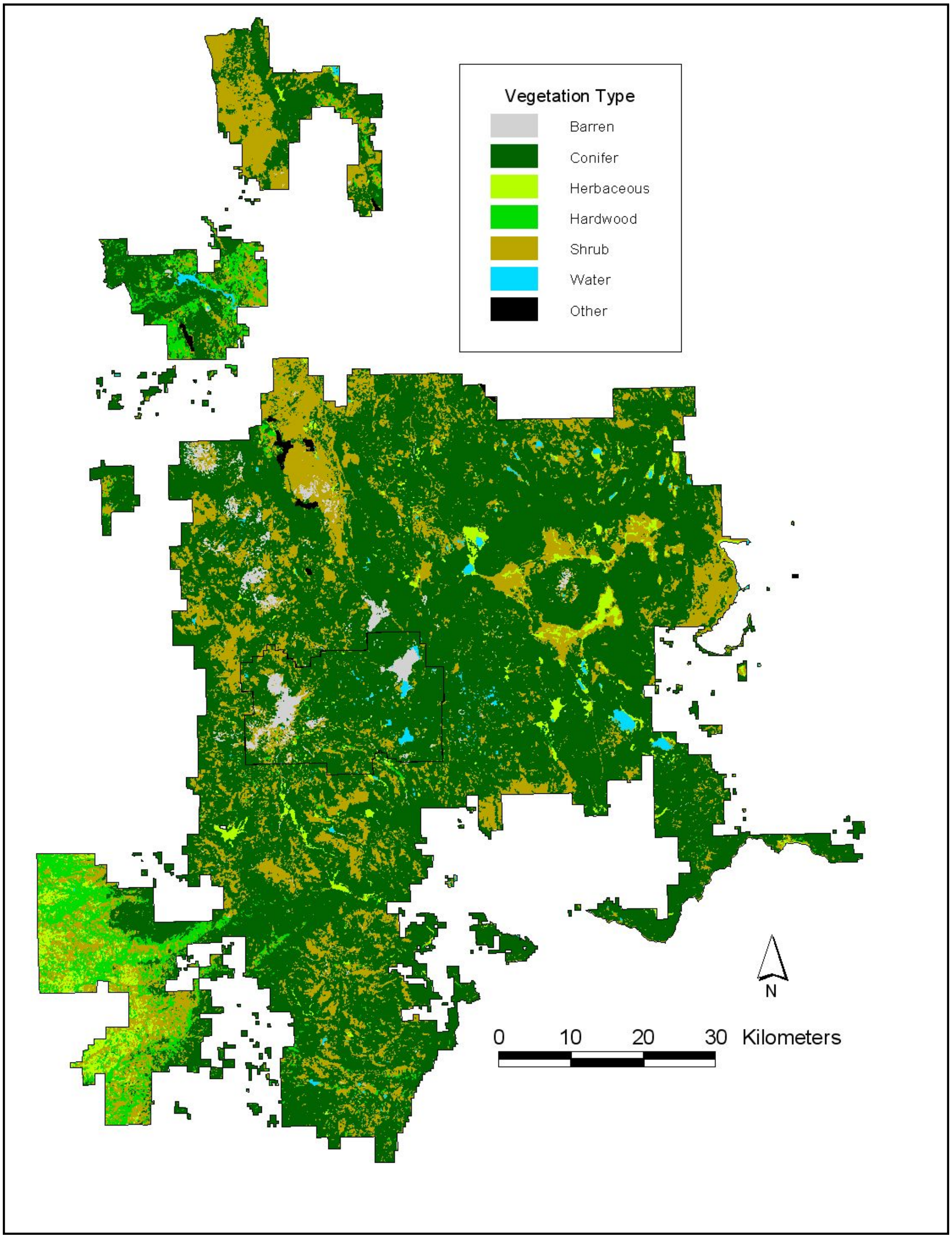


Figure 4: Elevation in the Lassen Peak area.

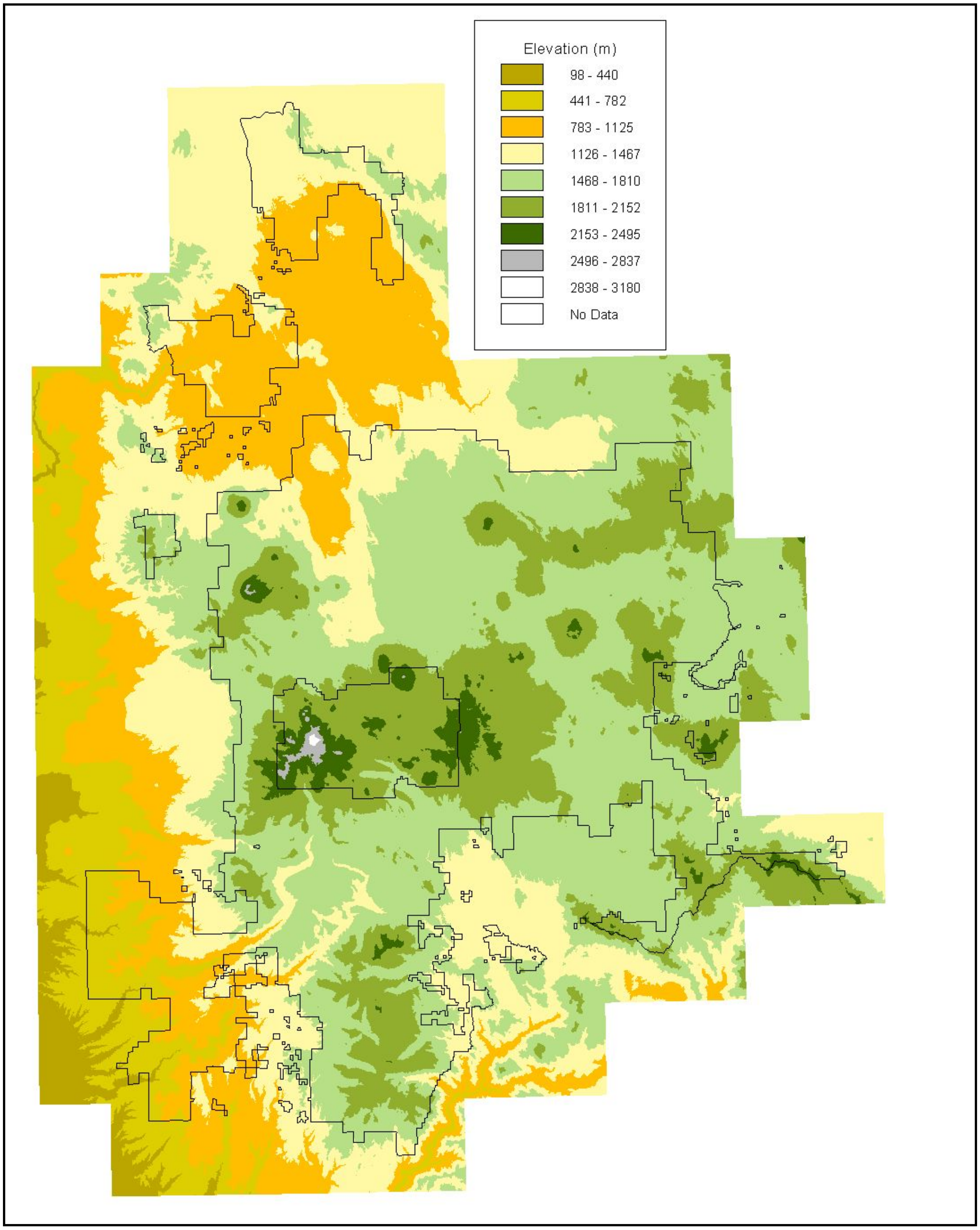


Figure 5: Places in and around the western half of Lassen Park that are frequently mentioned in the text.

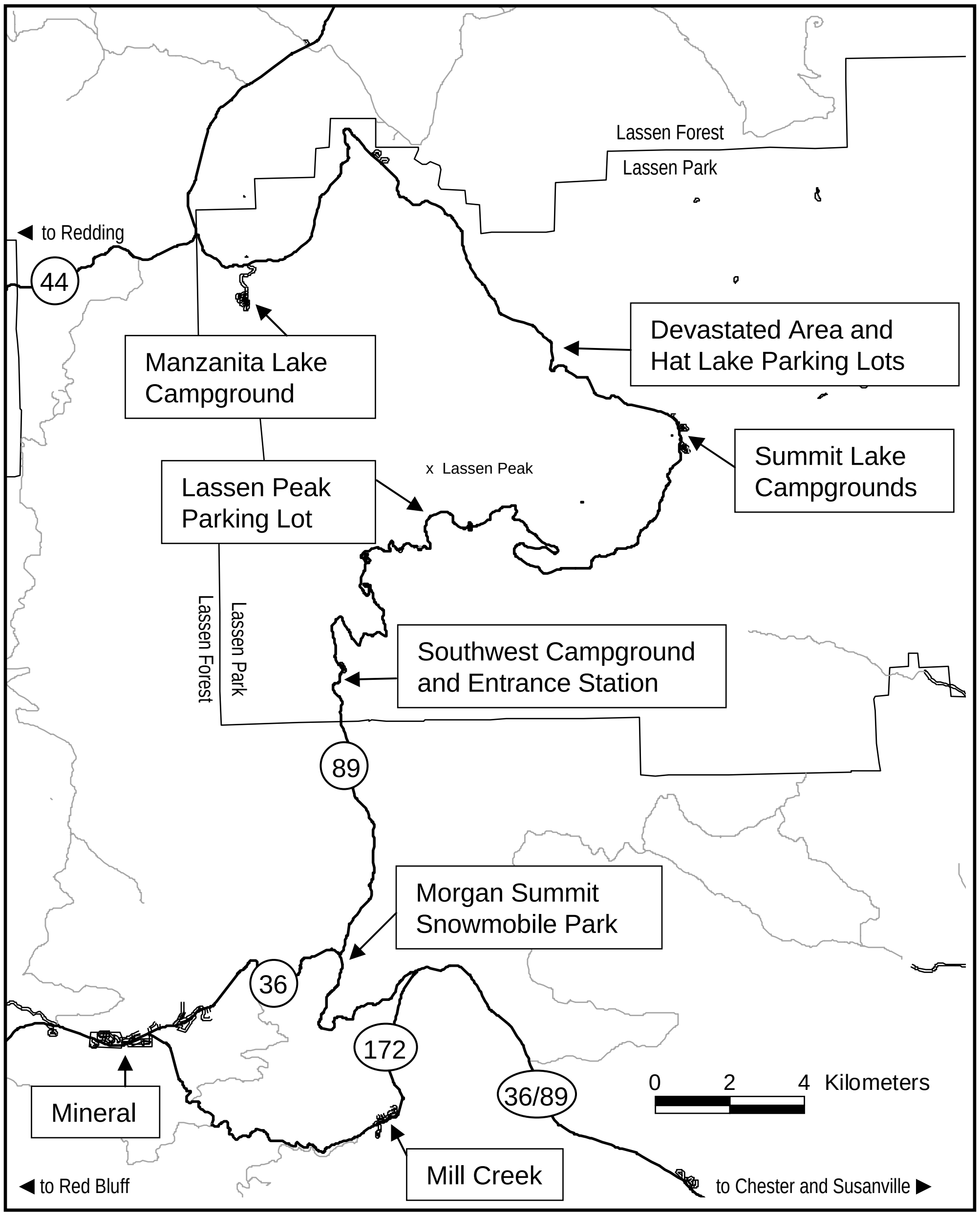
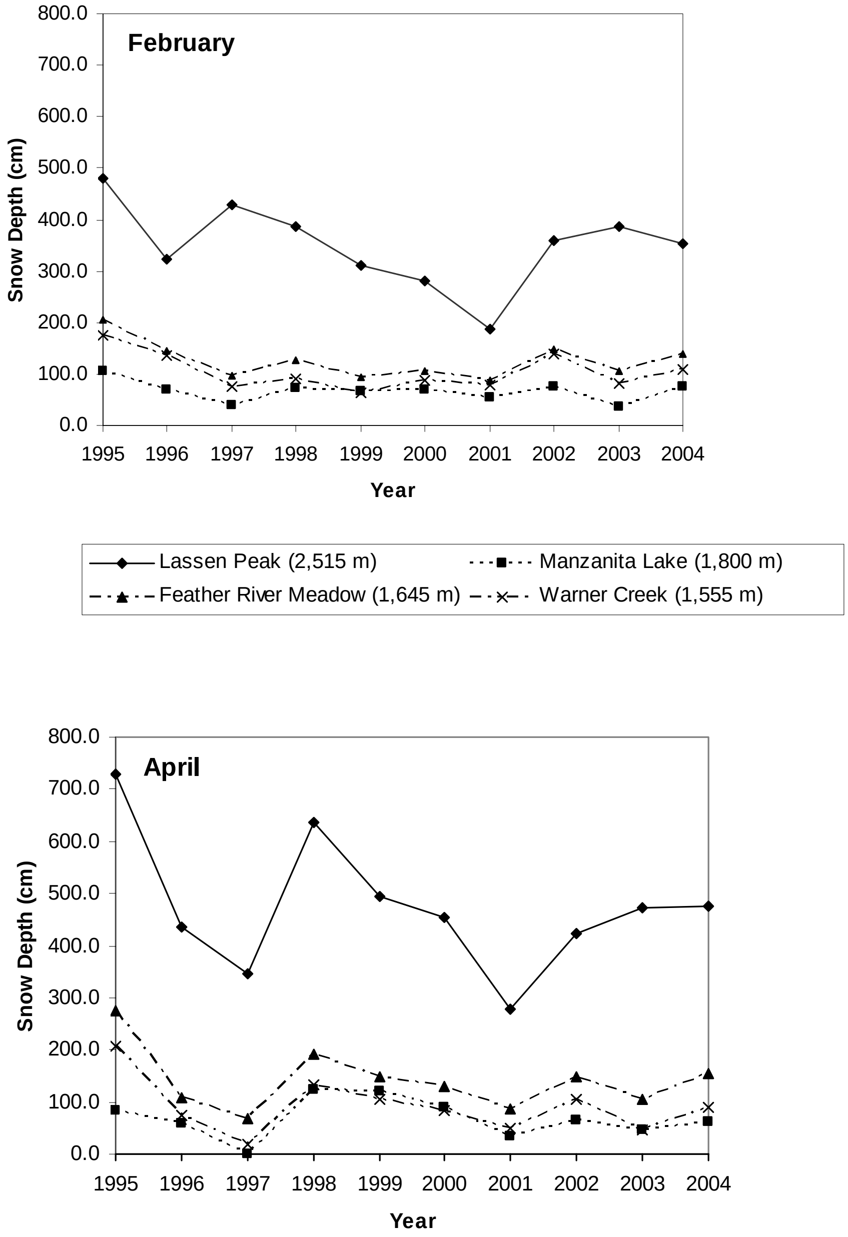


Figure 6: Monthly snow depths in the Lassen region.



CHAPTER 1

SEASONAL FOOD HABITS OF RED FOX, COYOTE AND MARTEN IN THE LASSEN PEAK REGION OF NORTHERN CALIFORNIA

INTRODUCTION

Dietary analysis is a frequent first step in studying an animal's ecology because diet directly reflects resource use and can provide insight into habitat utilization and competitive interactions (Litvaitis 2000). For carnivores, the availability and utilization of various food resources are important factors affecting population viability (Fuller and Sievert 2001). Additionally, competitive interactions among sympatric carnivore species are common and can have major impacts upon their ecology and management (Palomares and Caro 1999, Creel et al. 2001). Such interactions usually favor the larger competitor and can result in decreased fitness for the subordinate competitor due to direct mortality, reduced access or exclusion from preferred resources, and reduced foraging and reproductive efficiency (Johnson et al. 1996, Palomares and Caro 1999, Creel et al. 2001). Therefore, understanding such interactions can be critical when conservation of the subordinate competitor is a management goal.

My primary objective was to describe seasonal trends in the food habits of red fox (*Vulpes vulpes*) in the Lassen region of northern California. A secondary objective was to compare the red fox diet to that of two other generalist carnivores in the region, coyote (*Canis latrans*) and marten (*Martes americana*). It is unknown whether the red foxes currently inhabiting the Lassen region are native or exotic (Kucera 1995, Lewis et al. 1995). If they are native, competition with coyotes may be a conservation concern because coyotes are antagonistic toward red foxes (Dekker 1983, Sargeant and Allen 1989). If the Lassen red foxes are exotic, their potential competitive interactions with marten may also be of concern, because the latter is a US Forest Service Sensitive species (Zeiner et al. 1990). An analysis of the seasonal food habits of these three sympatric species is an important step toward their effective management.

Red foxes are generally characterized as opportunistic predators and scavengers that eat a wide variety of foods depending on seasonal availability. Small and medium-sized mammals dominate the diet, with birds, insects, fruit, carrion, garbage and other foods important seasonally (Ables 1975, Lloyd 1980, Samuel and Nelson 1982, Lariviere and Pasitschniak-Arts 1996, Verts and Carraway 1998, Nowak 1999). Although the red fox diet has been extensively studied in a variety of countries and habitats (Ables 1975, Lockie 1977, Lariviere and Pasitschniak-Arts 1996), their diet in mountainous areas of western North America has been largely overlooked. In California, mountain red fox diet and ecology have been addressed only in the context of regional or statewide natural history surveys (e.g., Grinnell et al. 1937, Sumner and Dixon 1953). These suggest that mountain red fox eat predominantly rodents and lagomorphs, along with a wide variety of other vertebrate, invertebrate and plant foods as seasonally available. However, these accounts lack comprehensive and quantitative seasonal dietary patterns, making them of minimal use for modern management purposes. The only recent, thorough and quantitative treatment of mountain red fox diet was in Washington’s Cascade Mountains (Aubry 1983). The Cascade red foxes’ summer diet consisted of *Thomomys talpoides, Clethrionomys gapperi, Phenacomys intermedius* and other rodents, along with fruit, insects, birds, grass and garbage. Their winter diet was more narrow, consisting largely of *Lepus americanus, C. gapperi, T. talpoides* and other mammals, with some birds and garbage taken opportunistically.

Coyote diets in California have been well documented in the Central Valley (Barrett 1983, Cypher et al. 1996, Neale and Sacks 2001), the Sierra Nevada and upper Great Basin (Bond 1939, Sumner and Dixon 1953, Hawthorne 1972, Bowyer et al. 1983, Smith 1990), and suburban areas (Fedriani et al. 2001), as well as statewide (Ferrel et al. 1953). In these studies, coyote diets were largely dominated by rodents, especially *Microtus*, along with larger mammals such as lagomorphs, *Odocoileus hemionus* and livestock (usually scavenged) as available. *Thomomys* sp. was usually present in the diet, although secondary to mice and squirrels in importance. Insects and fruit, especially *Arctostaphylos* at higher elevations, were seasonally important, with their peaks in the diet corresponding with peak availability. A wide variety of other items including birds, reptiles, amphibians and man-made items occurred in the diet but were of comparatively low importance. None of the studies in mountainous regions examined dietary overlap with sympatric red fox or marten.

Martin (1994) reviewed 22 dietary studies of *M. americana*, including 3 from California. Mammalian prey, especially voles (*Clethrionomys* and *Microtus*), were the primary dietary component for marten across their range. Larger mammals such as *L. americanus* were taken when available, and were more prevalent in the diets of marten in eastern and midwestern North America. Birds, insects, and vegetation frequently occurred in scats but generally at low volumes. She concluded that marten were opportunistic generalists, taking foods as seasonally available in the environment, with a likely preference for *Microtus*. A recent study of marten in the southern Sierra Nevada found that they ate primarily sciurids, murids, other rodents and birds, with insects and fruit consumed in summer and autumn (Zielinski and Duncan 2004). Although marten and mountain red fox ranges largely coincide in California (Kucera et al. 1995), their potential competitive interactions have not been examined.

METHODS

I collected carnivore scats (feces) opportunistically from June 1998 through December 2002 while performing radio telemetry and behavioral observations on collared red foxes, establishing and monitoring photosurvey stations, driving the park road and conducting other tasks. Pilot studies suggested that red foxes were too rare in the study area for formal transect methods to yield an adequate sample size for diet analysis. Most scats were collected in the western half of Lassen Volcanic National Park and the adjacent areas of the Lassen National Forest at 1600 to 3150 m elevation.

Species identity

Scats were preliminarily identified to species based upon field guides (Murie 1974, Halfpenny 1986, 1998) and scats of known origin from observed individuals. Scats with uncertain field identities were discarded. Locality data for each scat was recorded using a Trimble GeoExplorer II GPS unit. Scats were stored in individually-numbered zip-lock plastic baggies at 0°C pending analysis.

In the lab, I took several surface scrapes from each scat for genetic confirmation of the species identification. Genetic scrapings were placed in individual 2 ml vials containing 1 ml of Queen's tissue buffer (Seutin et al. 1991), then stored at -80°C. I extracted the genetic material using QiaGen Stool Kits (QiaGen Incorporated, Valencia, California) in the labs of Per Palsboll at UC Berkeley and Robert Wayne at UCLA. Technicians at the Wayne lab then amplified and sequenced a 370 bp segment of the mitochondrial cytochrome-*b* gene from randomly-selected scats using general mammal primers. The genetic identity of each sample scat was determined by comparing the resulting sequences to those from known species via GenBank's BLAST routine (National Center for Biotechnology Information, http://www.ncbi.nlm.nih.gov/BLAST). I contrasted the resulting genetic identities with their original field identifications to quantify my ability to correctly identify scats in the field.

Diet content

Scats were dried at 80°C for 24 hr to achieve constant weight and to kill *Echinococcus* parasites (Colli and Williams 1972), then weighed to the nearest 0.1 g. I measured the total length and widest diameter of scats collected during the 2001 and 2002 field seasons, representing about half the total. Scats were then placed into individually-numbered ripstop nylon bags, soaked and broken up by three cycles in a residential washing machine and then dried in a residential clothes dryer.

Mammal remains were identified to the most specific taxon possible using reference specimens and keys to skeletal remains (Glass 1951, Ingles 1965, Lawlor 1979) and guard hairs (Mayer 1952, Adjoran and Kolenosky 1969, Moore et al. 1974). Birds, reptiles and insects were identified only to Class. Seeds were identified using local floral guides (Nelson 1962, Gillett 1995) and the California Department of Food and Agriculture's reference collection (Sacramento, California). "Manmade" objects consisted of plastic, tinfoil, apple (*Malus* sp.) seeds and other material associated with humans. Non-food items included vegetative material, woody debris and rocks, which were presumably ingested incidentally while capturing other prey or accidentally collected along with the scat. Likewise, conspecific hairs were assumed to have been ingested during grooming and were not considered food items.

For each scat, I estimated the relative volume of 9 categories of material: hair, bone, feathers, scales, insects, seeds, other plant material, rocks and manmade items. Each category was assigned to one of the following volume classes: “trace” (1-10% of the total volume of the scat), “some” (11-49%) and “most” (>49%). The species identifications and volume classifications were determined by the same person to minimize observer bias (Spaulding et al. 2000).

A “food item” in a scat represented the presence of that item in the scat, not the number of individual prey. For example, a scat containing mule deer hair and parts of 20 insects would have two food items. For each taxon of food item I calculated the relative frequency of occurrence, representing the percentage of the total number of identifiable food items in the scats of a given carnivore within a season. I divided the calendar year into 4 seasons of 3 months each, corresponding to occurrence of spring (March-May), summer (June-August), autumn (September-November) and winter (December-February) in the Lassen region.

I used χ^2 tests to compare dietary trends among seasons and among carnivore species, with the food items consolidated into seven categories: Rodents, Artiodactyls, Other Mammals (insectivores, lagomorphs and carnivores), Birds, Arthropods, Fruit and

Manmade. Differences were considered significant if $p \leq 0.05$. I quantified each carnivore's dietary niche breadth using the Levins (1968) index,

$$B = 1 / \Sigma p_i^2$$

where p_i represents the relative proportion of food item i in the diet of a given species. Note that the Levins index is the reciprocal of Simpson's (1949) index of diversity, so it is highest when a species uses all resource states equally and lowest when a single resource out of many is used predominantly (Krebs 1989). For comparison with other studies, the Levins index is standardized (Hurlbert 1978, Krebs 1989) as follows:

$$B_A = \frac{(B - 1)}{(n - 1)}$$

where n equals the number of dietary categories.

Dietary overlap between pairs of carnivores was calculated via Renkonen's percentage overlap equation (Krebs 1989):

$$\mathrm{P}_{jk} = [\, \Sigma \,(\text{minimum } p_{ij}, p_{ik})] * 100$$

where P_{jk} represents the percentage overlap between species j and k, and p_{ij} and p_{ik} represent the proportion of food item i in the diet of species j and k, respectively. I modified Renkonen's equation to provide a three-way percentage overlap:

$$\mathrm{P}_{jkl} = [\, \Sigma \,(\text{minimum } p_{ij}, p_{ik}, p_{il})] * 100$$

where P_{jkl} represents the percentage overlap among all three species j, k, and l, and p_{ij}, p_{ik}, and p_{il} represent the proportion of food item i in the diets of species j, k, and l, respectively.

To facilitate comparisons with other studies, I also calculated Pianka's (1973) niche overlap index:

$$O_{jk} = \frac{\Sigma\, p_{ij} p_{ik}}{\sqrt{(\Sigma\, p^2_{ij}\ \Sigma\, p^2_{ik})}}$$

where p_{ij}, p_{ik}, and n are defined as above. I excluded non-identifiable food items from all niche breadth and overlap calculations.

RESULTS

Genetic identity

I collected 359 scats from the study area between 1998 and 2002. The genetic identities of 68 randomly-selected scats were determined and compared with their field identifications. I tested an additional five red fox scats whose identities were known because the defecation had been directly observed, and the genetic test correctly identified all five as red fox. A total of 22 scats (32.4%) failed to amplify sufficient genetic material for analysis. This failure rate varied from 0% for the coyote scats to 66.7% for the marten scats. Of the 34 putative red fox scats that amplified successfully, 88.2% (± 5.6%; SE) were correctly identified in the field. The remainder were coyote scats, except for one domestic dog scat collected the first field season. Putative coyote scats were either correctly identified (77.8%) or were actually red fox scat (22.2%).

The number of putative marten scats that amplified successfully was much lower than the other two carnivores. These results were insufficient to quantify my ability to identify marten scats in the field, but suggested that misidentification as red fox might be occurring. Therefore, I used other evidence to verify the identities of the putative marten scats used for the diet analysis. I considered a marten scat to be of known identity if any of the following seven criteria were met: a) the cytochrome-*b* sequence matched that from other marten samples in GenBank's library; b) the scat was collected in association with capturing a marten in a trap; c) the scat was collected from a photostation where marten were detected but red fox were not; d) the scat was collected at a photostation where both marten and red fox were detected, but the camera station recorded the defecation or clearly indicated that red fox had not deposited the scat; e) the scat was collected from marten snow tracks, which are easily distinguished from those of red fox (Halfpenny 1986); f) the scat was collected by marten specialists from the US Forest Service's Pacific Southwest Research Station working in areas where red fox were not known to occur; or g) the scat was collected at a trap site where marten were captured but red fox were not. A total of 37 putative marten scats (48.7%) met these criteria. I calculated the mean mass, length and maximum width of these known scats and confirmed that measurements on all the remaining scats (n=39) were within 2 standard deviations from the means of the known group. The known marten scats and the remaining putative marten scats were collected in the same seasonal proportions ($\chi^2 = 3.23$, 3 df, $p = 0.357$) and contained the same pattern of food items ($\chi^2 = 1.24$, 6 df, $p = 0.975$), so I pooled them for all subsequent analyses.

Volume Assessment

Hair was the dominant scat component across all seasons for red fox, coyote and marten (Figure 7), although winter sample sizes for coyote and marten were too small for strong inference. Hair was present in >90% of scats and usually accounted for most of the material in the scat. Seeds were the only other component that dominated the scat volume, but did so almost exclusively in autumn. Feathers occurred infrequently in the scats and were usually a secondary component, although a few scats from each species were composed mainly of feathers. The presence of arthropods in scats peaked in summer, but even then rarely accounted for more than 10% of the total scat volume. Reptile scales were rare and occurred only in trace amounts when present.

Relative Occurrence

A total of 23 taxa of identifiable food items occurred in the red fox, marten and coyote scats (Table 1). Mammals dominated the diet of all three carnivores in all seasons with sufficient sample size. For red fox, rodents were the primary prey in all seasons, with mountain pocket gopher (*Thomomys monticola*) and mule deer (*Odocoileus hemionus*) the most prominent species (Table 1A). Small rodents (Murid rodents and *Zapus princeps*) were second only to Artiodactyls among winter foods, but their prominence diminished in the warmer months. For coyotes, *O. hemionus* was the most prominent single food item every season, and was surpassed only by rodents in the spring (Table 1B). Squirrels (Sciurid rodents) were a secondary summer food. Marten diet was similar to red fox, except that in the spring *T. monticola* was superceded by *Peromyscus*, *Microtus* and *Spermophilus* (Table 1C). Small rodents were the most common marten food item in spring, and were second only to insects in summer and fruit in autumn. Lagomorphs were virtually absent from all three carnivores’ diets. The carnivores took birds at a moderate level, accounting for less than 15% of the food items for any season with adequate sample size. Reptiles were a minor component, with most occurrences being alligator lizard (*Elgaria* sp.). Manmade items included fishing line, tinfoil, cellophane food wrappers and seeds of domestic fruit, and were more common in the red fox diet than for the other two carnivores.

Each carnivore had significant seasonal differences in its consumption of the seven food categories (red fox: $\chi^2 = 89.39$, 18 df, $p < 0.001$; coyote: $\chi^2 = 33.34$, 12 df, $p < 0.001$; marten: $\chi^2 = 32.62$, 12 df, $p = 0.001$). Consumption of fruit, primarily *Arctostaphylos nevadensis*, was minimal except during autumn, and consumption of arthropods peaked in summer. There was no significant difference among the three carnivores' diets in spring ($\chi^2 = 13.03$, 12 df, $p = 0.367$) or summer ($\chi^2 = 16.29$, 12 df, $p = 0.178$), but in autumn the differences were significant ($\chi^2 = 31.18$, 12 df, $p = 0.002$) primarily due to the larger proportion of deer in the coyote diet relative to red fox and marten.

Niche Breadth and Overlap

Dietary niche breadth varied by species and season (Table 1). Red fox and coyote in spring had the widest dietary niches, indicating their broad use of food types. In contrast, coyote in summer and autumn had the narrowest dietary niche, reflecting the large proportion of *O. hemionus* in the diet. Niche breadth for all three carnivores showed a general pattern of being widest in spring and narrowest in autumn, although coyotes were marginally lower in summer. Coyotes showed the greatest change in niche breadth between spring and autumn ($B_{spring} / B_{fall} = 2.48$), followed by red fox (1.53) and marten (1.17). Percent overlap among carnivore pairs ranged from 55.9% to 75.5% depending on the season and species pair (Table 2). Both the Renkonen and Pianka indices revealed that the overlap between red fox and marten was highest, and the overlap between red fox and coyote was lowest. Three-way overlap was >50% in all seasons, indicating that most of the pairwise overlaps were actually food categories used by all three species (Table 3). The three-way overlap varied little across seasons but was highest in the summer. The food categories comprising the overlap and their relative contributions differed by season, but *O. hemionus*, *T. monticola*, birds and arthropods were components in all three seasons (Table 3).

DISCUSSION

Identification of scats

The primary goal of this study was to describe the diet of red fox in the Lassen Peak region of northern California and how it overlapped with two potential competitors, coyote and marten. The ability to correctly assign scats to species is crucial for any dietary study, especially when comparing diets of sympatric species (Green and Flinders 1981, Farrell et al. 2000). Absent direct observation of the defecation, carnivore ecologists usually base the field identity of scats on morphological characteristics. Although scats of uncertain origin are usually discarded, many studies simply assume that those remaining were correctly identified. Unfortunately, morphological identification can be prone to errors that can bias results, especially among carnivores (Halfpenny 1986). Analysis of fecal DNA, or “molecular scatology” (Kohn and Wayne 1997, Reed et al. 1997, Farrell et al. 2000) can confirm fecal identities independent of morphological traits, but can be expensive, time-consuming, and the DNA can degrade quickly under certain field conditions (Farrell et al. 2000, Davison et al. 2002).

I used mitochondrial DNA from a sample of scats to quantify the accuracy of my field identifications. The genetic results confirmed that the field identification of red fox and coyote scats was correct 88% and 78% of the time, respectively. On occasion, coyote scats were misidentified in the field as red fox, and red fox scats were misidentified as coyote, marten or bobcat. Wild canids have similar scats, and a large red fox scat can easily be mistaken for a small coyote scat and vice versa (Murie 1974, Green and Flinders 1981, Halfpenny 1986).

Red fox and marten scats are more easily differentiated (Halfpenny 1986), although they may be confused in areas where red fox are common and marten are rare (Davison et al. 2002). In the Lassen region, photosurveys indicate that marten are far more abundant than red fox (unpublished data). Unfortunately, the amplification rate for my putative marten scats was too low to assess their field identification rate, necessitating the use of other evidence to verify their identity. The amplification success rates among the three carnivore species is proportional to, and likely a function of, the mass of the original scat. Putative coyote scats were the largest collected, and a larger genetic sample could be taken without interfering with the dietary analysis of the same scat. These larger scats had an amplification success rate of 100%. Putative marten scats were the smallest collected, and comparatively little fecal tissue could be collected for the genetic test while still leaving most of the material for the diet content analysis. These smaller samples likely did not contain sufficient epithelial cells to amplify successfully, despite the general mammal primers used. One of the scats that failed to amplify was collected from a trapped marten, so its identity was known. However, this scat had been trampled and broken up by the trapped marten, so its overall mass was small and the genetic sample comparatively even smaller. The primers and lab technique are likely not at fault, because 2 other marten scats (not included in the random sample) did amplify successfully. Neither of these 2 scats were collected at a trap site, so their overall condition was better, their mass was larger and the genetic sample likely somewhat larger. Additionally, these 2 scats were <24 hrs old, suggesting that the smaller genetic sample in the other marten scats may have been further reduced by degradation due to weathering over multiple days.

Genetic testing of every scat may be prohibitively expensive and impractical, and field identification errors can only be minimized, not eliminated (Green and Flinders 1981, Halfpenny 1986, Farrell et al. 2000, Davison et al. 2002). This underscores the importance of training field technicians in the morphological variation of scats (Halfpenny 1986) as well as documenting extra evidence such as tracks or camera station photographs to support the species identification (Davison et al. 2002). Inexperienced field technicians may be more prone to identification errors, but even seasoned researchers may benefit from a tabulation of the physical characteristics of scats of verified identity (see Appendix A).

Diet content

With a few notable exceptions, the dietary patterns of red fox, marten and coyote in the Lassen Peak region of California were similar to those described in dozens of other studies of these species throughout North America. Mammals dominated their diets in all seasons, and hair represented a large proportion of the indigestible material in most of the scats. There was a general trend that coyote ate more mule deer and fewer rodents, while red fox and marten did the opposite, but the trend was significant only in autumn. The presence of insects and birds in scats peaked in spring and summer, but even then usually represented a low percentage of scat volume. Fruit, mostly *Arctostaphylos nevadensis*, was important in autumn. Garbage and manmade items varied by season and species.

Thomomys monticola was the most common rodent in the diet of all 3 carnivores, increasing in their diets throughout the year until peaking in autumn. For red foxes, the importance of *T. monticola* in summer and autumn surpassed all other rodent species combined. Aubry (1983) concluded that *T. talpoides* was an important seasonal prey of red foxes in the Cascade Mountains of Washington and Oregon, and Chase et al. (1982) considered red and gray fox “common predators” on pocket gophers in Oregon. Coyotes in California apparently take pocket gophers when available (Ferrel et al. 1953, Hawthorne 1972, Barrett 1983, Bowyer et al. 1983, Smith 1990, Cypher et al. 1996), and where gophers were not a food item, it is questionable if they occurred in the environment (Bond 1939, Fedriani et al. 2000). Murie (1940) considered pocket gopher a staple of the Yellowstone coyote diet from April through November, peaking from July through October. Marten in California did not prey heavily upon pocket gopher but used them when available (Martin 1994). In the southern Sierra Nevada, *T. bottae* occurred in only 1.3% of marten scats (Zielinski and Duncan 2004).

The virtual absence of lagomorphs from the diets of all 3 carnivores was unexpected. Grinnell et al. (1937) noted that lagomorph remains were common in the Sierra Nevada red fox droppings they examined. Their current absence may indicate low population levels in the Lassen region during this study. Murie (1944) reported that the low proportion of *L. americanus* in the diet of Alaskan red fox reflected their scarcity and contended that had the hares been more numerous, they would have composed a greater proportion of the red fox diet. Snowshoe hare was the most common winter prey species for Cascade red foxes (Aubry 1983), and was important prey for marten in eastern North America (Martin 1994). However, it is apparently absent from the southern Sierra Nevada (Zielinski et al. 1999, Zielinski and Duncan 2004) and uncommon in the northern Sierra Nevada and southern Cascades in California (Zeiner et al. 1990). I found *L. americanus* in a single scat from Thousand Lakes Wilderness, and *Ochotona princeps* in a single scat collected in the southwestern portion of Lassen Volcanic National Park. However, both scats were excluded from the final diet analysis because their species identity could not be confidently determined. The abundance of *L. americanus* and other lagomorphs in the Lassen region is unknown, and targeted surveys should be conducted in light of their apparent absence in the carnivores' diets.

Mule deer was eaten by all three carnivores year-round. It dominated the Lassen coyote diet in summer and fall, but was most prominent in the red fox and marten diets in winter and spring. This probably represents carrion, although coyote are known to kill fawns, infirm individuals and even healthy deer that become mired in deep snow (Ferrel et al. 1953, Sumner and Dixon 1953). Ungulate carrion can be an important winter food for red fox and other carnivores, even if carcasses are relatively rare in the environment (Murie 1940, Schofield 1960, Goszczynski 1989, Jedrzejewski et al. 1993, Borkowski 1994, Lanszki et al. 1999, Sidorovich et al. 2000). Their role in the winter diet is even more surprising given that mule deer in the Lassen region typically descend to below 1200 m once heavy snows begin (Grinnell et al. 1930, Sumner and Dixon 1953, Ramsey 1981). The importance of ungulate carrion in winter may have increased due to the unavailability of lagomorphs. Mule deer was a minor component of Cascade red fox diet in winter when snowshoe hare was a principal food item, although sample sizes were low

(Aubry 1983). Red fox in Maine showed a similar pattern, with snowshoe hare dominating the winter diet despite the availability of white-tailed deer (*Odocoileus virginianus*) carcasses (Major and Sherburne 1987). In winter, coyotes may cache deer and other prey remains for later consumption (Murie 1940), representing an important food source for other scavengers. I noted several occasions when red foxes had dug through >50 cm snow to uncover a deer carcass. Marten consume ungulate carrion when available, but it rarely accounts for a large portion of their overall diet (Martin 1994, Zielinski and Duncan 2004).

Shrews (*Sorex* sp.) and moles (*Scapanus latimanus*) were rare in the coyote and marten diet, but red fox took them every season, especially in spring when they were one of the top food items. Insectivores are considered distasteful to predators (Murie 1940, Sumner and Dixon 1953, Lloyd 1980), and red fox consume them only when other prey is unavailable (Macdonald 1977). Ferrell et al. (1953) found shrews in only 6 of 2,222 coyote stomachs containing food remains. Yellowstone coyotes and Alaskan red foxes apparently avoided eating shrews despite their availability (Murie 1940, Murie 1944). Shrews and moles were each present in 6.7% of marten scats in the southern Sierra Nevada (Zielinski and Duncan 2004). Insectivores were a critical winter food for *Martes martes* in Poland when rodent populations were low (Jedrzejewski et al. 1993). In general, an abundance of shrews in the diet may indicate a low availability of more palatable prey.

Only coyote scats contained the remains of other carnivore species. The single occurrence of *Felis* sp. likely represents predation upon a domestic or feral housecat. More intriguing is the presence of *Ursus americana* in scats collected in December 2001, March 2001 and March 2002. Although some Lassen coyotes may be preying upon bears, they may also be scavenging the carcasses of bears killed by automobiles or hunters. Similar cases in Yellowstone were all near where problem bears had recently been killed (Murie 1940). Sumner and Dixon (1953) reported an instance of coyotes killing and eating a young black bear in the Sierra Nevada, but Ferrel et al. (1953) found no *Ursus* remains in any coyote stomachs collected anywhere in California. As for other carnivores, red foxes may occasionally consume mustelids, but it is unclear whether this represents predation or scavenging (Aubry 1983, Padial et al. 2002). Marten in Lassen Park apparently scavenged a red fox carcass during the winter 2000-2001, but I did not include those scats in these analyses.

Birds were seasonally common in the carnivores' diets but usually accounted for a small proportion of scat volume. Consumption of birds by red fox and coyote is likely opportunistic and much of it may represent scavenging. Birds killed by automobiles were fairly common along the road through Lassen Park in summer and autumn. In April 2000, I saw a red fox eat a pile of *Corvus corax* feathers atop the snow, and Lassen park rangers witnessed red fox capture and consume *Dendragapus obscurus* several times in winter and early spring (Steve Zachary, pers.com.). The higher incidence of birds in the marten diet in summer and autumn is likely attributable to their ability to climb trees, increasing their opportunities to prey upon birds. Birds were present in 18.7% of marten scats in the southern Sierra Nevada (Zielinski and Duncan 2004).

Fruit of *Arctostaphylos nevadensis* was an important autumn food for all 3 carnivores. It is common throughout the study site (Gillett 1995), and in autumn I frequently found carnivore scats composed entirely of its hard seeds. *Arctostaphylos* sp.

berries were a primary summer and autumn food for coyotes in Tehama County (Barrett 1983), Mendocino County (Neale and Sacks 2001) and Fresno County (Smith 1990), and were the most common fruit in the coyote diet in the coastal, northeast and inland-Sierra regions of California (Ferrel et al. 1953). Cascade red fox consumed strawberry (*Frageria* sp.) and blueberry (*Vaccinium* sp.) in summer and early autumn (Aubry 1983); it is unclear whether *Arctostaphylos* was present in the study site. Marten in the southern Sierra Nevada ate a variety of wild fruits including *Arctostaphylos, Ribes, Rhamnus, Rubus* and *Sambucus* (Zielinski and Duncan 2004). In general, these 3 carnivores probably take fruit whenever it is available.

All 3 carnivores ate manmade foods, although these rarely accounted for more than 10% of the food items. Canids and mustelids often consume garbage and other human-associated foods if available, and the levels in this study are at the lower end of the range documented for red fox and coyote in particular (Fedriani et al. 2001). However, human-associated foods often contain few indigestible items that would appear in the scat, so their consumption may be underestimated in this study. Several red foxes in the study site were known to scavenge and beg for food at campgrounds, parking lots and snowmobile parks, and they also likely scavenged pet food set outside local residences. The presence of apple seeds, sesame seeds and popcorn husks can only suggest what other man-made foods might have been eaten by these scavenging foxes. But these individuals clearly ate natural foods as well, as evidenced by the hairs, bones, feathers and seeds in their scats.

Niche breadth and overlap

Red fox, coyote and marten had relatively wide trophic niches, reflecting their consumption of rodents, ungulates, insectivores, birds, insects, fruit and manmade items (Table 1), and consistent with their reputations as opportunistic generalists. Coyotes had the greatest seasonal change in niche breadth and marten had the least. Note that similarity in niche breadth between two seasons does not imply similarity in diet composition; the actual food categories used by marten in spring and autumn were quite different (Table 1C, Figure 7C). Marten dietary diversity at Lassen was narrower in all 3 seasons than the overall value ($B_A = 0.36$) reported from the southern Sierra Nevada (Zielinski and Duncan 2004). This is consistent with the general trend of increasing dietary diversity with decreasing latitudes within marten range (Martin 1994, Zielinski and Duncan 2004), but may also be an artifact of the level of prey identification in this study (Greene and Jaksic 1983).

Trophic niche varied consistently by season for all three species, being narrowest in autumn and widest in spring. Cascade red fox display the opposite pattern (Figure 9), with their diet becoming increasing diverse throughout the year until peaking in autumn (Aubry 1983). Unlike Lassen red fox, Cascade red fox winter diet was dominated by a single taxon, namely lagomorphs. In contrast, coyote dietary breadth in an agricultural area of Mendocino County was widest in spring and winter and was narrowest in autumn (Neale and Sacks 2001), identical to the pattern of all 3 carnivores in this study, despite the differences in habitat and prey availability between the two study sites.

Foods such as insects and fruit have distinct seasonal cycles of abundance. I did not quantify the abundance of any food resources, so I cannot make definitive statements about their seasonal availability in the Lassen region. However, red fox diet niche was clearly wider during winter and spring when environmental conditions were severe than during summer and autumn when conditions were benign. Winter niche breadth for coyote and marten could not be determined due to small sample size, but in other seasons their patterns paralleled that of red fox. It appears that during the snowy months, the absence of lagomorphs as a critical food resource requires that carnivores take a wide variety of alternative prey.

Dietary overlap among all 3 species was high, indicating that they used many of the same foods during the same season (Tables 2, 3). In none of the seasons with adequate sample size did any carnivore pair overlap less than 55%. Moreover, overlap across all 3 species was approximately 50% in all seasons, large relative to the pairwise overlap values and remarkably consistent across seasons. This overlap is again consistent with the scenario of 3 opportunistic generalists eating seasonally available foods.

Extensive dietary overlap is not in itself evidence of competition among these species. Niche overlap is not necessarily indicative of, or even correlated to, interspecific competition (Wiens 1977). Extensive overlap may indicate a high potential for competition or merely a superabundant resource. Likewise, low overlap may indicate a low potential for competition or complete competitive exclusion (Litvaitis et al. 1996). In a variable environment, truly limiting resource availability sufficient to spur competition may occur only infrequently, perhaps not for generations (Wiens 1977). If resources are extremely scarce, potential competitors may have to take what is available, resulting in increased niche overlap (Wiens 1993). Lastly, competition may also manifest itself along other resource axes such as habitat utilization or activity pattern as opposed to diet (Wiens 1993).

However, interspecific intolerance has been well documented between red fox and coyote, and may exist between marten and both canids. Coyotes chase red foxes and may kill them (Dekker 1983, Sargeant and Allen 1989). Red foxes appear to minimize such interactions by avoiding areas occupied by coyotes (Dekker 1983, Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989, Gosselink et al. 2003). There has been little documentation of antagonistic interactions between coyote and marten. Coyote scat occasionally contain marten remains (Murie 1940, Arjo et al. 2002), but these likely represent scavenging as carnivores rarely eat the competitors they kill (Creel et al. 2001). Red fox may occasionally kill marten (Thompson 1994), and the risk of such predation may contribute to marten avoidance of open areas (Brainerd et al. 1994, Thompson and Harestad 1994). Despite the dietary overlap among these 3 carnivores, the seasonal abundance of most of their foods may reduce competition pressure. However, during the snowy months mule deer carcasses are an important and presumably limited food, and agonistic interactions between red fox and coyote or marten may be common.

CONCLUSIONS

My results are consistent with the characterization of red fox, coyote and marten as opportunistic predators and scavengers whose dietary patterns reflect the availability of food items, especially those with seasonal peaks such as insects and fruit (Murie 1940, Ferrel et al. 1953, Ables 1975, Samuel and Nelson 1982, Storch et al. 1990, Martin 1994, Sidorovich et al. 2000, Padial et al. 2002). Consistent with numerous other studies (see Rosenzweig 1966), the larger-bodied coyote took more large prey such as *O. hemionus*, the smaller-bodied marten took more small prey such as mice, and the red fox was intermediate in both respects. The virtual absence of lagomorphs and the year-round role of *O. hemionus* in the diets of all 3 carnivores are atypical patterns and may be related. My results suggest that leporids may be functionally absent from this system, which warrants further investigation. The absence of a usual critical food resource may require red foxes in particular to rely upon other sources for winter food. The seasonal movement of Lassen red foxes to lower elevations (see Chapter 4) may be due to the lack of sufficient winter food on their summer range. The advent of heavy snows in the Lassen region apparently prompts red foxes to seasonally relocate to lower elevations where they subsist on ungulate carrion, insectivores, birds and anthropogenic foods. No such seasonal movement was documented for red foxes in the Cascades, where lagomorphs dominated the winter diet and winter consumption of ungulate carrion, insectivores and birds was negligible (Aubry 1983). Furthermore, the importance of ungulate carrion as a winter food, paired with its apparently limited supply, may increase the possibility of fatal interactions with coyotes. Therefore, the absence of lagomorphs as winter food may be an important factor limiting the abundance, and perhaps even contributing to the decline, of red fox in the Lassen region. The low absolute abundance of red fox in the region suggests that their competitive impacts on marten may be negligible.

Table 1: Field identity versus cytochrome-*b* identity of scats.

Field Identification	Number Tested	Test Failed	Results of cytochrome-*b* test				% Correct	Std Error
			Red Fox	Coyote	Marten	Dog		
Red Fox	50	16	30	3	-	1	88.2	5.6
Coyote	9	-	2	7	-	-	77.8	14.7
Marten	9	6	2	-	1	-	33.3	5.6

Table 2: Seasonal diet composition for Lassen red fox, coyote and marten.

A) Red Fox	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
Number of Scats Collected:	41	38	93	55
Number of Food Items:	63	64	218	126
Relative Percent Occurrence				
Mammalia	**77.8**	**76.6**	**58.3**	**60.3**
Rodentia	41.3	43.8	37.2	45.2
Aplodontia rufa	1.6	1.6	2.3	0.8
Clethrionomys sp.	1.6	0.0	0.9	0.8
Microtus sp.	4.8	0.0	3.2	3.2
Ondatra zibethicus	0.0	0.0	0.0	0.0
Peromyscus sp.	7.9	4.7	0.5	6.3
Reithrodontomys megalotis	1.6	0.0	0.9	0.0
Spermophilus sp.	3.2	6.3	3.2	2.4
Tamias sp.	1.6	0.0	1.4	1.6
Tamiasciurus douglasii	0.0	3.1	0.5	0.8
Thomomys monticola	9.5	10.9	17.4	26.2
Zapus princeps	0.0	3.1	0.9	0.0
unidentified Murid	0.0	4.7	1.4	0.8
unidentified Sciurid	1.6	1.6	0.9	0.8
unidentified Rodent	7.9	7.8	3.7	1.6
Insectivora	6.3	10.9	4.1	2.4
Scapanus latimanus	1.6	3.1	1.8	1.6
Sorex sp.	4.8	7.8	2.3	0.8
unidentified Insectivore	0.0	0.0	0.0	0.0
Artiodactyla	22.2	15.6	13.8	11.1
Odocoileus hemionus	17.5	14.1	12.4	8.7
unidentified Artiodactyl	4.8	1.6	1.4	2.4
Lagomorpha	0.0	1.6	0.9	0.0
unidentified Leporid	0.0	0.0	0.9	0.0
unidentified Lagomorph	0.0	1.6	0.0	0.0
Carnivora	0.0	0.0	0.0	0.0
Felis sp.	0.0	0.0	0.0	0.0
Ursus americana	0.0	0.0	0.0	0.0
unidentified Mammal	7.9	4.7	8.6	1.6
Aves	**6.3**	**6.3**	**8.7**	**8.7**
Reptilia	**1.6**	**1.6**	**0.5**	**0.0**
Arthropoda	**3.2**	**10.9**	**20.2**	**7.9**
Fruits	**0.0**	**0.0**	**2.3**	**20.6**
Arctostaphylos nevadensis	0.0	0.0	1.4	19.8
other fruit	0.0	0.0	0.9	0.8
Manmade	**11.1**	**4.7**	**10.1**	**2.4**
Levins Index (B):	8.61	9.67	7.52	6.32
standardized (B_A):	0.346	0.394	0.296	0.242

Table 2, continued.

B) Coyote	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
Number of Scats Collected:	5	18	12	23
Number of Food Items:	13	42	24	44
Relative Percent Occurrence				
Mammalia	**46.2**	**66.7**	**75.0**	**72.7**
Rodentia	15.4	28.6	33.3	27.3
Aplodontia rufa	0.0	0.0	0.0	0.0
Clethrionomys sp.	0.0	2.4	4.2	0.0
Microtus sp.	0.0	2.4	0.0	2.3
Ondatra zibethicus	0.0	2.4	0.0	0.0
Peromyscus sp.	0.0	4.8	0.0	0.0
Reithrodontomys megalotis	0.0	0.0	0.0	0.0
Spermophilus sp.	0.0	2.4	4.2	0.0
Tamias sp.	0.0	0.0	0.0	4.5
Tamiasciurus douglasii	0.0	0.0	4.2	2.3
Thomomys monticola	0.0	4.8	8.3	13.6
Zapus princeps	0.0	0.0	0.0	0.0
unidentified Murid	0.0	2.4	0.0	0.0
unidentified Sciurid	15.4	2.4	8.3	0.0
unidentified Rodent	0.0	4.8	4.2	4.5
Insectivora	0.0	2.4	0.0	2.3
Scapanus latimanus	0.0	2.4	0.0	2.3
Sorex sp.	0.0	0.0	0.0	0.0
unidentified Insectivore	0.0	0.0	0.0	0.0
Artiodactyla	23.1	21.4	37.5	40.9
Odocoileus hemionus	15.4	19.0	37.5	40.9
unidentified Artiodactyl	7.7	2.4	0.0	0.0
Lagomorpha	0.0	0.0	0.0	0.0
unidentified Leporid	0.0	0.0	0.0	0.0
unidentified Lagomorph	0.0	0.0	0.0	0.0
Carnivora	7.7	7.1	0.0	0.0
Felis sp.	0.0	2.4	0.0	0.0
Ursus americana	7.7	4.8	0.0	0.0
unidentified Mammal	0.0	7.1	4.2	2.3
Aves	**23.1**	**11.9**	**4.2**	**2.3**
Reptilia	**0.0**	**4.8**	**0.0**	**0.0**
Arthropoda	**15.4**	**7.1**	**20.8**	**2.3**
Fruits	**7.7**	**2.4**	**0.0**	**22.7**
Arctostaphylos nevadensis	7.7	2.4	0.0	22.7
other fruit	0.0	0.0	0.0	0.0
Manmade	**7.7**	**7.1**	**0.0**	**0.0**
Levins Index (B):	--	8.89	3.51	3.58
standardized (B_A):	--	0.359	0.114	0.117

Table 2, continued.

C) Marten	Dec-Feb	Mar-May	Jun-Aug	Sep-Nov
Number of Scats Collected:	2	25	26	23
Number of Food Items:	5	36	50	39
Relative Percent Occurrence				
Mammalia	**60.0**	**77.8**	**64.0**	**59.0**
Rodentia	40.0	52.8	40.0	43.6
Aplodontia rufa	0.0	0.0	2.0	2.6
Clethrionomys sp.	0.0	2.8	0.0	2.6
Microtus sp.	0.0	11.1	0.0	7.7
Ondatra zibethicus	0.0	0.0	0.0	0.0
Peromyscus sp.	0.0	11.1	8.0	0.0
Reithrodontomys megalotis	0.0	0.0	0.0	0.0
Spermophilus sp.	0.0	11.1	2.0	2.6
Tamias sp.	0.0	2.8	0.0	2.6
Tamiasciurus douglasii	0.0	0.0	0.0	0.0
Thomomys monticola	0.0	2.8	12.0	12.8
Zapus princeps	0.0	0.0	0.0	0.0
unidentified Murid	0.0	2.8	8.0	2.6
unidentified Sciurid	20.0	0.0	4.0	0.0
unidentified Rodent	20.0	8.3	4.0	10.3
Insectivora	0.0	0.0	4.0	0.0
Scapanus latimanus	0.0	0.0	0.0	0.0
Sorex sp.	0.0	0.0	4.0	0.0
unidentified Insectivore	0.0	0.0	0.0	0.0
Artiodactyla	20.0	22.2	14.0	5.1
Odocoileus hemionus	20.0	19.4	12.0	5.1
unidentified Artiodactyl	0.0	2.8	2.0	0.0
Lagomorpha	0.0	0.0	0.0	0.0
unidentified Leporid	0.0	0.0	0.0	0.0
unidentified Lagomorph	0.0	0.0	0.0	0.0
Carnivora	0.0	0.0	0.0	0.0
Felis sp.	0.0	0.0	0.0	0.0
Ursus americana	0.0	0.0	0.0	0.0
unidentified Mammal	0.0	2.8	6.0	10.3
Aves	**0.0**	5.6	**12.0**	**10.3**
Reptilia	**0.0**	**2.8**	**2.0**	**0.0**
Arthropoda	**20.0**	**5.6**	**18.0**	**10.3**
Fruits	**0.0**	**0.0**	**0.0**	**20.5**
Arctostaphylos nevadensis	0.0	0.0	0.0	20.5
other fruit	0.0	0.0	0.0	0.0
Manmade	**20.0**	**8.3**	**4.0**	**0.0**
Levins Index (B):	--	7.63	6.69	6.52
standardized (B_A):	--	0.301	0.258	0.251

Table 3: Dietary niche overlap between pairs of Lassen carnivores. Renkonen's index is given as a percentage (possible range: 0% to 100%), followed by Pianka's index as a decimal (possible range: 0.0 to 1.0). Winter was omitted due to small sample size for coyote and marten. Overlap calculations were based on the same categories used for the Levins index in Table 2.

	Mar-May	June-Aug	Sep-Nov
Red Fox + Coyote:	59.8%	56.1%	57.0%
	0.802	0.741	0.673
Red Fox + Marten:	55.9%	75.5%	72.1%
	0.730	0.920	0.896
Coyote + Marten:	66.9%	57.1%	56.3%
	0.824	0.752	0.625

Table 4: Seasonal dietary overlap among all three carnivores. Percent overlap values represent the sum of the lowest percent use of each food item across the three carnivores' diets for that season. Food items comprising the overlap are listed in order of their proportional contribution to the total overlap for that season; their proportions sum to 1.0. Mule deer, pocket gopher and birds were eaten by all three carnivores every season. The presence of arthropods in spring and summer scats, and manzanita (*Arctostaphylos nevadensis*) berries in autumn, likely reflect their seasonal availability.

Mar - May		Jun - Aug		Sep - Nov	
Three-way overlap: 51.0%		53.7%		51.7%	
Proportional contributions:					
Odocoileus hemionus	0.346	Arthropods	0.416	*Arctostaphylos nevadensis*	0.413
Birds	0.131	*Odocoileus hemionus*	0.255	*Thomomys monticola*	0.283
Arthropods	0.131	*Thomomys monticola*	0.186	*Odocoileus hemionus*	0.129
Manmade	0.115	Birds	0.093	Birds	0.047
Peromyscus sp.	0.115	*Spermophilus* sp.	0.049	Arthropods	0.047
Thomomys monticola	0.065			*Microtus* sp.	0.047
Spermophilus sp.	0.058			*Tamias* sp.	0.033
Reptiles	0.038				

Figure 7: Seasonal composition of Lassen carnivore scats by volumetric index. Asterisks denote seasons with <6 scats analyzed. Hair was present in almost all scats and was usually the dominant component by volume. Feathers, insects and seeds occurred in fewer scats and were usually low volume. Seeds in autumn were the only food item other than hair to regularly dominate the scat volume. Scales (not shown) were rare in the diet, occurring in <5% of scats and only in trace amounts when present. Vegetation, primarily *Abies magnifica* needles, and rocks occurred in many scats but were not considered food items.

Figure 7:

A) Hair

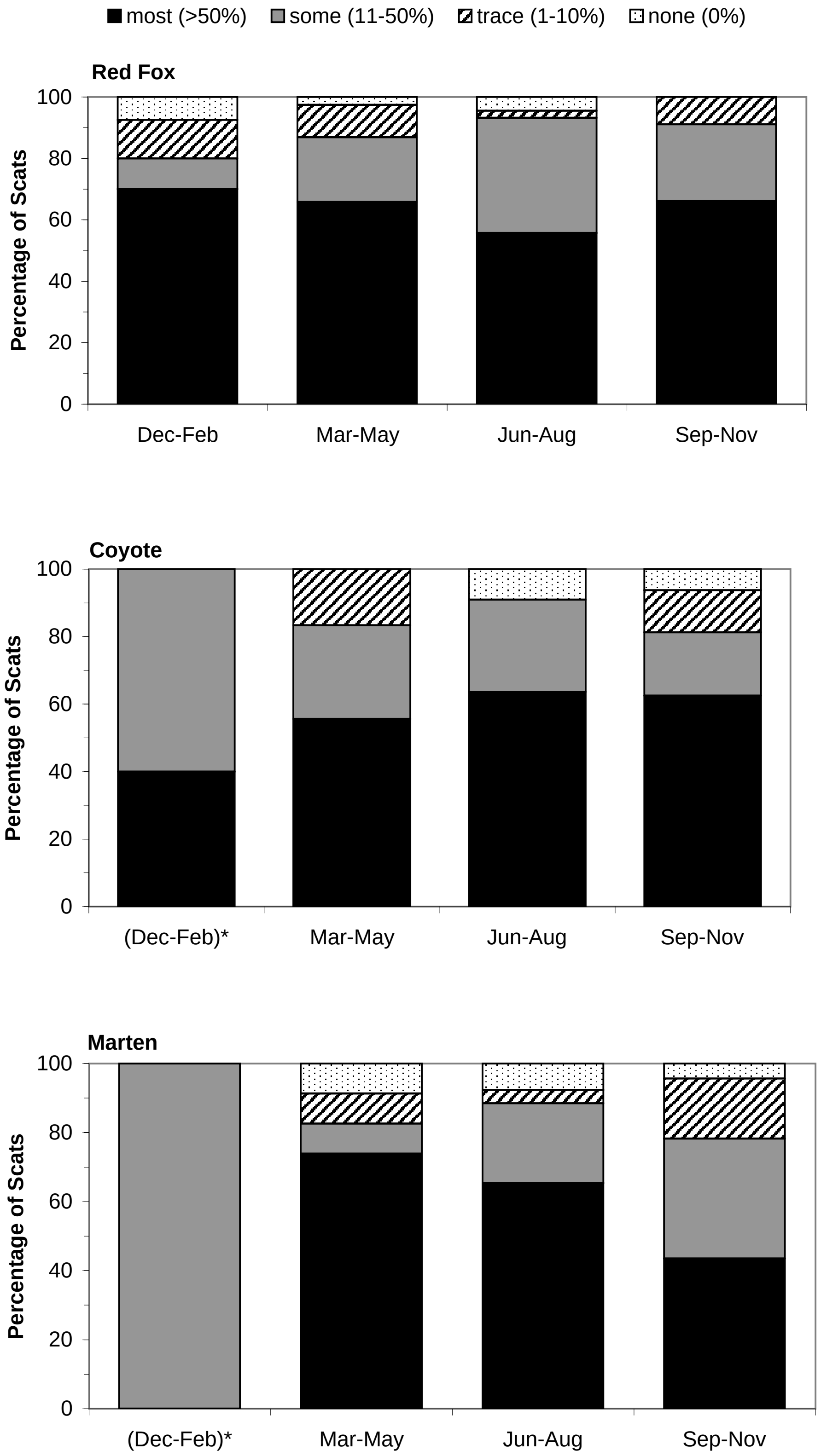


Figure 7, continued.

B) Feathers

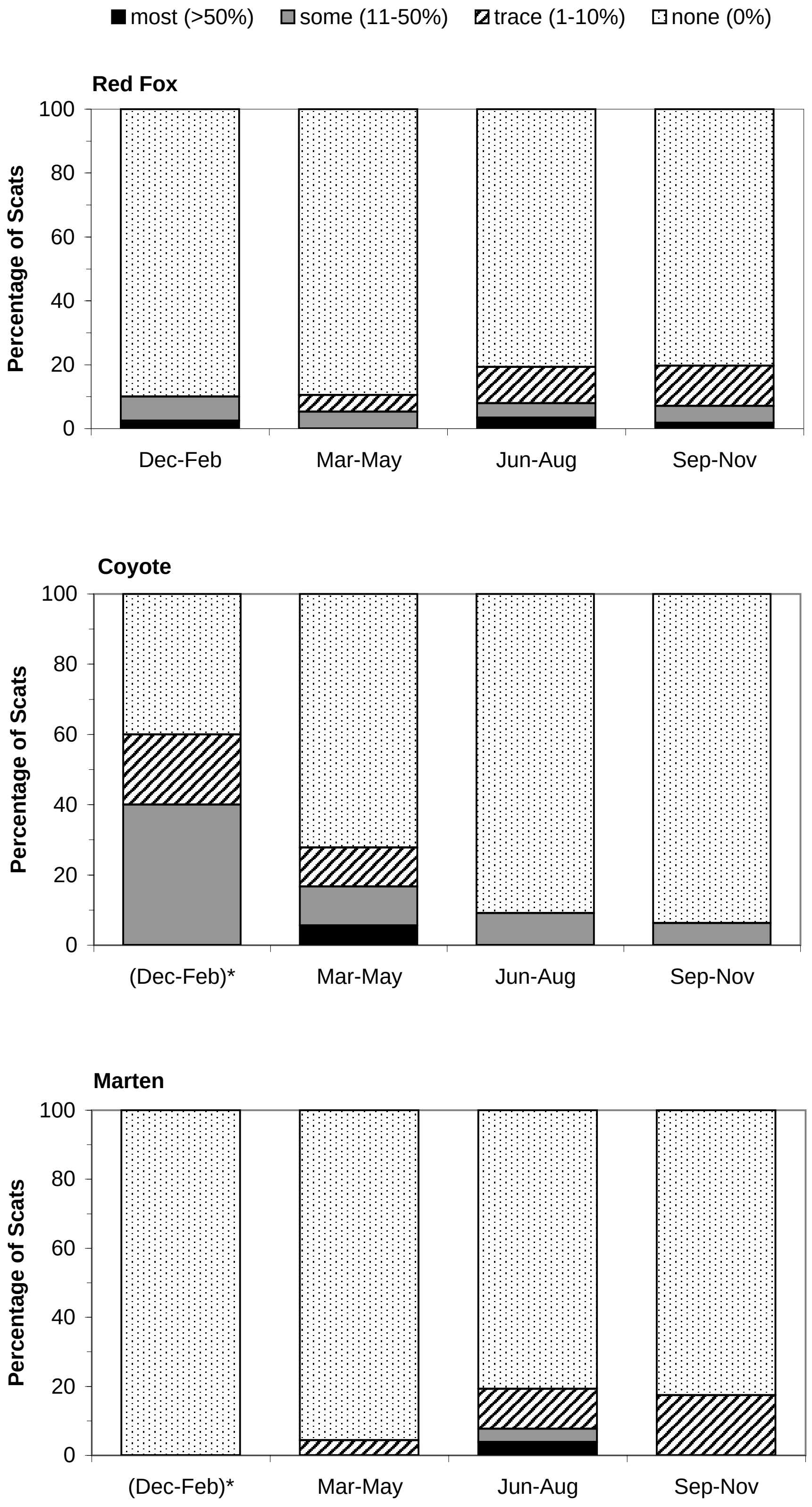


Figure 7, continued.

C) Insects

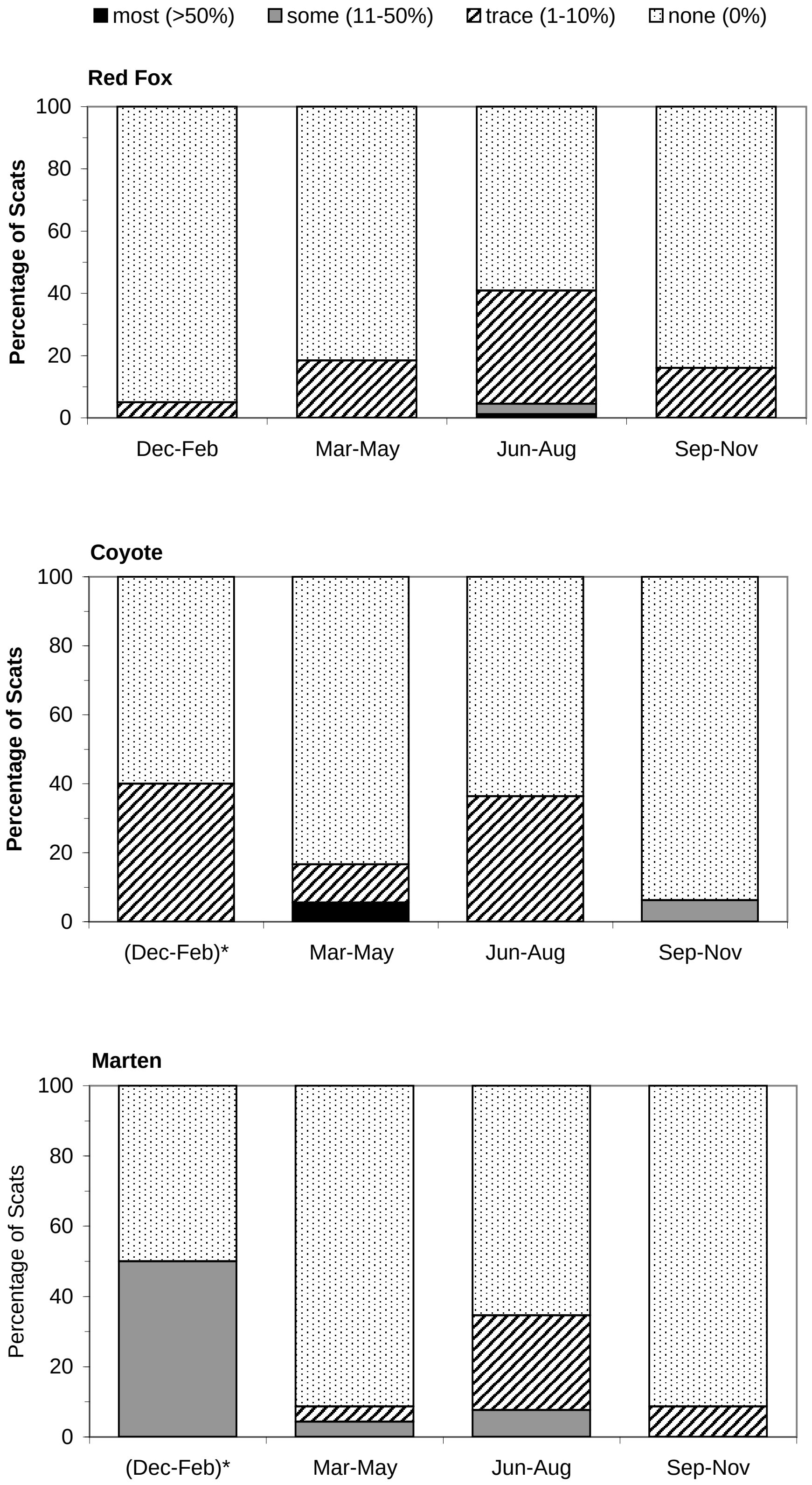


Figure 7, continued.

D) Seeds

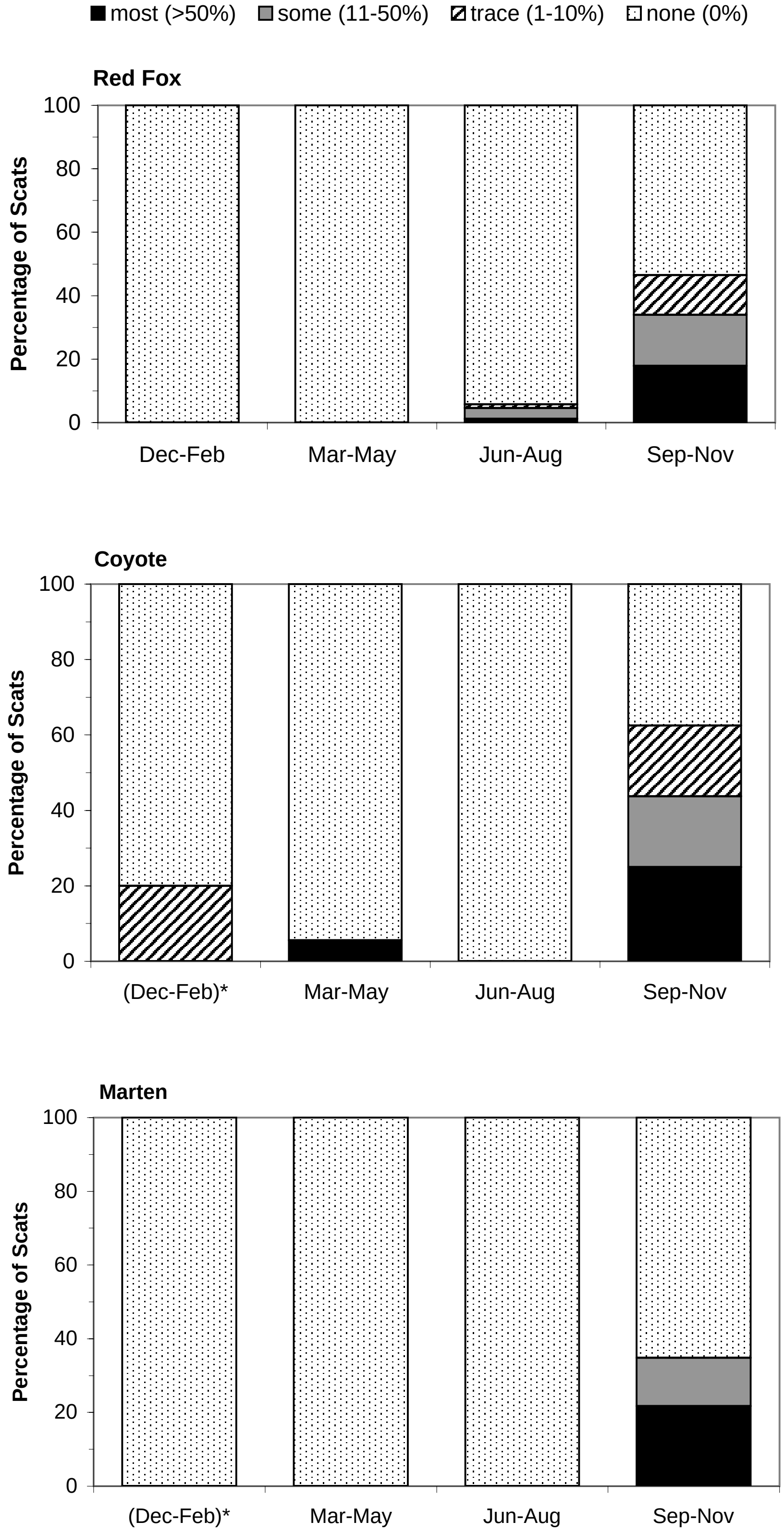


Figure 8: Seasonal trends in diet composition for red fox, coyote and marten in the Lassen Peak region of northern California, as composite food categories used for statistical testing. Note that the same season (winter) is shown at the beginning and ending of each figure. Asterisks denote seasons with <10 scats analyzed; see Table 1 for actual sample sizes. "Other Mammals" = insectivores, lagomorphs and carnivores. Other categories are as reported in Table 2. "Unidentified Mammal" food items were omitted and the proportions re-calculated.

Figure 8:

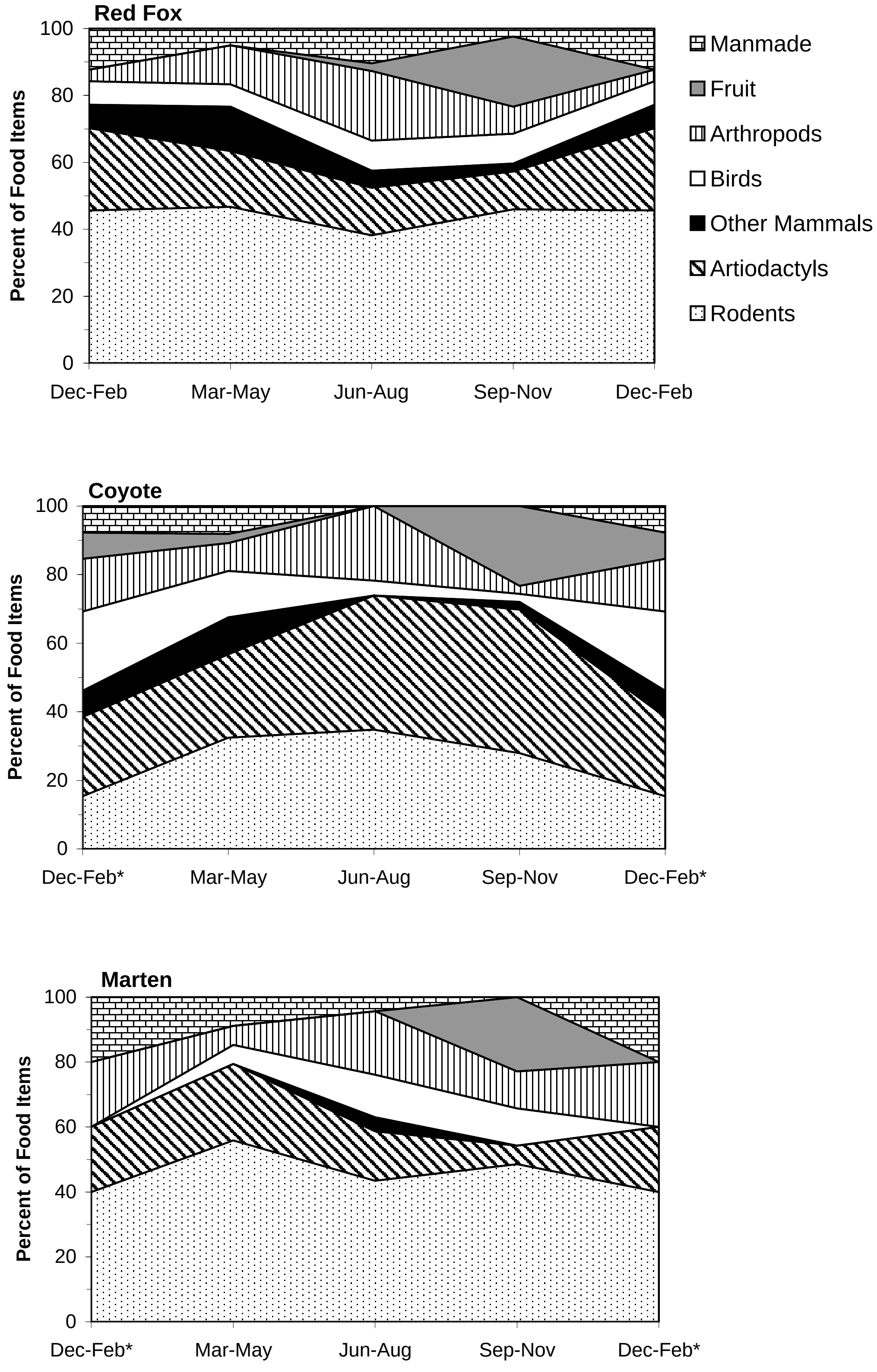
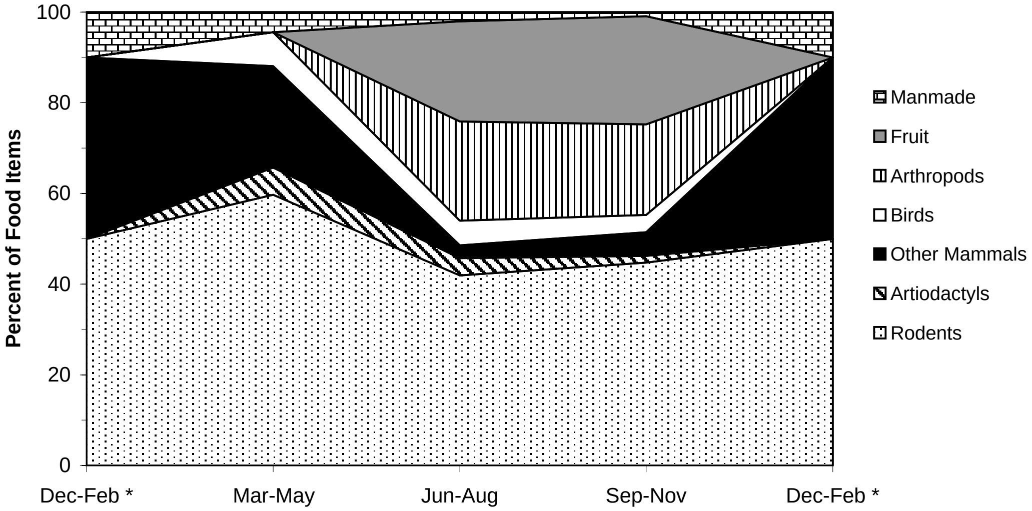

Red Fox
Percent of Food Items
100
80
60
40
20
0
Dec-Feb
Mar-May
Jun-Aug
Sep-Nov
Dec-Feb
Manmade
Fruit
Arthropods
Birds
Other Mammals
Artiodactyls
Rodents
Coyote
Percent of Food Items
100
80
60
40
20
0
Dec-Feb*
Mar-May
Jun-Aug
Sep-Nov
Dec-Feb*
Marten
Percent of Food Items
100
80
60
40
20
0
Dec-Feb*
Mar-May
Jun-Aug
Sep-Nov
Dec-Feb*

Figure 9: Seasonal diet trends for Cascade red fox, based on data in Aubry (1983: Table 9). As with Figure 8, the same season is shown at the beginning and ending of the figure. In the winter and spring diet, note the low level of artiodactyls and the prominent role of "Other Mammals," composed almost exclusively of lagomorphs. This pattern is the opposite of that seen for the Lassen carnivores, where lagomorphs were absent and artiodactyls were prominent. Seasonal trends in niche breadth for Cascade red fox are also the opposite of those seen for Lassen carnivores, presumably due to the presence of lagomorphs as a critical winter food in the Cascades. "Rodents" = *Clethrionomys gapperi, Glaucomys sabrinus, Marmota caligata, Microtus* sp.*, Neotoma cinerea, Peromyscus maniculatus, Phenacomys intermedius, Spermophilus saturnatus, Tamias townsendii* and *Zapus trinotatus*. "Artiodactyls" = *Cervus elephus, Odocoileus hemionus* and *Oreamnos americanus*. "Other Mammals" = *Lepus americanus, Mustela frenata, Ochotona princeps, Scapanus* sp. and *Sorex* sp. "Fruits" = *Frageria* sp. and *Vaccinium* sp. For comparison with the Lassen carnivores, "Grass" food items were omitted and the proportions recalculated; these items represented 1.2% and 4.1% of total food items in summer and autumn, respectively. Niche calculations were based on the highest taxonomic level of food identification (26 categories), with "Unidentified Mammals" omitted and the proportions recalculated.

Figure 9:



Season:	Dec-Feb *	Mar-May	Jun-Aug	Sep-Nov	Dec-Feb *
Scats:	8	51	228	133	
Food Items:	10	67	394	220	
B_A:	0.127	0.280	0.300	0.392	

CHAPTER 2

DISTRIBUTION AND HABITAT ASSOCIATIONS OF RED FOX, COYOTE AND MARTEN IN THE LASSEN REGION AS INDICATED BY CAMERA TRAP SURVEYS

INTRODUCTION

A species' habitat associations are a fundamental factor of its ecology. Restricting or partitioning these associations is a primary means by which sympatric competitor species can coexist (Schoener 1974). Habitat partitioning may arise solely through exploitative competition, but is exacerbated by interference competition (Case and Gilpin 1974). Interspecific competition has been documented in a wide range of carnivore communities (Johnson et al. 1996, Johnson and Crabtree 1999, Palomares and Caro 1999). Along with the physical structure of the habitat, the strength of interspecific interactions is one of the primary factors shaping many mesocarnivore communities (Buskirk 1999).

Red fox (*Vulpes vulpes*) occur in a wide variety of habitats throughout their global range, including deserts, tundra, mountains, agricultural lands and urban areas (Lloyd 1980, Voigt 1987, Lariviere and Pasitschniak-Arts 1996). Their ability to thrive in such diverse habitats is a function of their intermediate body size, generalist body plan and adaptive dietary tolerances (Lloyd 1980, Buskirk 1999). Yet three North American red fox subspecies are apparently restricted to the subalpine meadows and parklands of the montane boreal forests, in marked departure with the generalist tendencies of other subspecies (Aubry 1983, Buskirk and Zielinski 2003). One of these mountain subspecies, the Sierra Nevada red fox (*V. v. necator*), is listed as a State Threatened species in California and is considered “critically endangered” (CDFG 2004). Its current distribution and habitat associations are unknown, as are many other fundamental aspects of its ecology.

The Lassen Peak region of northern California is within the historic range of the Sierra Nevada red fox (Grinnell et al. 1937, Schempf and White 1977, Zeiner et al. 1990). However, the exotic red fox (*V. vulpes* sp.) that are common at lower elevations throughout central and southern California may have dispersed into these higher elevations, possibly displacing the native red fox (Lewis et al. 1995, Lewis et al. 1999). Regardless of the status or origin of the Lassen region’s red fox population, documenting its local distribution and habitat affiliations is essential to its effective management. Also important is evidence of competition with other native carnivores, specifically coyote (*Canis latrans*) and marten (*Martes americana*), both of which are common in the Lassen region (Campbell and Perrine *in prep*).

Coyotes are one of the most widespread and adaptable terrestrial carnivores in North America (Bekoff and Gese 2003, Buskirk and Zielinski 2003). They evolved in the prairies and are believed to have become abundant in the western mountains only within the past 150 years (Nowak 1999, Buskirk et al. 2000, but see Sacks et al. 2004). Coyotes now inhabit a wide variety of habitat types throughout their range but apparently prefer shrublands, woodlands and other open habitats (Nowak 1999, Bekoff and Gese 2003). In Maine and the Yukon, coyotes selected for open habitats such as grasslands, alpine meadows and fens (Major and Sherburne 1987, Theberge and Wedeles 1989). Within California, coyotes occur in many habitats including deserts, grasslands, woodlands, forest and alpine areas (Grinnell et al. 1937, Ingles 1965, Zeiner et al. 1990).

Their ecology and habitat use has been well-studied at lower elevations throughout the state (e.g., Barrett 1983, Bowyer 1987, Cypher et al. 1996, Fedriani et al. 2000, Neale and Sacks 2001, Crooks 2002, Riley et al. 2003, Mitchell 2004). However, it is unclear whether the habitat associations documented in the lowlands of California and in eastern states extend to coyote populations in the Sierra Nevada and Cascade mountains. Few ecological studies (e.g., Hawthorne 1971, Shivik 1995, Shivik et al. 1996, 1997) have been conducted at high elevations (>1500 m) in the Sierra Nevada and Cascade ranges, and none have specifically addressed habitat use or interaction with sympatric carnivores.

Interspecific aggression between coyote and red fox has been well documented, with the larger-bodied coyote the dominant competitor (Johnson et al. 1996). Coyotes chase red foxes and may kill them (Dekker 1983, Sargeant and Allen 1989). Red foxes minimize such interactions by avoiding areas occupied by coyotes (Dekker 1983, Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989, Gosselink et al. 2003). In some areas, red fox live in the interstitial spaces between coyote territories (Sargeant et al. 1987, Harrison et al. 1989), but the complete exclusion of red fox from coyote-occupied areas is rare (Voigt and Earle 1983, Johnson and Crabtree 1999). None of these studies have been conducted in the Sierra Nevada or Cascades ranges, and it is unclear if these mountainous areas display the same patterns documented in the flatter agricultural lands of eastern and midwestern North America.

Marten habitat affiliations have been well-studied in recent decades (Buskirk and Powell 1994, Harrison et al. 2004). Their strong association with mature, structurally complex forests has led to their characterization as one of the most habitat-specialized mammals in North America (Buskirk and Powell 1994). Snags, downed logs, abundant low-level cover and other structural elements may be more important than species composition or forest type (Spencer et al. 1983, Buskirk and Powell 1994, Chapin et al. 1997, Krohn et al. 2004). Within California, marten occur throughout the higher elevations of the Sierra Nevada and southern Cascade ranges, as well as in the northern coastal forests (Grinnell et al. 1937, Ingles 1965, Kucera et al. 1995, Zielinski et al. 2001). The Lassen Park region has been characterized as "excellent marten habitat" due to its high elevations, mature red fir stands and long-term prohibition on fur trapping (Schempf and White 1977: 17).

Interactions between sympatric red fox and American marten have been poorly studied in North America. Several studies in northern Europe have examined habitat partitioning and competitive interactions between red fox and *M. martes* (Lindstrom 1989, Storch et al. 1990, Overskaug 2000), but similar studies are lacking in North America despite the extensive range overlap between *V. vulpes* and *M. americana.* Red fox occasionally kill marten and avoidance of red fox has been hypothesized as a factor behind marten habitat use (Drew and Bissonette 1997). In California, marten occur throughout the entire historic range of the Sierra Nevada red fox (Grinnell et al. 1937, Kucera et al. 1995) but there has been no examination of their interactions or habitat partitioning.

Camera traps are a useful tool for determining the distribution of medium- and large-size mammals among various habitat types (Kucera and Barrett 1993b, Foresman and Pearson 1998, Cutler and Swann 1999, Hilty and Merenlender 2004). They are especially valuable for monitoring rare or low density carnivores of conservation concern (Kucera and Barrett 1993a, Mace et al. 1994, Zielinski and Kucera 1995, Karanth and

Nichols 1998). Cameras can collect data on multiple sympatric species, allowing species co-occurrence patterns to be examined with little additional cost or effort.

Carnivore surveys utilizing baited camera traps have been conducted in the Lassen Peak region since 1992. The goal of this study was to use the data from these surveys to quantify the distribution and habitat utilization of red fox, coyote and marten in the Lassen Peak region. Specific research objectives included documenting where each species was detected, quantifying the time necessary for camera traps to detect them, identifying species-specific habitat attributes and testing for patterns of co-occurrence among these potential competitors. Quantification of mountain red fox habitat associations is an essential step in developing predictive models of their distribution within their historic range, thereby identifying high-priority areas for additional camera surveys. However, species interactions and sampling effort may also affect the observed pattern of habitat use. Such covariates are usually not available when developing predictive models to guide future surveys. Therefore, management of mountain red fox would benefit from comparing models that include these covariates against models that omit them.

METHODS

I pooled the results from multiple photostation surveys conducted in the Lassen region from 1992 through 2002, totaling 998 camera traps (Table 5). All the surveys used baited TrailMaster camera stations (Goodson and Associates, Lenexa, KS) and followed the same general protocol for surveying forest carnivores (Zielinski and Kucera 1995), although with slight differences in methodology such as the volume of bait used and the frequency of checking stations. I confirmed that all the camera traps were positioned so that all 3 target species could be detected. Many of the stations were established specifically to monitor for marten and red fox, usually in areas where timber harvest was planned (T. Rickman, Lassen National Forest, pers.com.). Because most stations were placed opportunistically, the resulting data are best characterized as “retrospective” (Carroll et al. 1999). Such data are useful for delineating trends and developing testable hypotheses, but they should be interpreted with caution because each camera may not be a statistically independent sample.

Station-level analyses

I pooled the camera trap data into a single database and then used the Animal Movement Extension (Hooge and Eichenlaub 1997) for ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA) to generate 95% minimum convex polygons (MCPs) based upon the detection sites for each species. I determined the elevation and vegetation characteristics of each camera site using an existing 30 m digital elevation model and the US Forest Service “Existing Vegetation 1997” data layer (US Forest Service, Sacramento, CA, unpublished data). Vegetation classifications were based upon the California Wildlife Habitat Relationships (CWHR) system (Mayer and Laudenslayer 1988). Elevation and vegetation classifications were not ground-truthed. To be conservative, I converted individual CWHR vegetation types to general cover type descriptors for most analyses (Table 6). I used chi-square analysis and follow-up tests (Neu et al. 1974, Alldredge and Ratti 1992) to identify habitat selection among these cover types, using an alpha level of 0.10 and Bonferroni corrections to maintain the family alpha level for each comparison.

For each camera station with nightly records of detection (n = 134), I calculated latency to first detection ("LFD", Zielinski and Stauffer 1996) for each of the 3 target species for each station where they were detected. LFD is simply the number of survey nights needed to first detect a species at a given site. However, LFD does not provide any information on the proportion of survey nights that the target species was detected at a site. Therefore, I define a species' "return ratio" (R_S) as:

$$R_S = \frac{(D_S - 1)}{(A - 1)}$$

where D_S is the number of sampling nights that species *S* was detected, and A is the total number of sampling nights, for each station detecting species *S*. Return ratio is a measure of the proportion of total survey nights the target was detected, not including the night of the first detection; it is an indicator of the target's proclivity to return to a site. The subscript differentiates the return ratio for species (R_S) from that for individually marked animals (R_I). Return ratio was calculated only for stations with >9 survey nights (n = 127) to prevent the non-representative extreme values that could occur from stations with fewer nights.

Seasonal differences in habitat use have been documented for marten (Buskirk and Powell 1994) and suggested for red fox and coyote in the Sierra Nevada (Grinnell et al. 1937). To incorporate such seasonal trends, I classified camera traps by their dates of operation. "Summer" stations (n = 380) operated between 1 May and 31 October and "winter" stations (n = 463) operated between 1 November and 30 April; these dates correspond to the general pattern of snow-free ("summer") and snowy ("winter") months in the study site. Stations that began in summer but continued into winter (n = 100), or vice versa (n = 55), were excluded from the seasonal analysis because their results could not be allocated to only 1 season.

Seasonal Habitat Models

To reduce the pseudoreplication (Hurlbert 1984) in the camera data I placed a 2.6 km^2 (1 mi^2) grid over the survey area, with each cell indicating the results of the stations within it. Species detections at the grid cell level were binomial: the species was "detected" in a cell if any cameras within that cell detected the species, and it was "not detected" if none of the cameras within the cell detected it. Non-detections at cameras could indicate that the species was not present or could be a failure to detect the species. Therefore, non-detections were made more robust by including only those cameras that were active and operational during the entire 28+ night survey period recommended for forest carnivores (Zielinski and Kucera 1995); i.e., non-detection results were included only from cameras that were operational for >27 survey nights and that detected at least 1 species (of any taxon, not limited to the 3 target carnivores).

I calculated elevation, cover type, forest structure and highway density attributes for each cell, along with survey effort and species co-occurrence variables (Table 7). For each of the 6 scenarios (3 species * 2 seasons), I first conducted a univariate analysis of each variable (using the Wilcoxan rank-sum test for continuous variables and the chi-square test for categorical variables) to determine whether the values differed between cells that did and did not detect the target species. I then constructed a multivariate logistic regression model comprised of landscape-level variables: elevation, vegetation and highway attributes. Interactions and higher-order terms were not included due to the preliminary and exploratory nature of the analysis (Burnham and Anderson 2002) and because models with such terms were frequently unstable. Unstable variables and those with correlation $|r| > 0.7$ were not included in the starting models (Hosmer and Lemeshow 2000). I then removed terms from the global model using a backward stepwise approach until all remaining terms were significant at alpha = 0.10 using the Wald test (Hosmer and Lemeshow 2000). For each term retained in the final model, I exponentiated the parameter estimate and the 95% confidence interval to generate an odds ratio, which indicates the change in the odds of detecting the target carnivore per unit change in the covariate (Hosmer and Lemeshow 2000).

To determine whether the addition of species co-occurrence and sampling effort terms improved the fit compared to the landscape-only model resulting from the stepwise regression, I used an information theoretic approach (Burnham and Anderson 2002). Burnham and Anderson (2002) caution against mixing frequentist and information theoretic paradigms in a single analysis. Yet in this case the two paradigms are not mixed; rather, each is used within its own appropriate context. The information theoretic approach is not suitable for analyzing all possible model combinations, for which the stepwise regression approach has been widely used, albeit in the absence of robust statistical theory (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). But the information theoretic approach is appropriate for direct comparisons among a limited set of *a priori* models; in this case, between the models that did and did not include the species co-occurrence and sampling effort terms. For comparison, univariate models of species co-occurrence, sampling effort and elevation were also included. The model with the lowest AICc value was considered the most parsimonious (Burnham and Anderson 2002). I generated odds ratios for the terms in the most parsimonious model and compared them to the odds ratios from the landscape-only model.

The grid-cell data used in the above analyses would not detect fine-scale patterns of pairwise species association within cells where both species were detected. Although both species might occupy the same cell, they might be positively or negatively correlated at the scale of the individual camera trap. To identify such fine-scale patterns, I used Fisher's exact test (2-tailed) on the individual camera results within cells where both species were detected.

RESULTS

The 998 camera stations were distributed widely throughout Lassen Volcanic National Park and the Lassen National Forest (Figure 10), although coverage was spatially and temporally uneven (Table 5). Sampling effort within Lassen Park varied greatly, with numerous stations along the main road and few in the eastern half of the park. Sampling effort was also high along roads in the southern and eastern portions of the Lassen National Forest. Forest areas to the southwest of Lassen Park and to the east of the Caribou Wilderness were heavily sampled, while the northern extremes of the Forest were lightly sampled. Mean (± SD) elevation of camera traps was 1749.7 ± 256.4 m (range: 798-2612 m). Few cameras were >5 km from their nearest neighbor, the recommended distance to ensure independence of marten detections (Zielinski and Stauffer 1996). Several radio-collared red foxes were detected at multiple sites, indicating that camera trap results were not independent for red fox and were likely not independent for coyote or marten either.

Red fox were detected at the fewest stations (53) and had the smallest areal extent as indicated by their 95% MCP (Figure 10). Median elevation for these stations was 2000 m (range: 1379-2612 m). Marten were detected at more stations (132) across a larger area, and coyotes were detected at the most stations (159) across roughly the entire study area (Figure 10). Median elevations for marten and coyote detections were 1959 m (range: 1305-2612 m) and 1718 m (range: 929-2469 m), respectively. The 95% MCPs for the 3 carnivores were roughly concentric, centering upon the southeastern portion of Lassen Volcanic National Park (Figure 10).

Red fox were detected in 9 of 18 CWHR community types sampled, while coyote and marten were detected in 10 and 13 types, respectively (Table 8). Within the 8 community types receiving ≥10 camera stations, red fox were detected at 7 and coyote and marten at all 8. None of the 41 cameras in Sagebrush habitat detected red fox. For community types with <10 stations, there was a tendency for coyotes to be detected in different community types than red fox or marten. Of the 3 camera traps in Barren areas, 2 detected marten and 1 detected red fox.

When I consolidated the CWHR communities into general cover types, I pooled the Hardwood and Herbaceous community types into a single category because they received comparatively few cameras (0.7% and 1.4% of camera sites, respectively), and I eliminated Barren altogether (0.3% of sites). Also, I split the Conifer community type (88.8% of sites) into 2 groups: High-elevation Conifer (consisting Red Fir and Subalpine Conifer; 7.7% of sites) and Mid-elevation Conifer (all other CWHR Conifer types in the study area; 81.1% of sites). Chi-square tests indicated significant selection among these 4 cover types by red fox (χ^2 = 18.17, 3 df, p = 0.004) and marten (χ^2 = 58.71, 3 df, p < 0.001) but not coyote (χ^2 = 4.27, 3 df, p = 0.234). Follow-up tests (Table 9) indicated that both marten and red fox avoided Mid-elevation Conifer community types and selected for High-elevation Conifer community types.

Species' responses to cameras

The median number of nights required to detect red fox and marten was 2 to 3, but detection of coyote required a median of 12 nights (Table 10). Seasonal differences in LFD were not significant (Wilcoxan rank-sum test; red fox: Z = -0.09, p = 0.929; marten: Z = -0.89, p = 0.375; coyote: Z = 0.36, p = 0.716), so I pooled the summer and winter data for between-species comparisons. LFD for coyote was greater than for red fox (Z = 2.49, p = 0.013) and for marten (Z = 3.21, p = 0.001), but red fox and marten did not differ (Z = 0.03, p = 0.974). All red fox detections occurred in <28 nights regardless of season, but at several summer stations the first detection of marten or coyote occurred after the 28th survey night (Table 10). These species would not have been detected at these sites if the camera trap had been removed after 28 nights.

Coyote were detected on only a single sampling night at 17 of 19 cameras (89.5%) resulting in a return ratio of 0.0 for these sites; the remaining 2 stations each detected coyote on only 2 nights. In contrast, red fox and marten were usually detected on multiple nights, including several stations where detections occurred on >50% of the survey nights (Table 10). Seasonal differences in return ratio were not significant (Wilcoxan rank-sum test; red fox: Z = -0.11, p = 0.916; marten: Z = 0.98, p = 0.329;

coyote: Z = 0.84, p = 0.399), so summer and winter data were pooled (n = 111) for between-species comparisons. Return ratio for coyotes ratio was significantly lower than for red fox (Z = -3.88, p < 0.001) or marten (Z = -4.42, p <0.001), and red fox and marten were not significantly different (Z = -0.87, p = 0.382).

Modeling Occurrence in Relation to Landscape Variables

The 998 camera stations occurred in 668 of the 2.6 km^2 (1 mi^2) grid cells. Retaining only the cameras that either detected the target species, or that were operational for >27 active nights and detected ≥1 species, resulted in 145 summer and 301 winter cells (Figure 11). Few cells (n = 24) were sampled in both summer and winter. Summer sampling was sparse, with cameras concentrated in and around the western half of Lassen Volcanic National Park and the national forest lands east and north of the Park. Red fox were detected in 11 (7.5%) summer cells, all of which were within or adjacent to Lassen Park (Figure 12). Marten were detected in 24 (16.2%) summer cells, primarily within Lassen Park and the nearby Caribou and Thousand Lakes wilderness areas. In contrast, the 21 (14.2%) summer cells detecting coyote were widely distributed throughout the study area. Winter sampling was more comprehensive, with increased coverage of the southern and north-eastern portions of the Lassen National Forest. Red fox were detected in 25 (8.3%) winter cells (Figure 13). In addition to areas within Lassen Park, red fox were detected on national forest lands several miles to the south and east of the Park. Marten were detected in 71 (23.6%) cells across a wider area than in summer. Marten were detected in virtually every sampled cell in or immediately adjacent to Lassen Park and the Caribou Wilderness, but were also widely detected southwest of Lassen Park and at the southern extent of the National Forest where they were not detected in summer. As in summer, coyote were detected throughout the study area, in 93 (30.9%) winter-surveyed cells. They were widely detected throughout the eastern half of the forest but at only a few sites within Lassen Park and the Caribou Wilderness.

Univariate analysis

In a univariate context, many of the landscape attributes of the 2.6 km² cells were significantly related to the detection of the target carnivores (Table 11). Red fox and marten were positively associated with mean elevation in both summer and winter, but for coyote the association was negative in winter and not significant in summer. Standard deviation of elevation was not significant for all 3 carnivores in winter, but red fox and marten both had positive associations in summer. CONIFER was the primary cover type within the cells in both summer and winter. All 3 species were negatively associated with it in summer but had no significant association in winter. SHRUB was the second most prominent cover type in all cells except red fox in summer, when it was surpassed by BARREN. Although SHRUB was prominent in cells, it was significant only for marten in winter (negative association) and coyote in summer (positive association). Detection of marten and red fox was positively associated with BARREN cover in both seasons. HARDWOOD, HERBACEOUS and OTHER cover were minor on average, but abundant in occasional cells. Detection of the carnivores was positively associated with HARDWOOD cover in all scenarios except for coyote in summer. In contrast, coyote in summer had a positive association with OTHER cover, which was not significant in any other scenarios. HERBACEOUS cover was not significant in any scenario.

Of the 6 forest structure categories assessed, mid-sized closed-canopy forest (34MD) was the most abundant within the sampled cells (Table 11). All 3 species were negatively associated with this structure type in summer, but in winter the association was not significant. The forest area with trees <15cm DBH, regardless of canopy closure (i.e., PCT12SP and PCT12MD), was miniscule (<3.5%) in all scenarios, and was significantly associated only with coyote in winter (negative association). Mature closed-canopy forest (56MD) was also a minor (<7%) cell component, but it was positively associated with red fox and marten detections in both seasons. The remaining forest structure types varied in association by species and seasons. Mature open-canopy forest (56SP) was positively associated with detection of red fox in winter and marten in both seasons. Mid-sized open-canopy forest (34SP) was common in most cells but was significant only for marten in winter (negative association). Detection of the target carnivores was positively associated with highways in all scenarios except for coyote in summer.

Stepwise Multivariate Analysis

Many of the landscape variables were significantly correlated (Table 12). PCTCON was dropped from all starting models due to its high correlation ($|r| > 0.7$) with PCTSHB and PCT34MD. PCT12MD or PCT12SP was unstable in most analyses due to its absence in most cells where the target carnivores were detected, and was therefore dropped prior to the backward stepwise analysis. A linear combination of the remaining

13 or 14 landscape-level variables constituted the starting global model. Due to the number of significant correlations among the variables, the final multivariate model contained few of the variables that were significant in a univariate context, and included some that were not significant in the univariate context.

In summer, the final red fox landscape model retained positive associations with mean elevation and highways, and negative associations with HERBACEOUS and SHRUB cover (Table 13). Marten detections were positively associated with mean elevation and negatively associated with the standard deviation of elevation and with mid-sized and mature closed-canopy forest (34MD and 56MD). Coyote detections were negatively associated with the standard deviation of elevation and with mid-sized closed canopy forest. The final multivariate landscape models explained much more of the variability in the red fox ($R^2 = 0.58$) and marten ($R^2 = 0.61$) detections than for coyote ($R^2 = 0.09$).

In winter, red fox detections were positively associated with mean elevation, highways and mature closed-canopy forest. The marten model retained these same associations plus a negative association with the standard deviation of elevation. The amount of variability explained by these winter landscape models (red fox $R^2 = 0.27$, marten $R^2 = 0.12$) was considerably less than in summer. The coyote model retained many terms: a negative association with mean elevation and positive associations with BARREN, HERBACEOUS, SHRUB, and OTHER cover, as well as mature closed canopy forest, mid-sized open-canopy and mid-sized closed canopy forest. Despite the number of terms in the model, it explained little of the variability in the data ($R^2 = 0.08$).

Incorporating Species Co-Occurrence and Sampling Effort

In summer, 13 cells (9.0%) detected >1 of the target carnivores. Red fox and coyote were detected in 2 cells, red fox and marten in 6 cells, and coyote and marten in 3 cells; an additional 2 cells contained detections of all 3 species (Figure 12). In winter, 24 cells (7.8%) detected >1 of the target carnivores. Red fox and coyote were detected in 4 cells, red fox and marten in 7 cells, and coyote and marten in 8 cells; an additional 5 cells contained detections of all 3 species (Figure 13). In both seasons, the least common pairwise association at the grid-cell scale was red fox and coyote.

Whether the detection of one species within a cell was significantly related to the detection of a second species depended upon the species pair and the season. Detection of red fox was positively associated with the detection of marten in both summer (χ^2 test; 1 df; $p < 0.001$) and winter ($p < 0.001$), and was positively associated with the detection of coyote in summer ($p = 0.008$) but not winter ($p = 0.657$). Detection of marten in a cell was negatively associated with the detection of coyotes in winter ($p = 0.008$) but not summer ($p = 0.116$).

The number of cameras within a grid cell provided a measure of sampling effort, and averaged 1.6 (range: 1-9) cameras per cell in summer and 1.3 (range: 1-9) cameras per cell in winter. In a univariate context, the number of cameras within the cell was positively associated with red fox detection in both summer and winter, but was not significant for marten or coyote (Table 11).

The addition of species co-occurrence and effort terms to the multivariate landscape models improved the model fit for both canids but not for marten (Table 14). In summer, the most parsimonious red fox model included the landscape terms along with COYOTE; adding CAMERAS to this model caused a slight decrease in overall fit. Likewise, the addition of REDFOX improved the fit of the summer coyote model. In winter, the most parsimonious red fox model included CAMERAS along with the landscape terms, and the further addition of species co-occurrences caused a reduction in fit. In contrast, inclusion of effort and species co-occurrence terms reduced the overall fit of the marten models; the landscape model was the most parsimonious in both summer and winter. The best model for coyote detections in winter included only mean elevation, confirming that the landscape model was over-parameterized.

Regardless of season, the addition of sampling effort and species co-occurrence variables resulted in a substantial improvement (ΔAICc > 2) in model fit only for red fox. For marten and coyote, incorporating the detection of red fox and the number of cameras resulted in models that had comparable fit (ΔAICc < 2) to the landscape-only model resulting from the stepwise regression. Models consisting solely of effort and species co-occurrence terms generally had far poorer fit than models that also included landscape terms. This pattern was most pronounced for marten, where removal of the landscape terms resulted in a fit reduction of >50 AICc units in both seasons (Table 14). As in the landscape-only analysis, more of the data variance was explained for marten and red fox than for coyote, and for summer detections than for winter detections.

At the scale of individual camera stations within the grid cells where both species of a pair were detected, there was no significant association between detection of coyote and red fox or coyote and marten in either season (Table 16). Detections of red fox and marten at the same camera were not significantly associated in summer. In winter, however, there was a positive association between red fox and marten; stations detecting one species were more likely to detect the other as well.

DISCUSSION

The goal of this study was to use data from camera trap surveys to quantify distribution, habitat associations and species co-occurrence relationships for red fox, marten and coyote in the Lassen region of northern California. Multiple lines of evidence indicate that red fox had the most restricted distribution of the 3 target species. Red fox were detected at fewer stations, within fewer habitat types, and across a smaller area than either marten or coyote. Red fox were detected only within Lassen Volcanic National Park and its immediate surroundings, which contain the highest elevations in the region. In contrast, coyote detections were widely distributed across the entire study site. Marten detections were intermediate in their extent, with seasonal patterns similar to red fox but not as highly restricted in vegetation type or area.

Red fox and marten were readily detected by camera traps. Median detection time for these species was 3 nights regardless of season, and each species was usually detected on multiple nights per site. Previous studies have found that marten are usually detected by camera traps within 8 to 14 nights (Jones and Raphael 1993, Zielinski and Kucera 1995, Foresman and Pearson 1998). No prior studies have quantified mountain red fox response to camera stations. These results indicate that standard photostation methods for other forest carnivores are sufficient to detect mountain red fox. All stations detecting red fox did so within 28 nights, the recommended length for forest carnivore surveys (Zielinski and Kucera 1995). However, >28 survey nights were required to detect marten and coyote at several stations. Had the stations been operated for only 28 nights, as suggested by the protocol, these species would not have been detected at these stations. Median detection time for coyote was 12 nights, and coyotes were rarely photographed >1 night at the same station. These results are similar to those from the Dye Creek Preserve in the foothills of northern California, where coyotes were first detected at unbaited camera stations primarily during the second week of operation, usually after 10 to 12 sampling nights (E. Sequin, unpublished data). Coyotes, especially those maintaining territories, may actively avoid camera stations (Sequin et al. 2003). Automatic telemetry recorders at Dye Creek and snow tracks at Lassen indicated that coyotes approached some camera stations without being photographed, although this usually occurred after the coyote had previously been detected at the site. Avoidance of camera stations may make photographic mark-recapture estimates impractical for coyotes, but their use for red fox and marten appears plausible.

My analyses implicitly assume a detection probability for each species of 1.0 at camera stations operating for the entire 28-night survey period. The data suggest that this assumption may have been violated, and that coyote detection probability may have been substantially lower than that of red fox or marten. Unequal detection probabilities among species may complicate deeper analysis of camera station data, and a more thorough investigation of species-specific detection probabilities at camera stations is warranted.

Habitat Associations

Ascertaining habitat associations from the camera trap data was complicated by multiple factors. Due to the lack of a consistent underlying sampling approach, camera trap results were not independent and sampling was likely spatially and temporally biased. Conversion to a grid-cell approach reduced but did not eliminate this pseudoreplication and bias. Additionally, local vegetation attributes were not measured at most camera sites. Vegetation attributes were assigned to each site based upon existing GIS layers, but these layers were not fully ground-truthed and did not contain some habitat elements that are known to be important, such as quantitative assessment of snags and coarse woody debris for marten. Furthermore, the 2.6 km^2 grid cell approach I used may not contain the necessary detail at the appropriate scale to fully represent habitat selection by the target species. Carnivores may assess and select habitat based upon multiple spatial scales (Johnson 1980, Minta et al. 1999), and interaction between adjacent habitat types may also be important. Despite these complications, the camera traps represent the most comprehensive sampling of the Lassen region to date. Mountain red fox ecology is poorly known and these data provide the best available information on their distribution and habitat associations. Previous studies of marten and coyote distribution and habitat associations provide important comparisons with the results from these camera surveys. The conclusions and models resulting from this analysis should be viewed as hypotheses that warrant testing with new data collected with a statistically-robust sampling design.

Carnivores in the Lassen region appear stratified by elevation. Detections of red fox and marten were centered upon the highest elevation regions of the study area, whereas coyote were detected throughout the lower elevations, especially in winter (Figure 10). Elevation was the best univariate predictor of red fox in summer and marten in both seasons, and a positive association with elevation was retained in the multivariate models for both species in both seasons. In summer, an increase of 100 m caused the odds of detecting red fox to increase by 4.3 times and the odds of detecting marten to increase by 5.2 times (Tables 13, 15). Neither species was detected below 1300 m. This is consistent with previous reports that have found red fox and marten only at high elevations in the Sierra Nevada (Grinnell et al. 1937, Sumner and Dixon 1953, Ingles 1965, Schempf and White 1977). In contrast, the association between coyote detections and elevation depended upon the season. In summer, coyote were detected at all elevations, but in winter the most parsimonious model consisted solely of a negative association with elevation. On average, each 100 m *decrease* in elevation caused the odds of detecting coyote to *increase* by 1.3 times (Table 15). Coyote apparently use high-elevation habitats in the summer but do not remain there during winter, presumably due to deep snow (see below). The unevenness of the terrain, as indicated by the standard deviation of elevation, was not significant in a univariate context in most scenarios but became significant in the final multivariate models for marten (negative association, both seasons) and coyote (negative association in summer).

Red fox detections were disproportionately abundant at cameras in high-elevation conifer community types and were under-represented at cameras in mid-elevation conifer communities. They also tended to be detected at cameras in Barren areas such as talus slopes. No forest structure terms were retained in the summer multiple logistic regression model, but mature closed-canopy forest was a significant predictor in winter. On average, a 1% increase in the extent of mature closed canopy forest caused a 3.5% increase in the odds of detecting red fox (Table 15). In Washington, mountain red fox did not inhabit the dense mid-elevation western hemlock (*Tsuga heterophylla*) and

Douglas fir (*Pseudotsuga menzeisii*) forest, but were found in the drier, more open grand fir (*Abies grandii*) and ponderosa pine (*Pinus ponderosa*) forest on the eastern slopes of the Cascade Range (Aubry 1984). Use of mature upland conifer forest by Lassen red fox suggests that elevation, not structure, may be the ultimate cause of such patterns. It remains unclear if such forests act as barriers to red fox movement and dispersal, as hypothesized for the Cascades (Aubry 1984).

Red fox association with shrub communities depended on elevation and the scale of the analysis. Red fox detections appeared disproportionately abundant at cameras in Montane Chaparral, but none were detected in lower elevation Sagebrush despite extensive sampling. When camera results were consolidated across 2.6 km^2 grid cells, shrub cover was not significantly different in cells where red fox were and were not detected (Table 11). But the most parsimonious multiple regression model for summer contained a negative association with Shrub cover (Table 14). Consolidating high and low elevation shrub communities into a single variable probably obscured finer-scale patterns of association. Other studies have documented red fox preferentially using shrub communities (Schofield 1960, Jones and Theberge 1982, Halpin and Bissonette 1988, Theberge and Wedeles 1989). Although the use of Herbaceous areas was not significant in a univariate context, a strong negative relationship was retained in the summer multivariate model. Barren areas were strongly significant in a univariate context, reflecting the foxes' use of talus slopes and areas above treeline. The absence of this term in the multivariate model is likely due to its strong correlation with elevation.

Multiple studies have shown that marten are closely associated with mature closed-canopy conifer forest (Buskirk and Powell 1994). In the northern Sierra Nevada range, marten selected riparian lodgepole pine and red fir associations and avoided brush, mixed conifer and Jeffrey pine associations (Spencer et al. 1983). Marten sightings from the northern Sierra Nevada occurred primarily in fir, lodgepole and mixed conifer forest (Schempf and White 1977). The Lassen cameras yielded similar findings, with marten detected disproportionately in Red Fir, Sub-Alpine Conifer and Lodgepole Pine community types and less than expected in Sagebrush, Sierran Mixed Conifer and East-Side Pine community types. Like the red fox, marten selected for high-elevation forest types and avoided mid-elevation forests. They had no significant univariate or multivariate association with Herbaceous cover. Although marten may avoid open meadows (Hargis and McCullough 1984), they commonly use talus slopes and boulder fields in alpine areas, probably due to the high availability of prey and cover (Grinnell et al. 1937, Ingles 1965, Streeter 1968). Talus slopes were included in the Barren cover type in this analysis, which was significant at the camera- and grid-cell level. As with red fox, the absence of Barren cover in the final multivariate model is presumably due to its strong positive correlation with elevation (Table 12).

For marten, the species composition of forests may be less important than the physical structure, especially in regard to canopy closure and coarse woody debris (Buskirk and Powell 1994, Chapin et al. 1997, Krohn et al. 2004). I did not include woody debris as a variable but it is strongly associated with mature conifer stands (Buskirk and Powell 1994, Hemstrom 2003). Marten may require a minimum of 30% canopy cover in conifer forests (Thompson and Harestad 1994). In the northern Sierra Nevada, marten preferred forest stands with 40-60% canopy closure and avoided stands with <30% canopy closure (Spencer et al. 1983). Again, results from the Lassen cameras were largely consistent with these findings. The multivariate logistic regression model for marten in winter included a positive association with mature forest with >40% canopy cover (56MD). In the summer, however, the association was positive in a univariate context (Table 11) but negative in a multivariate context (Table 13). This may be a consequence of the 0.10 alpha level chosen for the stepwise analysis; had alpha been set at 0.05, the negative association with PCT56MD would not have been retained in the summer model. The association may also reflect the presence of marten in the more open hemlock and red-fir forests at higher elevation as opposed to the more dense mixed-conifer forest at lower elevations.

In contrast to red fox and marten, coyotes were detected in a wide variety of habitat types. At both the camera and grid cell levels of analysis, vegetation type was a poor predictor of coyote detection. This is consistent with their characterization as highly adaptable habitat generalists even in montane areas (Ingles 1965, Johnson and Crabtree 1999, Buskirk and Zielinski 2003). As comparatively large carnivores, coyotes have fewer enemies and dominant competitors than smaller species such as red fox and marten, resulting in less need for protective cover and reduced associations with specific cover types (Buskirk 1999). For example, coyote in the Santa Monica Mountains of southern California were captured in virtually every habitat type in the study area, including chaparral, sage scrub, grassland, oak, walnut, riparian and human-developed areas (Fedriani et al. 2000). In some areas coyotes prefer open and shrub communities, presumably due to the higher availability of preferred prey (Major and Sherburne 1987, Theberge and Wedeles 1989, Holzman et al. 1992). However, coyotes in Oregon’s Coast Range used forested and open habitats in proportion to their availability (Witmer and

Decalesta 1986). For the Lassen coyotes, the best univariate predictor was percent conifer cover (negative correlation), but this term was removed prior to the stepwise analysis in all scenarios because of high correlation with other terms. The only vegetation attribute retained in the final coyote models was a slight negative association with mid-sized closed-canopy forest in summer (Table 15). Inclusion of other vegetative terms in the stepwise regression produced a model that was over-parameterized and still had poor fit to the data (Table 14).

Seasonal Differences

The distribution of camera sampling in the Lassen region varied seasonally. But even accounting for the uneven sampling effort, both marten and red fox were detected across a larger geographic area in winter than in summer (Figures 12 and 13). Several mechanisms could generate such patterns, including seasonal range expansion, seasonal differences in detectability or a source-sink dynamic whereby animals dispersing to lower elevations in autumn fail to persist there through the spring. Historical reports suggest that Sierra Nevada red fox descend to lower elevations (1400-2000 m) during the winter and then return to higher elevations for the summer (Grinnell et al. 1937). Radio-collared red foxes in the Lassen area confirm this pattern (see Chapter 4). Detection of several collared foxes at camera traps indicated that the same individuals residing at high elevations in the western half of Lassen Park in the summer were also frequenting mid-elevation sites south and east of the Park in winter. Foxes descend to lower elevations in winter presumably due to heavy snows at higher elevations; why they do not remain at these lower elevations in the spring is unclear, but may relate to the presence of coyotes (see below). This is the only red fox population in North America with a seasonal elevational migration, but a similar pattern has been documented for red fox in the mountains of central Asia (Heptner et al. 1998). Cascade red fox showed no such seasonal migration although their home ranges expanded in winter (Aubry 1983).

The apparent seasonal expansion pattern for marten was more dramatic and less easily explained due to the lack of marked individuals. Sampling in the southern and eastern portions of the Lassen National Forest was less intensive in summer than in winter, but it is surprising that not a single summer camera in these areas detected marten outside of designated wilderness areas. This pattern is consistent with the results of a recent regional carnivore survey using track plates and baited cameras, which detected marten only within wilderness areas of the Lassen region during summer (Zielinski et al. *in press*). In some areas marten may not be attracted to camera stations or track plates in summer due to the availability of alternate prey (Bull et al. 1992). However, marten LFD and return ratio for Lassen cameras did not differ between summer and winter as would be expected if detectability differed by season. Unfortunately, LFD and return ratio data were not available for most of the cameras within the marten's apparent winter range expansion, and such data by definition were not available from cameras where marten were not detected. Some grid cells in the southern portion of the Lassen National Forest received considerably more camera effort in summer than in winter, and yet marten were detected there only in winter. The possibility that marten may be dispersing to these areas and then not persisting seems unlikely but cannot be discounted without further investigation using radio-collared individuals. If detectability or habitat use varies by season, as suggested by the Lassen data, then habitat models based solely upon summer sampling may have significant bias.

In this study, the presence of mature closed-canopy forest was a significant predictor for both red fox and marten in winter but not summer. In winter, marten are more strongly associated with late-successional conifer forests and reduce their use of open areas (Spencer et al. 1983, Hargis and McCullough 1984, Buskirk and Powell 1994). Forested areas have more downed woody debris, which provides important access to subnivean prey (Hargis and McCullough 1984, Buskirk and Powell 1994). Snow tracking suggests that Lassen red fox use forests extensively during winter and prefer these areas to open or shrub communities (Benson et al. 2005). I observed numerous instances of red fox day rests in the tentlike cavities formed by snow-laden red fir boughs; marten also use such areas for cover (Hargis and McCullough 1984). In the mountains of western Switzerland, red fox used forests and wooded areas more often during snow cover, and reduced their use of grasslands (Weber and Meia 1996). In Maine, red fox avoided hardwood stands in winter, where snow depth was deeper and more powdery, and selected for softwood stands and open areas, where snow was shallower and more often covered with an icy crust (Halpin and Bissonette 1988). The softwood stands also had higher densities of snowshoe hare (*Lepus americanus*), a critical winter food (Halpin and Bissonette 1988). Snowshoe hare habitat affiliations in the Lassen region have not been studied, but they were virtually absent from the winter diets of all 3 target carnivores (see Chapter 1).

Deep and persistent snow packs are common in the upper montane and subalpine forests of northern California and are strongly correlated with carnivore distribution and abundance (Krohn et al. 1997, Buskirk and Zielinski 2003, Hemstrom 2003). The presence of snow is likely a primary factor behind the seasonal difference in habitat associations documented in this study. Deep snow increases the energetic costs of movement and changes the relative availability of prey (Murray and Lariviere 2002, Buskirk and Zielinski 2003). These factors may cause habitat preferences to change, especially if certain habitat types are usable only during summer. Marten are the most snow-adapted of the 3 carnivores in this study. Their lighter foot-loading and subnivean abilities give marten a competitive advantage in areas with persistent, deep soft snows (Buskirk et al. 2000, Krohn et al. 2004). Other carnivores lacking these adaptations would be expected to migrate seasonally to lower elevations with less snow or to south-facing slopes where snow was crusted (Buskirk and Zielinski 2003). As mentioned above, cameras and telemetry confirm that Lassen red foxes do conduct such a seasonal elevational migration.

Coyotes are disproportionately affected by snow due to their greater mass and higher foot loading (Krohn et al. 2004). They sink into soft snow, resulting in increased energy expenditures and reduced travel speed (Crete and Lariviere 2003). In western North America the presence of deep soft snow can create elevational separation between coyotes and more snow-adapted carnivores such as lynx (Buskirk et al. 2000). Such separation is not absolute and in some areas coyotes may be common above 2450 m (8000 ft) in winter (Byrne 1998 in Buskirk et al. 1999), but this seems to be the exception rather than the rule. Coyotes in the Sierra Nevada occur up to 3950 m (13,000 ft) during summer but are forced to lower elevations by heavy winter snows, at least in some areas (Grinnell et al. 1937, Sumner and Dixon 1953). A similar pattern has been reported for coyotes in the Cascades (Bond 1939). Such a pattern would be consistent with the fact that in winter, the best model of coyote detection consisted solely of elevation, which is highly correlated with snow depth. Surveys in Yellowstone National Park indicate that only transitory coyotes use areas above 2450 m in winter. Once the snows begin to melt in early spring, subadults and transients move to these higher elevations and establish territories, but they apparently do not remain through the winter (Crabtree and Sheldon 1999). The coyotes documented at high elevations in the Lassen region during summer may also be juvenile and transients. These non-territorial coyotes are more likely to be detected by camera stations (Sequin et al. 2003). They also do not howl (Gese and Ruff 1998), and during several summers of nocturnal fieldwork I never heard coyote howls above 1800 m elevation, although they were common at lower elevations. A formal test of this hypothesis would require monitoring marked individuals, preferably of known social status, across several seasons.

Species co-occurrence

Red fox and marten were positively associated with each other in both summer and winter. In summer, this association may simply be due to similar habitat use patterns by these species. In winter, however, individual camera stations were more likely to detect both species or neither species rather than just one species of the pair. This likely reflects the importance of winter scavenging by both species. Easily-accessible winter bait would attract both species, assuming that both were present in the local area. In winter, the detection of marten in a cell was the best univariate predictor of whether red fox would be detected in that cell. Interactions and habitat associations between sympatric red fox and marten populations have been poorly examined in North America.

In northern Europe, where the range of red fox and pine marten (*M. martes*) overlap extensively, dietary overlap has received far more attention than sympatric habitat associations. In general, the red fox inhabits grasslands, woodlands and clearcuts, while *M. martes* is more restricted to mature boreal forests (Lindstrom 1989, Storch et al. 1990, Overskaug 2000). Their interspecific interactions have been poorly studied, although the red fox is an occasional predator of *M. martes* and is hypothesized to be a primary factor behind their avoidance of clear cuts, meadows and other open areas (Lindstrom 1989, Brainerd et al. 1994, Overskaug 2000). A similar relationship between American marten and red fox has been suggested (Thompson and Harestad 1994, Drew and Bissonette 1997) but empirical data are lacking. If such a pattern of antagonism and avoidance were occurring at Lassen, it was at a scale not discernable by this analysis.

Surprisingly, red fox and coyote were positively associated with each other in summer. This association remained in the most parsimonious multivariate model for each species even after controlling for elevation and vegetation characteristics. Cells where coyote were detected were 5 times as likely to detect red fox, and cells where red fox were detected were 2.2 times as likely to detect coyote (Table 15). However, at the scale of individual cameras within the grids, coyote and red fox detections were not significantly associated. These patterns may be due to the proximity of roads, which both species often used at high elevations (see below). Numerous previous studies have documented negative associations between coyotes and red fox, with particular emphasis upon coyotes excluding red fox from habitats that would otherwise be used, especially in winter. In southwest Yukon, coyotes selected open communities (e.g., grasslands, wet meadows and fens) and red fox selected brush communities (Theberge and Wedeles

1989). Coyotes in western Maine used open habitats and softwood-dominated forest types while red fox used hardwood forests and avoided open habitats (Major and Sherburne 1987). Areas avoided by coyotes may become red fox refugia (Sargeant et al. 1987, Gosselink et al. 2003). This can lead to elevational stratification, with coyotes in preferable habitats at lower elevations and red fox relegated to poorer habitat at higher elevations. Such elevational stratification between coyotes and red fox has been documented in Alberta (Dekker 1989) and Maine (D. Harrison, unpublished data). A similar elevational stratification has been documented in Sweden, where red foxes exclude arctic foxes (*Alopex lagopus*) from lower elevation habitats (Tannerfeldt et al. 2002). Interspecific competition and snowfall patterns are likely the primary mechanisms behind the elevational stratification seen between red fox and coyotes in the Lassen region. Coyote population densities in the Lassen area are unknown but their prevalence at mid-elevations may restrict red fox abundance in habitats such as sagebrush that might otherwise be suitable. Quantifying the change in coyote population density, age structure and social status along the elevational gradient in the Lassen region would shed additional light on these interactions.

Camera and Road Density

The number of cameras within a grid cell was a significant univariate predictor of red fox detection in both seasons (Table 11), but only in winter was this term included in the most parsimonious multivariate model. This association is probably an artifact of biased sampling. The low LFD and high return ratio scores indicate that the Lassen red fox were readily detected by camera traps. Increasing the number of cameras within a grid cell would therefore have little impact on the binomial outcome of detection within the cell. In practice, cameras were frequently placed in areas already known to be occupied by red fox, both to document the activity times of these animals and to detect uncollared red fox. Areas occupied by red fox therefore received more cameras than areas not occupied by foxes. In other words, the detection of red fox was the cause, not the consequence, of increased sampling effort.

The effect of road density may also be an artifact of sampling bias and the scale of analysis. Many cameras were placed <0.75 km from a road to facilitate operating multiple cameras simultaneously. Road density comprises a variety of positive and negative factors that are difficult to individually quantify, but their overall effect is generally believed to be negative with regard to mesocarnivore conservation in western forests (Buskirk and Zielinski 2003). These factors, however, may have more impact upon reproduction, survivorship and activity patterns than upon presence or detectability. Robitaille and Aubry (2000) found that the occurrence of marten tracks did not differ between areas near (<300 m) and away from (>300 m) roads, and they therefore recommended sampling along road corridors for detection surveys. Red fox and coyote may benefit from the increased fragmentation associated with higher road densities and the ease of travel that roads offer (Meek and Saunders 2000, Buskirk and Zielinski 2003, Gosselink et al. 2003). Snow tracks, feces and sightings indicated that red fox and coyote commonly travel along roads in the Lassen region. The impacts of road density upon montane carnivores warrants additional study.

Management considerations

The distribution and habitat associations of Lassen red fox are consistent with the historical characterizations of the native Sierran subspecies, *V. v. necator*, and are not consistent with expectations for exotic red fox. Grinnell et al. (1937: 386) described the Sierra Nevada red fox as “restricted to the highest timbered peaks and ridges of the main Sierra Nevada,” and they considered the Lassen Peak region to be a major population center. Ingles (1965) concluded that red fox in the Sierra Nevada inhabited alpine fell-fields and subalpine red fir and lodgepole pine forests. Red fox sighting reports from the northern Sierra Nevada were concentrated in fir and mixed-conifer habitats, usually between 1650 and 2250 m (5,400 and 7,400 ft) elevation (Schempf and White 1977). Grinnell et al. (1937) reported that the Sierra Nevada red fox did not occur below 1370 m (4500 ft); in this study, the lowest elevation at which camera stations detected red fox was 1379 m. The restricted nature of the Sierra Nevada red fox contrasts starkly with the wide habitat tolerances shown by red fox in other portions of their range (Buskirk and Zielinski 2003). California’s exotic red fox were imported from the eastern and midwestern United States starting in the late 19th century (Lewis et al. 1999). Their rapid expansion throughout much of central and southern California indicates a broad tolerance of many habitat types despite the presence of sympatric coyotes. If exotic red fox had dispersed into the Lassen region, they would probably inhabit numerous habitat types including the sagebrush areas to the northeast. Until definitive genetic evidence becomes available, Lassen’s red fox population should continue to be managed as the threatened, native *V. v. necator*.

The current distribution of *V. v. necator* throughout its historic range is unknown. If range-wide surveys are to be conducted, this study suggests the habitat types where red fox may be most likely to be detected: high-elevation conifer forest, subalpine woodlands, talus slopes and barren areas above treeline. Baited camera stations are only survey instrument that has been demonstrated to detect mountain red fox populations. Surveys for marten, fisher, wolverine and other forest carnivores within the historic range of *V. v. necator* should be administered in a fashion that would also detect red fox. Specifically, the bait should be near the ground and the camera should be positioned so the ground is included in the photograph. Otherwise, the station may attract red fox but fail to record their presence -- the occasional tree-climbing red fox notwithstanding (Kucera 1993). (See Appendix B for the field protocols I used for my camera stations.)

Biologists with the US Forest Service's Pacific Southwest Research Station ("PSW") recently completed an extensive carnivore survey throughout California's Sierra Nevada and southern Cascade ranges using sooted track plates and baited camera traps along a statistically-defensible sampling grid (Zielinski and Stauffer 1996, Zielinski et al. *in press*). The Lassen region was included in this survey, as was most of the historic range of *V. v. necator*, but no detections of red fox were obtained. Why the survey did not detect the Lassen red fox population is unclear, but may be due to the fact that the range of this population is so restricted that the PSW sites simply missed them. Their surveys were conducted only during the summer when the red fox range was at its most restricted, and none of the PSW plots fell within grid cells where red foxes were detected in summer by the camera traps analyzed here. Only 2 of the PSW sites were in cells adjacent to cells where red fox were detected in summer, but only 2 of the 24 cameras within those cells detected red fox in the same years as the PSW survey. Although the Lassen cameras indicate that red fox may be readily detected at camera traps, the PSW survey suggests that their patchy population distribution and density may prevent them from being detected at sites that are indeed occupied habitat. This illustrates the benefit of using all available sample data, not just those sites that were conducted using a statistically-rigorous sampling protocol, and re-emphasizes the caution that failure to detect does not provide conclusive evidence of absence.

The high elevation, low productivity habitats occupied by mountain red fox should not be assumed to be preferred or ideal habitats. Population density is not necessarily correlated with habitat suitability (Pulliam 1988). Red fox habitat use is likely a function of several factors, including the availability of prey and the avoidance of dominant competitors (e.g., coyotes) or harsh environmental conditions (e.g., deep soft snow). Changes in these factors, such as might occur with global climate change, could have important impacts upon the survival of mountain red fox, especially if the high elevation areas currently represent “escape habitat.” Habitat quality for an organism should be assessed in terms of the fitness it confers upon its occupants (Powell 2004). Such an assessment cannot be achieved using camera stations. Studies using individually marked and monitored individuals are necessary to test the hypotheses generated by the camera station data.

Table 5: Annual camera sampling effort in the Lassen region.

Year	Perrine	Lassen National Forest Almanor	Eagle Lake	Hat Creek	Lassen Park	total
1992	--	--	2	5	--	7
1993	--	--	9	1	--	10
1994	--	--	18	5	--	23
1995	--	--	17	11	7	35
1996	--	25	14	15	9	63
1997	--	57	66	19	6	148
1998	13	26	22	48	--	109
1999	10	20	98	26	--	154
2000	40	21	77	39	--	177
2001	38	10	86	35	--	169
2002	25	30	40	--	8	103
total:	126	189	449	204	30	998

Note: Cameras that I operated as part of this dissertation were located on both the Lassen National Forest and the Lassen Park. Cameras operated by other agencies were located within their own administrative boundaries.

Table 6: CWHR communities represented in general cover types.

Cover Type	Variable	CWHR Community Type
Barren	BAR	Barren
Conifer	CON	Closed Cone Pine Cypress, Douglas Fir, East-Side Pine, Jeffrey Pine, Juniper, Klamath Mixed Conifer, Lodgepole Pine, Montane Hardwood-Conifer, Ponderosa Pine, Red Fir, Sierran Mixed Conifer, White Fir
Hardwood	HWD	Aspen, Blue-Oak Woodland, Montane Hardwood, Montane Riparian
Herbaceous	HRB	Annual Grassland, Wet Meadow
Shrub	SHB	Bitterbrush, Mixed Chaparral, Montane Chaparral, Sagebrush
Other	OTH	Water, Urban, Crops

Table 7: Variables used in the grid cell analyses.

Variable	Definition (units)
ElevMn	Mean of 2,878 elevation pixels, each 30m x 30m, within cell (meters)
ElevSTD	Standard deviation of elevation pixels within cell (meters)
pctBAR	Percentage of cell in BARREN lifecover
pctCON	Percentage of cell in CONIFER lifecover
pctHRB	Percentage of cell in HERBACEOUS lifecover
pctHWD	Percentage of cell in HARDWOOD lifecover
pctSHB	Percentage of cell in SHRUB lifecover
pctOTH	Percentage of cell in OTHER lifecover
pct12MD	Percentage of cell in CON or HWD with trees <15cm dbh and >40% canopy closure; "small open-canopy forest"
pct12SP	Percentage of cell in CON or HWD with trees <15cm dbh and <40% canopy closure; "small closed-canopy forest"
pct34MD	Percentage of cell in CON or HWD with trees 15-60cm dbh and >40% canopy closure; "mid-sized open-canopy forest"
pct34SP	Percentage of cell in CON or HWD with trees 15-60cm dbh and <40% canopy closure; "mid-sized closed-canopy forest"
pct56MD	Percentage of cell in CON or HWD with trees >60cm dbh and >40% canopy closure; "mature open-canopy forest"
pct56SP	Percentage of cell in CON or HWD with trees >60cm dbh and <40% canopy closure; "mature closed-canopy forest"
HWYm	Length of paved road within cell (meters)
CAMERAS	Number of camera stations within cell
MARTEN	Marten detected in cell? (Yes/No)
REDFOX	Red Fox detected in cell? (Yes/No)
COYOTE	Coyote detected in cell? (Yes/No)

Table 8: Distribution of camera traps and carnivore detections by CWHR community type.

CWHR Type	Cameras	Red Fox	Marten	Coyote
Annual Grassland	2	0	0	1
Aspen	2	0	2	0
Barren	3	1	2	0
East-Side Pine	254	3	8	53
Juniper	2	0	0	0
Lodgepole Pine	42	7	17	4
Mixed Chapparal	2	0	0	0
Montane Chapparal	44	8	12	6
Montane Hardwood-Conifer	1	0	0	0
Montane Hardwood	4	0	1	0
Montane Riparian	1	0	1	0
Ponderosa Pine	7	0	0	3
Red Fir	71	10	27	6
Sub-Alpine Conifer	5	1	5	0
Sagebrush	41	0	1	7
Sierran Mixed Conifer	465	20	46	70
White Fir	33	1	9	5
Wet Meadow	12	1	1	4

Table 9: Detection of red fox and marten at camera traps in varying cover types. Coyote detections were not significantly different by cover type and are therefore not included. Cameras in Barren cover type were not incuded due to small sample size (0.3% of camera sites).

Species	Cover Type	Observed	Expected	χ^2	Observed Proportion	Observed CI lower	Observed CI upper	Expected Proportion	Effect
Red Fox:	High-elevation Conifer	11	3.9	12.77	0.216	0.083	0.349	0.077	**select**
	Mid-elevation Conifer	31	41.5	2.66	0.608	0.450	0.766	0.814	**avoid**
	Hardwood-Herbaceous	1	1.1	0.01	0.020	-0.025	0.065	0.021	ns
	Shrub	8	4.5	2.74	0.157	0.039	0.275	0.088	ns
	subtotal:	51	51	18.17					
	p-value:			$p = 0.0004$					
Marten:	High-elevation Conifer	32	10.0	48.40	0.216	0.160	0.332	0.077	**select**
	Mid-elevation Conifer	80	105.8	6.29	0.608	0.519	0.712	0.814	**avoid**
	Hardwood-Herbaceous	5	2.8	1.81	0.020	0.000	0.077	0.021	ns
	Shrub	13	11.4	0.21	0.157	0.040	0.160	0.088	ns
	subtotal:	130	130	56.71					
	p-value:			$p < 0.0001$					

Observed: The number of camera traps in the cover type that detected the target species.

Expected: The number of cameras expected to detect the target species based on the null hypothesis of no habitat selection.

Observed Proportion: The distribution of camera detections by cover type.

Observed CI: Upper and lower bounds of 90% confidence interval around the observed proportion.

Expected Proportion: Expected distribution of camera detections by camera types, under the null hypothesis of no selection.

Effect: Indicates whether cover type was selected, avoided or not significantly different from expected, based upon whether the 90% CI was entirely above, entirely below or included the expected proportion.

Table 10: Detection statistics for each target species.

		Latency to First Detection			Return Ratio		
Species	Season	n	Median	Range	n	Median	Range
Red Fox	all	27	3	1 - 27	25	0.14	0.00 - 0.72
	summer	13	3	1 - 27	12	0.14	0.00 - 0.41
	winter	6	3	1 - 23	5	0.11	0.00 - 0.37
Marten	all	46	3	1 - 34	40	0.16	0.00 - 0.53
	summer	33	3	1 - 34	28	0.14	0.00 - 0.50
	winter	7	2	1 - 10	6	0.18	0.00 - 0.40
Coyote	all	19	12	2 - 34	19	0.00	0.00 - 0.05
	summer	12	12	2 - 34	12	0.00	0.00 - 0.03
	winter	4	15	4 - 23	4	0.00	0.00 - 0.05

"n" is the number of camera traps where the species was detected.
Sample sizes are smaller for return ratio because cameras with <10 nights were excluded.

Table 11: Univariate analysis of landscape variables in 2.6 km² cells. Z and p values are from the Wilcoxan rank-sum test, used to test whether the given variable was significantly different in sampled cells where the target species was and was not detected. For significant differences ($p < 0.10$), “Assoc” indicates whether the variable was positively or negatively correlated with the carnivore’s detection. Asterisks denote variables that were retained in the stepwise logistic regression. CAMERAS was not a landscape variable and was not included in the stepwise logistic regression, but is included here for comparison with the other variables.

Table 11:

A) Summer: 145 cells sampled

			Detected			Not Detected					
Species	n	Variable	Mean	SD	Range	Mean	SD	Range	Z	p	Assoc
Red fox	11	ElevMn *	2261.1	282.4	1823 - 2727	1751.9	221.7	956 - 2328	4.71	<0.001	+
		ElevSTD	76.5	35.4	29 - 138	51.9	33.1	5 - 160	2.37	0.018	+
		pctBAR	18.4	26.7	0.0 - 86.8	0.8	2.7	0 - 17.0	5.42	<0.001	+
		pctCON	59.2	32.8	6.9 - 97.3	83.2	17.9	12.3 - 100.0	-2.72	0.007	-
		pctHRB *	0.8	2.1	0.0 - 6.7	2.1	5.9	0.0 - 47.4	-0.75	0.454	ns
		pctHWD	1.2	2.2	0.0 - 6.0	0.4	2.3	0.0 - 23.0	1.97	0.049	+
		pctSHB *	18.1	16.6	0.0 - 51.3	12.1	14.6	0.0 - 64.8	1.29	0.198	ns
		pctOTH	2.4	6.1	0.0 - 20.4	1.4	6.4	0.0 - 66.4	0.38	0.706	ns
		pct12MD	0.0	0.0	0.0 - 0.0	0.0	0.2	0.0 - 2.7	-0.27	0.788	ns
		pct12SP	0.0	0.0	0.0 - 0.0	0.0	0.4	0.0 - 3.4	-0.58	0.559	ns
		pct34MD	23.2	25.7	0.0 - 68.6	55.6	22.6	4.4 - 97.5	-3.57	0.000	-
		pct34SP	18.6	18.7	0.6 - 52.9	11.9	14.1	0.0 - 58.8	1.34	0.179	ns
		pct56MD	15.6	21.0	0.0 - 58.2	13.6	18.3	0.0 - 87.1	0.98	0.325	ns
		pct56SP	1.6	2.3	0.0 - 6.6	0.3	0.9	0.0 - 5.8	2.66	0.008	+
		HWYm *	1518.9	876.0	0.0 - 2894.7	418.9	877.9	0.0 - 4224.3	4.11	<0.001	+
		CAMERAS	3.1	2.2	1 - 9	1.4	0.7	1 - 6	4.06	<0.001	+
Marten	24	ElevMn *	2158.0	236.6	1756 - 2727	1722.8	203.0	956 - 2213	6.72	<0.001	+
		ElevSTD *	67.7	35.5	15 - 143	50.8	32.7	5 - 160	2.27	0.023	+
		pctBAR	10.6	19.5	0.0 - 86.8	0.4	1.7	0.0 - 14.0	4.67	<0.001	+
		pctCON	67.1	29.5	6.9 - 99.2	84.4	16.5	12.3 - 100.0	-2.80	0.005	-
		pctHRB	1.6	2.9	0.0 - 12.3	2.0	6.1	0.0 - 47.4	1.16	0.244	ns
		pctHWD	1.1	2.1	0.0 - 7.6	0.4	2.2	0.0 - 23.0	2.97	0.003	+
		pctSHB	17.5	18.1	0.0 - 54.8	11.4	13.9	0.0 - 64.8	1.07	0.287	ns
		pctOTH	2.1	4.4	0.0 - 18.9	1.4	6.7	0.0 - 66.4	1.63	0.104	ns
		pct12MD	0.0	0.0	0.0 - 0.0	0.0	0.2	0.0 - 2.7	-0.44	0.662	ns
		pct12SP	0.1	0.4	0.0 - 1.8	0.1	0.4	0.0 - 3.4	0.39	0.693	ns
		pct34MD *	34.3	28.0	0.0 - 83.4	57.2	21.7	4.4 - 97.5	-3.69	0.000	-
		pct34SP	13.5	14.8	0.0 - 52.9	12.2	14.5	0.0 - 58.8	0.77	0.440	ns
		pct56MD *	16.6	17.6	0.0 - 63.8	13.1	18.2	0.0 - 87.1	2.32	0.020	+
		pct56SP	1.7	2.2	0.0 - 6.6	0.2	0.7	0.0 - 4.8	5.37	<0.001	+
		HWYm	1226.9	1284.2	0.0 - 4224.3	366.0	761.0	0.0 - 2971.6	4.13	<0.001	+
		CAMERAS	2.0	1.7	1 - 9	1.5	0.8	1 - 6	1.75	0.080	ns
Coyote	21	ElevMn	1806.2	288.9	1331 - 2444	1774.8	255.6	956 - 2727	0.27	0.786	ns
		ElevSTD *	47.0	35.2	5 - 121	54.6	33.6	6 - 160	-1.09	0.276	ns
		pctBAR	2.8	8.6	0.0 - 38.3	1.7	8.5	0.0 - 86.8	0.82	0.414	ns
		pctCON	69.2	24.8	6.9 - 99.2	83.4	18.4	9.9 - 100.0	-2.68	0.007	-
		pctHRB	3.9	10.5	0.0 - 47.4	1.6	4.3	0.0 - 32.3	0.43	0.664	ns
		pctHWD	0.7	1.7	0.0 - 6.0	0.5	2.3	0.0 - 23.0	2.10	0.036	+
		pctSHB	21.0	19.9	0.8 - 66.0	11.5	13.9	0.0 - 64.8	2.39	0.017	+
		pctOTH	2.4	5.4	0.0 - 20.4	1.3	6.6	0.0 - 66.4	1.98	0.047	+
		pct12MD	0.0	0.0	0.0 - 0.0	0.0	0.2	0.0 - 2.7	-0.40	0.689	ns
		pct12SP	0.0	0.1	0.0 - 0.2	0.1	0.4	0.0 - 3.4	0.53	0.599	ns
		pct34MD *	40.4	24.6	0.5 - 79.0	55.8	23.4	0.0 - 97.5	-2.55	0.011	-
		pct34SP	13.8	14.3	0.0 - 44.3	12.0	14.6	0.0 - 58.8	1.04	0.299	ns
		pct56MD	12.5	13.9	0.0 - 42.5	13.5	18.6	0.0 - 87.1	0.48	0.631	ns
		pct56SP	0.5	1.3	0.0 - 4.7	0.3	1.0	0.0 - 6.6	0.18	0.854	ns
		HWYm	875.8	1273.1	0.0 - 4080.9	438.2	848.8	0.0 - 4224.3	1.59	0.111	ns
		CAMERAS	1.6	0.9	1 - 4	1.5	1.1	1 - 9	0.37	0.709	ns

Table 11, continued.

B) Winter: 301 cells sampled

			Detected			Not Detected					
Species	n	Variable	Mean	SD	Range	Mean	SD	Range	Z	p	Assoc
Red fox	25	ElevMn *	1878.2	264.0	1396 - 2494	1753.7	217.9	787 - 2416	2.11	0.035	+
		ElevSTD	51.2	40.0	6 - 117	47.6	31.2	3 - 139	-0.01	0.992	ns
		pctBAR	2.3	5.6	0.0 - 20.1	0.5	2.1	0.0 - 20.0	3.00	0.003	+
		pctCON	83.0	16.6	43.0 - 99.8	84.4	20.7	4.0 - 100.0	-1.42	0.155	ns
		pctHRB	1.9	4.3	0.0 - 17.6	3.0	9.0	0.0 - 60.3	-0.06	0.956	ns
		pctHWD	0.9	2.0	0.0 - 6.0	1.1	5.5	0.0 - 53.3	1.83	0.067	ns
		pctSHB	10.9	12.5	0.0 - 54.4	10.4	15.9	0.0 - 83.1	1.17	0.242	ns
		pctOTH	0.9	3.8	0.0 - 18.9	0.6	3.4	0.0 - 46.4	-0.14	0.887	ns
		pct12MD	0.0	0.0	0.0 - 0.0	0.0	0.1	0.0 - 1.8	-0.83	0.409	ns
		pct12SP	0.0	0.1	0.0 - 0.6	0.1	0.9	0.0 - 10.0	-0.33	0.742	ns
		pct34MD	49.6	25.3	0.5 - 89.3	58.3	23.0	0.9 - 100.0	-1.42	0.155	ns
		pct34SP	12.1	19.0	0.0 - 78.9	12.1	13.1	0.0 - 71.1	-1.38	0.168	ns
		pct56MD *	19.0	16.3	0.0 - 47.7	10.6	15.8	0.0 - 71.5	3.26	0.001	+
		pct56SP	0.9	1.8	0.0 - 6.6	0.2	0.7	0.0 - 5.6	2.95	0.003	+
		HWYm *	902.2	1069.9	0.0 - 4080.9	492.4	851.1	0.0 - 3679.2	2.16	0.031	+
		CAMERAS	1.8	1.7	1 - 9	1.2	0.1	1 - 4	2.48	0.013	+
Marten	71	ElevMn *	1900.0	191.0	1372 - 2494	1372.0	216.5	787 - 2162	6.00	<0.001	+
		ElevSTD *	45.8	30.5	3 - 135	48.4	31.9	3 - 139	-0.52	0.603	ns
		pctBAR	1.3	3.8	0.0 - 20.1	0.5	2.1	0.0 - 20.0	3.33	0.001	+
		pctCON	87.7	16.7	4.0 - 100.0	83.7	21.0	7.7 - 100.0	0.64	0.526	ns
		pctHRB	2.3	6.0	0.0 - 37.5	3.0	9.1	0.0 - 60.3	0.89	0.374	ns
		pctHWD	0.6	1.5	0.0 - 7.6	1.3	5.8	0.0 - 53.3	1.93	0.054	ns
		pctSHB	7.2	12.0	0.0 - 69.0	11.1	16.3	0.0 - 83.1	-1.99	0.046	-
		pctOTH	0.9	3.1	0.0 - 18.9	0.5	3.4	0.0 - 46.4	1.00	0.318	ns
		pct12MD	0.0	0.0	0.0 - 0.0	0.0	0.1	0.0 - 1.8	-1.50	0.135	ns
		pct12SP	0.1	0.5	0.0 - 3.2	0.1	0.9	0.0 - 10.0	0.85	0.398	ns
		pct34MD	55.5	24.6	0.5 - 99.0	57.8	22.8	0.9 - 100.0	-0.63	0.526	ns
		pct34SP	10.1	14.6	0.0 - 78.9	12.4	13.3	0.0 - 71.1	-1.75	0.080	ns
		pct56MD *	19.2	18.3	0.0 - 58.2	10.0	15.4	0.0 - 71.5	4.69	<0.001	+
		pct56SP	0.6	1.4	0.0 - 6.6	0.2	0.7	0.0 - 5.6	3.01	0.003	+
		HWYm *	740.7	1022.5	0.0 - 4080.9	469.1	824.7	0.0 - 3679.2	2.06	0.039	+
		CAMERAS	1.4	1.1	1 - 9	1.3	0.6	1 - 4	0.47	0.638	ns
Coyote	93	ElevMn *	1690.5	232.1	787 - 2494	1802.6	210.6	910 - 2416	-5.15	<0.001	-
		ElevSTD	47.0	36.6	3 - 139	48.1	29.4	3 - 139	-1.08	0.279	ns
		pctBAR *	0.6	2.8	0.0 - 20.1	0.6	2.5	0.0 - 20.0	-0.27	0.789	ns
		pctCON	84.1	20.6	7.7 - 100.0	84.6	20.4	4.0 - 100.0	-0.01	0.992	ns
		pctHRB *	2.4	5.5	0.0 - 28.1	3.1	9.9	0.0 - 60.3	1.43	0.153	ns
		pctHWD	1.4	6.0	0.0 - 46.3	0.9	4.9	0.0 - 53.3	0.27	0.788	ns
		pctSHB *	10.8	16.3	0.0 - 80.4	10.2	15.4	0.0 - 83.1	-0.18	0.855	ns
		pctOTH *	0.7	4.9	0.0 - 46.4	0.5	2.4	0.0 - 18.9	0.96	0.337	ns
		pct12MD	0.0	0.1	0.0 - 0.7	0.0	0.2	0.0 - 1.8	-0.24	0.814	ns
		pct12SP	0.0	0.3	0.0 - 2.5	0.2	1.0	0.0 - 10.0	-1.67	0.096	ns
		pct34MD *	56.7	23.8	0.5 - 98.5	58.2	23.1	2.3 - 100.0	-0.46	0.647	ns
		pct34SP *	13.9	15.6	0.0 - 78.9	11.2	12.7	0.0 - 71.1	0.92	0.359	ns
		pct56MD *	11.8	18.2	0.0 - 71.5	10.9	14.7	0.0 - 55.6	-0.67	0.504	ns
		pct56SP	0.2	0.9	0.0 - 6.6	0.3	0.8	0.0 - 5.6	-0.68	0.497	ns
		HWYm	625.9	904.5	0.0 - 3679.2	474.7	861.1	0.0 - 4080.9	1.77	0.076	ns
		CAMERAS	1.4	1.0	1 - 9	1.3	0.6	1 - 3	0.97	0.332	ns

Table 12: Pairwise Pearson correlations among cell-level variables. Summer data are above the diagonal and winter data are below. Significant correlations ($p < 0.05$) had $|r|$ values exceeding 0.17 in summer and 0.12 in winter and are printed in bold font.

a) Red Fox

	Marten	Coyote	Cameras	ElevMN	ElevSTD	pctBAR	pctCON	pctHRB	pctHWD	pctSHB	pctOTH	pct12MD	pct12SP	pct34MD	pct34SP	pct56MD	pct56SP	HWYm
Marten		0.16	**0.22**	**0.62**	**0.23**	**0.47**	**-0.38**	-0.02	0.13	**0.21**	0.03	-0.04	0.03	**-0.39**	0.05	0.04	**0.45**	**0.37**
Coyote	-0.11		0.05	0.12	-0.05	0.06	**-0.23**	**0.18**	0.05	**0.19**	0.05	-0.03	-0.04	**-0.25**	0.10	0.00	0.07	**0.18**
Cameras	**0.12**	0.09		**0.33**	**0.27**	0.16	-0.05	-0.08	-0.02	0.02	-0.02	-0.05	-0.08	-0.07	0.00	0.03	0.09	0.14
ElevMN	**0.29**	**-0.24**	0.00		**0.46**	**0.57**	**-0.20**	-0.04	-0.13	-0.03	-0.01	-0.01	0.10	**-0.24**	**-0.26**	**0.27**	**0.48**	**0.17**
ElevSTD	-0.03	-0.01	0.04	0.08		**0.38**	-0.09	-0.07	0.00	-0.04	-0.07	-0.08	-0.02	**-0.31**	**-0.26**	**0.50**	**0.24**	**0.18**
pctBAR	**0.14**	-0.01	0.00	**0.28**	**0.12**		**-0.54**	-0.04	0.05	0.16	-0.03	-0.02	-0.03	**-0.42**	0.02	-0.06	**0.32**	**0.30**
pctCON	0.06	-0.02	-0.04	**0.24**	**0.22**	**-0.14**		-0.17	**-0.24**	**-0.80**	**-0.33**	0.08	0.11	**0.70**	**-0.14**	**0.27**	**-0.34**	**-0.35**
pctHRB	-0.01	-0.04	-0.01	-0.04	**-0.31**	-0.04	**-0.53**		-0.04	-0.11	-0.03	-0.03	-0.05	-0.10	-0.06	0.02	0.00	0.02
pctHWD	-0.07	0.05	-0.03	**-0.52**	**0.16**	-0.03	**-0.27**	-0.06		**0.17**	-0.02	-0.02	-0.03	**-0.23**	0.06	0.00	0.11	**0.33**
pctSHB	-0.08	0.02	0.08	**-0.17**	**-0.17**	0.06	**-0.85**	**0.15**	0.07		0.06	-0.07	-0.09	**-0.56**	**0.24**	**-0.33**	**0.26**	**0.27**
pctOTH	0.05	0.02	-0.06	0.02	-0.11	-0.01	**-0.19**	0.12	-0.03	-0.02		-0.02	-0.03	**-0.18**	-0.10	-0.02	-0.02	-0.07
pct12MD	-0.06	-0.02	0.03	0.09	0.01	-0.03	0.08	-0.04	-0.03	-0.07	-0.02		-0.01	0.08	-0.06	-0.03	-0.03	-0.05
pct12SP	0.00	-0.09	-0.04	**0.12**	0.04	-0.04	0.10	-0.04	-0.03	-0.09	-0.03	**0.38**		0.11	-0.09	0.01	-0.05	-0.08
pct34MD	-0.02	-0.04	-0.04	**0.15**	0.01	**-0.23**	**0.66**	**-0.31**	**-0.16**	**-0.58**	-0.07	0.03	0.03		**-0.35**	**-0.26**	**-0.44**	**-0.38**
pct34SP	-0.03	0.10	-0.02	0.03	**-0.26**	**0.16**	-0.04	-0.05	-0.03	0.08	-0.07	0.06	-0.02	**-0.35**		**-0.45**	0.11	0.13
pct56MD	**0.15**	0.02	0.04	-0.06	**0.48**	0.00	**0.25**	**-0.15**	0.02	**-0.23**	-0.05	-0.06	0.00	**-0.25**	**-0.38**		0.06	-0.01
pct56SP	**0.17**	-0.02	-0.01	**0.25**	**0.17**	**0.43**	-0.09	-0.06	0.10	0.06	-0.05	-0.04	-0.04	**-0.28**	**0.17**	**0.12**		**0.44**
HWYm	**0.14**	0.09	**0.25**	**-0.25**	0.02	0.09	**-0.17**	0.06	**0.12**	**0.12**	0.03	-0.06	-0.10	**-0.17**	0.03	0.05	0.10	

Table 12, continued.

b) Marten:

	RedFox	Coyote	Cameras	ElevMN	ElevSTD	pctBAR	pctCON	pctHRB	pctHWD	pctSHB	pctOTH	pct12MD	pct12SP	pct34MD	pct34SP	pct56MD	pct56SP	HWYm
RedFox		**0.25**	**0.47**	**0.53**	**0.23**	**0.55**	**-0.36**	-0.05	0.10	0.14	0.05	-0.02	-0.04	**-0.36**	0.15	-0.04	**0.31**	**0.35**
Coyote	0.06		0.05	0.11	-0.05	0.06	**-0.23**	**0.18**	0.05	**0.19**	0.04	-0.03	-0.04	**-0.25**	0.10	0.00	0.05	**0.18**
Cameras	**0.24**	0.09		**0.32**	**0.27**	0.16	-0.06	-0.08	-0.02	0.02	-0.02	-0.04	-0.08	-0.08	0.00	0.03	0.06	**0.13**
ElevMN	**0.16**	**-0.25**	-0.01		**0.45**	**0.55**	**-0.19**	-0.04	-0.13	-0.04	0.00	-0.01	0.09	**-0.23**	**-0.26**	**0.29**	**0.47**	0.17
ElevSTD	0.03	-0.01	0.04	0.08		**0.38**	-0.10	-0.07	0.00	-0.04	-0.08	-0.08	-0.01	**-0.32**	**-0.25**	**0.52**	**0.22**	0.16
pctBAR	**0.20**	-0.02	0.00	**0.29**	**0.13**		**-0.55**	-0.04	0.05	0.16	-0.03	-0.02	-0.03	**-0.42**	0.02	-0.06	**0.28**	**0.30**
pctCON	-0.03	-0.03	-0.04	**0.24**	**0.21**	**-0.15**		-0.17	**-0.24**	**-0.80**	**-0.33**	0.08	0.10	**0.71**	-0.13	**0.26**	**-0.28**	**-0.33**
pctHRB	-0.02	-0.03	-0.01	-0.05	**-0.30**	-0.05	**-0.53**		-0.04	-0.11	-0.03	-0.03	-0.05	-0.10	-0.06	0.02	-0.01	0.02
pctHWD	-0.02	0.05	-0.03	**-0.50**	**0.17**	-0.02	**-0.28**	-0.06		**0.17**	-0.02	-0.02	-0.03	**-0.23**	0.06	0.00	0.09	**0.33**
pctSHB	0.02	0.03	0.08	**-0.17**	**-0.16**	0.06	**-0.85**	**0.15**	0.07		0.05	-0.07	-0.09	**-0.57**	**0.23**	**-0.32**	**0.21**	**0.25**
pctOTH	0.03	0.02	-0.05	0.02	-0.11	-0.01	**-0.19**	0.11	-0.03	-0.02		-0.02	-0.03	**-0.18**	-0.11	-0.01	-0.02	-0.08
pct12MD	-0.03	-0.02	0.04	0.09	0.01	-0.03	0.08	-0.04	-0.03	-0.07	-0.02		-0.01	0.08	-0.06	-0.03	-0.03	-0.05
pct12SP	-0.04	-0.08	-0.03	0.11	0.04	-0.04	0.10	-0.04	-0.03	-0.09	-0.03	**0.38**		0.11	-0.09	0.01	-0.05	-0.08
pct34MD	-0.10	-0.03	-0.04	**0.14**	0.01	**-0.25**	**0.65**	**-0.30**	**-0.17**	**-0.57**	-0.08	0.03	0.03		**-0.36**	**-0.26**	**-0.42**	**-0.36**
pct34SP	0.02	0.11	0.00	0.02	**-0.26**	**0.16**	-0.05	-0.05	-0.02	0.09	-0.07	0.06	-0.02	**-0.34**		**-0.44**	0.12	0.12
pct56MD	0.11	-0.02	0.02	-0.02	**0.45**	0.01	**0.25**	**-0.15**	0.02	**-0.24**	-0.05	-0.07	-0.01	**-0.27**	**-0.38**		0.10	-0.01
pct56SP	**0.22**	-0.04	0.00	**0.26**	**0.16**	**0.43**	-0.10	-0.06	0.10	0.06	-0.01	-0.04	-0.04	**-0.30**	**0.16**	**0.14**		**0.38**
HWYm	**0.13**	0.08	**0.25**	**-0.25**	0.01	0.10	**-0.17**	0.06	0.12	**0.12**	0.05	-0.06	-0.10	**-0.18**	0.05	0.05	**0.12**	

Table 12, continued.

c) Coyote:

	Marten	RedFox	Cameras	ElevMN	ElevSTD	pctBAR	pctCON	pctHRB	pctHWD	pctSHB	pctOTH	pct12MD	pct12SP	pct34MD	pct34SP	pct56MD	pct56SP	HWYm
Marten		**0.48**	**0.24**	**0.59**	**0.22**	**0.44**	**-0.32**	-0.01	0.13	0.16	0.02	-0.03	0.03	**-0.36**	0.05	0.07	**0.42**	**0.34**
RedFox	**0.25**		**0.51**	**0.51**	**0.23**	**0.50**	**-0.29**	-0.04	0.10	0.08	0.04	-0.02	-0.04	**-0.32**	0.16	-0.01	**0.27**	**0.32**
Cameras	0.11	**0.24**		**0.36**	**0.27**	**0.18**	-0.05	-0.08	-0.01	0.00	-0.02	-0.04	-0.08	-0.08	0.00	0.04	0.11	0.13
ElevMN	**0.30**	**0.17**	0.00		**0.46**	**0.52**	-0.11	-0.03	-0.12	-0.11	-0.01	-0.01	0.10	**-0.18**	**-0.26**	**0.31**	**0.43**	0.12
ElevSTD	-0.03	0.03	0.05	0.07		**0.39**	-0.09	-0.07	0.00	-0.04	-0.08	-0.08	-0.01	**-0.32**	**-0.26**	**0.52**	**0.24**	0.14
pctBAR	**0.14**	**0.21**	0.00	**0.28**	0.11		**-0.49**	-0.03	0.05	0.11	-0.04	-0.02	-0.03	**-0.38**	0.02	-0.04	**0.24**	**0.27**
pctCON	0.06	-0.02	-0.04	**0.25**	**0.22**	**-0.14**		**-0.18**	**-0.23**	**-0.81**	**-0.32**	0.08	0.11	**0.71**	-0.13	**0.26**	**-0.26**	**-0.32**
pctHRB	-0.02	-0.03	-0.01	-0.05	**-0.30**	-0.04	**-0.54**		-0.05	-0.10	-0.03	-0.03	-0.05	-0.11	-0.06	0.02	0.01	0.04
pctHWD	-0.07	-0.02	-0.03	**-0.52**	**0.16**	-0.03	**-0.27**	-0.06		0.16	-0.02	-0.02	-0.03	**-0.22**	0.06	0.00	0.11	**0.32**
pctSHB	-0.08	0.01	0.08	**-0.17**	**-0.17**	0.05	**-0.85**	**0.15**	0.07		0.03	-0.07	-0.09	**-0.57**	**0.22**	-0.32	**0.21**	**0.24**
pctOTH	0.05	0.03	-0.06	0.02	-0.11	-0.01	**-0.19**	0.12	-0.03	-0.02		-0.02	-0.03	**-0.18**	-0.11	-0.01	-0.03	-0.08
pct12MD	-0.06	-0.04	0.03	0.09	0.01	-0.02	0.08	-0.04	-0.03	-0.07	-0.02		-0.01	0.08	-0.06	-0.03	-0.03	-0.05
pct12SP	0.00	-0.04	-0.04	**0.12**	0.04	-0.04	0.10	-0.04	-0.03	-0.09	-0.03	**0.38**		0.11	-0.09	0.01	-0.05	-0.08
pct34MD	-0.02	-0.11	-0.04	**0.16**	0.02	**-0.23**	**0.66**	**-0.31**	**-0.16**	**-0.58**	-0.07	0.03	0.03		**-0.36**	**-0.26**	**-0.40**	-0.36
pct34SP	-0.04	0.02	-0.02	0.04	**-0.26**	**0.16**	-0.05	-0.05	-0.02	0.08	-0.07	0.06	-0.02	**-0.36**		**-0.44**	0.12	0.14
pct56MD	**0.16**	**0.13**	0.05	-0.07	**0.47**	-0.01	**0.25**	**-0.15**	0.02	**-0.24**	-0.05	-0.06	0.00	**-0.24**	**-0.37**		0.10	-0.01
pct56SP	**0.17**	**0.25**	-0.01	**0.25**	**0.17**	**0.43**	-0.09	-0.05	0.10	0.06	-0.05	-0.04	-0.04	**-0.28**	**0.17**	0.12		**0.42**
HWYm	**0.13**	**0.14**	**0.26**	**-0.25**	0.01	0.09	**-0.17**	0.07	**0.12**	**0.12**	0.03	-0.06	-0.10	**-0.17**	0.04	0.04	0.09	

Table 13: Parameter estimates and odds ratios for terms in the landscape-only model resulting from the stepwise logistic regression. Note that ElevMn and HWYm have been multiplied by 100 so that their odds ratios reflect a 100 m change in these terms.

A) Summer

		Parameter				Odds Ratio		
Species	Effect	Estimate	Std Error	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Red Fox	Intercept	-25.91	7.71	-41.15	-10.67	0.00	0.00	0.00
	ElevMn * 100	1.19	0.38	0.44	1.94	3.29	1.55	6.99
	pctSHB	-0.14	0.07	-0.28	0.00	0.87	0.76	1.00
	pctHRB	-0.60	0.27	-1.13	-0.07	0.55	0.32	0.93
	HWYm * 100	0.19	0.08	0.04	0.35	1.21	1.04	1.42
Marten	Intercept	-27.78	6.20	-40.04	-15.52	0.00	0.00	0.00
	ElevMn * 100	1.65	0.37	0.92	2.38	5.20	2.50	10.80
	ElevSTD	-0.03	0.02	-0.06	0.00	0.97	0.94	1.00
	pct34MD	-0.05	0.02	-0.10	-0.01	0.95	0.91	0.99
	pct56MD	-0.05	0.03	-0.11	0.01	0.95	0.90	1.01
Coyote	Intercept	0.52	0.73	-0.93	1.96	1.67	0.39	7.10
	ElevSTD	-0.01	0.01	-0.03	0.00	0.99	0.97	1.00
	pct34MD	-0.03	0.01	-0.05	-0.01	0.97	0.95	0.99

B) Winter

		Parameter				Odds Ratio		
Species	Effect	Estimate	Std Error	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Red Fox	Intercept	-9.33	2.08	-13.42	-5.24	0.00	0.00	0.01
	ElevMn * 100	0.34	0.11	0.13	0.55	1.40	1.14	1.73
	pct56MD	0.03	0.01	0.01	0.06	1.03	1.01	1.06
	HWYm * 100	0.06	0.02	0.01	0.10	1.06	1.01	1.11
Marten	Intercept	-14.14	2.11	-18.30	-9.98	0.00	0.00	0.00
	ElevMn * 100	0.72	0.12	0.49	0.94	2.05	1.63	2.57
	ElevSTD	-0.03	0.01	-0.04	-0.01	0.97	0.96	0.99
	pct56MD	0.06	0.01	0.04	0.08	1.06	1.04	1.08
	HWYm * 100	0.07	0.02	0.03	0.10	1.07	1.03	1.11
Coyote	Intercept	-1.91	2.27	-6.37	2.56	0.15	0.00	12.96
	ElevMn * 100	-0.30	0.07	-0.44	-0.17	0.74	0.64	0.85
	pctBAR	0.12	0.06	-0.01	0.24	1.13	0.99	1.28
	pctHRB	0.05	0.03	-0.01	0.11	1.05	0.99	1.11
	pctSHB	0.06	0.02	0.01	0.11	1.06	1.01	1.11
	pctOTH	0.09	0.04	0.00	0.17	1.09	1.00	1.19
	pct34MD	0.07	0.02	0.02	0.11	1.07	1.02	1.12
	pct34SP	0.08	0.03	0.03	0.13	1.08	1.03	1.14
	pct56MD	0.07	0.03	0.02	0.12	1.07	1.02	1.13

Table 14: Comparative fit of models by species and season. The "BASE" model is the one resulting from the stepwise logistic regression (Table 13). Models are ranked by AICc value, with the lowest value indicating the most parsimonious model. K = number of terms in the model; w*i* = relative weight of the model (Σw*i* = 1).

a) Summer

Species	Model	R^2	-LogLik	K	AICc	Δ AICc	w*i*
Red Fox	BASE, Coyote	0.67	12.74	7	40.35	0.00	0.40
	BASE, Coyote, Cameras	0.68	12.34	8	41.80	1.45	0.19
	BASE, Marten, Coyote	0.67	12.73	8	42.59	2.24	0.13
	BASE, Cameras	0.63	14.14	7	43.14	2.80	0.10
	BASE, Marten, Coyote, Cameras	0.68	12.28	9	43.97	3.62	0.07
	BASE (= ElevMn - pctHRB - pctSHB + HWYm)	0.58	15.96	6	44.57	4.22	0.05
	BASE, Marten, Cameras	0.63	14.09	8	45.31	4.96	0.03
	BASE, Marten	0.58	15.95	7	46.76	6.41	0.02
	ElevMn	0.47	20.42	3	47.02	6.67	0.01
	Marten, Coyote, Cameras	0.46	20.72	5	51.90	11.55	0.00
	Marten, Cameras	0.43	21.87	4	52.03	11.68	0.00
	Marten, Coyote	0.31	26.59	4	61.49	21.14	0.00
	Marten	0.27	27.88	3	61.94	21.59	0.00
	Coyote, Cameras	0.27	27.91	4	64.13	23.78	0.00
	Cameras	0.20	30.45	3	67.09	26.74	0.00
	Coyote	0.07	35.74	3	77.66	37.31	0.00
Marten	BASE (= ElevMn - ElevSTD - pct34MD - pct56MD)	0.61	24.97	6	62.58	0.00	0.36
	BASE, RedFox	0.62	24.55	7	63.95	1.37	0.18
	BASE, Cameras	0.61	24.80	7	64.46	1.88	0.14
	BASE, Coyote	0.61	24.97	7	64.79	2.21	0.12
	BASE, RedFox, Cameras	0.62	24.54	8	66.19	3.60	0.06
	BASE, RedFox, Coyote	0.62	24.54	8	66.19	3.61	0.06
	BASE, Coyote, Cameras	0.61	24.80	8	66.71	4.12	0.05
	BASE, RedFox , Coyote, Cameras	0.62	24.54	9	68.47	5.89	0.02
	ElevMn	0.50	31.80	3	69.77	7.19	0.01
	RedFox	0.17	53.36	3	112.90	50.32	0.00
	RedFox, Cameras	0.17	53.24	4	114.77	52.19	0.00
	RedFox, Coyote	0.17	53.33	4	114.97	52.38	0.00
	RedFox, Coyote, Cameras	0.17	53.22	5	116.88	54.30	0.00
	Cameras	0.03	62.12	3	130.41	67.83	0.00
	Coyote, Cameras	0.04	61.13	4	130.56	67.98	0.00
	Coyote	0.02	62.88	3	131.93	69.35	0.00
Coyote	BASE, RedFox	0.12	52.17	5	114.78	0.00	0.31
	BASE (= -ElevSTD - pct34md)	0.09	53.90	4	116.10	1.32	0.16
	BASE, RedFox, Cameras	0.12	51.83	6	116.28	1.50	0.15
	BASE, Marten, RedFox	0.12	52.17	6	116.97	2.18	0.10
	BASE, Marten	0.09	53.63	5	117.71	2.92	0.07
	BASE, Cameras	0.09	53.83	5	118.12	3.33	0.06
	BASE, Marten, RedFox, Cameras	0.12	51.83	7	118.50	3.72	0.05
	RedFox	0.04	56.74	3	119.66	4.88	0.03
	BASE, Marten, Cameras	0.09	53.61	6	119.85	5.07	0.02
	RedFox, Cameras	0.06	55.83	4	119.96	5.18	0.02
	Marten, RedFox	0.04	56.73	4	121.76	6.97	0.01
	Marten, RedFox, Cameras	0.06	55.82	5	122.09	7.31	0.01
	Marten	0.01	58.37	3	122.91	8.13	0.01
	ElevMn	0.00	59.05	3	124.28	9.49	0.00
	Cameras	0.00	59.17	3	124.52	9.74	0.00
	Marten, Cameras	0.01	58.35	4	124.99	10.20	0.00

Table 14, continued.

b) Winter

Species	Model	R^2	-LogLik	K	AICc	Δ AICc	w_i
Red Fox	BASE, Cameras	0.16	71.08	6	154.47	0.00	0.28
	BASE, Marten, Cameras	0.17	70.10	7	154.61	0.14	0.26
	BASE, Coyote, Cameras	0.16	70.66	7	155.74	1.27	0.15
	BASE, Marten, Coyote, Cameras	0.18	69.66	8	155.84	1.38	0.14
	BASE, Marten	0.14	72.80	6	157.89	3.43	0.05
	BASE, Marten, Coyote	0.15	72.05	7	158.50	4.03	0.04
	BASE (= ElevMn + pct56MD + HWYm)	0.12	74.14	5	158.50	4.03	0.04
	BASE, Coyote	0.13	73.47	6	159.24	4.77	0.03
	Marten, Cameras	0.10	75.85	4	159.84	5.37	0.02
	Marten, Coyote, Cameras	0.11	75.71	5	161.63	7.16	0.01
	Marten	0.07	78.77	3	163.63	9.16	0.00
	Marten, Coyote	0.07	78.37	4	164.89	10.42	0.00
	Cameras	0.05	80.54	3	167.16	12.70	0.00
	ElevMn	0.05	80.62	3	167.32	12.85	0.00
	Coyote, Cameras	0.05	80.54	4	169.22	14.75	0.00
	Coyote	0.00	84.52	3	175.13	20.66	0.00
Marten	BASE (= ElevMn - ElevSTD + pct56MD + HWYm)	0.27	119.11	6	250.51	0.00	0.27
	BASE, RedFox	0.28	118.43	7	251.25	0.74	0.18
	BASE, Cameras	0.27	118.64	7	251.66	1.16	0.15
	BASE, Coyote	0.27	118.94	7	252.27	1.76	0.11
	BASE, RedFox, Cameras	0.28	118.02	8	252.54	2.03	0.10
	BASE, RedFox, Coyote	0.28	118.11	8	252.72	2.21	0.09
	BASE, Coyote, Cameras	0.28	118.41	8	253.32	2.81	0.07
	BASE, RedFox, Coyote, Cameras	0.28	117.85	9	254.33	3.82	0.04
	ElevMn	0.12	144.11	3	294.30	43.79	0.00
	RedFox, Coyote	0.06	153.52	4	315.17	64.66	0.00
	RedFox, Coyote, Cameras	0.06	153.14	5	316.49	65.98	0.00
	RedFox	0.03	158.14	3	322.35	71.84	0.00
	RedFox, Cameras	0.03	157.99	4	324.12	73.61	0.00
	Coyote, Cameras	0.03	158.23	4	324.59	74.08	0.00
	Coyote	0.02	159.59	3	325.27	74.76	0.00
	Cameras	0.01	162.47	3	331.02	80.51	0.00
Coyote *	ElevMn	0.04	171.29	4	292.68	0.00	0.57
	BASE (= -ElevMn + pctBAR + pctHRB + pctSHB + pctOTH + pct34MD + pct34sp + pct56MD)	0.08	164.47	11	296.18	3.50	0.10
	BASE, Cameras	0.09	163.54	12	296.81	4.13	0.07
	BASE, RedFox	0.09	163.62	12	296.95	4.27	0.07
	BASE, Marten	0.08	164.12	12	297.79	5.11	0.04
	BASE, Marten, Redfox	0.09	163.04	13	298.18	5.51	0.04
	BASE, RedFox, Cameras	0.09	163.04	13	298.19	5.51	0.04
	BASE, Marten, Cameras	0.09	163.05	13	298.19	5.52	0.04
	BASE, Marten, RedFox, Cameras	0.09	162.36	14	299.28	6.60	0.02
	Marten, Cameras	0.02	176.30	5	303.07	10.40	0.00
	Marten	0.01	177.65	4	303.25	10.57	0.00
	Marten, RedFox	0.01	176.76	5	303.84	11.16	0.00
	Cameras	0.01	178.20	4	304.16	11.48	0.00
	Marten, RedFox, Cameras	0.02	175.79	6	304.31	11.64	0.00
	RedFox	0.00	178.86	4	305.25	12.57	0.00
	RedFox, Cameras	0.01	178.08	5	306.03	13.35	0.00

* overdispersion present. Correction factor $\hat{c} = 1.204$ used to calculate QAICc instead of AICc.

Table 15: Parameter estimates and odds ratios for the most parsimonious multivariate models for red fox and coyote. Marten are not included here because in both summer and winter their most parsimonious model was the landscape-only model resulting from the stepwise logistic regression; see Table 13. As in Table 13, ElevMn and HWYm have been multiplied by 100 so that their odds ratios reflect a 100 m change.

A) Summer

Species	Effect	Estimate	Parameter Std Error	Lower CI	Upper CI	Estimate	Odds Ratio Lower CI	Upper CI
Red Fox	Intercept	-30.22	9.24	-48.50	-11.94	0.00	0.00	0.00
	ElevMn * 100	1.46	0.47	0.54	2.38	4.30	1.71	10.82
	pctSHB	-0.21	0.10	-0.40	-0.02	0.81	0.67	0.98
	pctHRB	-0.90	0.34	-1.58	-0.23	0.41	0.21	0.80
	HWYm * 100	0.25	0.10	0.05	0.46	1.29	1.05	1.58
	COYOTE	1.62	0.71	0.21	3.03	5.03	1.23	20.59
Coyote	Intercept	1.15	0.83	-0.50	2.80	3.16	0.61	16.42
	ElevSTD	-0.02	0.01	-0.04	0.00	0.98	0.96	1.00
	pct34MD	-0.03	0.01	-0.05	-0.01	0.97	0.95	0.99
	REDFOX	0.80	0.42	-0.03	1.64	2.23	0.97	5.16

B) Winter

	Term	Estimate	Parameter Std Error	Lower CI	Upper CI	Estimate	Odds Ratio Lower CI	Upper CI
Red Fox	Intercept	-10.32	2.19	-14.64	-6.01	0.00	0.00	0.00
	ElevMn * 100	0.35	0.11	0.14	0.57	1.42	1.15	1.76
	pct56MD	0.03	0.01	0.01	0.06	1.04	1.01	1.06
	HWYm * 100	0.04	0.02	0.00	0.09	1.04	1.00	1.09
	CAMERAS	0.54	0.23	0.10	0.99	1.72	1.10	2.69
Coyote	Intercept	3.38	1.10	1.21	5.55	29.49	3.36	258.46
	ElevMn * 100	-0.23	0.06	-0.36	-0.11	0.79	0.70	0.90

Table 16: Pairwise species associations at cameras within grid cells where both species of the pair were detected.

Season	Species Pair	Cells	Cameras Total	Both	Final	p-value
Summer	Coyote + Marten	5	10	4	6	1.000
	Coyote + Red fox	4	12	1	7	1.000
	Marten + Red fox	8	26	10	21	0.586
Winter	Coyote + Marten	13	25	12	19	0.222
	Coyote + Red fox	9	23	8	17	0.131
	Marten + Red fox	12	28	10	21	0.032

Cells: number of cells where both species were detected
Total: number of cameras within these cells
Both: number of cameras where both species detected
Final: final number of cameras used in the analysis. Cameras operational <28 nights were not included unless both species were detected.
p-value: results of Fisher exact test, 2-tailed.

Figure 10: Camera sampling in the Lassen Peak region, 1992-2002 (n = 998). 95% minimum convex polygons delimit detection areas for red fox (red), marten (green) and coyote (blue).

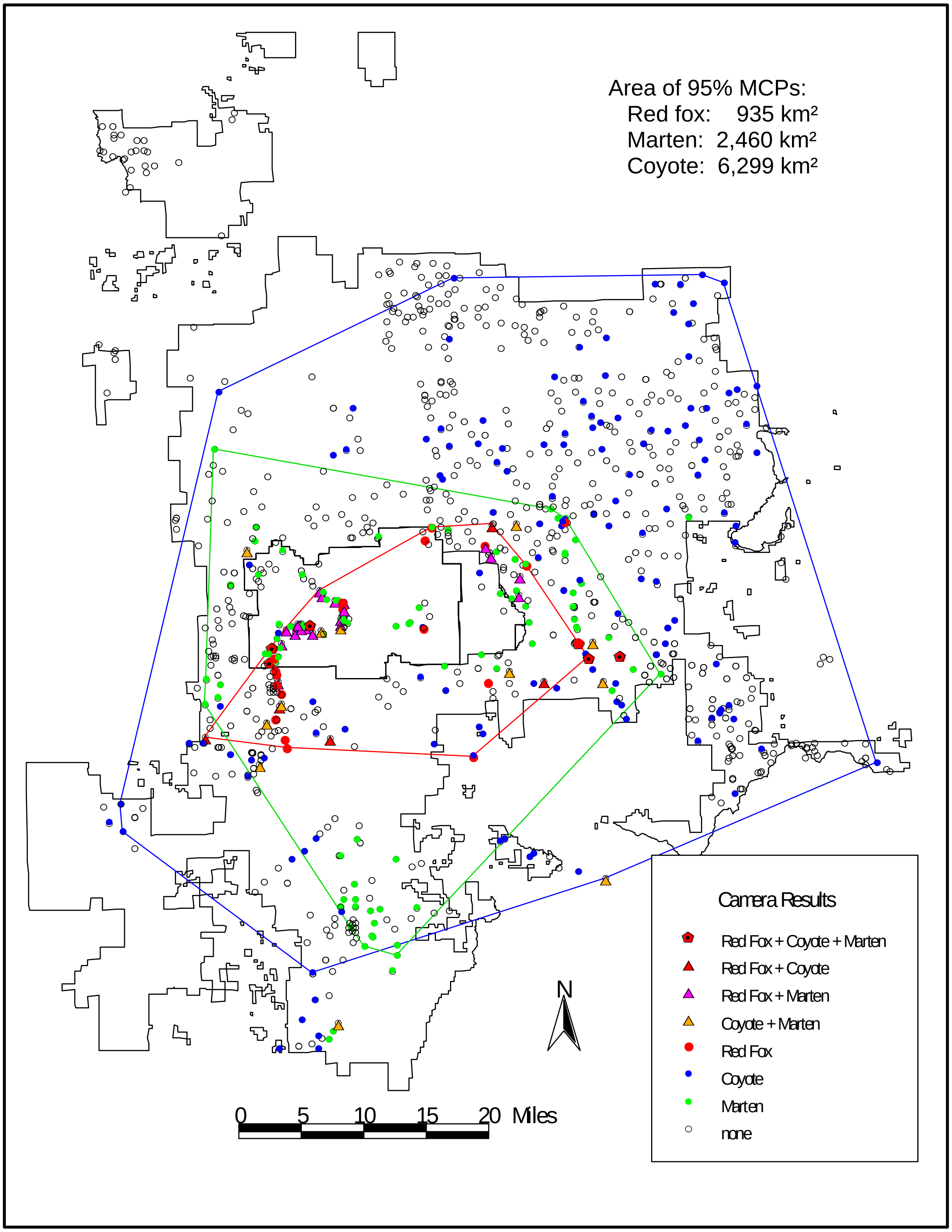


Figure 11: Distribution of seasonal camera sampling of 2.6 km² (1 mi²) grid cells. Open boxes indicate cells sampled in summer (n = 148) and dark circles indicate cells sampled in winter (n = 301). Cells with both symbols (n = 24) were sampled in both seasons.

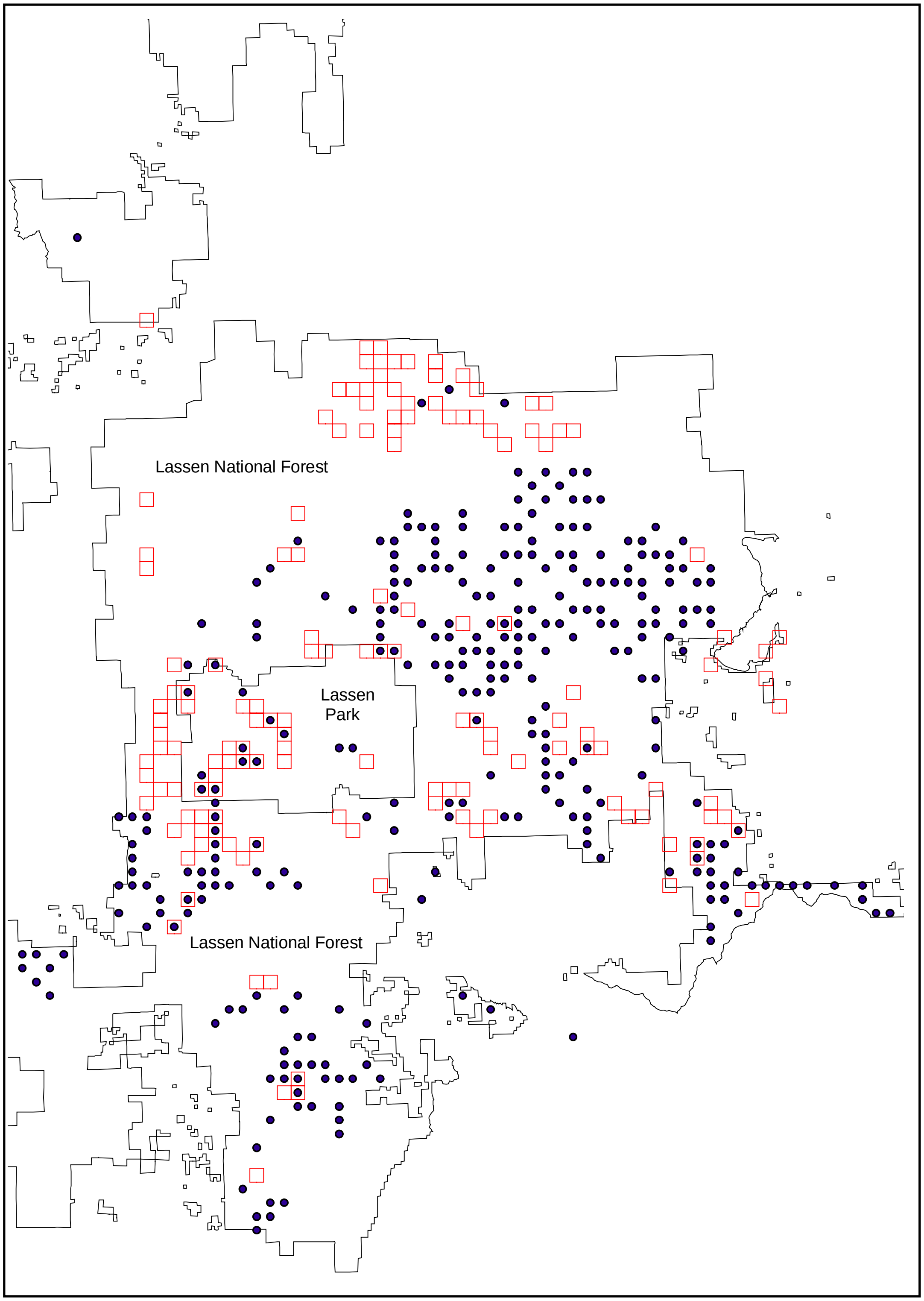


Figure 12: Distribution of red fox, marten and coyote detections in summer grid cells.

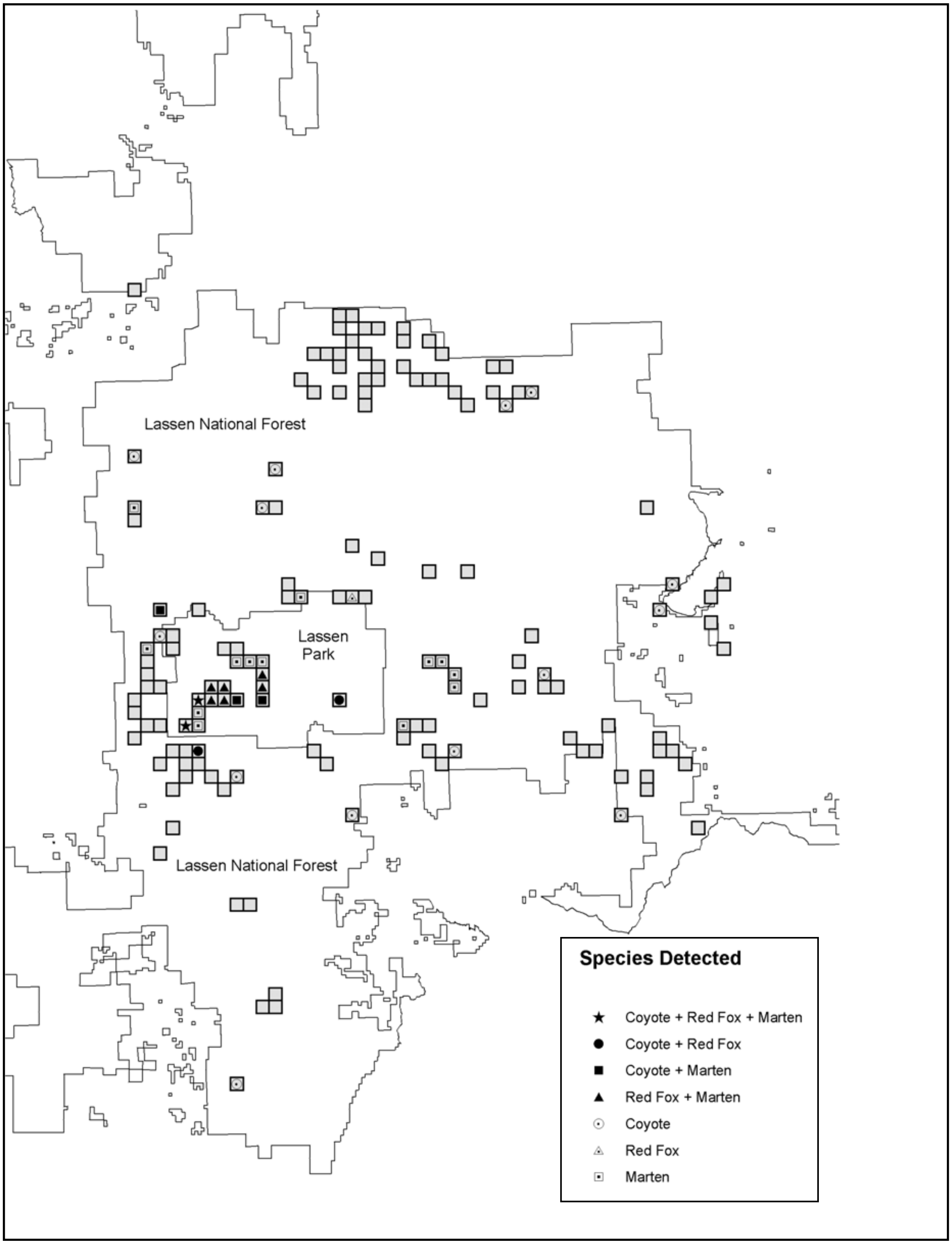
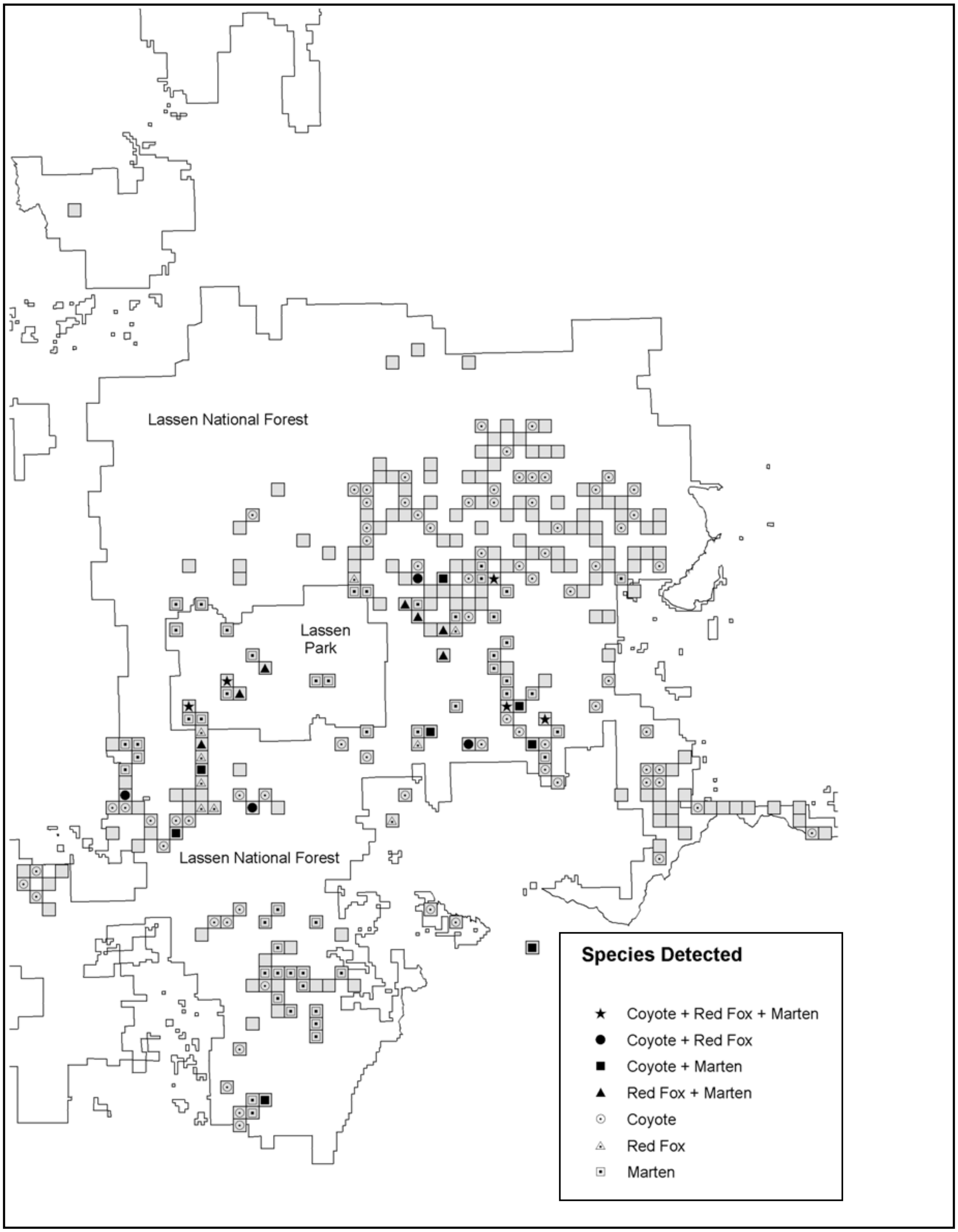


Figure 13: Distribution of red fox, marten and coyote detections in winter grid cells. Note the expanded detection area of red fox and marten to the south and east of Lassen Park, as compared to summer (Figure 12).



CHAPTER 3

ACTIVITY PATTERNS OF SYMPATRIC RED FOX, COYOTE AND MARTEN IN THE LASSEN PEAK REGION

INTRODUCTION

Carnivores may modify their temporal activity patterns to reduce interactions with sympatric competitors (Case and Gilpin 1974, Schoener 1974). Specifically, the smaller competitor usually alters its activity pattern to avoid encountering the larger, dominant competitor (Crabtree and Sheldon 1999, Palomares and Caro 1999). Agonistic interactions between red fox (*Vulpes vulpes*) and coyote (*Canis latrans*) have been well documented (Litvaitis 1992, Johnson et al. 1996). However, most of these studies (e.g., Voigt and Earle 1983, Major and Sherburne 1987, Sargeant et al. 1987, Harrison et al. 1989, Sargeant and Allen 1989, Gosselink et al. 2003) have been conducted in eastern and midwestern North America at elevations below 1500 m and have concentrated on spatial, not temporal, avoidance. Interactions between red fox and coyote have been poorly documented in the mountainous regions of the western United States except for a few studies in Yellowstone National Park (Gese et al. 1996, Crabtree and Sheldon 1999).

The Cascade and Sierra Nevada mountains of California comprise the range of the critically endangered Sierra Nevada red fox (*V. v. necator*) (Schempf and White 1977, CDFG 2004). Agonistic interactions with coyotes and other sympatric carnivores represent a potentially important threat to the survival and recovery of *V. v. necator* (Campbell and Perrine *in prep*). The American marten (*Martes americana*) is another common carnivore within the historic range of the Sierra Nevada red fox and with similar habitat use (Grinnell et al. 1937, Schempf and White 1977, Zeiner et al. 1990). Competitive interactions between red fox and *Martes* sp. have been studied in Europe (Lindstrom 1989, Storch et al. 1990, Overskaug 2000) but not in North America despite the range overlap between these species.

Red fox and coyote are primarily nocturnal and crepuscular, becoming active at twilight and foraging until dawn, although both may occasionally be active during the day (Ables 1975, Voigt 1987, Bekoff and Gese 2003). Both canids may become more nocturnal to avoid interactions with humans (Kavanau and Ramos 1975, Eguchi and Nakazono 1980, Weber et al. 1994, Kitchen et al. 2000). The daily activity patterns of marten are highly variable, with activity periods distributed throughout the 24-hour diel period (Powell et al. 2003). Seasonal variations in activity pattern of all 3 species may be linked to temperature, prey availability, reproductive status or other factors (Ables 1975, Bekoff and Gese 2003, Powell et al. 2003).

The diel activity patterns for red fox, coyote and other carnivores are driven largely by changes in photoperiod (Kavanau and Ramos 1975). Unfortunately, many field studies of red fox and coyote diel patterns to date have utilized time periods defined by anthropogenic clock times (e.g., “6-9 AM”) that do not maintain a constant relationship to seasonal changes in photoperiod, especially at higher latitudes. The primary goal of this project was to examine the diel activity patterns of sympatric red fox, coyote and marten relative to local photoperiod. Departures from their activity patterns in other regions, especially where the other species are not present, would suggest that competitive interactions may be occurring in the Lassen region.

To date, radio telemetry has been the primary means of determining activity patterns. Tip switches, activity sensors and fluctuations in signal amplitude can all be used to detect movement by a collared animal (Mech 1983, Rodgers 2001). In the past decade, camera traps have become increasingly common in wildlife research (Cutler and Swann 1999). Because camera traps can record the time of each detection event (Kucera and Barrett 1993), they can be used to compile activity patterns for multiple sympatric species without capture or telemetry. However, the detection biases of camera stations remain poorly quantified. In particular, no published studies have directly compared the activity patterns generated by telemetry and camera station methods. The utility of camera traps for determining activity patterns will be limited until such comparisons are conducted. Therefore, a secondary goal of this study was to directly compare red fox activity patterns from telemetry and camera stations.

METHODS

I captured red foxes in boxtraps (Tomahawk Live Trap Co., Tomahawk, WI) baited with 2 rancid chicken legs, commercially-available fox urine and Gusto or Canine Call trapping lure (M&M Fur Company, Bridgewater, SD). Boxtraps were pre-baited for 2 weeks to increase probability of capture. Trapping effort was year-round and was concentrated in the western half of Lassen Volcanic National Park and the adjacent Lassen National Forest. Captured red foxes were fitted with radio collars (Telonics, Inc., Mesa, AZ) containing activity sensors. Collared foxes were located approximately 3 times per week, with at least 1 location in each of 3 time bins: 0600-1359h, 1400-2159h, and 2200-0559h. At each bearing I noted whether the fox was “active” or “not active” based upon the telemetry signal. I generated activity profiles for each collared fox based on the proportion of the bearings that were active for each hour.

I created similar activity profiles for red fox, coyote and marten using the date-time stamps of their detections at baited TrailMaster camera traps (Goodson and Associates, Lenexia, KS) throughout the study area. Both passive (models TM 500 and 550) and active (TM 1500 and 1550) camera trap sensors were used. Camera traps were placed using several different sampling protocols, including opportunistic placement in areas where the target species were known to occur. Camera traps used the same attractants as the boxtraps but were not pre-baited. At each camera trap, detection times were recorded by 2 devices: the camera's date-time stamp and the sensor unit's internal memory. I checked each station weekly to ensure that both devices kept the correct time and to refresh the attractants, change the film and keep the station in good working order.

I obtained the daily sunrise and sunset times for Lassen Peak from 1998 through 2002 from the U.S. Naval Observatory (http://aa.usno.navy.mil/data) and corrected for Daylight Savings Time as necessary. I divided each 24-hour day into 4 periods: "dawn" = sunrise ± 2 hr; "dusk" = sunset ± 2 hr; "day" = time between when dawn ended and dusk began; "night" = time between when dusk ended and dawn began. Baited camera traps often acquire multiple photos of the same animal during a single feeding bout, and these detections are not independent. To reduce this pseudoreplication (Hurlbert 1984), I eliminated photos of the same species (or, for radio-collared red foxes, of the same individual) detected at the same photostation within a pre-determined time after the first photograph ("time lag"). I compared how 1 hr, 5 hr and 8 hr time lags affected the resulting activity profile. To be conservative, I used the 8 hr time lag for all statistical analyses.

To assess seasonal patterns, I defined “summer” as 1 May – 31 October and “winter” as 1 November – 30 April for both telemetry and camera data. These dates corresponded to the usual snow-free and snow-cover periods in the study area. I used chi-square tests to examine whether the species’ detections were distributed proportionally to the amount of time within the 4 time periods, to assess seasonal differences in activity pattern within species and to compare activity patterns among species. If the chi-square test indicated a significant difference I conducted follow-up tests to identify which individual categories were used more or less than expected (Neu et al. 1974, Alldredge and Ratti 1992). These comparisons used a Bonferroni correction to maintain a “family” alpha of 0.05 for each test. Only the camera station data were used for comparisons among seasons and species, as the telemetry data were limited to red fox.

RESULTS

I captured and tracked a total of 5 (4 females, 1 male) red foxes from 2000-2002. Recaptures of these individuals and the low number of uncollared red fox detected at camera stations in the western half of Lassen Park suggest that these 5 individuals comprised virtually all of the local red fox population during this period. I acquired an average of 626 (range: 137-1029) telemetry bearings per fox (Table 17). Due to the sampling schedule used to conduct telemetry, no bearings were acquired from 0300-0600h and 2000-2200h.

The 5 collared red foxes had similar activity profiles in both summer and winter (Figure 14). Activity was low (<20% bearings active) during the day and was high (>60% bearings active) at night. In both summer and winter there was a sharp decline in activity several hours before daybreak (0300-0400h in summer, 0200h in winter), although sample sizes for these times were low. There was individual variation from these patterns, with the male fox (M01) in particular more active during the day and less active at night than the other foxes.

I operated a total of 144 camera traps in the study area from 1997 through 2002. Red fox were detected at 27 cameras (18.8%) yielding a total of 349 photos. Detection of the same collared red foxes at multiple sites indicated that not all camera traps were independent. Eliminating the photos taken >1 hr after the first photo at a feeding bout reduced the number of photo detections by 46-50% depending on season; increasing the time lag to 5 hr or 8 hr had little additional effect on sample size or activity profile (Figure 15). Telemetry and camera detections produced similar activity profiles, although camera detections were consistently lower than telemetry activity at the same time (Figure 16). In summer, activity levels between 2300h and 0400h via camera detections were far lower than those from telemetry. In both summer and winter, camera detections were rare during daylight hours, then peaked following sunset, with a secondary peak in the hours prior to sunrise (Figure 16).

Marten and coyote were detected at 47 (32.6%) and 19 (13.2%) camera stations, yielding a total of 535 and 38 photos, respectively. As with red fox, the choice of 1, 5 or 8 hr time lag resulted in little difference in the marten activity pattern (Figure 17). Use of the 8 hr lag resulted in 278 (238 summer, 40 winter) marten detections and 22 (17 summer, 5 winter) coyote detections. Marten detections were distributed throughout the diel period although they also had activity peaks soon after sunset in both summer and winter (Figure 17). Diurnal detections were more common in winter than in summer. In contrast, coyote were never detected during daylight hours and were most often detected from 0200-0300h (Figure 18). There were too few coyote detections to assess seasonal trends.

The distribution of red fox detections was significantly different from the proportion of time within the 4 diel periods in summer ($\chi^2 = 70.93$, 3 df, $p < 0.001$) and winter ($\chi^2 = 18.15$, 3 df, $p = 0.004$). In summer, there were more red fox detections than expected during Dusk and Night and fewer than expected during Day (Table 19). Detections at Dawn were proportional to the amount of time in that period. In winter, there were fewer detections than expected during Day, but the number of detections in the other time periods were proportional to the time in each period.

Marten showed temporal selection in summer ($\chi^2 = 15.97$, 3 df, $p = 0.001$) but not winter ($\chi^2 = 2.89$, 3 df, $p = 0.410$). In summer, there were fewer marten detections during Day than expected by chance. The number of detections in the other time periods was proportional to the time in each period, although there was a trend of more detections than expected during Dusk (Table 19). Coyote detections were not analyzed due to small seasonal sample sizes.

There was no seasonal difference in activity pattern for red fox ($\chi^2 = 1.81$, df = 3, $p = 0.613$) or marten ($\chi^2 = 4.47$, df = 3, $p = 0.215$), and coyote seasonal patterns could not be assessed due to small sample size. I therefore pooled the seasonal data for pairwise comparisons between species. The distribution of marten detections was significantly different than red fox ($\chi^2 = 46.26$, df = 3, $p < 0.001$) and coyote ($\chi^2 = 16.55$, df = 3, $p < 0.001$). Follow-up tests indicated that marten were significantly more diurnal and the canids were significantly more nocturnal; their proportions of detections at Dawn and Dusk did not differ (Table 20). Activity patterns for red fox and coyote were not significantly different ($\chi^2 = 4.76$, df = 3, $p = 0.190$), but there was a trend for coyote and red fox activity peaks to be out of phase during summer. No coyote detections were recorded during the primary red fox activity peak at 2100-2200h and red fox detections were low during the primary coyote activity peak at 0200-0300h (Figures 15, 17). Coyote sample sizes were too low to test these fine-scale patterns statistically.

DISCUSSION

Radio telemetry and camera traps indicated that red fox in the Lassen Peak region of northern California were largely inactive during daylight hours but roused after sunset and remained active until dawn. This is the usual red fox activity pattern (Ables 1975, Lariviere and Pasitschniak-Arts 1996) and has been widely documented in many regions and habitats worldwide (e.g., Storm 1965, Ables 1975, Eguchi and Nakazono 1980, Lloyd 1980, Voigt and Macdonald 1984, Cavallini 1992, Cavallini and Lovari 1994, Weber et al. 1994, Fedriani et al. 1999, Meek and Saunders 2000). Red fox in some areas may become more diurnal in winter (Ables 1975, Lloyd 1980) but this is not universal (Eguchi and Nakazono 1980, Weber et al. 1994). Lassen red fox had no seasonal difference in activity pattern after controlling for changing photoperiod. None of the radio-collared females reproduced during this study, so their activity patterns were not affected by the presence of pups.

Activity patterns recorded by camera traps were similar, but not identical, to the patterns documented by telemetry. Both telemetry and camera traps reflected the primarily nocturnal habits of red fox, but the cameras also indicated activity peaks just after sunset and prior to sunrise. These activity peaks were not an artifact of the time lag used (Figure 15). Unfortunately, little telemetry data was available during these time periods. Similar crepuscular patterns have been noted in many other red fox populations (Ables 1975, Cavallini and Lovari 1994, Fedriani et al. 1999), including Washington's Cascade Range (Aubry 1983). Camera traps also recorded lower activity levels during daylight hours than did telemetry. This was probably caused by the baited camera traps detecting foraging and ranging behavior, which is primarily nocturnal, whereas the telemetry also detected grooming, brief travel among day rests and other non-foraging movements that may be common during the day (Ables 1975, Voigt 1987).

The baited camera traps often acquired numerous photographs of the same individual animal during a single visit as it consumed the bait. These surplus photographs are not independent detections because they occur during the same feeding bout. It is necessary to use a time lag following the first photograph to differentiate lingering at the bait from distinct foraging bouts. For example, when Pierce et al. (1998) used camera traps at deer carcasses to test for temporal partitioning among social classes of mountain lions, they used only the first detection of each lion each evening to indicate its arrival time at the carcass. My results indicated that applying a 1 hr time lag reduced the number of photo detections by 40-50% but had little effect on the shape of the activity profile if drawn as a proportion of the total number of usable photographs. Use of longer lag times had little additional effect on the sample size or activity profile (Figures 15, 17 and 18). Red fox, coyote and marten could easily remove or consume the bait used in this study in <1 hr. Use of larger quantities of bait, such as entire deer carcasses or mounds of frozen fish, may result in longer feeding bouts and necessitate a longer lag time. In general, researchers using baited camera traps should use a lag time instead of the raw number of detections, and the lag time should exceed the length of the feeding bout.

Although all 3 target species were primarily nocturnal, marten had the greatest proportion of daytime detections (Table 18; Figures 15, 17, 18). Although marten were significantly more active than either canid during daytime, the majority of their activity remained in the crepuscular or nocturnal periods. These results do not conflict with previous studies that have found that marten may be active throughout the diel period (Zielinski et al. 1983, Thompson and Colgan 1994, Drew and Bissonette 1997), but direct comparisons are difficult due to different methods of partitioning the diel period. For marten in Newfoundland, Canada, in winter, the proportion of active telemetry fixes was highest (60% to 70%) during the nocturnal hours, but 30% to 40% of daytime fixes were also active (Drew and Bissonette 1997). In California’s Sierra Nevada mountains, the highest proportion of active telemetry fixes (>60% active) was during the dawn and daylight periods in both summer and winter, but nocturnal activity was higher in winter than in summer (Zielinski et al. 1983). In contrast, marten in Ontario were more diurnal in winter, possibly to limit activity during periods of extreme cold (Thompson and Colgan 1994). I found no seasonal change in marten activity patterns after controlling for changing photoperiod. Diurnal activity appeared greater in winter than in summer (Figure 17) but this was not statistically significant. A possible reason for this discrepancy would be that previous studies have addressed the total *length* of activity bouts (e.g., Thompson and Colgan 1994), whereas the cameras detected the *distribution* of such bouts throughout the diel period. Additionally, marten may have extensive subnivean movement in winter (Zielinski et al. 1983, Powell et al. 2003) and such movements may be more readily detected by telemetry than by camera traps above the snow. However, it is reasonable to assume that active, foraging marten would be attracted to bait atop the snow and therefore be photographed (Zielinski and Kucera 1995).

Of the 3 target carnivores, the fewest detections were obtained for coyotes. Small sample size precluded statistical analysis of these data except when both seasons could be pooled (Zar 1999). My cameras never detected coyote during the day (Table 18) but it is unclear whether this is an unbiased depiction of their activity patterns. Throughout their range, coyotes are predominantly nocturnal and crepuscular but may be active at any time of day (Bekoff and Gese 2003). In an agricultural area of northern California, coyotes were active throughout the diel period, but were most active at night (2100–0259h) and least active during the day (1200–1759h) (Neale and Sacks 2001). Similarly, coyotes in northern Wisconsin were most active between 1800h and 0600h (Smith et al. 1981). Persecution by humans may be a major factor in coyote activity: where such pressure is high, coyotes may reduce their daytime activity (Kavanau and Ramos 1975, Kitchen et al. 2000). Persecution of coyotes on my study site was minimal and probably insufficient to cause fully nocturnal behavior. It is possible that activity patterns from telemetry included non-foraging movements such as grooming and short travels among day rests, while baited cameras detect coyotes only during their more extensive nocturnal foraging movements.

In the few studies using cameras to document coyote activity, diurnal photo detections were uncommon. In the Santa Monica Mountains of southern California, approximately 90% of coyote photo detections were nocturnal or crepuscular (Fedriani et al. 2000). Likewise, in the foothills of the northern Sacramento Valley, 83% of adult coyote photo detections at unbaited cameras occurred between sunset and sunrise (Sequin et al. 2003). Most detections occurred between 2300h and 0000h, with secondary peaks just after sunset and just before sunrise (E. Sequin, unpublished data). However, telemetry revealed that these coyotes were active throughout the diel period, indicating that they might be detecting and avoiding camera stations during daytime (E. Sequin, unpublished data). Detectability was further biased by social status, with territorial alphas never photographed in their core areas (Sequin et al. 2003). It is unknown whether baited cameras share these detection biases, but temporal activity patterns derived from baited cameras should be interpreted with caution until such biases can be quantified. Red fox and marten do not have the pack structure or dominance hierarchy that coyotes do and are not as wary of camera traps, and there is no evidence that their camera detections are biased.

Lassen red fox, coyote and marten activity periods overlapped extensively, especially at night, indicating that these species were not avoiding each other temporally. In particular, red fox and coyote had the same distribution of detections throughout the diel period. However, some fine-scale temporal portioning may be occurring, with the red fox activity peak coinciding with a lull in coyote activity and vice versa. Such temporal avoidance, if present, is minor compared to that documented in Yellowstone National Park, where red fox were predominantly nocturnal while coyotes were more diurnal and crepuscular (Crabtree and Sheldon 1999). Camera stations would likely not detect fine scale avoidance involving both temporal and spatial patterns, e.g. with red fox active at the same time as coyote but avoiding direct interaction with them. Such avoidance may also be difficult to detect via telemetry (Kitchen et al. 1999). Marten were significantly more diurnal than red fox or coyote, but this pattern applies throughout much of their range and is probably not a response to the presence of the canids. Both marten and red fox had activity peaks at dusk in both seasons and at dawn in the summer (Figures 15 and 17). Although red fox may occasionally kill marten (Drew and Bissonette 1997, Palomares and Caro 1999), such antagonism is apparently not sufficient to preclude simultaneous activity in the Lassen region.

This study demonstrates that camera traps can successfully generate activity profiles for sympatric species and that such profiles, at least for red fox and marten, are in broad agreement with the results from other methods and study sites. It also demonstrates that red fox activity profiles generated by telemetry and by camera traps are in close agreement. But the choice of cameras over telemetry for such purposes incorporates important trade-offs. Camera traps provide the opportunity to study species less invasively than telemetry, but at the cost of deeper insight into the behavior of individual animals, including knowledge of their sex, age class, social rank and reproductive status. However, telemetry can be costly and impractical, particularly for studies of multiple sympatric species, rare species and in rugged terrain. Furthermore, data from activity sensors can be ambiguous unless the animal is observed visually.

Camera traps represent an important alternative to telemetry, especially when the latter is impractical, but may record different movement types than does telemetry. Activity patterns resulting from camera detections should be viewed with caution until the detection biases of camera traps are more fully documented.

Table 17: Number of telemetry fixes and monitoring dates for radio-collared Lassen red fox.

Red Fox	Telemetry Fixes	Start Date	End Date
F01	856	March 2000	December 2002
F02	915	April 2000	October 2002
F03	1029	August 2000	December 2002
F05	195	December 2000	May 2001
M01	137	May 2000	November 2000

Table 18: Distribution of seasonal detections of carnivores at baited camera stations. Detections of the same species at the same station within 8 hrs have been removed as pseudoreplicates.

Season	Period	Red Fox	Marten	Coyote
Summer	Dawn	18	37	2
	Day	5	70	0
	Dusk	36	57	3
	Night	55	74	12
Winter	Dawn	11	3	1
	Day	1	14	0
	Dusk	13	6	0
	Night	27	17	4

Summer: 1 May through 31 October.
Winter: 1 November through 30 April.
Dawn: Sunrise ± 2 hr.
Dusk: Sunset ± 2 hr.
Day: After dawn ends and before dusk begins.
Night: After dusk ends and before dawn begins.

Table 19: Was the number of detections proportional to the amount of time in each diel period? Marten in winter was not tested because the overall chi-square test did not indicate significant departure from the diel proportions ($\chi^2 = 2.89$, 3 df, $p = 0.410$). Coyote sample size was too small for seasonal tests.

Season	Species	Period	Observed Proportion	95% CI lower	95% CI upper	Expected Proportion	Effect
Summer	Red Fox	Dawn	0.158	0.072	0.243	0.167	ns
		Day	0.044	-0.004	0.092	0.399	**avoid**
		Dusk	0.316	0.207	0.425	0.167	**select**
		Night	0.482	0.365	0.600	0.268	**select**
	Marten	Dawn	0.155	0.097	0.214	0.167	ns
		Day	0.294	0.220	0.368	0.399	**avoid**
		Dusk	0.239	0.170	0.309	0.167	ns
		Night	0.311	0.236	0.386	0.268	ns
Winter	Red Fox	Dawn	0.212	0.070	0.353	0.167	ns
		Day	0.019	-0.028	0.067	0.284	**avoid**
		Dusk	0.250	0.100	0.400	0.167	ns
		Night	0.519	0.346	0.693	0.383	ns

Table 20: Follow-up tests of whether species pairs were similarly distributed within diel periods. Coyote + Red fox is not included because the null hypothesis of identical distributions was not rejected ($\chi^2 = 4.76$, 3 df, $p = 0.190$). The below test is based upon the difference between 2 proportions, using an individual test alpha of 0.00625 to maintain a family alpha of 0.05 per pair.

Species Pair	Diel Period	Marten Proportion	Species 2 Proportion	ΔP	SE	Z	Signif? *
Marten + Red Fox	Dawn	0.144	0.175	0.031	0.036	0.87	
	Day	0.302	0.036	0.266	0.039	6.75	* *
	Dusk	0.227	0.295	0.069	0.043	1.61	
	Night	0.327	0.494	0.167	0.048	3.48	* *
Marten + Coyote	Dawn	0.144	0.136	0.008	0.078	0.10	
	Day	0.302	0.000	0.302	0.099	3.04	* *
	Dusk	0.227	0.136	0.090	0.092	0.98	
	Night	0.327	0.727	0.400	0.106	3.77	* *

* asterisks indicate significant results; the calculated Z value exceeds the critical Z value of 2.50.

Figure 14: Percentage of active telemetry bearings by hour for individual Lassen red fox. "Summer and "Winter" are as defined in Table 2. Arrows indicate the average time of sunrise and sunset for each season, with the shaded areas denoting Dawn and Dusk.

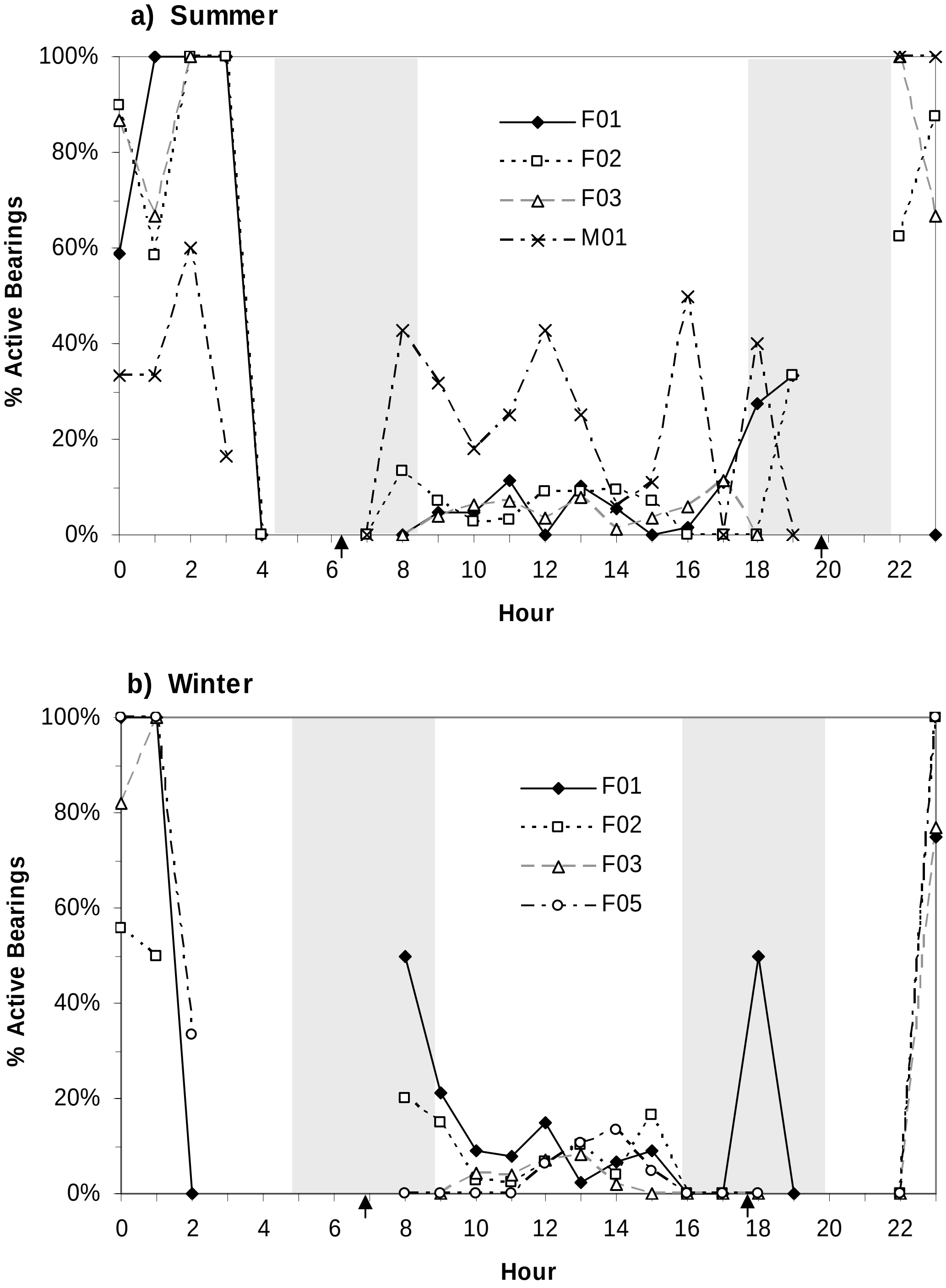
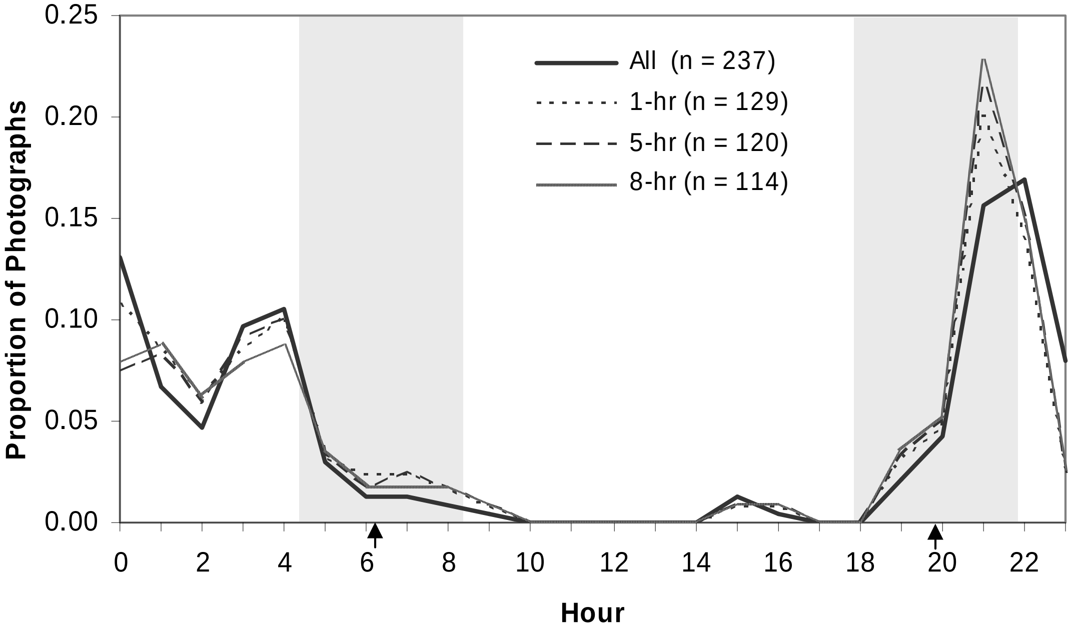


Figure 15: Hourly distribution of red fox photographs at baited camera traps. "All" incorporates all photos, whereas "1 hr", "5 hr" and "8 hr" denote different time periods before subsequent photos of the same individual at the same camera were included.

a) Summer



b) Winter

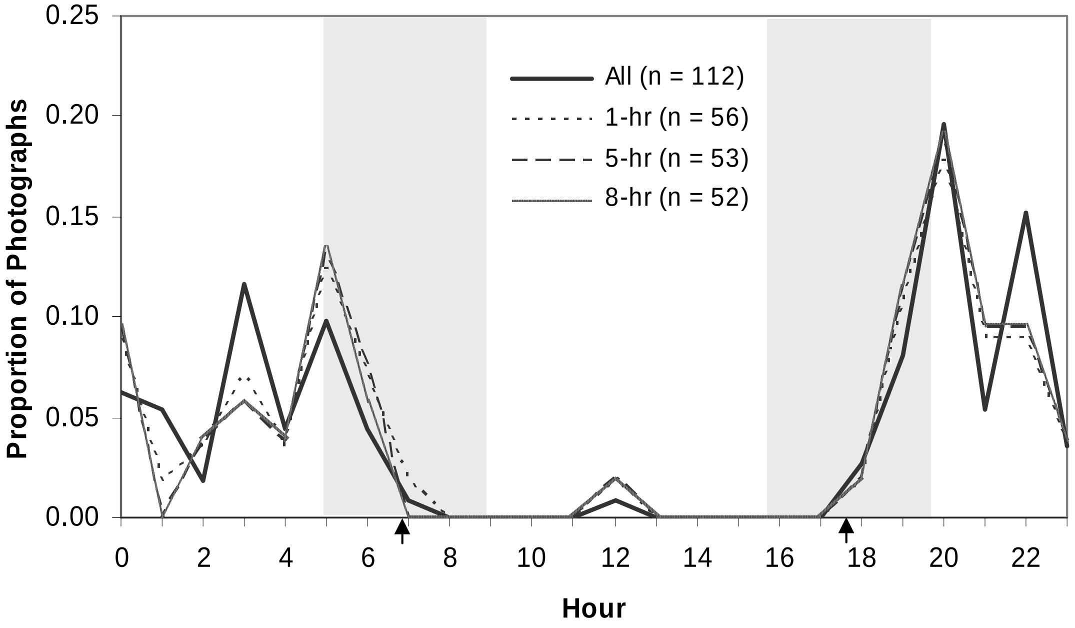
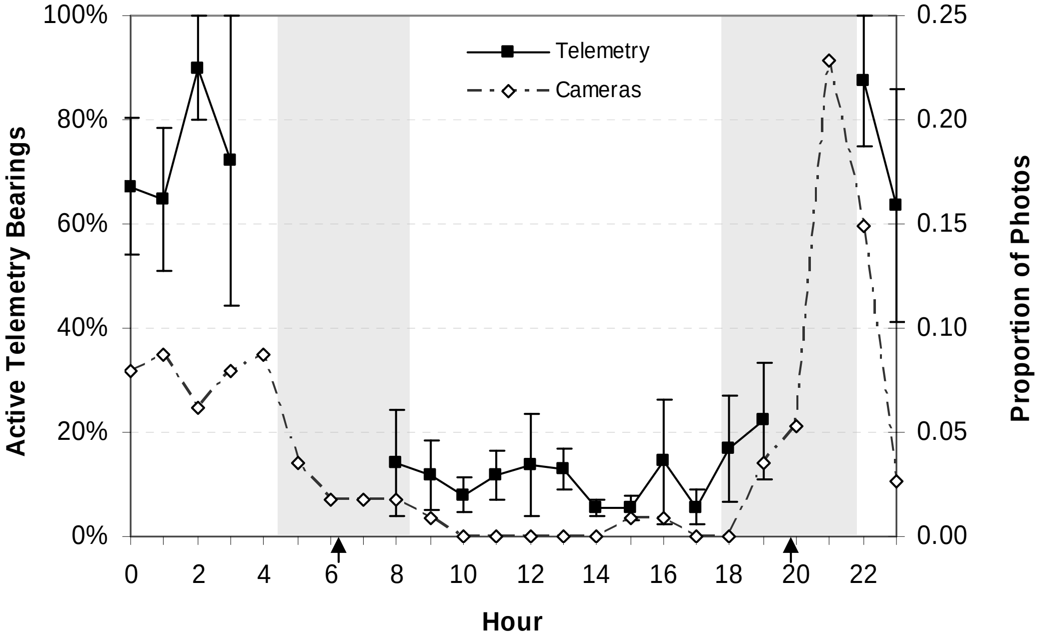


Figure 16: Comparison of red fox activity patterns generated from telemetry bearings and from camera trap detections using an 8 hr time lag. The telemetry profile is the mean (± SE) of the individual fox profiles from Figure 14; hours with data for <2 foxes have been omitted. Camera traps occasionally detected uncollared foxes in addition to the collared foxes.

a) Summer



b) Winter

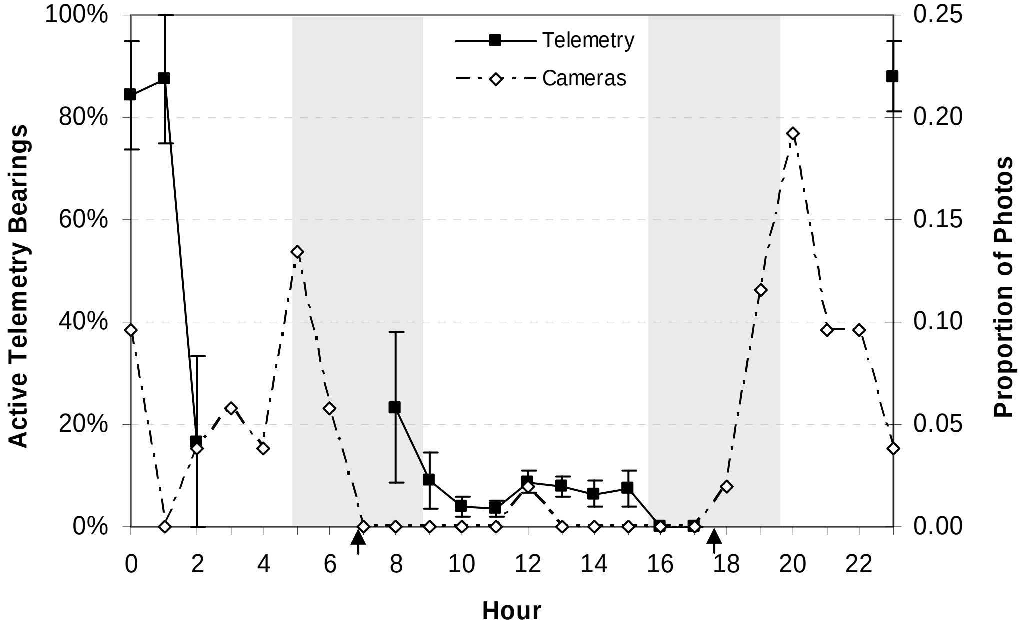
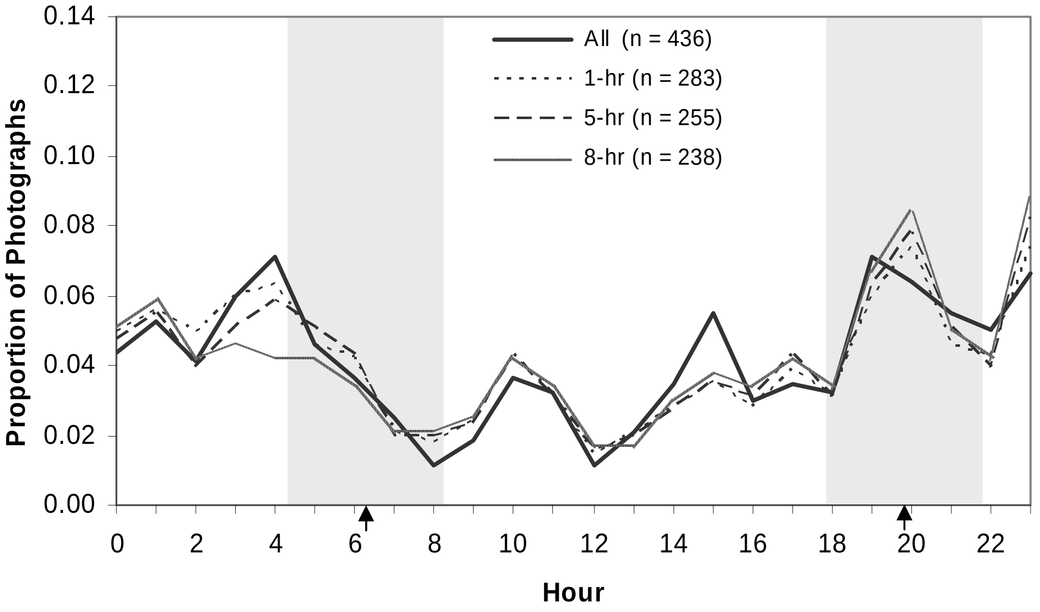


Figure 17: Hourly distribution of marten photographs at baited camera traps. Variables are the same as in Figure 15.

a) Summer



b) Winter

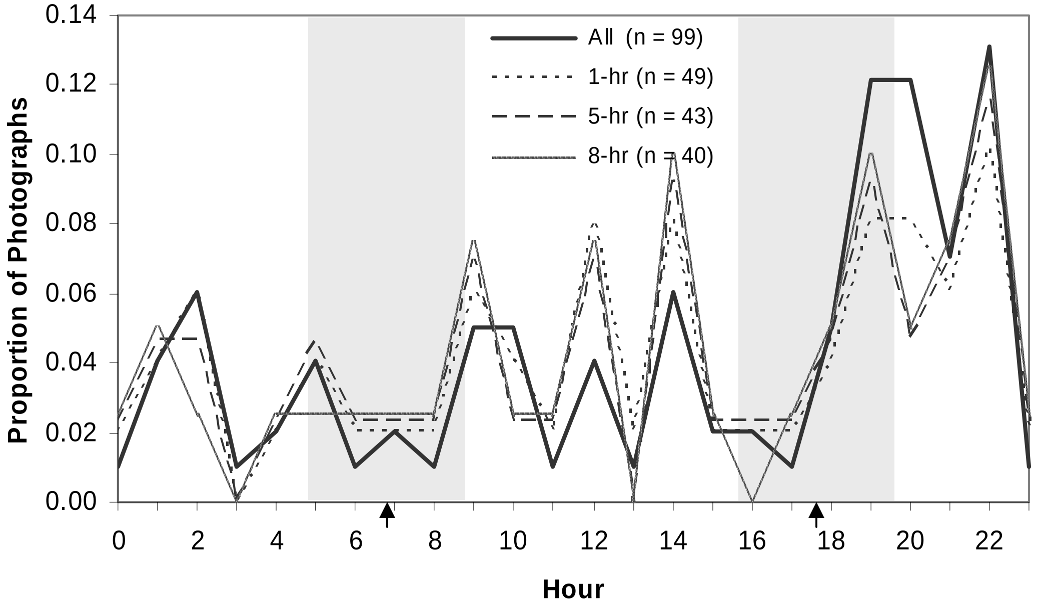
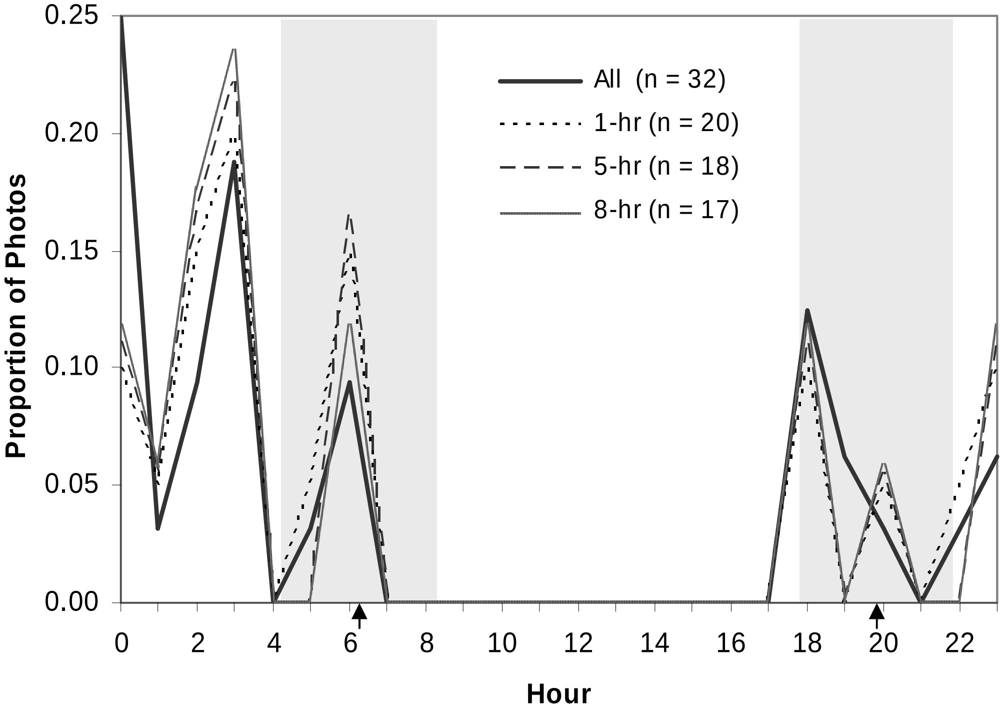


Figure 18: Hourly distribution of coyote photographs at baited camera traps in summer. Winter distribution could not be calculated due to small sample size, but consisted of 1 photo at 0100h, 0200h, 0500h and 2000h, and 2 photos at 1900h. Variables are the same as in Figure 15.



CHAPTER 4

HOME RANGE AND HABITAT USE OF RADIO-COLLARED MOUNTAIN RED FOXES

INTRODUCTION

Although the red fox (*Vulpes vulpes*) is among the world's most widely distributed and most thoroughly studied terrestrial carnivores (Lloyd 1980, Voigt 1987), the populations inhabiting the mountains of western North America are virtually unstudied (Aubry 1983). In California, the Sierra Nevada red fox (*V. v. necator*) is a State Threatened species and is considered critically endangered (CDFG 2004). Effective management of the Sierra Nevada red fox is hindered by a lack of basic ecological information (CDFG 1987, Aubry 1997). Its distribution and habitat associations have been described (Grinnell et al. 1937, Schempf and White 1977) based largely upon sighting reports and trappers' accounts, but no targeted ecological studies have been conducted. Specific details of home range size and composition, habitat selection for foraging and day rests, the extent of daily and seasonal movements, and estimates of reproduction and survival are currently unknown. *V. v. necator* "remains one of the few State-listed animals for which there is no information on current status other than periodic sightings filed mostly by inexperienced observers" (CDFG 1996: 17).

Radio telemetry can provide valuable insight into resource utilization and its effects on local population dynamics (White and Garrott 1990, Powell 2000, Garton et al. 2001). The goal of this study was to use telemetry to quantify resource utilization by red foxes in the Lassen region. Research objectives included documenting the size and composition of home ranges, daily and seasonal movements, and reproduction and mortality within the local population.

Research on the Lassen red fox population began in the winter of 1997-8, when Tom Kucera and biologists with the Lassen National Forest successfully captured and radio-collared a male and female red fox southwest of Lassen Park (Kucera 1999). My involvement began with pilot telemetry and camera sampling projects on these 2 animals in the summers of 1998 and 1999. My full-time research on the population began in March 2000 and continued through December 2002. Data and results presented in this chapter are largely from 2000-2002 but include the summer pilot projects when appropriate to present the most complete picture of red fox ecology in the region.

METHODS

Foxes were captured in boxtraps (Tomahawk Live Trap Co., Tomahawk, WI) baited with 2 rancid chicken legs, commercially-available fox urine and Gusto or Canine Call trapping lure (M&M Fur Co., Bridgewater, SD). Boxtraps were camouflaged with limbs and branches and were wired open and pre-baited for 2 weeks to increase capture success. Boxtraps with no evidence of red fox visitation during the pre-baiting session were not activated. Captured foxes were physically examined in the field and standard body measurements were recorded. Foxes were fitted with radio telemetry collars (Telonics Inc., Mesa, AZ) containing activity or mortality sensors and were marked with individually-identifying ear tags prior to their release at the site of capture. All capture and handling activities were in accordance with a Memorandum of Understanding with the California Department of Fish and Game (CDFG), U.C. Berkeley's Animal Care and Use Committee research protocol #R139, and state and federal collecting permits.

I used ground-based telemetry to determine the locations of collared foxes approximately 3 times weekly, with at least 1 location in each of 3 time bins: 0600-1359h, 1400-2159h and 2200-0559h. Locations of telemetry sites were determined using a Trimble GeoExplorer II GIS receiver. Fox locations were calculated using LOCATE II (Nams 2001) on ≥ 3 intersecting bearings. Location estimates with error polygons >100 ha were discarded. I attempted to obtain a visual sighting of each collared fox weekly by "walking in" on the telemetry signal. Additional locations were obtained through aerial telemetry (1-2 flights per month commencing in May 2000), photographs at camera stations, recaptures and sightings of collared animals. The locations of sightings reported by Lassen Park staff and visitors (Perrine and Arnold 2001) were estimated using ArcView GIS 3.2 (ESRI, Redlands, CA). The time of an individual telemetry location was calculated as the midpoint between the earliest and latest bearings used to calculate that animal's location. Captures were arbitrarily assumed to occur at 0200h. Aerial telemetry was usually conducted between 0800h and 1100h. The accuracy of aerial locations was assessed by a test collar with GPS coordinates; the pilot was unaware which collar was the test collar.

I used all available locations to generate 95% minimum convex polygons (MCPs) via the harmonic mean algorithm in the Animal Movement Extension (Hooge and Eichenlaub 1997) for ArcView GIS. To identify core use areas, I generated 50% fixed kernel isopleths using least-squares cross validation on a reduced data set of statistically-independent locations. This reduced data set did not contain sightings other than those achieved during telemetry efforts and included only the first detection of each fox at a camera station. The remaining telemetry and sighting locations were separated by at least 8 hr to minimize serial autocorrelation (Kernohan et al. 2001). This reduced data set was used for all statistical tests. I determined the elevation and vegetation characteristics of locations and home ranges using an existing 30 m digital elevation model and the US Forest Service "Existing Vegetation 1997" data layer (US Forest Service, Sacramento, CA, unpublished data). Vegetation classifications were based upon the California Wildlife Habitat Relationships (CWHR) system (Mayer and Laudenslayer 1988). Elevation and vegetation classifications were not ground-truthed. To be conservative, I grouped individual CWHR vegetation types into more general cover type descriptors for most analyses (see below). I obtained daily sunrise and sunset times for the study area from the U.S. Naval Observatory (http://aa.usno.navy.mil/data), and used these to allocate each fox location into 1 of 4 time periods: Dawn (sunrise ± 2 hr), Dusk (sunset ± 2 hr), Daytime (between Dawn and Dusk) and Nighttime (between Dusk and Dawn).

The study area boundary, representing the available habitat for the collared foxes, was determined by constructing the 98% MPC of all locations of all foxes. I compared the foxes' selection of habitat types within this area using chi-square analysis and follow-up tests on each habitat category (Neu et al. 1974, Alldredge and Ratti 1992). Separate analyses were conducted for each collared fox, thereby retaining the individual animal as the sample unit, and Bonferroni corrections were incorporated into the confidence intervals to maintain an overall significance level of 0.05 per test. Chi-square tests were also used to compare nighttime and daytime habitat usage, and t-tests were used to compare elevations between seasonal home ranges. Daily movements were quantified by calculating the straight-line distance between successive independent locations <24h apart. Analyses were conducted in JMP-IN 5.1 (SAS Institute Inc., Cary, NC) and Excel XP (Microsoft Inc., Redmond, WA).

RESULTS

During 2000 the 2 foxes captured in winter 1998 were re-captured and fitted with fresh telemetry collars, and 3 additional foxes (all female) were captured (Table 21). No additional individuals were captured after December 2000 despite ongoing trapping effort through May 2002. Therefore, a total of 669 trap nights yielded only 5 unique captures, a success rate of 0.7% despite pre-baiting. From 2000 through 2002, sightings or photo captures of uncollared foxes within the western half of Lassen Park were rare. The 5 captured animals likely represent virtually the entire red fox population within the study area at the time. These 5 foxes had a mean (± SD) body mass of 3.6 ± 0.4 kg. None of the females was pregnant or lactating at any capture. All 5 foxes were recaptured at least once, and F02 was recaptured a total of 17 times (Table 21). F02 shed her collar and ear tag in October 2000 but was recaptured and retagged shortly thereafter; she was called "F04" for the remainder of the study but these data were pooled under her original designation for all analyses.

Individual foxes were tracked for 3 to 60 months, yielding a total of 1,435 locations in the full data set of all location types (Table 22). The reduced data set of independent locations contained 840 locations, with 35 to 249 independent locations per fox (Table 23). Locations between 2200-0559h comprised only 13% of the reduced data set despite attempts to collect locations evenly throughout the diel period. Ground telemetry locations had a 95% error radius of 186 ± 245 m (n = 577). A sighting of the target animal was obtained in 8.5% of telemetry sessions. (A sighting was not attempted at every ground telemetry session, and when one was obtained its location was used instead of the estimated triangulation location.) Locations of test collars by aerial telemetry had a mean error of 589 ± 482 m (n = 48). No sightings of target animals were obtained during aerial telemetry.

The study area, as defined by the 98% MCP around the full set of all fox locations, encompassed most of the western half of Lassen Park plus a portion of the Lassen National Forest southwest of the Park roughly bounded by the communities of Mill Creek and eastern Mineral (Figure 19). The study area was 311.5 km^2 and was composed of 11 CWHR vegetative communities. I consolidated these to 5 cover types: barren, high-elevation conifer (consisting of the Red Fir and Subalpine Conifer CWHR communities), mid-elevation conifer (Lodgepole Pine, Sierran Mixed Conifer and White Fir), shrub (Montane Chaparral) and hardwood-herbaceous (Annual Grassland, Aspen, Montane Hardwood, Montane Riparian and Wet Meadow).

Home range and habitat use

The collared foxes had distinct seasonal movements between their summer and winter ranges, so the seasonal data were analyzed separately. The ranges were defined by the dates when a fox clearly transitioned from one center of activity to another. I used the full data set of all locations to identify the transition dates as closely as possible (Table 24). The specific transition dates varied slightly among individual foxes.

The foxes generally spent the summers at high elevations within the western half of Lassen Park. Summer home ranges (95% MCP, based upon >20 locations) ranged from 262 to 6,981 ha (Table 23). Mean summer MCP size varied among foxes but the mean across foxes ($n = 4$) was 2,323 ha. In summer, each fox demonstrated significant selection among the 5 available habitat types (all $p < 0.001$) (Table 25). All 4 foxes selected for barren areas and against mid-elevation conifer and hardwood-herbaceous cover types. In addition, F02 selected for high-elevation conifer and F03 selected for shrub. The summer dataset did not contain enough nighttime locations to test whether each individual fox used different habitats at night than during the day, so I pooled the data for all 4 foxes. The resulting test revealed no significant difference between daytime and nighttime habitat utilization ($\chi^2 = 2.97$, 4 df, $p = 0.562$) in summer.

In winter the foxes moved to lower elevations, usually to the south of their summer ranges. The winter locations for each fox were at significantly lower elevations (all $p < 0.0001$) than their summer locations (Table 26). The magnitude of the seasonal difference varied by individual but the overall mean difference was 479 m (range: 315–599 m). Winter detections were clustered along the road corridor between Mineral, Mill Creek and the Park’s southwest entrance. These locations were likely biased by my inability to access the higher elevations on foot during winter, so no habitat selection tests were conducted on these data. Winter home range sizes (Table 23) therefore represent minimum estimates; the actual area used may have been larger. The aerial telemetry locations likely had no seasonal bias so I repeated the elevation comparison using only these locations. Small sample sizes necessitated the use of nonparametric Wilcoxan tests (Zar 1999) but significant seasonal differences were confirmed for all 3 foxes with >5 aerial locations in both summer and winter (Table 27). Within the aerial telemetry locations, the mean seasonal elevation difference was 439 m. In most years a fox's summer core area did not overlap with its winter core area; often even the 95% MCPs did not overlap (see Appendix C for seasonal home range maps).

In both summer and winter, fox core areas (i.e., 50% fixed kernel isopleths) usually contained parking lots or campgrounds. In summer the Lassen Peak, Bumpass Hell and Devastated Area parking lots were frequented by multiple collared foxes, as were the Southwest Campground, McGowan Lake parking area and Morgan Snowmobile Park in winter (Appendix C). Foxes tended to return to the same geographic area for multiple seasons, but several range shifts also occurred. For example, in the summers of 1998-2000, F01 was detected on the north slopes of Reading Peak and near the Summit Lake Campgrounds. In 2001 she widened her area of use to most of the western half of the park, but her core use area was the Lassen Peak parking lot. She spent that winter near the Manzanita Lake Campground and remained nearby the following summer. F02 was near the Morgan Snowmobile Park and the hamlet of Mill Creek all 3 winters she was tracked and she was near the Lassen Peak or Devastated Area parking lots each summer. F03 had the smallest and most seasonally consistent summer home ranges, located on the southern slopes of Lassen and Reading Peaks. The male fox (M01) was often near the Southwest Campground and the Morgan Snowmobile Park for several seasons until he abruptly shifted to near Lassen Peak in summer 2000.

Rest sites

I documented 54 summer and 19 winter rest sites by walking in on collared animals until they could be observed. Rest sites were where foxes were observed laying down or sleeping. All rest sites were found during daylight because the foxes were actively foraging at night. Rest sites occurred in a variety of vegetative communities (Table 28). No quantitative vegetation data were collected at these sites; community characteristics were derived from GIS vegetation layers. In general, the foxes rested under conifer boughs, among boulders or in sunny patches near vegetative cover. None of the day rests were in earthen dens or dug-out cavities and I never encountered such structures that had evidence of fox utilization. Individual foxes often used the same rest site on multiple days, sometimes even in different seasons. For example, M01 often rested in a dense grove of small (<5 m tall) red firs near the Park's Southwest Campground and F01 often rested near several large boulders high on the northern slope of Reading Peak.

Daily movements

The foxes were highly mobile in both summer and winter. A total of 107 summer and 62 winter pairs of independent locations were <24 hr apart. Although most movements between such locations were <2 km, movements of 3-5 km were common, and occasional movements of 6-9 km occurred (Figure 20). The maximum daily movement documented was 14.2 km by F02 in March 2001. All 4 female foxes had at least 1 daily movement >5 km but the male fox had no daily movements >1.3 km. The full data set of all locations contained additional pairs of locations within 24 hr but none of these distances exceeded 14.5 km. Although some of the longer movements were associated with the seasonal transition between summer and winter ranges, most were conducted during the course of normal foraging within a season.

Mortality

Three of the 5 collared foxes died during the study period. None of these mortalities was within 4 weeks of a capture event and there was no evidence that capturing or collaring played any role in these animals' deaths. The male fox (M01) died in late October 2000 in the upper Kings Creek drainage 1.2 km southeast of the Lassen Peak parking area. Because his telemetry collar did not have a mortality sensor, his death was not noticed for several weeks. By then, heavy snows had closed the Park road and covered his carcass. His skeletal remains were recovered in early June 2001 and likely had been exposed from the melting snow for only a few days. No soft tissues remained, making necropsy impossible, but his skeleton and skull were intact and covered with fur, suggesting that depredation was not the cause of death. Several marten scats containing red fox fur were recovered at the site but these likely indicate scavenging rather than predation.

F05, the second mortality, died 0.7 km from M01. Her collar contained a mortality sensor so her demise was discovered during an aerial telemetry session on March 26, 2001. Her last prior telemetry location had been recorded on March 4 near the park's Southwest Campground. As with M01, heavy snows prevented recovery of her remains until the spring thaw. On May 14, 2001, I recovered all that remained of her carcass: clumps of golden fur in a 3 m radius patch atop the snow. Her telemetry collar was deep in a narrow crack in a nearby cliff and several fresh bird droppings were on the snow nearby. No cause of death could be determined but the tight pattern of fur on the snow suggested she had died, been covered by snow, and her carcass had been scavenged by birds and small mammals once it became exposed by the snowmelt.

The third mortality, F02, occurred in late October 2002. Her collar contained a mortality sensor and the lack of snow allowed her remains to be recovered almost immediately. She was found 175 m southwest of the ski chalet at the park's Southwest Campground. Her carcass was intact and in good condition and I first suspected she had been struck by a vehicle on the nearby road. A necropsy by Dr. Pamela Swift at CDFG's Wildlife Investigations Laboratory revealed puncture wounds on either side of F02's ribcage. The splintered ribs had punctured her lungs, causing death via pneumothorax. Dr. Smith concluded that F02 had been attacked by a dog and escaped, but died soon thereafter from the injuries (CDFG WIL Lab Report N-061-02). In accordance with the MOU with CDFG, the 3 foxes' remains were provided to the Museum of Vertebrate Zoology at UC Berkeley.

Reproduction

None of the 4 females was pregnant or lactating at any capture, and examination of their teats indicated that none of them had raised pups in prior seasons. F02's nulliparity was confirmed during a second necropsy conducted by Ben Sacks of UC Davis. Reproduction was not entirely absent in the population, however. An uncollared adult fox, presumably female, was seen with 2 pups multiple times near the Lassen Peak parking area in summer 1999. They were first reported by Lassen Park's road crew 3 days after the park road had opened for the season. The local newspaper, the Redding

Record Searchlight, ran a photograph of a pup walking along the roadside near Lassen Peak (Watters 1999). A camera trap on Lassen Peak that summer photographed a scruffy golden adult, a dark-shinned pup and a light-shinned pup. Their den was never discovered but was probably just east of the Lassen Peak parking lot (2,600 m elevation). The adult fox may have been the same uncollared golden fox seen and photographed near Lassen Peak the previous summer. This fox was never captured but the pups may have been captured the following seasons as F02 and F03. No uncollared foxes were detected on Lassen Peak after F02 and F03 were captured.

DISCUSSION

Home range and seasonal movement

Radio-collared red foxes in the Lassen Peak region of northern California had large home ranges for their body mass. Adult red foxes in North America typically weigh between 3.5 and 7 kg (Voigt 1987). Within this range, the average weight of male red foxes in North America is 4.5 to 5.4 kg, and of females is 4.1 to 4.5 kg (Ables 1975). With an average mass of 3.6 kg, Lassen red foxes were smaller than average but within the range documented for the species. Mountain red fox may be smaller than their lowland counterparts. A trapper quoted in Grinnell et al. (1937) said that the typical mass for Sierra Nevada red fox was 4.2 kg for males and 3.3 kg for females. Aubry (1983) captured 2 adult males, 2 adult females and 2 juvenile females on the eastern slopes of Mt. Rainier in Washington; the average mass was 4.3 kg for the males and 3.3 kg for the females. In the Lassen population the male was slightly larger than the females, which is typical for most red fox populations (Voigt 1987).

Seasonal home ranges for Lassen red foxes generally exceeded the largest values reported in the literature. Red fox home range size is a function of terrain, habitat complexity and food supply (Ables 1975), and since red fox occur in many habitat types throughout their global range (Lloyd 1980, Voigt 1987), their home ranges span 2 orders of magnitude. Red fox in the urban areas of Bristol and Oxfordshire, UK, had the smallest average home ranges, 45 ha, presumably due to abundant resources (Harris 1980, Voigt and Macdonald 1984). In Wisconsin, mean MCP was 141 ha (range: 71-220 ha) but the foxes were tracked for only 11-148 days (Ables 1969). Exotic red fox in Orange County, California had average MCP home ranges of 427 ha (Lewis et al. 1993). Family groups in Minnesota occupied areas that were ≤960 ha (Storm et al. 1976). In Ontario, home ranges were 900 ha (range: 500-2,000 ha), typical of most studies in the agricultural areas of central and eastern North America (Voigt and Tinline 1980, Voigt 1987). Red foxes at high latitudes have the largest home ranges, reflecting reduced habitat productivity due to the short growing season. Red foxes in eastern Maine had mean annual MCPs of 1,470 ha (range: 600-2,750 ha; Harrison et al 1989). Summer home ranges for red fox in the tundra of northwest British Columbia averaged 1,611 ha (range: 277-3,420 ha; Jones and Theberge 1982), and winter home ranges in Lapland were 3,000 to 5,000 ha (Heptner et al. 1998). Note that all these studies used the MCP method, which is comparable among studies; the size of home ranges and core areas constructed using fixed or adaptive kernel methods are not (Kernohan et al. 2001).

Only one previous telemetry study has been conducted on mountain red fox in western North America. Aubry (1983) captured and tracked 7 red fox (2 adult males, 3 adult females, 2 juvenile females) in the Washington Cascades near Mt. Rainier National

Park. Seasonal home ranges (100% MCPs) for 6 of these foxes averaged 152 ha (range: 26-308 ha); the remaining fox, an adult female, had a summer home range of 1,166 ha. With the exception of this latter female, the seasonal home ranges for Cascade red fox were far smaller than those documented for Lassen red fox. However, Aubry's home ranges may be underestimates. His seasonal sample sizes were small (11-34 locations per fox) so the MCPs may not have reached their asymptotes (Kernohan et al. 2001). More importantly, Aubry conducted his telemetry during mid-day when the foxes were presumably resting. Since red foxes generally forage at night (Voigt 1987), omitting nocturnal locations can dramatically reduce home range estimates (Smith et al. 1981).

Red foxes typically have larger home ranges in winter when resources are less abundant and less evenly distributed (Ables 1975, Lloyd 1980). In the Cascades, red fox winter home ranges were larger than summer home ranges but were not at lower elevations (Aubry 1983). In the Swiss Jura Mountains, red fox home ranges in winter were not significantly different than those in summer (Meia and Weber 1995). The seasonal migrations documented in the Lassen population are unique in the red fox literature from North America, Europe and Australia. However, this may merely reflect the paucity of research done in montane habitats with deep, soft snows. The only comparable pattern in the literature is from the central Asian mountains of the former Soviet Union, where red fox conduct a virtually identical seasonal migration. According to Heptner et al. (1998: 537), "…with the falling of deep snow, [red] foxes descend from the alpine and subalpine zones to the forest belt and lower… The reverse movement of foxes to the mountains in spring is less obvious." The latter sentence implies more individual variability in the spring return to higher elevations than in the fall descent; such was the pattern for the Lassen foxes as well (Table 20).

Although seasonal elevational migration is common among montane birds and ungulate populations (e.g., Inouye et al. 2000), few studies have documented this pattern for carnivores, perhaps due to the difficulty of monitoring collared animals in such areas during winter. But a seasonal movement to lower elevations with shallower snow may be common among carnivores that are too large for subnivean foraging and that incur high energetic costs when traveling in deep snow (Buskirk and Zielinski 2003). Coyote (*Canis latrans*), mountain lion (*Puma concolor*) and bobcat (*Lynx rufus*) in the mountains of central Idaho all descended to lower elevations during winter, concentrating their activities onto the relatively snow-free southwestern exposures (Koehler and Hornocker 1991). In the Sierra Nevada, mountain lion follow mule deer (*Odocoileus hemionus*) to lower elevations in winter, although not all members of the population may show this pattern (Pierce et al. 1999, Grigione et al. 2002). Likewise, coyote in the Sierra Nevada may descend to lower elevations to avoid deep winter snows (Grinnell et al. 1937, Sumner and Dixon 1953), but recent telemetry studies indicate that at least some individuals remain at high elevations in winter (Shivik 1995). Giant panda (*Ailuropoda melanoleuca*) in the Qinling Mountains of China also have a seasonal elevational migration, inhabiting mountain tops in the summer and descending to mid-latitudes in winter (Loucks et al. 2003). Although the red foxes in the Swiss Jura Mountains had no seasonal elevation shifts (Meia and Weber 1995), the wildcats (*Felis silvestris*) there descended to lower elevations after snowfalls and returned to higher elevations as soon as the snow disappeared (Mermod and Liberek 2002).

Snow depth at high elevation is likely the primary factor triggering Lassen red fox to descend to lower elevations in autumn. Transition dates were strongly correlated with the opening and closing of the park road due to snowfall (Table 24). The seasonal pattern and magnitude of these movements are consistent with historic accounts. Grinnell et al. (1937) reported that Sierra Nevada red fox descended to lower elevations in winter, as evidenced by winter records between 1,370-1,980 m (4,500-6,500 ft). Mean winter elevations for radio-collared Lassen red fox were very close to this range and almost all summer locations were higher (Table 26). Furthermore, Grinnell et al. (1937) reported that the summer range for Sierra Nevada red fox was 150-300 m (500-1000 ft) higher than the winter range; this value is comparable with the 439 m average seasonal difference for aerial telemetry locations for Lassen red fox. Although the high elevations are suitable habitat in the summer, the accumulation of deep soft snows prompts the foxes to descend to lower elevations, presumably where food is more accessible. It is unclear why they return to higher elevations in summer, but the higher density of coyotes on the winter range may be a factor. Avoidance of coyotes may also contribute to the foxes' close association with areas of human activity (Sargeant et al. 1987, Gosselink et al. 2003).

Lassen red foxes used a variety of above-ground day rests including the natural cavities among boulders and under snow-burdened conifer boughs, amid dense groves of young red fir and in openings among the pinemat manzanita (*Arctostaphylos nevadensis*). None of these sites were in earthen dens or other dug-out cavities underground. Individual foxes had rest sites they would use repeatedly, sometimes over multiple seasons. I did not quantify the physical and structural characteristics of these sites but there was no indication that suitable rest sites were limited in the landscape. Few studies have documented rest site use by mountain red fox. Aubry (1983) did not discuss the rest sites used by his study animals in the Cascades. Diurnal rest sites by adult female red fox in the Swiss Jura Mountains (1000-1300 m elevation) were always in cover, either within forest, woodlands or pasture with high grass. Underground dens were also common diurnal rest sites and were used more often by foxes with a higher percentage of open areas within their home ranges (Meia and Weber 1993).

Despite their small body size, the Lassen foxes conducted extensive daily movements. Daily movements were comparable to those of red fox in the Swiss Jura Mountains, which moved 4 to 12 km per day regardless of age class, season or home range size (Meia and Weber 1995). In winter, foxes in subalpine areas of New South Wales made nightly excursions to a ski resort 12 km away (Bubela et al. 1998). These daily movements are at the upper range of those documented by resident adults in other red fox populations (Voigt 1987), and are likely due to the differential distribution of available food resources and preferred bedding areas. The straight-line distances used in these study likely underestimate the total distance traveled by the collared animals during their nightly foraging bouts. My data did not include distances traveled during >1 day, such as F02’s excursion to the Swain Mountain snowmobile park approximately 37 km east of Lassen Peak in the winter of 2001 (see Figure 31). Long movements were common in the weeks before the foxes made their transition to a new seasonal range. It appeared that the foxes “scouted” the new range, returning to the old range for a few weeks if habitat conditions there remained preferable. The ability of these animals to cover extensive distances in rugged, mountainous terrain underscores the limitations of ground-based telemetry, especially in winter. In the absence of marked individuals, such movements may create the perception of a larger local population, as detections across the landscape may be attributable to only a few highly-mobile individuals.

Begging Behavior

Lassen red foxes were closely associated with roads, parking lots and campgrounds in both summer and winter. During this study, park staff and visitors reported numerous instances of red foxes, including collared individuals, scavenging and begging at campgrounds and parking lots (Perrine and Arnold 2001). Such sighting reports may reflect the density of human use more than the density of wildlife (Perrine and Arnold 2001), but the red fox core areas remained centered upon campgrounds and parking lots even after such sightings were removed (see Appendix C). Individual collared foxes had varied tolerances for human interactions. F03 was the least tolerant of human presence. She would scavenge in the Lassen Peak parking lot at night once the cars were gone, but she never approached people or cars. In fact she often fled from humans, which is why so few occupied rest sites were documented for her (Table 28). In contrast, F01, F02 and M01 were bold beggars who often approached humans and vehicles during the day. M01 became such a pest at the Southwest Campground that a part-time ranger was tasked with shooing him away in the evenings. On several occasions M01 and F02 entered tents, buildings and vehicles in search of handouts or unguarded food. Some park biologists expressed concern that someone attempting to hand-feed a fox might be bitten and require precautionary rabies treatment. Notices were posted at campgrounds and handed out at entrance stations informing visitors that feeding the foxes was illegal and unhealthy for foxes and humans alike. A few park rangers began carrying heavy-duty squirt guns to drive the foxes away from campgrounds without harming them; this approach was surprisingly effective.

It would be easy to conclude that the foxes' seasonal movements were directly related to their begging behavior: the foxes descended to lower elevations when the campgrounds at high elevations closed due to snow, and they returned to high elevations once the campgrounds re-opened in the summer. But several factors indicate that the situation is more complex. First, the foxes remained at high elevations in autumn after the campgrounds had closed and the visitors departed but before the heavy snows began. Second, the foxes were sometimes more closely associated with campgrounds when they were unoccupied. F01, for example, was more closely associated with the Summit Lake and Manzanita Lake campgrounds after they were closed for the season than while they were open. In two separate years she was also detected in the Drakesbad region when it was still inaccessible to visitors due to deep snow; while it was open to visitors, she was never detected there. Similarly, F02 spent most winters near the hamlet of Mill Creek when the vast majority of the houses (primarily vacation homes) were unoccupied. Third, the diet content analysis (Chapter 1) and nightly telemetry locations indicated that even the begging foxes utilized natural food resources and foraged well beyond the campgrounds; they were not dependent upon anthropogenic food. Fourth, the foxes often returned to their summer range before the park road opened and well before the campgrounds were open. Additionally, winter range areas such as Mineral and Mill Creek had greater scavenging and begging opportunities in summer, yet the foxes left these areas to return to the higher elevations. If access to handouts were the sole factor, one would expect the foxes to remain in Mineral and Mill Creek year-round. Lastly, the historic movements described by Grinnell et al. (1937) and the similar seasonal movements of red fox in the mountains of central Asia (Heptner et al. 1998) cannot be ascribed to beggar foxes. Although most of my study animals begged, it is doubtful that access to handouts was the primary factor behind their seasonal migrations.

Park records indicate that begging red foxes are a periodic problem, especially at high elevations. Begging foxes were reported in and around the Lassen Peak parking lot in the summers of 1970, 1977, 1978, 1979, 1980, 1987, 1989 and 1997. Several reports mention foxes approaching people or vehicles. In June 1968, a red fox reportedly stole a bag of trash from the Kings Creek Campground, which has since been decommissioned. No begging activity was reported from Manzanita Lake campground, the largest campground in the Park, but several sightings occurred there in January 1951, November 1960 and throughout the winter of 1966, all while the campground was unoccupied. In 1997 a begging fox was reported from the Butte Lake campground, in the northeast corner of the Park; a camera station near there detected an uncollared red fox in June 2000. Most fox sighting reports from Lassen Park do not explicitly mention begging or scavenging behavior. Given red foxes' intelligence and adaptable nature, it is likely that individual foxes occasionally learn that begging is a profitable way of life. Begging foxes but may be more common in mountainous regions where natural productivity is low and winter food scarce. For example, one of Aubry's study animals became a beggar at a nearby town (Aubry 1983), and begging foxes have been reported from subalpine parks in Hokkaido, Japan (Tsukada 1997) and New South Wales, Australia (Bubela et al. 1998).

Begging behavior can affect resource use by red foxes, as well as their management. Clearly, begging can have a major impact upon home range size. Foxes may have smaller home ranges if they always remain near a single campground, or they may have large home ranges if they move among widely-scattered campgrounds. Both patterns were observed in the Lassen population. M01 was tightly associated with the Park's Southwest Campground in the summers of 1998 and 1999 but then he abruptly re-located to Lassen Peak in 2000. F01 and F02 routinely visited several campgrounds, often traveling along the road corridor. Although the availability of abundant resources can increase local population density (Voigt and Macdonald 1984, Bubela et al. 1998), the occurrence of >1 fox at a time at Lassen's campgrounds was rare and may represent mated pairs or family groups. More importantly, begging can affect managers' *perception* of local population density because a few highly-visible animals can create the perception of an abundant local population. Scores of red fox sightings were reported throughout Lassen Park in 1999 and 2000 but most of these sightings could be attributed to ≤3 individual foxes (Perrine and Arnold 2001). Additionally, begging behavior can increase the risk of injury or death due to vehicle strikes, ingestion of toxic materials or attack by domestic dogs. F02's demise clearly illustrates these risks, even for a state-listed species within a national park where dogs are required to be leashed at all times.

Reproduction and Mortality

Red fox generally mate during winter and birth a litter of up to 12 pups after a gestation period of 52-54 days (Lloyd 1980, Voigt 1987). Virtually no data on red fox reproduction in the Sierra Nevada are available, likely due to the harsh winter conditions at high elevations and the extremely low fox population densities there. Grinnell et al. (1937) reported that Sierra Nevada red foxes began to pair up around February 15, but their evidence consisted solely of snow tracks. July is apparently “the proper season for finding young in a den” near Lassen Peak (Grinnell et al. 1930: 470).

The limited field data suggest that mountain red foxes may have lower fecundity and recruitment than other populations. Grinnell et al. (1937) reported that Sierra Nevada red fox litters averaged 6 pups and ranged from 3 to 9 pups. The weight of evidence behind this conclusion is unclear although the range apparently reflects trappers’ reports. More recent evidence indicates that litters of 2 to 3 pups may be more typical. Lassen Park records include a single report of a mother fox and 3 pups near Hat Creek in August 1979. The uncollared fox on Lassen Peak in 1999 raised only 2 pups. In 1980, Aubry (1983) captured and radio-collared a family group consisting of an adult male, an adult female and 2 female pups. The following year one of these pups produced her own litter of 3 pups, but at least 1 died by mid-June. Neither the other female pup nor her mother reproduced in 1981. Three collared females in the Lassen population were tracked for 3-5 breeding seasons and produced no litters despite the presence of a male fox in the local vicinity. None of 7 adult female red foxes monitored by Meia and Weber (1993) in the Swiss Jura Mountains (1000-1300 m) bred during their monitoring period, but one had reared pups just prior to the study. Globally, red fox litters average 3 to 6 pups with a range of 1-12 (Lariviere and Pasitschniak-Arts 1996), but litter size and pup survival are a function of local food availability (Voigt 1987). Limited resources may be preventing mountain red foxes from achieving the reproductive output typical of other populations in more productive environments. Whatever the cause, mountain red foxes appear to be at the lower range of typical litter size.

Den sites of mountain red foxes remain poorly characterized. The lack of reproduction among the red foxes collared for this study precluded additional insight into their denning behavior and habitats. Historic accounts indicate that Sierra Nevada red foxes denned in natural cavities amidst boulder piles and talus slopes (Grinnell et al. 1937). These dens were primarily located among the whitebark pines (*Pinus albicaulis*) and mountain hemlocks (*Tsuga mertensiana*) of the subalpine forest, not above treeline where the foxes commonly foraged. They apparently did not use the earthen dens typical of red fox populations in eastern North America and Europe (Storm et al. 1976, Lloyd 1980, Voigt 1987). The mother and 3 pups reported in Lassen Park in August 1979 had their den among large boulders near Hat Creek. However, Cascade red fox in Washington used earthen burrows with multiple entrances, generally situated in dense forest (Aubry 1983). None of Aubry's study animals denned among rocks although outcrops and talus slopes were available in his study area. It remains unclear whether Sierra Nevada red fox do not utilize earthen dens or whether such dens merely remain to be discovered. Aubry's (1997) hypothesis that Sierra Nevada red fox likely use any suitable denning site may be correct, but the limited available evidence suggests a consistent tendency toward natural cavities among rocks.

This study also shed little additional light on sources of mountain red fox mortality. In eastern North America, human activities such as hunting, trapping and vehicle collisions account for the vast majority of documented red fox mortality (Storm et al. 1976). These sources are probably much reduced in the snowy forests of the high

Sierra. Fur trapping was probably never a major source of mortality for mountain red fox in California, averaging around 21 foxes per year (Grinnell et al. 1937). From 1940 through 1959, only 135 pelts were taken throughout the state (Gray 1975). The statewide harvest had declined to 2 per year well before the state legislature banned red fox trapping in 1974 (Gray 1975). Both deaths during Aubry's study were human-related: one fox died of an infection caused by stepping through its radio collar and the other fox was caught by a trapper. Widespread use of poisons for predator and rodent control likely caused significant mortality in the past (Grinnell et al. 1937) but such practices have largely been discontinued. Little is known about natural mortality among mountain red foxes. Golden eagles (*Aquila chrysaetos*) were known to kill foxes caught in traps, and bobcats and coyotes likely killed occasional infirm individuals (Grinnell et al. 1937). There are no data on the impact of rabies, canine distemper or other diseases upon mountain red fox in North America; such diseases have significant impacts on other red fox populations (Voigt 1987).

MANAGEMENT CONSIDERATIONS

Mountain red foxes have large home ranges and extensive daily and seasonal movements. These characteristics may cause local population densities to be lower than otherwise expected. Furthermore, local management may need to be coordinated among multiple agencies and landowners. As with other migratory species, conservation activities on the summer range may have little success if threats are not addressed on the winter range, and vice versa.

Scavenging and begging foxes have been a historic problem in the Lassen region that will likely arise again in the future. Red foxes are intelligent and adaptable and can quickly learn to utilize human garbage and gullibility. Foxes that learn to beg on one portion of their seasonal range will likely exhibit such behavior on other portions of their range, even during different seasons. Such begging may increase their exposure to potential sources of disease and mortality. Resource managers should develop and implement proactive policies to prevent begging in campgrounds and parking lots and to discourage foxes from such actions before they become habitual beggars. The combination of visitor education and “super soaker” water guns helped reduce begging in Lassen Park during this study, but this was no substitute for effective, proactive law enforcement and animal management policies.

Red fox in the Sierra Nevada and Cascade Ranges may comprise a series of interconnected local populations, i.e., a metapopulation. As such, individual local populations may periodically go extinct and then be recolonized from other areas. Historically, the Lassen region had one of the highest red fox population densities in the mountains of California (Grinnell et al 1937, Schempf and White 1977). Currently, it is unclear whether local fecundity is sufficient to maintain the population. If mortality consistently exceeds local production, the Lassen area might be a “sink” population even if the local population density is higher than surrounding areas (Pulliam 1988). Sink populations can contribute to the long-term persistence of a metapopulation (Howe et al. 1991). However, the source of recolonization remains to be identified. Camera surveys on adjacent national forests have not detected red foxes to date (T. Rickman, Lassen National Forest, pers. com.) and the Lassen region has the only known red fox population in the Sierra Nevada. Additional surveys are needed throughout the historic range of the Sierra Nevada red fox to determine where local populations currently occur. Such surveys should employ camera traps, the only technique that has been empirically demonstrated to detect mountain red fox. Identifying other local populations and determining whether a red fox metapopulation exists in the Sierra Nevada are important steps toward the conservation of this state-listed species.

Most of what is currently known about mountain red fox distribution and ecology, especially in California, is derived from trappers' reports. In the absence of trapping, wildlife managers have had to rely upon sporadic sighting reports and anecdotes, often from people not familiar with the biology or taxonomic identity of the species. Trapping likely had negligible impact upon local red fox populations (Grinnell et al 1937), and it is worth asking whether the ecological information gained was worth the slight increase in mortality. Well-regulated trapping can provide insights into aspects of biology and natural history not otherwise available except through intensive field studies, such as identifying regional distribution and local population centers, and can provide specimens for morphometric and genetic analysis. Regardless of the potential benefits, however, resuming commercial trapping of mountain red fox in California is currently impractical: populations may now be critically low, little market remains for the pelts, and statewide bans on commercial fur trapping have eliminated opportunities for adaptive harvest management.

Table 21: Physical measurements at first capture for Lassen red foxes. Mass in kg; length and girth measurements in cm Values for adult Cascade red fox (3 males, 3 females) shown for comparison; data from Aubry 1983, Appendix B.

Fox	sex	Capture Date	Mass	Head length	Body length	Tail length	Hind foot length	Head girth	Neck girth	Max chest girth	Re-Captures
M01*	male	1-26-98	4.0	16.8	47.0	35.5	16.5	27.3	21.0	35.0	1
F01*	female	3-12-98	3.5	17.5	47.0	38.5	13.8	25.0	18.5	31.0	7
F02	female	4-14-00	2.9	15.7	47.0	38.1	13.6	23.6	19.3	29.9	17
F03	female	8-8-00	3.8	16.5	48.5	39.7	15.7	26.7	18.5	32.0	4
F05	female	12-11-00	3.6	16.0	49.4	36.3	14.9	24.0	19.8	31.4	0
Lassen:		Mean:	3.6	16.5	47.8	37.6	14.9	25.3	19.4	31.9	
		SE:	0.22	0.17	0.16	0.28	0.32	0.32	0.24	0.34	
Cascades:		Mean:	4.0 **	15.3	47.1 †	37.0	16.1	22.6	17.7	32.1	
		SE:	0.23	0.16	0.70	0.49	0.19	0.23	0.42	0.25	

* First capture by T. Kucera. Body measurements recorded at later recapture.
** 1 adult female (3.1 kg) omitted due to probable trap-induced weight loss before measurement taken.
† Body length calculated by subtracting head and tail length from Aubry's "total length."

Table 22: Number of locations, by type, for each collared red fox. Some of these locations were dropped to generate the set of "independent" locations used for statistical tests and kernel home ranges. Specifically, all park visitor / staff sighting reports were dropped, as were all but the *first* detection of each fox at a camera station or trap. Sightings were retained only if they occurred while conducting telemetry. The remaining locations had to be $\geq$ 8 hr apart to be retained in the "independent" set.

Location Type	M01	F01	F02	F03	F05
Aerial telemetry	7	40	40	34	3
Capture	2	8	18	5	1
Ground telemetry	37	24	162	199	34
Mortality	1	0	1	0	1
Park visitor / staff report	114	108	63	3	0
Photo station	63	76	62	29	0
Sighting	40	59	50	18	0

Table 23: Seasonal locations and home range size (ha) per collared red fox.

Season	Fox	Total locations	95% MCP	Indep locations	Core *
Winter 1998	F01	8	--	8	--
	M01	27	1,679.2	16	236.7
Summer 1998	F01	33	391.4	7	--
	M01	40	-- **	7	--
Winter 1999	F01	1	--	1	--
	M01	7	--	1	--
Summer 1999	F01	47	261.6	4	--
	M01	49	269.1	3	--
Winter 2000	F01	12	--	7	--
	F02	35	2,158.1	13	570.7
	M01	82	325.8	12	72.2
Summer 2000	F01	116	3,578.6	45	162.1
	F02	76	1,827.0	31	201.7
	F03	32	1,492.2	29	431.4
	M01	56	856.4	34	199.0
Winter 2001	F01	54	1,185.0	35	299.3
	F02	69	6,375.0	37	1,048.7
	F03	49	2,154.2	46	387.9
	F05	37	4,504.2	35	348.1
Summer 2001	F01	94	6,962.2	59	464.9
	F02	97	6,980.9	62	360.2
	F03	61	1,433.2	58	402.5
Winter 2002	F01	26	4,193.8	24	277.8
	F02	40	6,685.2	32	3,024.6
	F03	23	3,284.6	22	790.7
Summer 2002	F01	61	3,871.4	56	357.6
	F02	78	4,972.9	60	174.2
	F03	116	440.1	87	21.6
Winter 2003	F01	2	--	2	--
	F03	7	--	7	--

* 50% fixed kernel isopleth.

** MCP not calculated because 32 locations (80%) were sighting reports from one campground, making the MCP based upon only 8 unique points.

Table 24: Dates for seasonal home ranges. Winter seasons include Jan 1 of that year (e.g., Winter 2000 includes fall 1999 and spring 2000). Road dates are the opening of Highway 36 through Lassen Park at the end of winter and its closing at the end of summer.

	M01		F01		F02		F03		F05		Park Road
Season	start	end	start	end	start	end	start	end	start	end	Open/Close
Winter 1998	1-26-98	7-20-98	3-12-98	6-4-98	--	--	--	--	--	--	7-12-98
Summer 1998	7-26-98	10-6-98	7-14-98	10-1-98	--	--	--	--	--	--	11-10-98
Winter 1999	12-3-98	6-3-99	3-10-99		--	--	--	--	--	--	6-11-99
Summer 1999	6-9-99	10-24-99	6-6-99	10-20-99	--	--	--	--	--	--	11-19-99
Winter 2000	12-15-99	6-23-00	1-20-00	5-13-00	4-6-00	6-3-00	--	--	--	--	6-2-00
Summer 2000	6-24-00	10-16-00 *	5-18-00	11-7-00	6-15-00	11-7-00	8-8-00	11-02-00	--	--	11-17-00
Winter 2001	--	--	1-1-01	4-12-01	11-13-00	3-27-01	11-11-00	5-07-01	12-11-00	3-26-01 *	5-10-01
Summer 2001	--	--	4-13-01	10-04-01	3-30-01	11-19-01	5-16-01	11-14-01	--	--	11-15-01
Winter 2002	--	--	10-15-01	5-02-02	11-27-01	6-03-02	11-30-01	3-28-02	--	--	5-22-02
Summer 2002	--	--	5-26-02	11-4-02	6-14-02	10-31-02 *	4-4-02	11-06-02	--	--	11-13-02
Winter 2003	--	--	12-3-02	12-4-02	--	--	11-7-02	12-7-02	--	--	n/a

* animal died.

Table 25: Selection of cover types by individual red fox in summer. Chi-square tests indicated that the observed habitat use for each fox was significantly different from what was expected by chance. Follow-up tests (Neu et al. 1974, Alldredge and Ratti 1992) were used to determine which cover types were significantly selected or avoided. To retain a Type I error level of 0.05 for each fox, the individual alpha level was set at 0.005.

					Observed	Observed CI		Expected	
Fox	Cover type	Observed	Expected	χ^2	Proportion	lower	upper	Proportion	Effect
F01	Barren	47	15.9	60.6	0.276	0.188	0.365	0.094	**select**
	High-elevation conifer	60	48.1	3.0	0.353	0.259	0.447	0.283	ns
	Mid-elevation conifer	45	78.6	14.4	0.265	0.178	0.352	0.463	**avoid**
	Hardwood-Herbaceous	1	4.6	2.8	0.006	-0.009	0.021	0.027	**avoid**
	Shrub	17	22.8	1.5	0.100	0.041	0.159	0.134	ns
	subtotal:	170	170	82.2					
	p-value:			p<<0.001					
F02	Barren	83	14.3	329.0	0.542	0.439	0.646	0.094	**select**
	High-elevation conifer	29	43.3	4.7	0.190	0.108	0.271	0.283	**avoid**
	Mid-elevation conifer	14	70.8	45.5	0.092	0.031	0.152	0.463	**avoid**
	Hardwood-Herbaceous	1	4.1	2.3	0.007	-0.010	0.023	0.027	**avoid**
	Shrub	26	20.5	1.5	0.170	0.092	0.248	0.134	ns
	subtotal:	153	153	383.1					
	p-value:			p<<0.001					
F03	Barren	51	16.3	73.9	0.293	0.204	0.382	0.094	**select**
	High-elevation conifer	57	49.2	1.2	0.328	0.236	0.419	0.283	ns
	Mid-elevation conifer	0	80.5	80.5	0.000	0.000	0.000	0.463	**(avoid) ***
	Hardwood-Herbaceous	1	4.7	2.9	0.006	-0.009	0.021	0.027	**avoid**
	Shrub	65	23.3	74.3	0.374	0.279	0.468	0.134	**select**
	subtotal:	174	174	232.8					
	p-value:			p<<0.001					
M01	Barren	16	4.1	34.2	0.364	0.177	0.550	0.094	**select**
	High-elevation conifer	8	12.4	1.6	0.182	0.032	0.332	0.283	ns
	Mid-elevation conifer	8	20.4	7.5	0.182	0.032	0.332	0.463	**avoid**
	Hardwood-Herbaceous	0	1.2	1.2	0.000	0.000	0.000	0.027	n/a
	Shrub	12	5.9	6.3	0.273	0.100	0.446	0.134	ns
	subtotal:	44	44	50.8					
	p-value:			p<<0.001					

Observed: The number of independent telemetry locations within each cover type.
Expected: The expected number of telemetry locations, if proportional to the amount of each cover type.
χ^2: The chi-square value for each cover type; the subtotal and p-value indicate the results of a chi-square test with 4 df.
Effect: "Select" and "avoid" indicate habitats used significantly more or less than expected; "ns" = not significant.

* There were no detections in this cover type, so no confidence interval can be created. However, the sampling intensity strongly suggests that the fox was avoiding this cover type. Had 1 or 2 detections occurred, the effect would have been significant.

Table 26: Elevation (m) of independent locations, by season. For the 4 foxes with both summer and winter locations, the winter locations were at significantly lower elevations than the summer locations (t-tests; all p < 0.0001).

	Summer				Winter			
Fox	n	Mean	SD	Range	n	Mean	SD	Range
M01	44	2456	248	(1912 - 2816)	29	1956	171	(1550 - 2308)
F01	171	2233	263	(1808 - 3130)	77	1918	173	(1500 - 2527)
F02	153	2470	346	(1755 - 3089)	82	1872	296	(1410 - 2601)
F03	174	2506	134	(2200 - 3113)	75	2004	169	(1500 - 2624)
F05	--	--	--	--	35	1994	200	(1497 - 2477)

Table 27: Elevation (m) of aerial telemetry locations, by season.

	Summer				Winter				Wilcoxan
Fox	n	Mean	SD	Range	n	Mean	SD	Range	p-value
M01	5	2580	157	(2304 - 2672)	2	1998	23	(1981 - 2014)	0.08
F01	30	2299	197	(2036 - 2732)	10	1950	202	(1730 - 2330)	0.0003
F02	27	2505	257	(1908 - 2926)	13	1980	327	(1423 - 2441)	<0.0001
F03	27	2488	119	(2200 - 2689)	7	2191	257	(1914 - 2624)	0.0064

Table 28: Vegetation characteristics of occupied rest sites in summer (n = 54) and winter (n = 19). California Wildlife Habitat Relationships (CWHR) community type, tree diameter at breast height (DBH) and canopy closure were determined from a GIS data layer, as opposed to site-specific measurements.

Season	Cover Type	CWHR type	DBH (cm)	Closure	F01	F02	F03	M01
Summer	Barren	Barren	-	-	5	6	3	3
	High-elevation conifer	Red fir	28-61	25-39%	7	5	-	-
			28-61	40-59%	2	-	-	-
		Subalpine conifer	15-28	10-24%	-	1	-	-
			28-61	25-39%	-	-	-	1
	Mid-elevation conifer	Lodgepole pine	28-61	40-59%	3	-	-	-
			28-61	>59%	2	-	-	-
		Sierran mixed conifer	28-61	>59%	2	-	-	-
		White fir	15-28	40-59%	-	-	-	6
			28-61	>59%	-	-	-	2
	Shrub	Montane chaparral	-	-	2	3	-	1
Winter	Hardwood-Herbaceous	Aspen	15-28	>59%	1	-	-	-
	Mid-elevation conifer	Sierran mixed conifer	28-61	40-59%	-	-	-	1
			28-61	>59%	3	1	-	-
			>61	>59%	2	2	-	3
		White fir	28-61	>59%	-	-	-	1
			>61	40-59%	-	1	-	-
	Shrub	Montane chaparral	-	-	-	-	2	2

Figure 19: Study area boundary (red polygon), defined as the 98% MCP for all collared fox locations. Note the extreme eastern location (orange arrow) for F02 at a camera trap at the Swain Mountain snowmobile park, 37 km east of Lassen Peak, in winter 2002.

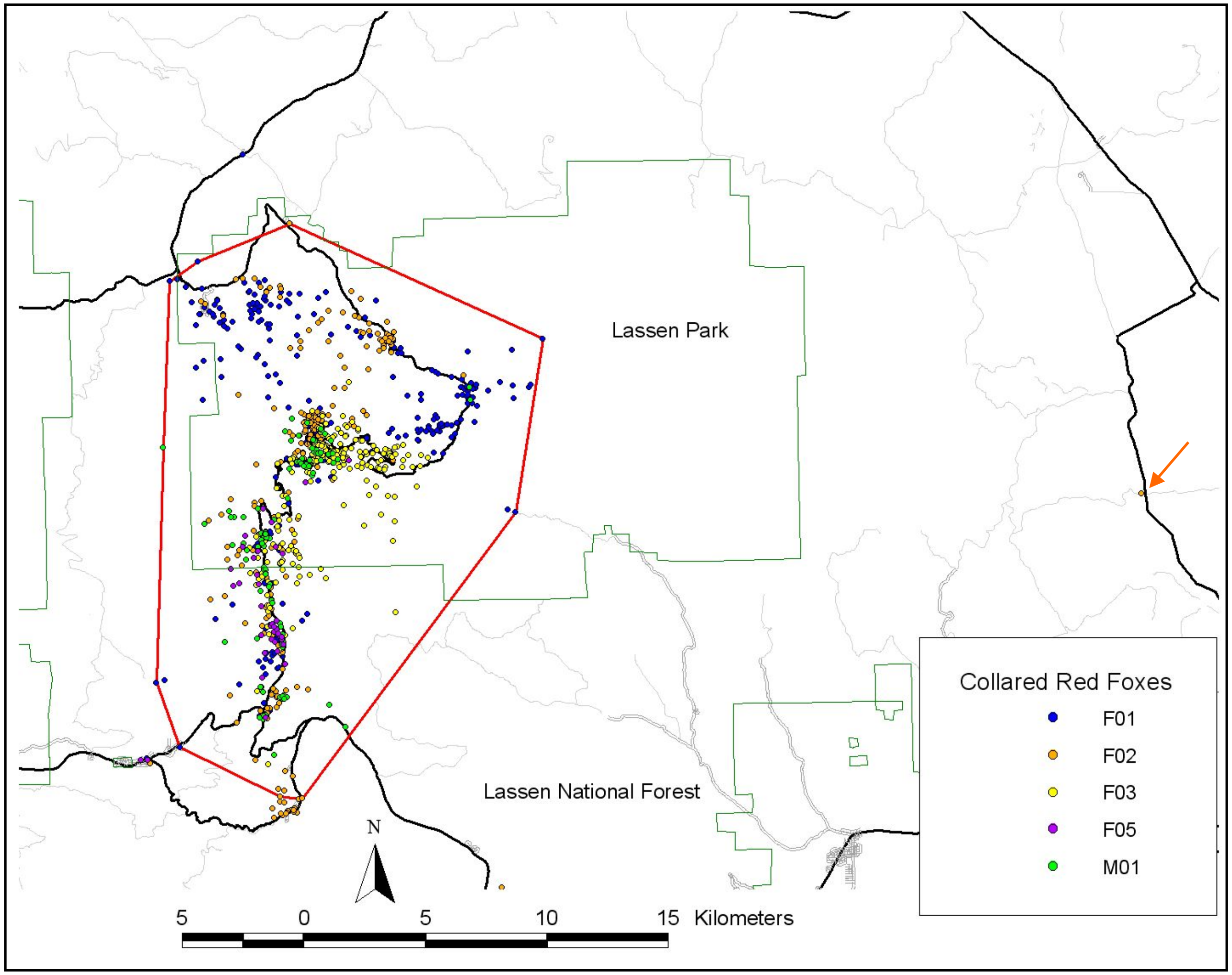
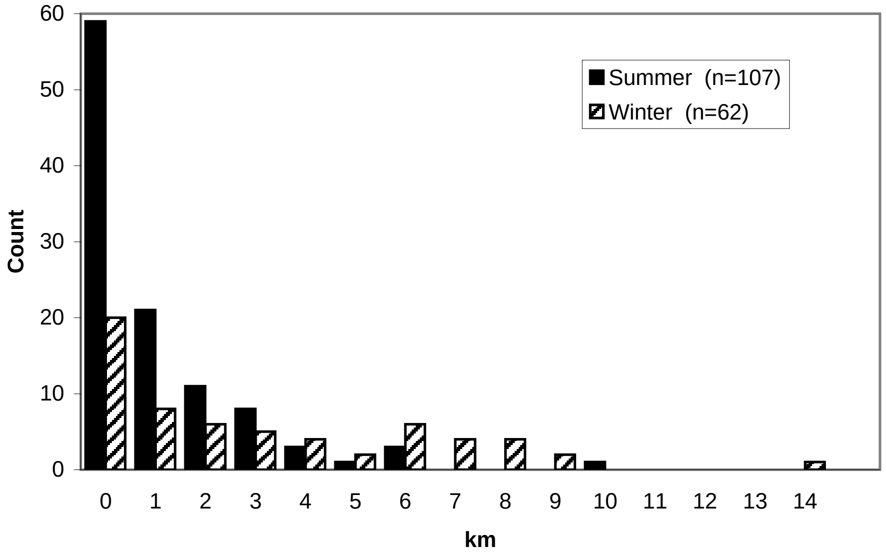


Figure 20: Distance between independent telemetry points <24 hrs apart.



CHAPTER 5

RED FOX POPULATION STRUCTURE IN CALIFORNIA

INTRODUCTION

Historically, California has been home to two separate red fox (*Vulpes vulpes*) populations, putatively of different origins. The Sierra Nevada and Cascade mountain ranges are the domain of the native Sierra Nevada red fox (*V. v. necator*). For ecological reasons that have yet to be identified, this rare fox is apparently restricted to subalpine areas and rarely descends below 1525 m (5000 ft) (Grinnell et al. 1937, Schempf and White 1977). The Sierra Nevada red fox was never common, but concerns about population declines led state wildlife managers to prohibit red fox trapping throughout California in 1974 and to list *V. v. necator* as a State Threatened species in 1980 (Gould 1980, Lewis et al. 1999). Its current distribution and population trend are unknown (CDFG 1996).

The second red fox population in California inhabits the lowland areas and is presumably descended from individuals introduced by humans. These exotic foxes were first recorded from the northern Sacramento Valley (Grinnell et al. 1937). Their origin is uncertain, but morphological analysis suggested that they derived from the red fox of the northern Great Plains, *V. v. regalis* (Roest 1977). These were probably introduced to California in the 1880s and they remained restricted to the Sacramento Valley through the 1930s (Grinnell et al. 1937). In subsequent decades, however, lowland red fox have been documented throughout much of central and southern California, and now occur in at least 36 counties in California (Figure 21). In addition to the Sacramento Valley, their current range includes virtually the entire area between the San Francisco Bay region and San Diego, and extends eastward through the San Joaquin Valley to the Sierra Nevada foothills (Lewis et al. 1999). This dramatic range expansion has been facilitated by ongoing anthropogenic introductions and translocations, likely from multiple source populations (Fitzpatrick 1999, Lewis et al. 1999). It is unclear whether the exotic red fox has expanded into the historic range of the native mountain red fox (Lewis et al. 1995).

For management purposes, it is important to be able to differentiate the native, state-threatened red fox from the exotic nuisance red fox. Although the mountain red foxes are generally smaller than their lowland counterparts, morphological variation within populations prevents individuals from being assigned to either population with certainty based solely on physical characteristics (Roest 1977). Therefore, elevation has been used to differentiate the two populations: those above 1066 m (3500 ft) are considered native and those below 1066 m are considered exotic (e.g., Lewis et al. 1993). Whether foxes from either population have crossed this elevation boundary is unknown. Recently, researchers and wildlife managers have called for a genetic comparison of the mountain and lowland populations in California (Kucera 1995, Lewis et al. 1995, Aubry 1997, Kucera 1999), largely in hope of finding a unique genetic signature that would allow individuals to be confidently classified as exotic or native. Such an analysis has been hindered in part by the paucity of samples from the mountain population, especially specimens collected since the dramatic range expansion of the exotic lowland foxes in the mid-20th century.

In 1993, a population of mountain red foxes was discovered in the Lassen Peak region of northern California (1900-3150 m) (Kucera 1995). Historically, this area was one of the main population centers for the Sierra Nevada red fox (Grinnell et al. 1937, Schempf and White 1977). But despite its elevation, the Lassen region is <70 km from the Sacramento Valley population of exotic red fox. The average dispersal distance for rural red fox is approximately 30 km, but instances of up to 300 km have been documented (Lariviere and Pasitschniak-Arts 1996). Therefore, the Lassen region should be considered within dispersal range of the Sacramento Valley population. Furthermore, several red fox fur farms were located in the Lassen region during the 1940s and 1950s, and escapees from these farms might have become naturalized in the local area (Lewis et al. 1995, Lewis et al. 1999). A subsequent ecological investigation of the Lassen red foxes (Chapters 1-4) quantified their local distribution, resource utilization and movement patterns, which were similar to those of the historic native mountain red fox. However, ecological characteristics alone could not satisfactorily answer the question of highest importance to wildlife managers: Do the Lassen red foxes represent a remnant of the native mountain population or the establishment of exotic individuals at high elevations?

Therefore, the primary goal of this project is to use population genetic methods to determine whether the Lassen red foxes most likely descended from the mountain or lowland foxes in California. Secondary goals include quantifying the diversity and distribution of mitochondrial haplotypes within California, especially those that are unique to the mountain or lowland populations, and assessing the extent of structure among sub-populations within the state.

METHODS

Acquisition of samples

I collected tissue samples from 5 red foxes (4 females, 1 male) from the Lassen Peak population in 1998-2000. I compared these to red foxes from the collection of the Museum of Vertebrate Zoology at the University of California, Berkeley. Additional specimens were acquired from other university and municipal natural history collections, and from several road-killed red foxes collected in the Sacramento Valley. Roadkills were collected in accordance with a salvage permit from the California Department of Fish and Game. I acquired a total of 78 specimens from throughout California, collected from 1904 through 2004 and representing 22 counties. For comparative purposes, I also acquired 4 specimens from 3 counties in Nevada and 15 specimens from 3 counties in Washington. Mountain red fox from Nevada are also considered *V. v. necator* but those from Washington are considered *V. v. cascadensis* (Hall 1981). These 2 subspecies, along with the Rocky Mountain red fox (*V. v. macroura*), are believed to have originated from the same ancestral population and are probably more closely related to each other than to other red fox subspecies in North America (Roest 1977, Aubry 1983). Specimen types included muscle tissue, untanned hide, nasal turbinate bone and feces.

I classified specimens based upon the elevation and date of their collection. Specimens collected above 1066 m were considered “mountain” and those below 1066 m were “lowland.” Similarly, those collected prior to 1950 were considered “historic” and those collected after 1950 were “modern.” I chose 1950 as a temporal boundary based upon a natural separation in the collection times of the available museum specimens and because the range of the lowland red fox had not expanded beyond the Sacramento

Valley by this date (Lewis et al. 1999). Based upon these elevational and temporal criteria and the geographic distribution of the available specimens, I made the *a priori* decision to recognize 7 sub-populations in California: 3 from the mountains (Modern Lassen Peak (MLP), Historic Cascades (HCS), and Historic Sierra Nevada (HSN)) and 4 from the lowlands (Historic Sacramento Valley (HSV), Modern Sacramento Valley (MSV), Modern Bay Area (MBA), and Modern Southern California (MSC)) (Figure 21). The 4 specimens from Nevada were all historic mountain samples (HNM), and the 15 specimens from Washington were all modern mountain samples (MWM). One Washington specimen collected at 1040 m was included as a "mountain" specimen due to the higher latitude of that population; all other specimens were >100 m from the elevational boundary.

DNA Extraction

Hide and tissue samples were cut into 100-200 mg pieces, diced with a sterile blade, and then soaked in sterile 1X PBS solution for 24 hours to dilute any preservatives that may have been present. DNA was then extracted using a QIAamp minikit (Qiagen Incorporated, Valencia, CA) and the standard tissue extraction protocol. DNA was extracted from nasal turbinate samples using the method of Wandeler et al. (2003). Specifically, a 100-300 mg sample of bone fragments was chilled in liquid nitrogen in a sterile vial for 2 min, then pulverized into a fine powder using a UV- and bleach-sterilized mortar and pestle. The powder was decalcified for 72 hr by suspension and agitation in 1.5 ml of 0.5M EDTA. Samples were then digested with 60 ml of 10% N-sarcosyl and 600 mg of proteinase K for 24 hr at 56^{o}C, followed by an additional 300 mg of proteinase K and 24 additional hr at 56^{o}C. Samples were then centrifuged and 1 ml of the supernatant was transferred to a 10 ml tube containing 5 ml of Qiagen Buffer PB. The DNA was then bound, washed and resuspended in 50 µl of TE buffer using the Qiagen Qiaquick PCR Purification Kit.

Sequencing Mitochondrial DNA

A 354 basepair (bp) sequence of the cytochrome-*b* gene was isolated using primers RF14724 (5'-CAACTATAAGAACATTAATGACC-3') and RF15149 (5'-CTCAGAATGATATTTGTCCTC-3'). Since the nasal turbinate samples were typically degraded, with fragment lengths potentially shorter than the desired products, a set of shorter overlapping PCR products was used to generate the same DNA sequence: RF14724-RFCYTB3R and RFCYTBBF-RF15149 (RFCYTB3R: 5'-GATGCTCCGT-TTGCATGTATG-3', and RFCYTBBF: 5'-CTGCCGAGACGTTAACTATGGCTG-3').

PCR cycle conditions were 94 ^{o}C for 3 min; then 45 cycles of 94 ^{o}C for 30 sec, 50^{o}C for 30 sec and 72 ^{o}C for 45 sec; followed by 10 min at 72 ^{o}C. PCR products were run on agarose gels and extracted using Ultraclean 15 DNA purification kits (Mo Bio, Solana Beach, CA). Dye terminator sequencing reactions were performed for each PCR product for each primer using Beckman DTCS reagents and products sequenced on a Beckman CEQ2000XL capillary sequencer (Fullerton, CA).

Population Analysis

I used Arlequin 2.000 (Schneider et al. 2000) to determine the distribution of alleles within sub-populations and to conduct AMOVA analyses (Excoffier et al. 1992).

Both hierarchical and non-hierarchical AMOVAs were conducted; the hierarchical AMOVA contained 1 group of mountain sub-populations (HSN, HCS, MLP) and 1 group of lowland sub-populations (MSV, MBA, MSC). I used Arlequin to generate F_{ST} values (Wright 1978) for all pairs of sub-populations within California based upon haplotype frequencies. Multiple comparisons among these pairwise F_{ST} values were accounted for via Rice's (1989) sequential Bonferroni procedure. Only Californian sub-populations with ≥ 4 specimens were included in these analyses; the specimens from Nevada and Washington and from Californian sub-populations with <4 specimens were used for only qualitative, non-statistical comparisons.

RESULTS

Usable cytochrome-*b* sequences were obtained from 63 California (80.8%), 4 Nevada (100%) and 11 Washington (73.3%) specimens (Table 29). The 7 sub-populations in California had a mean usable sample size of 9 (range: 2 to 17). Usable sequences were obtained from all 22 counties with specimens, with 1 to 12 sequences per county. Usable sequences were obtained from 54 of 64 (84.4%) tissue specimens, 24 of 30 (80%) nasal turbinate specimens, and 1 of 1 (100%) fecal specimen, for an overall success rate of 83.2%. (One fox had both tissue and nasal turbinate material, but only the nasal turbinate material sequenced successfully.) The success rate for nasal turbinate material was 80% for both the historic (12 of 15) and the modern (12 of 15) specimens; the success rate for tissue was lower for the historic specimens (16 of 24, 66.7%) than for the modern specimens (38 of 40, 95%).

There were 26 variable sites in the 354 bp sequence, consisting of 18 transitions and 8 transversions (Figure 22). These resulted in a total of 20 haplotypes, including 17 in the 63 California specimens, 4 in the 4 Nevada specimens, and 4 in the 11 Washington specimens (Table 29). Differences between haplotypes ranged from 1 to 8 bp relative to haplotype A, with a median difference of 2 bp (Figure 22).

Within California, only haplotypes A and D occurred in both mountain and lowland populations (Table 30). Haplotype A was present in 20 of 26 (76.9%) mountain specimens and 2 of 37 (5.4%) lowland specimens. Haplotype D was present in 1 of 26 (3.8%) mountain specimens and 10 of 37 (27.0%) lowland specimens, all of which were from the Modern Sacramento Valley (MSV) sub-population. The remaining 18 haplotypes in California, Nevada and Washington were exclusive to either the mountains or the lowlands, and 12 were unique to a single sub-population. These unique haplotypes were represented by a single individual in all cases except haplotype K, which occurred in the 6 foxes from Santa Barbara County, part of the Modern Southern California (MSC) sub-population.

The mountain foxes from Nevada shared 3 haplotypes with California, including 1 haplotype (F) that was otherwise found only in the modern lowland sub-populations of Southern California (MSC) and the San Francisco Bay area (MBA). The remaining Nevada haplotype (R) was unique. The mountain foxes from Washington had 2 haplotypes (Q and T) that did not occur in California or Nevada, and one Washington fox had the haplotype (A) that was most common among the California mountain foxes. The 8 remaining Washington mountain foxes (72.7%) had a haplotype (O) that occurred only in 1 individual from California, from the Historic Sierra Nevada (HSN) sub-population.

All 5 specimens in the Modern Lassen sub-population had haplotype A, which was also the most common haplotype in the Historic Cascades (75%) and Historic Sierra Nevada (70.6%) sub-populations. Three haplotypes occurred in the Modern Sacramento Valley sub-population but D was the most prevalent (83.3%). The Modern Sacramento Valley and Bay Area sub-populations shared no haplotypes despite their geographical proximity. The Bay Area and Southern California sub-populations were the most diverse, both in terms of the number of haplotypes and in their sequence differentiation (Table 30).

None of haplotypes found in the mountains of California, Nevada or Washington differed from haplotype A by >3 bp (Figure 22). Furthermore, the haplotype with the 3 bp difference (Q) occurred in the Washington population, the farthest away geographically, and was represented by a single individual. The dominant haplotype in the Washington mountains (O) differed by only 1 bp from the dominant haplotype in the California mountains (A). In contrast, the lowland haplotypes differed from haplotype A by 1 to 8 bp. One of the 1 bp variations (haplotype D) was the most common in the Sacramento Valley and also occurred in the mountains. All haplotypes that differed from A by ≥6 bp (i.e., B, L, M) occurred exclusively in the Bay Area; the one differing by 5 bp (N) occurred in both the Bay Area and in Southern California; and the one differing by 4 bp (G) occurred in both Southern California and in the Modern Sacramento Valley.

The non-hierarchical AMOVA indicated significant structure among the 6 California sub-populations with ≥4 specimens ($F_{\mathrm{ST}} = 0.46$, $p < 0.0001$). The hierarchical AMOVA allocated 24.9% of the variation between the mountain and lowland groups of sub-populations ($F_{\mathrm{CT}} = 0.25$) and 21.1% of the variability among the populations within the 2 groups (F_{SC} = 0.28). Pairwise F_{ST} values indicated significant structure between the Modern Sacramento Valley and both the Bay Area and Southern California, but not between the Bay Area and Southern California (Table 31). There was also significant structure between each mountain-lowland pair, but not among the 3 mountain sub-populations (Table 31).

DISCUSSION

The current analysis is preliminary, consisting of small sample sizes and a relatively short portion (354 bp) of the mitochondrial genome. Due to its matrilineal inheritance, mtDNA can give a biased perspective of gene flow, especially among animals with male-based dispersal such as the red fox (Avise 1994). Nevertheless, this study is still the most comprehensive examination of red fox population genetics in California to date, and is the first to incorporate specimens collected >1000 m elevation and prior to 1990. Unfortunately, many of the historic (pre-1950) specimens from the Sacramento Valley failed to yield usable sequences and therefore could not be included in most analyses. Note that no historic specimens were available from the San Francisco Bay Area and Southern California regions because these populations did not exist prior to 1950 (Fitzpatrick 1999, Lewis et al. 1999).

Wright (1978) provided some general guidelines for interpreting F_{ST} values: 0.00-0.05 indicates *little* genetic differentiation, 0.05-0.15 indicates *moderate* genetic differentiation, 0.15-0.25 indicates *great* genetic differentiation, and >0.25 indicates *very great* genetic differentiation. Values <0.05 can still indicate significant structure, just with little absolute difference between the respective populations.

According to the cytochrome-*b* haplotype frequencies, there was no significant structure among one modern and two historic sub-populations within the historic range of the Sierra Nevada red fox (*V. v. necator*). All 5 of the modern Lassen Peak specimens had the haplotype (A) that was most abundant in the Cascade and Sierra Nevada populations in California nearly a century ago. The prominence of this haplotype in the mountain populations and its scarcity among the lowland populations is strong evidence that the red fox population currently inhabiting the Lassen Peak region is a remnant of the native mountain red fox. The lack of haplotype diversity within this local population may be due to fixation as a result of genetic drift within a small population (Wright 1978), or may indicate that these 5 individuals were from a single matrilineage. In either case, it appears highly unlikely that these individuals are descended from exotic lowland red foxes or fur farm escapees.

The red foxes of the southern Cascade Mountains in California were originally considered the same subspecies as in Oregon and Washington (*V. v. cascadensis*) and distinct from those in the Sierra Nevada (*V. v. necator*) (Grinnell et al. 1930, also see Appendix E). However, Grinnell et al. (1937) found insufficient morphological evidence to support such a distinction and therefore considered all mountain red fox in California to be *V. v. necator*. The current genetic analysis supports this conclusion, finding no significant differentiation between these historic mountain sub-populations. But the predominance of a different haplotype (O) among the Washington specimens suggests that the mountain red foxes of the Pacific states are not panmictic. Additional analyses incorporating specimens from Oregon are necessary to determine the boundary between *V. v. necator* and *V. v. cascadensis,* which is currently arbitrarily delimited at the

California-Oregon border. Roest (1979) suggested grouping the red fox populations of the Sierra Nevada and Cascades as a single subspecies with those of the Rocky Mountains (*V. v. macroura*), based on morphological similarities. Analysis of specimens from the Rocky Mountains could clarify whether such a revision is warranted. Such an analysis would also help answer the question of whether the red foxes from these three regions were originally part of a single population that became isolated in the mountains following the Pleistocene, as hypothesized by Aubry (1983).

In contrast to the mountain sub-populations, significant structure was found among the modern lowland sub-populations in California. But the structure was solely between the Sacramento Valley and the other lowland populations; there was no significant structure between the San Francisco Bay Area and the Southern California sub-populations. In the only prior population genetic study of California red foxes, Fitzpatrick (1999) examined 3 microsatellite loci and a 240 bp portion of the mitochondrial control region from red foxes collected in San Francisco, Monterey and Los Angeles, and found significant structure ($F_{ST} = 0.139$) among these areas. Fitzpatrick concluded that multiple successful red fox introductions had occurred in both San Francisco and Los Angeles, which was consistent with historic records (Lewis et al. 1999). He also concluded that the Monterey population represented an admixture of the San Francisco and Los Angeles populations. In Fitzpatrick's analysis, San Francisco and Los Angeles had the lowest genetic distance despite being the furthest apart geographically. The cytochrome-*b* data in this study paint a similar picture, with the Bay Area and Southern California having the lowest pairwise F_{ST} value among the modern lowland populations, with no significant structure after correcting for multiple comparisons. The genetic similarity among these areas is likely due to recent anthropogenic introductions from similar source populations as opposed to gene flow between them (Fitzpatrick 1999).

No previous genetic study has included specimens from the Sacramento Valley, the first population of lowland exotic red foxes documented in California (Grinnell et al. 1937). Despite its geographic proximity to the San Francisco Bay Area, gene flow between these regions appears low. Presumably the San Francisco Bay Delta and the Sacramento River are barriers to gene flow between these two areas. The distinction between the red foxes of the Sacramento Valley and other coastal regions of the state has been noted previously, albeit not quantitatively. According to a brochure on the ecology and management of exotic red fox in California, “Little is known about the origin of coastal red foxes, except that they are not the same as red foxes from the [Sacramento] valley and were probably imported from some other region of the United States” (CDFG 1999: 2).

Given the availability of red fox specimens from these areas due to roadkills and control operations, a more detailed investigation of population structure among the lowland exotic red fox population, consisting of both mitochondrial and microsatellite analyses, is warranted. Such an analysis could examine whether additional structure exists within the *a priori* sub-populations recognized in this study. For example, the Southern California sub-population might consist of additional sub-populations in the San Joaquin Valley, Santa Barbara County and Los Angeles County. The prevalence of a unique haplotype (K) within all 6 specimens from Santa Barbara county would seem to support this hypothesis but limited sample size prevented this from being tested in the current analysis.

The Sacramento Valley region is the most likely source of exotic lowland red fox dispersing into the Lassen region, based both on geographic distance and the age of the Valley population, yet the pairwise F_{ST} value between the Lassen region and the modern Sacramento Valley sub-population was the largest of any in this study. Grinnell et al. (1937: 385) found the presence of the Sacramento Valley sub-population to be “altogether anomalous” considering the boreal habitats favored by the native red fox. Although this population had existed since at least the 1880s, it had remained restricted to the Sacramento Valley. The establishment of exotic red fox populations in the San Francisco Bay area, the San Joaquin Valley and the southern coastal regions of California is apparently due to multiple anthropogenic translocations as opposed to natural dispersal from the Sacramento Valley population (Fitzpatrick 1999). Assuming a 2-year generation time, the Sacramento Valley population has existed for >50 generations, and the mechanism that has prevented immigration from the valley to the mountains, or vice versa, is unclear. A barrier apparently also exists between the mid-elevation and high-elevation red fox populations in Yellowstone National Park, but also remains unidentified (Swanson 2005). In the Cascades of Washington a dense belt of conifer forest separates the exotic lowland red fox from the native mountain red fox, but since this habitat could easily be crossed by the red foxes, the forest itself is probably not the barrier to gene flow (Aubry 1984).

It is possible that whatever barrier may be restricting mountain red foxes to high elevation habitats may also be preventing lowland red foxes from dispersing into or establishing within these high-elevation areas. To date, the usual perspective (e.g., Aubry 1983, Lewis et al. 1995, Kamler and Ballard 2002) has been that mountain red fox are specialists that have become restricted to high-elevation habitats, presumably following the retreat of the glaciers at the end of the Pleistocene, and that lowland red fox are dietary and habitat generalists that will inevitably disperse into the mountainous areas and out-compete the mountain red fox. The persistence of the dominant mountain haplotype in the Lassen region despite nearby exotic red foxes in the Sacramento Valley and in local fur farms suggests that unidentified factors may be preventing exotic red fox from establishing in these mountainous areas. Such barriers might be intrinsic, such as fine-scale local adaptations within both the lowland and mountain red fox populations that prevent them from persisting in each other’s habitats. Dispersing red foxes may select habitats that are similar to their natal habitats, as has been hypothesized for similar habitat-based population structure in coyotes (*Canis latrans*) in California (Sacks et al. 2004). On the other hand the barrier could be extrinsic, such as the presence of coyotes or other dominant competitors occurring between the mountain and lowland red fox populations. An elevational stratification apparently exists between red fox and coyote populations in the Lassen region (Chapter 2) and this same mechanism may prevent dispersal among the mountain and lowland red fox populations. Although the causal mechanism remains unclear, the available genetic evidence, although limited, suggests that such barriers exist and have restricted gene flow for more than a century. Clearly, additional research needs to be conducted to understand dispersal and gene flow among disparate habitats and elevations for a species that is otherwise regarded as a highly mobile habitat generalist. Such research is especially important given the apparent population declines, protected status, and unique evolutionary history of the mountain red foxes in North America.

MANAGEMENT IMPLICATIONS

Several western states, including California, Oregon, Washington and Idaho, apparently have native mountain and exotic lowland red fox populations (Aubry 1983, Kamler and Ballard 2002). Yet only California has separate management strategies for mountain and lowland areas and explicitly acknowledges that one population is native and the other is exotic (Kamler and Ballard 2002). Although the elevation boundary of 1066 m is arbitrary and likely varies with latitude, this genetic analysis indicates that such a boundary exists and that the modern mountain red foxes, at least in the Lassen area, have the same mtDNA haplotype as most of the red foxes that inhabited the mountains prior to the range expansion of the exotic red fox in California. However, it would be premature to conclude that no exotic red foxes have dispersed into the historic range of the Sierra Nevada red fox. No modern specimens from the Sierra Nevada Mountains were available to be included in this study. Prior to the acquisition of the Lassen specimens, the most recent red fox specimen taken from the historic range of *V. v. necator* was collected in 1941. In fact, it is unclear whether any red fox population remains in the Sierra Nevada Mountains. Recent surveys using baited camera traps and track plates have failed to detect red fox anywhere in the Sierra Nevada (Zielinski et al. *in press*), including historic population centers such as Sequoia and Kings Canyon National Parks (R. Green, unpublished data). Additional targeted surveys are necessary to determine whether any red fox population remains in these areas, and such surveys should be conducted using methods such as hair snares or collection of feces that would allow genetic material to be obtained for comparison with other red fox populations statewide. Collaborative efforts with CalTrans, the highway patrol and other agencies should be established so that any road-killed red fox within the historic range of *V. v. necator* are collected for analysis.

The distribution of mountain red fox may be extremely limited in California and their population density and distribution may be declining, but there is no evidence that these factors are due to competition with or displacement by the exotic red fox. But the fact that the modern Lassen population appears to be native does not justify ignoring the potential threat from exotic red fox, either dispersing from the west (Lewis et al. 1995) or from the east (Kamler and Ballard 2002). The distribution and range expansion of these exotic populations should be carefully monitored, not just for the benefit of the native red fox but also for numerous other native species that may be negatively impacted (Lewis et al. 1999). A more thorough understanding of barriers to dispersal may facilitate regional control efforts for the exotic red fox, although it is unlikely that they can ever be fully eradicated in California.

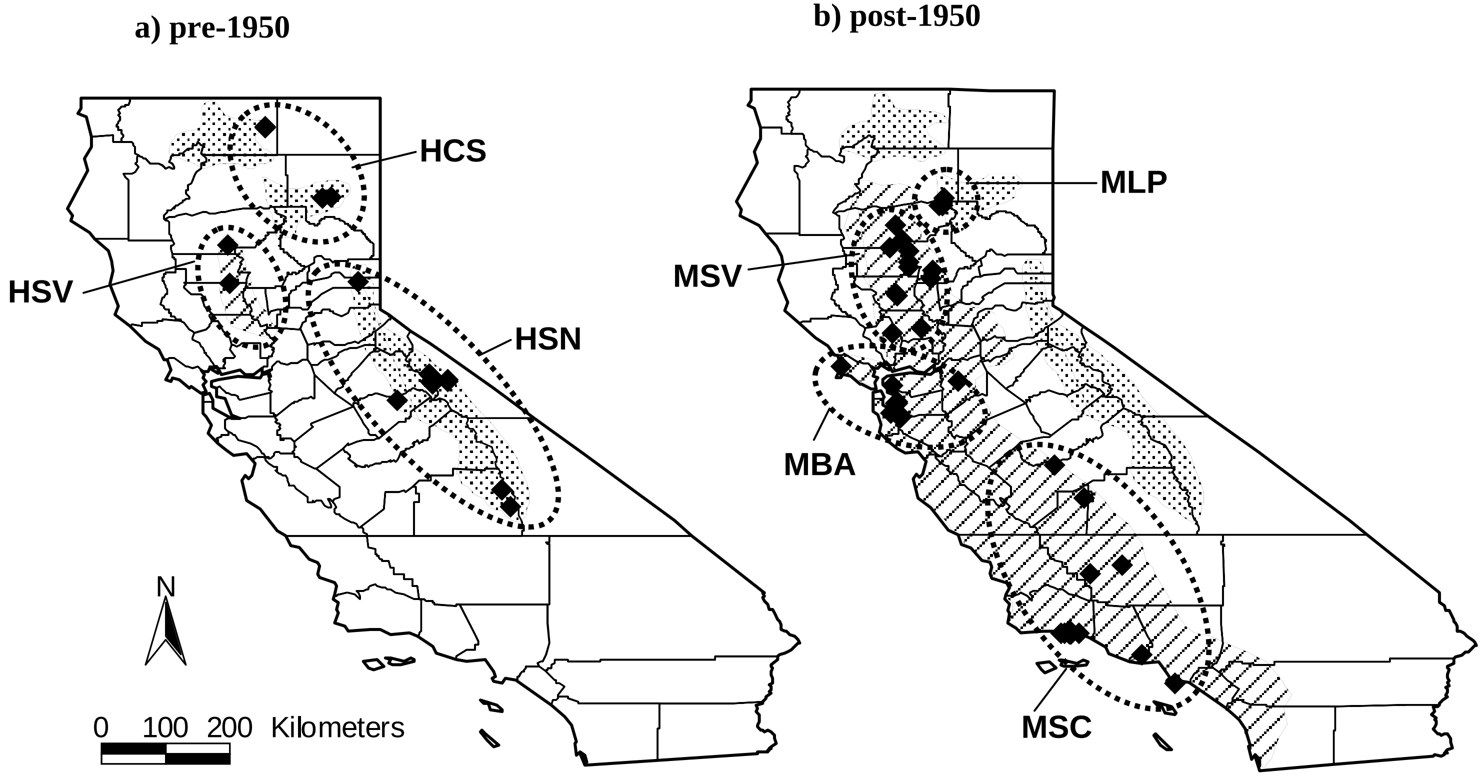


Figure 21: Distribution of red fox specimens and 7 putative sub-populations in California, relative to the range of the native Sierra Nevada red fox (stippling) and the exotic lowland red fox (diagonal lines). Note the increase in the lowland red fox's range from the 1930s to the 1990s. The current distribution of the Sierra Nevada red fox is unknown and is therefore assumed to be the same as its historic distribution. HCS = Historic Cascades; HSN = Historic Sierra Nevada; HSV = Historic Sacramento Valley; MBA = Modern Bay Area; MLP = Modern Lassen Peak; MSC = Modern Southern California; MSV = Modern Sacramento Valley. Not shown are 4 pre-1950 specimens from the mountains of Nevada (HNM) and 11 post-1950 specimens from the mountains of Washington (MWM). Distributions based upon Grinnell et al. 1937 and Lewis et al. 1999.

Figure 22: Variable sites in the 354 bp region of the cytochrome-*b* gene in red foxes from California, Nevada and Washington.

```
                     10        20

               11111122 2222222222 333333
             3834679914 5555577889 023345
Haplotype    9424848993 2456758387 844911

   A         CCATTATATT TTCTGGGTCT TTTGTG
   B         ....CT..CC .......ATC ..C...
   C         ...C...... .......... .....A
   D         .......... .......... C.....
   E         T......... .......... ...A..
   F         T......... .......... ......
   G         ....CT..C. ........T. ......
   H         T......... ......A... ......
   I         T......... .......... ....G.
   J         .......... .......... .....A
   K         .........C C......... ......
   L         T......... .CTGC..... .G....
   M         ..G.CTA.C. ........T. ......
   N         ..G.CT..C. ........T. ......
   O         .T........ .......... ......
   P         .......T.. .......... C.....
   Q         .T........ .....AA... ......
   R         ...C...... .......... ......
   S         ...C...... .......... C.....
   T         .T........ .......... .....A
```

Table 29: Locality data for red fox specimens used in the genetic analysis. Elevations rounded to the nearest 50 m.

State	Pop'n*	County	Sample ID	Year	Locality	Elev (m)	Type	Haplotype	Institution
CA	HCS	Lassen	MVZ-34984	1925	8 km SE of Eagle Lake	1850	skinsnip	A	MVZ
		Lassen	MVZ-35280	1925	8 km SE of Eagle Lake	1850	turbinate	C	MVZ
		Siskiyou	MVZ-68857	1934	Medicine Lake	2050	skinsnip	A	MVZ
		Siskiyou	MVZ-68858	1934	Medicine Lake	2050	skinsnip	A	MVZ
	HSN	Mariposa	MVZ-23696	1916	Big Meadows, Yosemite National Park	1350	skinsnip	A	MVZ
		Mono	MVZ-32800	1921	Ellery Lake, Yosemite National Park	2950	turbinate	D	MVZ
		Mono	MVZ-32809	1922	Virginia Lakes	3000	skinsnip	A	MVZ
		Mono	MVZ-33381	1922	near Mono Lake	3050	skinsnip	A	MVZ
		Mono	MVZ-33382	1922	near Mono Lake	3050	skinsnip	A	MVZ
		Mono	MVZ-33472	1923	19 km SW of Mono Lake	3000	skinsnip	A	MVZ
		Mono	MVZ-33473	1923	19 km SW of Mono Lake	3000	turbinate	A	MVZ
		Mono	MVZ-33474	1923	23 km SW of Mono Lake	3050	skinsnip	C	MVZ
		Mono	MVZ-33586	1923	Saddlebag Lake near Tioga Pass	3100	turbinate	A	MVZ
		Mono	MVZ-41004	1928	Between Ellery and Tioga Lakes	2950	skinsnip	J	MVZ
		Mono	MVZ-41468	1928	Between Ellery and Tioga Lakes	2950	turbinate	A	MVZ
		Mono	MVZ-44097	1929	near Camp Tioga	2950	turbinate	A	MVZ
		Mono	MVZ-46663	1929	1 km W of Ellery Lake	2950	turbinate	A	MVZ
		Nevada	MVZ-95401	1941	Euer Valley, appx. 16 km N of Truckee	1850	turbinate	S	MVZ
		Tulare	MVZ-16251	1911	Whitney Meadow	3000	skinsnip	A	MVZ
		Tulare	MVZ-16252	1911	2.5 km E of Whitney Meadow	3000	skinsnip	A	MVZ
		Tulare	MVZ-16374	1911	Monache Meadows	2450	turbinate	O	MVZ
	HSV	Colusa	MVZ-33550	1923	11 km NE of Maxwell	<50	skinsnip	P	MVZ
		Tehama	MVZ-115439	1948	2.5 km SW Vina-Corning Bridge	50	turbinate	A	MVZ
	MBA	Alameda	LF-42	1995	Strawberry Canyon	350	muscle	F	MVZ
		Alameda	REJ-1535	1996	Hayward Shoreline	50	muscle	N	MVZ
		Alameda	REJ-1537	1996	Hayward Shoreline	50	muscle	M	MVZ
		Alameda	REJ-1540	1996	Hayward Shoreline	50	muscle	F	MVZ
		Marin	MVZ-175993	1982	Point Reyes National Seashore	<50	turbinate	B	MVZ
		San Joaquin	REJ-1624	1997	Stockton	<50	muscle	F	MVZ
		San Mateo	REJ-1555	1996	Palo Alto	100	muscle	F	MVZ
		San Mateo	REJ-1573	1996	Palo Alto	100	muscle	H	MVZ
		San Mateo	REJ-1575	1996	Palo Alto	100	muscle	L	MVZ
		San Mateo	REJ-1588	1997	Redwood City, South Bay Refuge	50	muscle	F	MVZ

Table 29, continued.

State	Pop'n	County	Sample ID	Year	Locality	Elev (m)	Type	Haplotype	Institution
CA	MLP	Shasta	F03	2000	Lassen Volcanic National Park	2550	earsnip	A	J. Perrine
		Tehama	F01	1998	Lassen National Forest	1900	earsnip	A	J. Perrine
		Tehama	F02	2000	Lassen National Forest	1700	earsnip	A	J. Perrine
		Tehama	F05	2000	Lassen National Forest	1750	earsnip	A	J. Perrine
		Tehama	M01	1998	Lassen National Forest	1750	earsnip	A	J. Perrine
	MSC	Fesno	FRC-027	1997	Hwy 41 at San Joaquin River	<200	muscle	N	FRVC
		Kern	R003	2003	Roadkill, Bakersfield	50-150	muscle	E	MVZ
		Kern	FRC-061	1999	Elk Hills Petroleum Reserve	<200	muscle	G	FRVC
		Kings	FRC-087	2000	3 km E of Hanford	<200	muscle	G	FRVC
		Los Angeles	LA-4	1990	Agoura Hills	250-400	liver	I	LA NHM
		Los Angeles	LA-5	2002	Roadkill, San Pedro	<150	liver	F	LA NHM
		Los Angeles	LA-6	1989	Roadkill, San Pedro	<150	liver	F	LA NHM
		Santa Barbara	SB-1	2002	Roadkill, Hope Ranch	<150	earsnip	K	SB MNH
		Santa Barbara	SB-2	1993	Arroyo Borro Beach Park	<150	earsnip	K	SB MNH
		Santa Barbara	SB-3	1990	Hope Ranch, Las Palmas Dr	<150	earsnip	K	SB MNH
		Santa Barbara	SB-4	1994	Shoreline Drive	<150	earsnip	K	SB MNH
		Santa Barbara	SB-5	1995	West Ortega	<150	earsnip	K	SB MNH
		Santa Barbara	SB-6	1996	Hope Ranch Beach	<150	earsnip	K	SB MNH
	MSV	Butte	CSU-2530	1966	11 km S of Ord Ferry, Sacramento River	<100	skinsnip	D	CSU
		Butte	CSU-3943	1970	Oroville (Thermolito) Afterbay	<150	skinsnip	D	CSU
		Butte	X-2	2001	Roadkill, Gridley	<50	earsnip	D	R. Alessio
		Colusa	CSU-2588	1968	3 km S of Williams	<50	skinsnip	D	CSU
		Colusa	X-1	2000	Roadkill, I-5 near Williams	<50	muscle	D	J. Perrine
		Glenn	CSU-2589	1969	Hwy 32 at Sacramento River	<100	tissue	G	CSU
		Glenn	CSU-5128	1973	6 km S of Ord Ferry	<100	skinsnip	D	CSU
		Glenn	PW-1	2004	North Diversion Dam, NW of Orland	100	tissue	A	P. Weliver
		Napa	CSU-2591	1968	Lake Berryessa	<350	skinsnip	D	CSU
		Tehama	CSU-3504	1970	1.5 km S of Woodson Bridge, Corning	<100	skinsnip	D	CSU
		Tehama	H-1	1986	Roadkill, Sacramento Valley	<350	earsnip	D	HSU
		Yolo	W-1	2002	1 km W of Woodland	50	fecal	D	J. Perrine

Table 29, continued.

State	Pop'n	County	Sample ID	Year	Locality	Elev (m)	Type	Haplotype	Institution
NV	HNM	Carson City	MVZ-69635	1934	near Marlette Lake	1700-2000	skinsnip	J	MVZ
		Carson City	MVZ-69636	1934	near Marlette Lake	2440	turbinate	R	MVZ
		Churchill	MVZ-16381	1911	Fairview (Hwy 50 at SR-839)	1400	skinsnip	A	MVZ
		Clark	MVZ-90621	1940	1.5 km W of Hidden Forest	2750	turbinate	F	MVZ
WA	MWM	Pierce	UW-31868	1974	Mt. Rainier National Park	1300	turbinate	T	UWB
		Pierce	UW-32523	1980	Crystal Mountain Ski Area	1350	turbinate	O	UWB
		Pierce	UW-32550	1981	Crystal Mountain Ski Area	1600	turbinate	O	UWB
		Pierce	UW-32554	1982	Mt. Baker - Snoqualmie National Forest	1500	turbinate	O	UWB
		Pierce	UW-32559	1982	Crystal Mountain Ski Area	1200	turbinate	O	UWB
		Pierce	UW-32953	1982	Crystal Mountain Ski Area	1550	turbinate	Q	UWB
		Pierce	UW-32954	1983	Crystal Mountain Ski Area	1550	turbinate	O	UWB
		Pierce	UW-33375	1983	Crystal Mountain Ski Area	1550	turbinate	A	UWB
		Skamania	UW-33377	1984	Gifford Pinchot National Forest	1050	turbinate	O	UWB
		Yakima	UW-32525	1980	Potato Hill	1200-1600	turbinate	O	UWB
		Yakima	UW-32524	1980	Potato Hill	1200-1600	turbinate	O	UWB

* See Figure 1 for the location and definition of sub-populations.

Institutions (all are in California unless otherwise noted):
CSU = California State University, Chico
FRVC = Fort Roosevelt Vertebrate Collection, Hanford
HSU = Humboldt State University, Arcata
LA NMH = Los Angeles County Natural History Museum
MVZ = Museum of Vertebrate Zoology, UC Berkeley
SB NHM = Santa Barbara Natural History Museum
UWB = Burke Museum of Natural History and Culture, University of Washington, Seattle, WA
Other names indicate specimens not from official collections, such as field study animals or roadkills.

Table 30: Distribution of cytochrome-*b* haplotypes among putative red fox sub-populations.

Sub-	Haplotypes																						
Pop'n	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	n	H ± sd	π
HCS	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	0.50 ± 0.27	0.0028
HSN	12	-	1	1	-	-	-	-	-	1	-	-	-	-	1	-	-	-	1	-	17	0.51 ± 0.15	0.0022
HSV	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2	1.00 ± 0.50	0.0057
MLP	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	0.00 ± 0.00	0.0000
MBA	-	1	-	-	-	5	-	1	-	-	-	1	1	1	-	-	-	-	-	-	10	0.78 ± 0.14	0.0138
MSC	-	-	-	-	1	2	2	-	1	-	6	-	-	1	-	-	-	-	-	-	13	0.78 ± 0.11	0.0100
MSV	1	-	-	10	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	12	0.32 ± 0.16	0.0027
HNM	1	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	-	-	4	1.00 ± 0.18	0.0042
MWM	1	-	-	-	-	-	-	-	-	-	-	-	-	-	8	-	1	-	-	1	11	0.49 ± 0.18	0.0021

n: sample size
H: haplotype diversity
π: nucleotide diversity

Table 31: Matrix of pairwise F_{ST} values for California sub-populations with ≥ 4 specimens. Note that the 3 mountain sub-populations are listed first, followed by the 3 lowland populations. Values that were not significant after correcting for multiple comparisons are indicated by "(ns)".

	HCS	HSN	MLP	MBA	MSC	MSV
HCS	--					
HSN	-0.115 (ns)	--				
MLP	0.063 (ns)	-0.003 (ns)	--			
MBA	0.323	0.371	0.514	--		
MSC	0.315	0.360	0.487	0.148 (ns)	--	
MSV	0.604	0.521	0.760	0.465	0.437	--

CONCLUSIONS

NICHE OVERLAP AMONG RED FOX, COYOTE AND MARTEN IN THE LASSEN REGION

I used Pianka's index (see p. 21) to quantify the niche overlap between each pair of carnivores for each resource type (Figure 23). Diet was divided into 7 categories: Rodents, Artiodactyls, Other Mammals (insectivores, lagomorphs and carnivores), Birds, Insects, Fruit and Manmade Items. Habitat was divided into 6 cover types: Barren, High-elevation Conifer, Mid-elevation Conifer, Herbaceous, Hardwood and Shrub. Activity was divided into 4 diel periods: Dawn, Day, Dusk and Night. (See Chapters 1, 2 and 3 for additional details about the definition and composition of the dietary, cover type and diel categories, respectively.)

Dietary overlap was assessed for 4 seasons of 3 months each (winter, spring, summer and autumn), but the winter overlap was dropped due to small sample size for coyote and marten. The winter diets are likely quite similar to the spring diets given the extent of spring snow cover in the Lassen region (Figure 6). Habitat and activity overlap were assessed for 2 seasons of 6 months each (winter and summer). The use of separate seasonal definitions for the scat and camera data was unavoidable. There were not enough camera detections to recognize 4 seasons for the habitat and activity assessments, and pooling the dietary data to 2 seasons caused the autumn foods to be split between "winter" and "summer," subsequently eliminating most seasonal patterns.

Similarly, it would have been ideal to have had telemetry-based habitat and activity time data for all 3 carnivores, but this was not possible given the limited resources available for this project. Therefore I used camera traps to obtain these data, but this added new assumptions regarding equal detectability, sampling effort, bias and independence. Although some of these assumptions were surely violated (see Chapters 2 and 3 for details), the available data provide useful insight into the interspecific dynamics among red fox, coyote and marten in the Lassen region and suggest several new hypotheses.

PAIRWISE NICHE OVERLAPS

Red Fox and Coyote

The red fox and coyote diets were most similar in spring. This was due primarily to the limited availability of prey in the snowy months caused by rodent hibernation cycles, deep snow, the availability of mule deer carcasses and the apparent absence of snowshoe hare and other lagomorphs. Their diets diverged through the summer and autumn because the coyotes continued to use large prey while the red fox used seasonally-available fruit and pocket gophers. Habitat use overlap decreased in summer when the red fox moved to higher elevations. Their activity patterns were virtually identical regardless of season, although some fine scale temporal partitioning may have occurred at night (see Chapter 3).

Red Fox and Marten

Niche overlap between red fox and marten was high (>0.8) for all 3 resource types and showed virtually no seasonal variation. Diet had the highest overlap and increased from spring through summer and autumn. This reflected the use of seasonally-available rodents, insects, and manzanita berries by these generalist carnivores. Activity had the least overlap because the red fox were primarily nocturnal and crepuscular while the marten were active throughout the diel period.

Coyote and Marten

Niche overlap between coyote and marten was similar to the overlap between coyote and red fox. This is consistent with the virtually identical resource utilization patterns of red fox and marten. Coyote and marten diets were most similar in the spring and least similar in autumn. Habitat use varied from very similar in winter to quite different in summer. Activity patterns showed little seasonal change, with the comparably low overlap value due to coyotes being detected at camera traps almost exclusively at night while marten were detected throughout the diel period.

IMPLICATIONS FOR THE RED FOX

The available data suggest that seasonal patterns of food availability, snow depth and interspecific antagonism may be central to red fox ecology in the Lassen region. During the snow-free months, interspecific competition and the availability of sufficient food resources at high elevations (pocket gophers and manzanita berries in particular) causes an elevational separation, with coyotes at lower elevations and red fox at higher elevations. This separation is not absolute, as some coyotes occur at higher elevations, but the coyote population density is likely negatively correlated with elevation while the red fox population density is positively correlated with elevation. Red fox niche overlap with marten is high but resources do not appear to be limiting in these snow-free months.

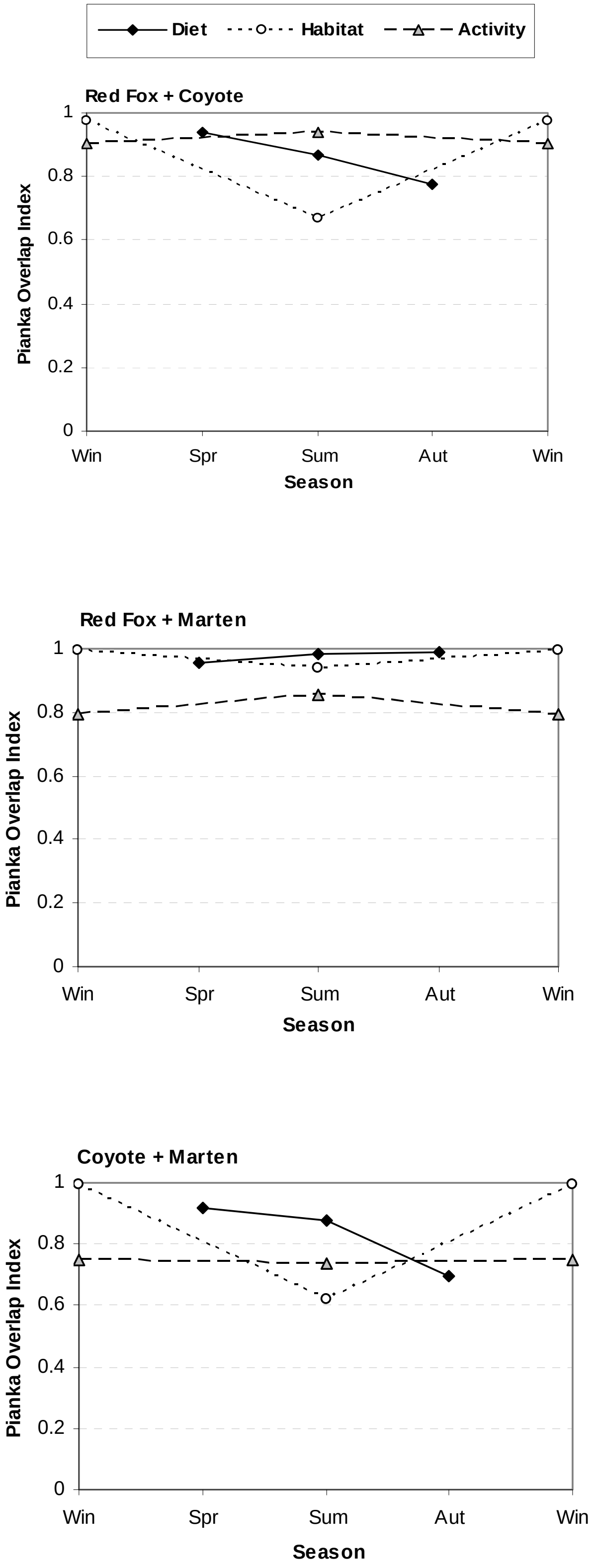
In the winter, however, the accumulation of deep, soft snow at high elevations has direct and indirect effects upon the red fox, because the snow increases the energy required for locomotion and restricts the availability of prey. As a result, the red fox descend to lower elevations as soon as the snow begins to accumulate. Here they subsist on whatever foods are available, predominantly mule deer carrion, rodents, insectivores and garbage. The snow not only remains throughout the spring months but is often deeper in spring than in winter (Figure 6). Therefore, the spring months are likely the time of resource scarcity in the Lassen area. This coincides with the foxes' peak consumption of insectivores, which are otherwise shunned if more palatable prey are available (Macdonald 1977, Lloyd 1980). Spring is also the breeding season for red fox, and food availability is an important factor for successful reproduction (Lloyd 1980, Voigt 1987). The scarcity of prey in spring may contribute to the low level of reproduction observed in this population. When the snows finally begin melt, the red foxes promptly return to the higher elevations, presumably to reduce their interactions with coyotes and to utilize the prey that are now available due to the firmness and shallowness of the melting snow.

The deep snows and the apparent lack of lagomorphs likely have a greater impact upon the red fox than upon coyote or marten. Of these carnivores, marten are the best adapted to snowy conditions (Buskirk et al. 2000, Krohn et al. 2004). Their lighter foot-loading and subnivean and arboreal abilities permit them to successfully forage for rodents atop the snow, beneath the snow and in the trees, in addition to utilizing other foods such as mule deer carrion. On the other hand, coyotes are the least adapted to snowy conditions but their larger body size permits them to take large prey such as mule deer and allows them to dominate the smaller carnivores in direct interactions. The red fox is intermediate in foot-loading and body mass, and its food options during the snowy months are largely restricted to prey available atop or just beneath the snow, along with carrion and manmade foods. As the intermediate-sized carnivore, it would likely be most dependent upon the intermediate-sized prey, namely snowshoe hares and other lagomorphs.

Numerous lines of evidence suggest that resources in the Lassen area are limiting for red foxes. Lassen red foxes have below-average body sizes, massive home ranges, low population density and negligible observed reproduction. They undergo a seasonal elevational migration that appears to be unique in North America. Starvation foods are present in their diet in all seasons and peak in the snowy months. Many individuals become beggars at campsites and parking lots. It is difficult to believe that these factors are unrelated to the apparent population declines of *V. v. necator* and its listing as a State Threatened species -- characteristics of no other red fox population worldwide (Nowak 1999).

Far from being a high elevation specialist, California's mountain red fox may instead have become isolated in a narrow ecological pocket, bounded by interspecific competition with coyotes and harsh winter conditions that restrict the available prey. If lagomorphs were a critical winter prey, as is the case with many other red fox populations, then a reduction in lagomorph populations would likely have a more profound effect upon the red fox than upon coyotes or marten. Furthermore, changes in climate might reduce the available refugia from the competitively-dominant coyote. These factors may be important contributors to the apparent reduction in mountain red fox populations in California over the past century. Additional research is necessary to test these hypotheses.

Figure 23: Pairwise niche overlap among Lassen red fox, coyote and marten. Note that winter is shown at both ends of each chart.



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APPENDIX A

MEASUREMENTS OF SCATS OF KNOWN SPECIES IDENTITY

Table 32: Measurements of scats of known species identity. Identities were known by observing the defecation or by genetic analysis.

Measurement	Species	Mean	SD	Min	Max	n
Dry mass (g)	Red Fox	4.7	4.0	0.7	23.2	77
	Coyote	18.8	12.2	1.7	51.4	22
	Marten	1.5	0.8	0.3	2.2	5
Length (mm)	Red Fox	90.9	45.1	27.3	275.0	31
	Coyote	216.8	80.0	105.6	330.0	8
	Marten	69.6	6.9	64.7	77.5	3
Max. diameter (mm)	Red Fox	14.0	3.3	8.4	21.5	33
	Coyote	21.4	4.3	14.0	30.6	13
	Marten	9.8	2.3	8.0	12.4	3

Figure 24: Distribution of scat length among Lassen red fox, coyote and marten.

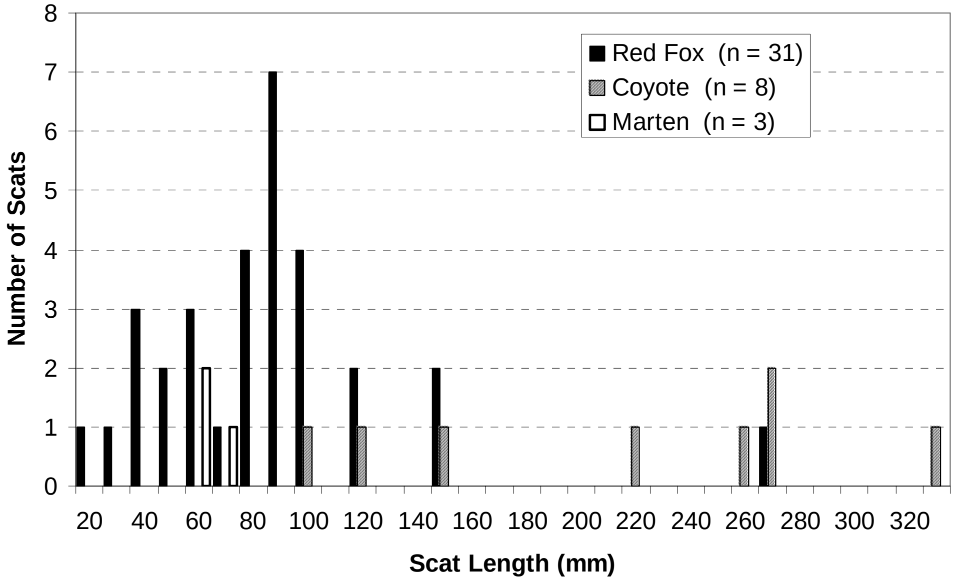
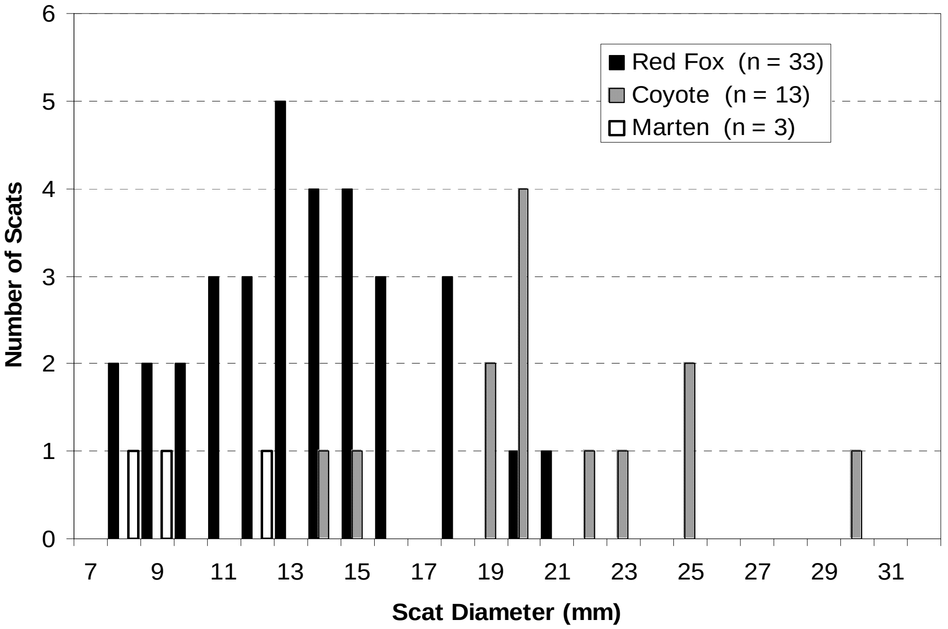


Figure 25: Distribution of scat width among Lassen red fox, coyote and marten.



APPENDIX B

TRAILMASTER CAMERA PROTOCOL

I followed the usual protocol for detecting forest carnivores (Zielinski and Kucera 1995), except that all stations were operated for approximately 28 nights instead of relocating the station after the target species were detected. Given the rarity of the mountain red fox, and that camera traps are the only method that has been shown to reliably detect them, a more explicit summary of my methodology appears warranted.

Each camera trap station consisted of a sensor unit and a single 35 mm camera. In summer 1998 I used mostly TrailMaster TM-1500 active sensors, but in the following seasons (summer 1999 through autumn 2002) I used TM-500 and TM-550 passive sensors. Cameras were a variety of Yashika, Olympus and Canon models as supplied by TrailMaster.

In general, the camera and TM 500 / 550 sensor were attached to a tree, approximately 1.2 m from the ground. The camera was mounted using the small plastic tripod that came with the unit and the sensor was mounted using a customized pair of angle brackets that permitted the sensor to be pointed in any direction. I put electrical tape over the sensor's window until only a slit 0.5 to 1 cm remained exposed. This created a "trigger zone" approximately 1 m^2 at a distance of 3 to 5 m. Standard settings for the sensor were P = 2.0, PT = 2.0, and Camera Delay = 3.0 min. The cameras were loaded with Fuji 400 sp, 24 exp print film and the camera flash was set to "Fill-In" mode so the flash fired with every exposure. Stations with passive sensors were usually arranged to point as close to north as possible to prevent sunlight from falling directly onto the sensor window and triggering photographs ("sunsplash"). I also cut back any tall grass, tree boughs or other items between bait and sensor that could move and trigger photos. By waving my hand around near the bait, I could determine the borders of the sensor's "trigger zone." I outlined this with sticks and then ensured the full area was within the camera's field of view.

Each trap station was baited with a pair of rancid (>1 week at room temperature) chicken drumsticks. These were wired to tree, preferably >75 cm DBH, approximately 30 cm from ground, or occasionally to large (>30 cm) flat rock on open ground. The bait was 3 to 5 m from the camera station and sensor unit. The camera and sensor were aimed so that a photograph would be triggered by any animal approaching the bait, either from ground-level (e.g., a fox) or from above on the tree (e.g., a marten). Immediately below the bait at ground level I placed 2 small dollops (each about size of pea) of commercial scent lure, usually Gusto or Canine Call (M&M Fur Company, Bridgewater, SD), and usually alternating by week. I placed another dollop on tree branches or other features approximately 2 m above ground and 5 m from either side of bait to act as "draw in" scent lures. I also put small splash (10-15 drops) of red fox urine (M&M Fur Company, Bridgewater, SD) immediately below the bait. I put an index card labeled with the station identification code near the bait, close enough to be in every photo but not so close that it would be obscured by an animal investigating the bait. Tinted index cards worked better than white cards, which tended to wash out with the flash. I covered the index card with a sandwich baggie to repel moisture and discourage rodent chewing.

To minimize the risk of bear damage I used a 2-person field crew to establish, bait and monitor all camera traps. Each day, one person handled only the bait and scent lure while the other person handled only the sensor equipment and recorded all the data. This method kept the bait and lure scents off the camera gear. In addition, the “draw in” scent lures were placed at least 5 m from the camera and sensor gear. This approach worked well even in summer and bear damage was minimal (1 to 2 sensors chewed up annually, with a usual repair charge of $100 each). Often I covered the wire between the camera and the sensor unit with duct tape to discourage rodent chewing.

My goal was 28 successful trap nights per station (the “survey period”). Stations were left at the same site for at least 4 weeks and were continued for another week if I suspected that 28 trapnights had not yet been achieved due to battery failure, animal damage, etc. Reflected sunlight (“sunsplash”) was a common problem with the passive units and would consume the entire roll of film in an hour or two. To minimize the number of trap nights lost, I would check each station 2 days after setup to ensure that it was working correctly. Sunsplash or other problems usually became evident after just a day or two (the sensor event record would list hundreds of events within a particular time window, and if this happened on 2 consecutive days I could be reasonably sure that it was not due to an animal lingering at the bait). If sunsplash was a problem at a site, I usually programmed the sensor not to trigger photos during the problematic times. This was more efficient than moving the station and starting over. Stations were re-checked in another 3 days to see if the sunsplash was still causing trapnights to be lost. Once stations were working properly, they were monitored weekly.

Battery failure in the sensor or camera can also cost trapnights. I used fresh C batteries in the sensor each 4-5 week survey period. If the camera used AA batteries I replaced them weekly. 3 volt lithium cells generally lasted for the whole 4-5 week survey period, so I just replaced them at the start of each survey period.

To ensure that the equipment was working properly, I triggered a test photo at the beginning and end of each monitoring visit by waving my hand near the bait. Stations were never left until a successful test photo was taken. At each return visit I recorded the status of station, including whether the test photo was successful, whether the bait had been taken or disturbed and whether there was any damage to the camera or sensor. I also confirmed that both the sensor and camera had the correct date and time and were still aimed correctly at the bait. I recorded from the sensor's memory the time and date of the first 30 events when a photo had been triggered. I replaced the film if >13 exposures had been taken. I erased the event records from the sensor's memory only when I changed the film roll; otherwise, I left both for the next visit. Each film roll was labeled with the date, camera station code and the number of photos exposed, and then taken to Wal-Mart for developing as 4x6 single prints. The amount of data recorded per monitoring visit may seem excessive but this took only a few minutes and was very helpful in later determining the number of active nights per station. I refreshed the bait and lure at every visit regardless of whether the old bait had been removed. If the old drumsticks had not been taken I merely piled them below the new bait. Refreshing the bait and lure took about the same time as checking the camera equipment, recording the event data and replacing the batteries and film: about 10 minutes per station for an experienced team.

I was not consistent about recording the presence of animal tracks and sign near each camera station, but this would be a valuable addition to the protocol because it would indicate whether the station was detecting all the species that were nearby.

APPENDIX C

RED FOX LOCATIONS AND HOME RANGES BY SEASON

The following maps illustrate the seasonal locations and home ranges of each individual red fox in the telemetry study (January 1998 through December 2002). The size of these seasonal home ranges and their seasonal variability cannot be fully appreciated without such maps.

Triangles denote independent locations and small circles denote other locations; see Chapter 4 for the criteria for independent locations. 95% MCP home ranges are bounded by thin straight lines and core areas (50% adaptive kernel isopleths) are bounded by bold curved lines. See Table 24 for the dates for each season and Table 23 for the number of locations for each fox and the sizes of their 95% MCPs and core areas.

Cast of characters (in order of appearance):

Red symbols:	F01 (adult female).
Green symbols:	M01 (adult male).
Blue symbols:	Uncollared adult fox and 2 pups on Lassen Peak in Summer 1999.
Tan symbols:	F02 (adult female).
Yellow symbols:	F03 (adult female).
Purple symbols:	F05 (adult female).

Figure 26: Fox locations, winter 1998.

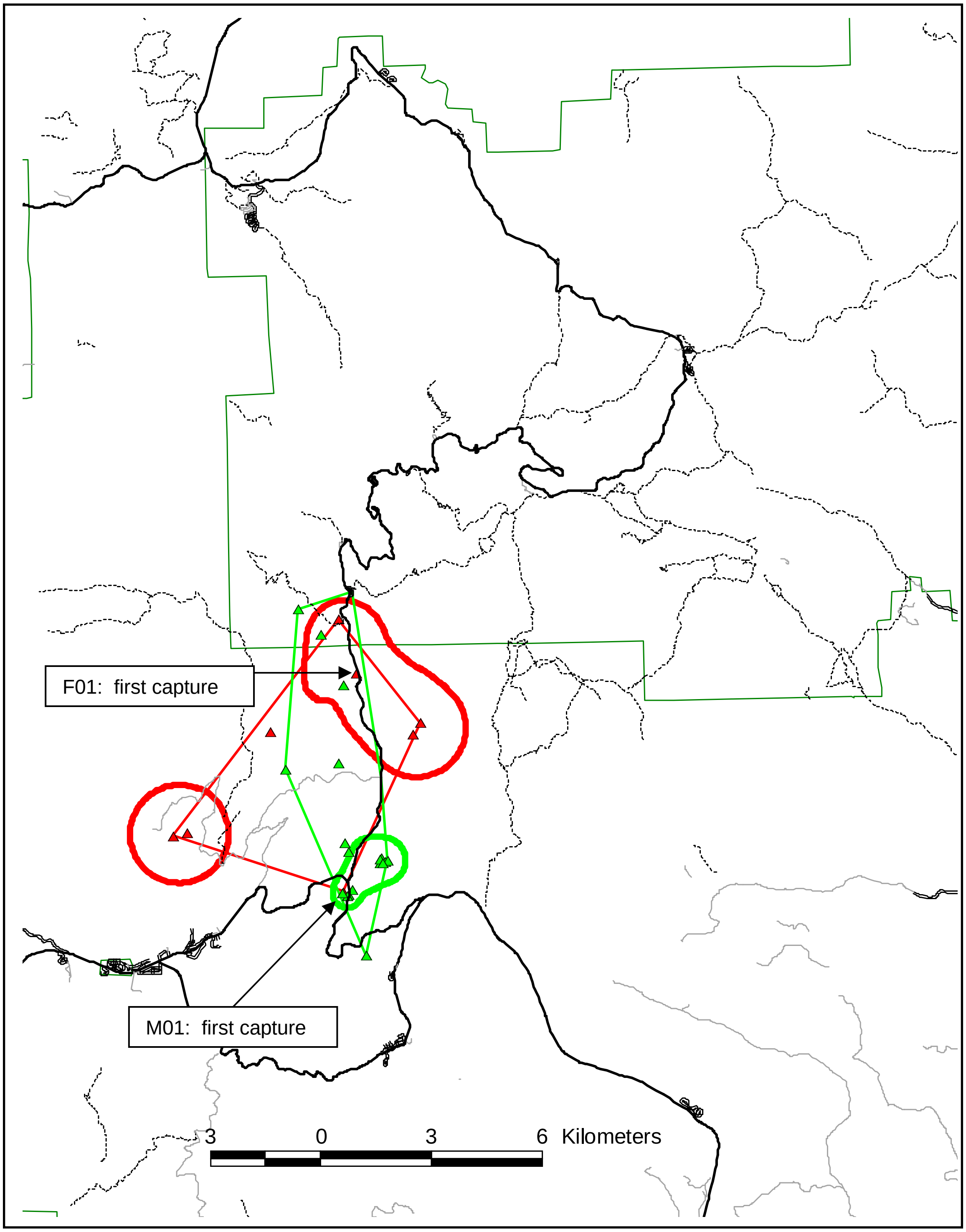


Figure 27: Summer 1998.

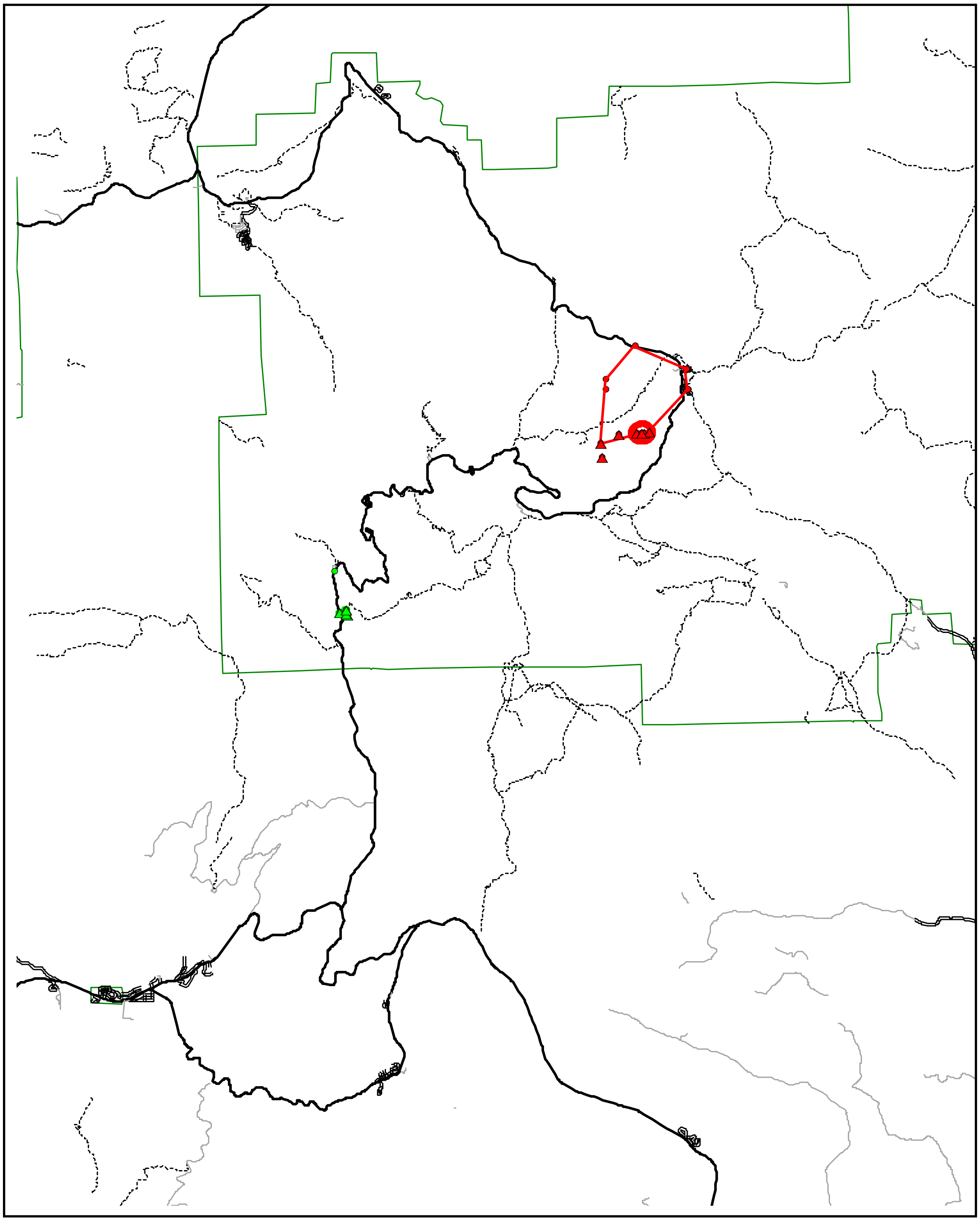


Figure 28: Winter 1999.

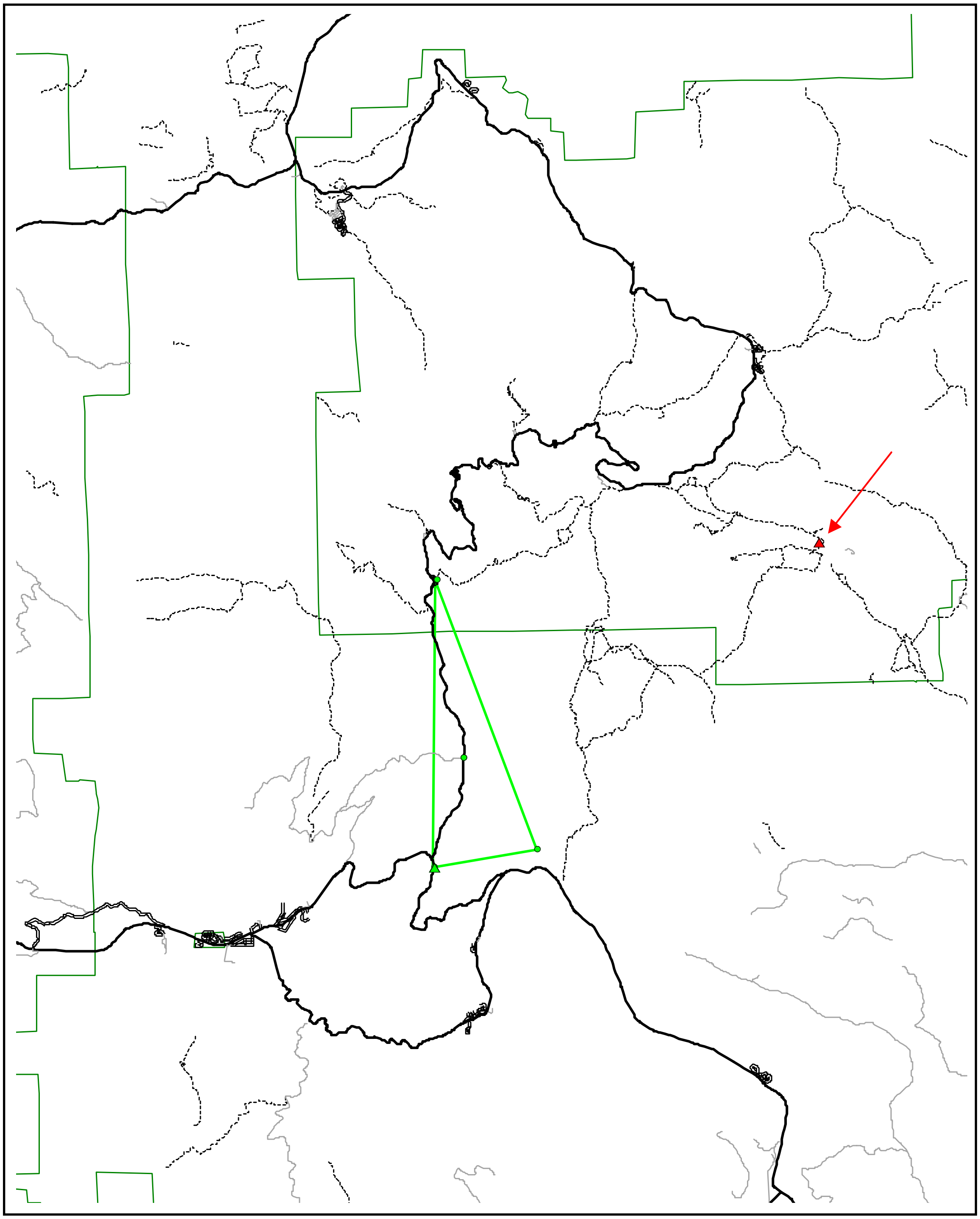


Figure 29: Summer 1999.

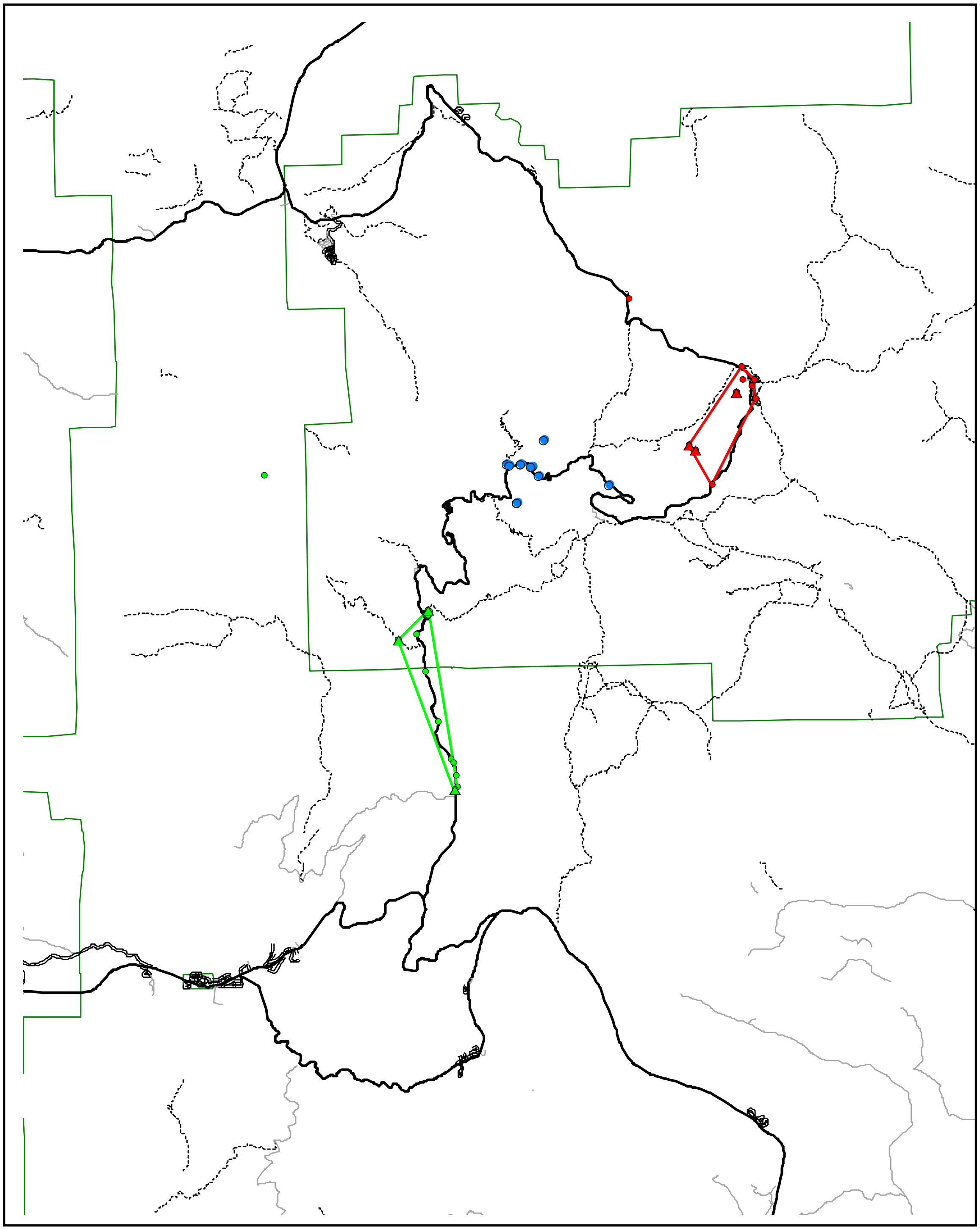


Figure 30: Winter 2000.

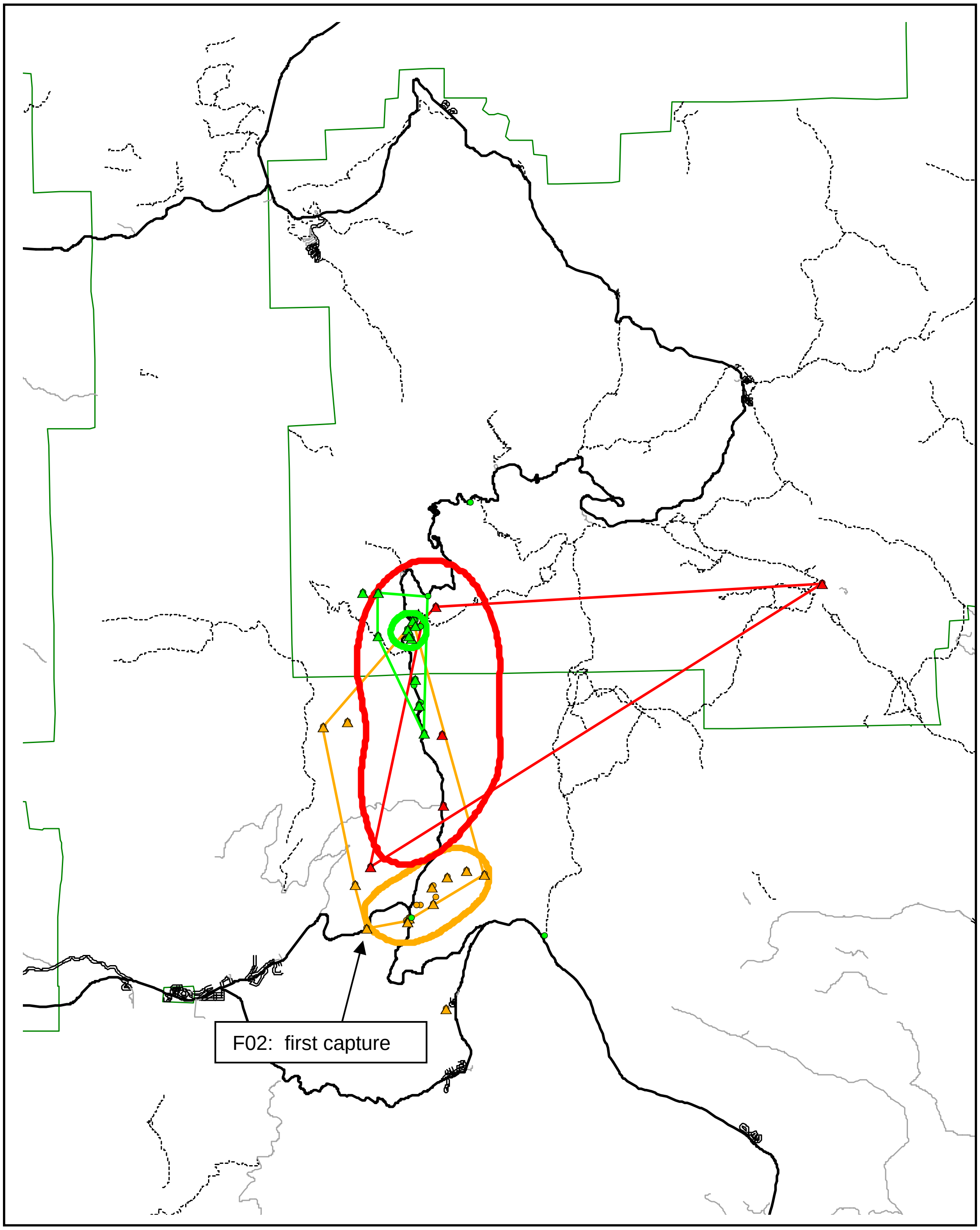


Figure 31: Summer 2000.

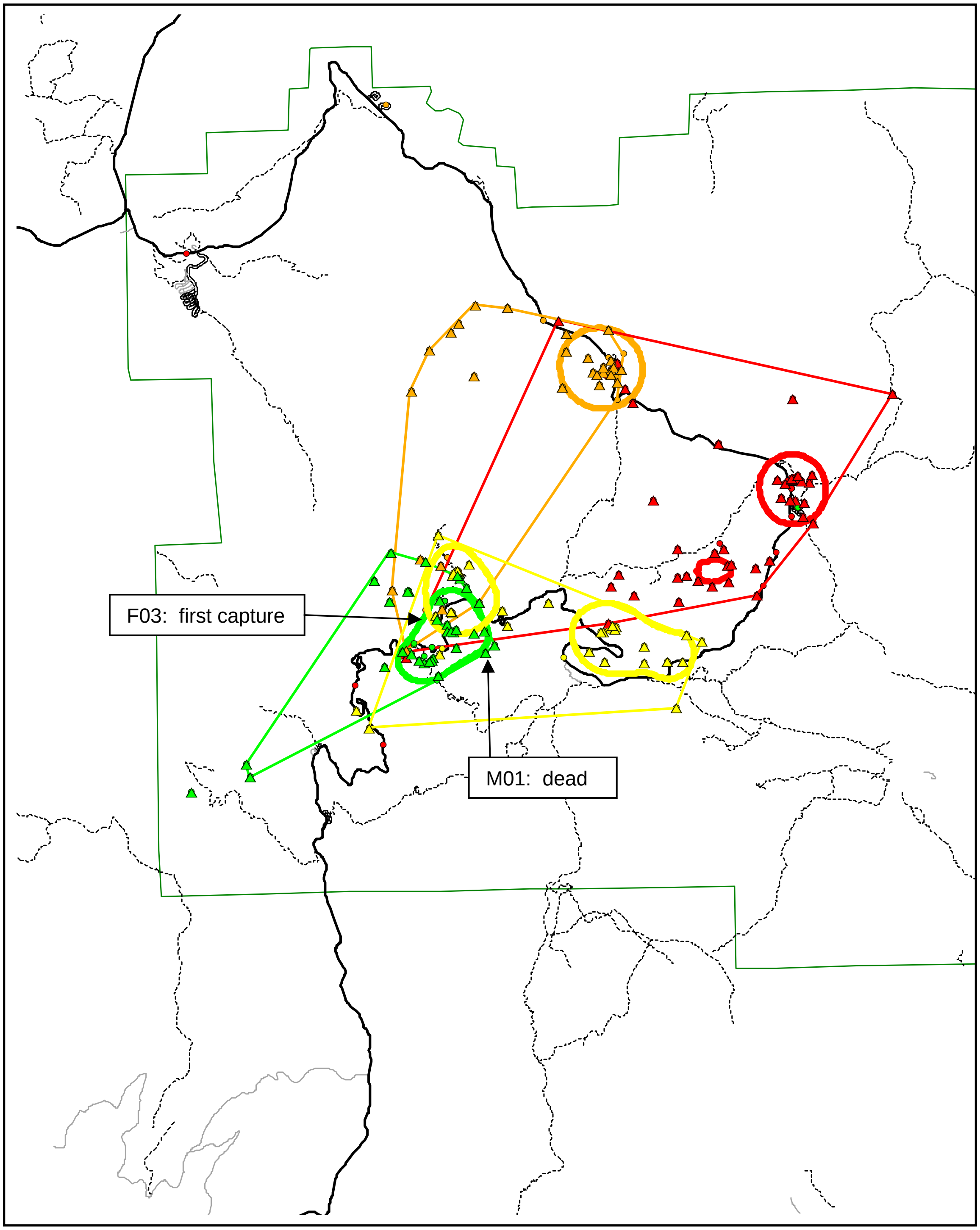


Figure 32: Winter 2001.

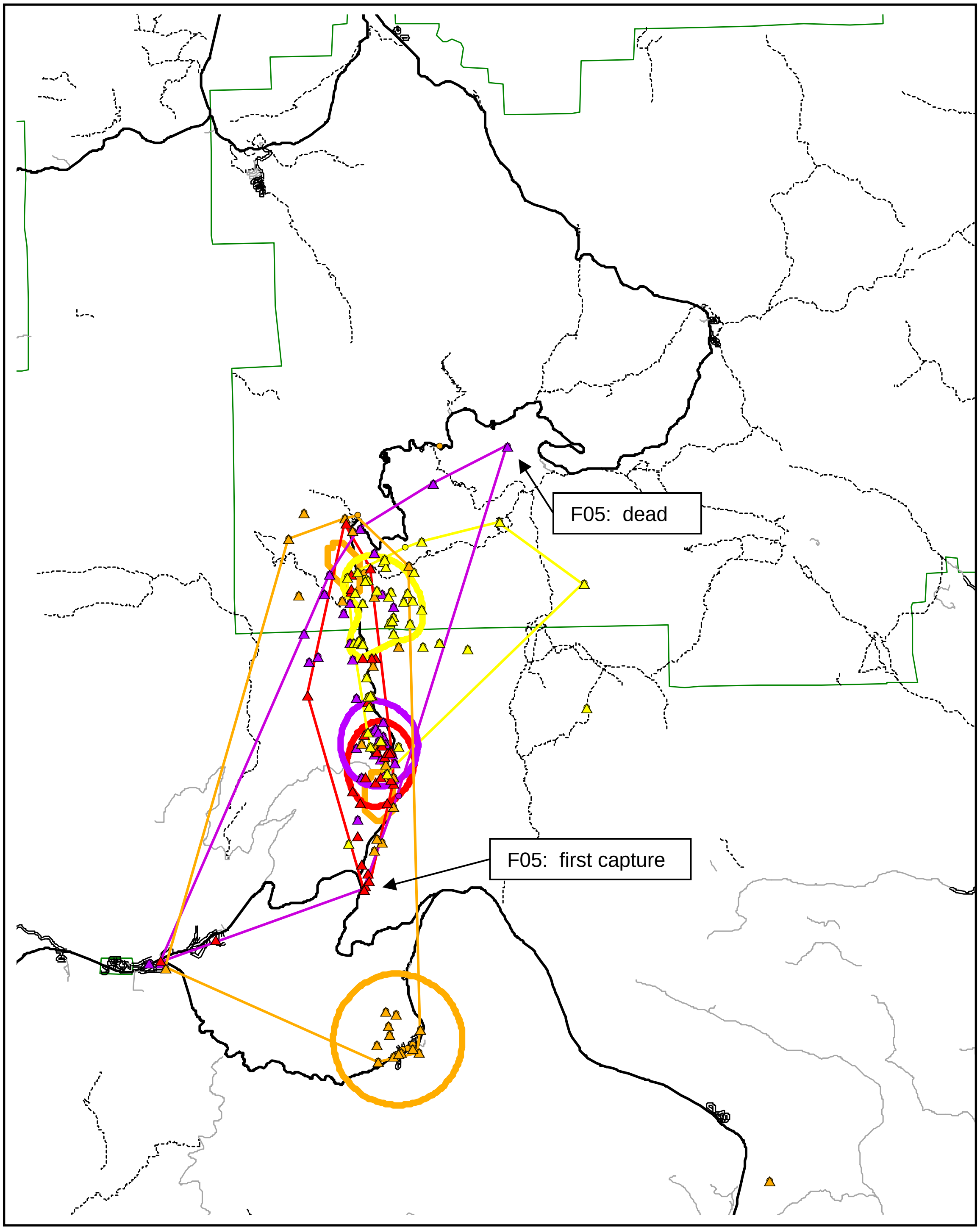


Figure 33: Summer 2001.

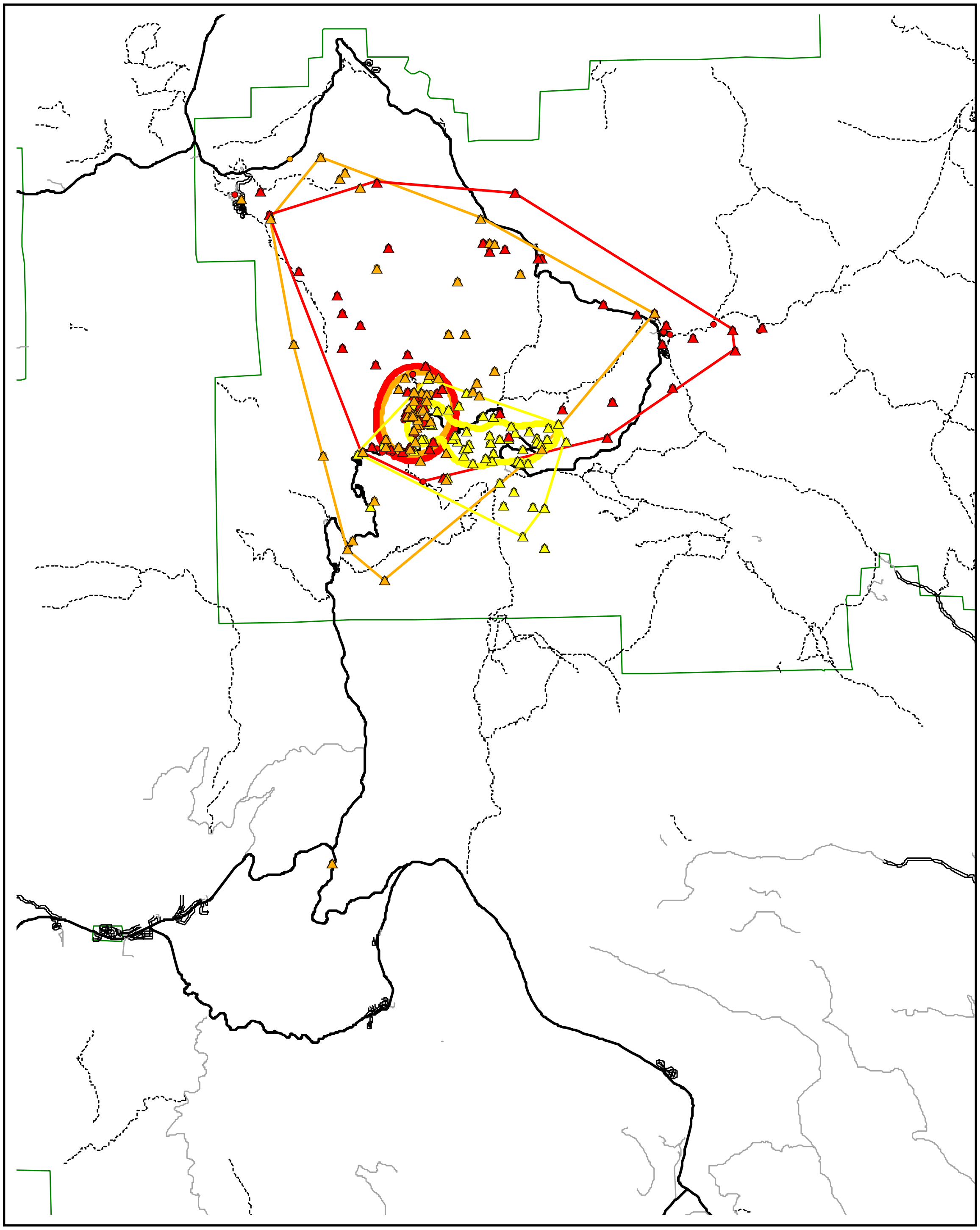


Figure 34: Winter 2002.

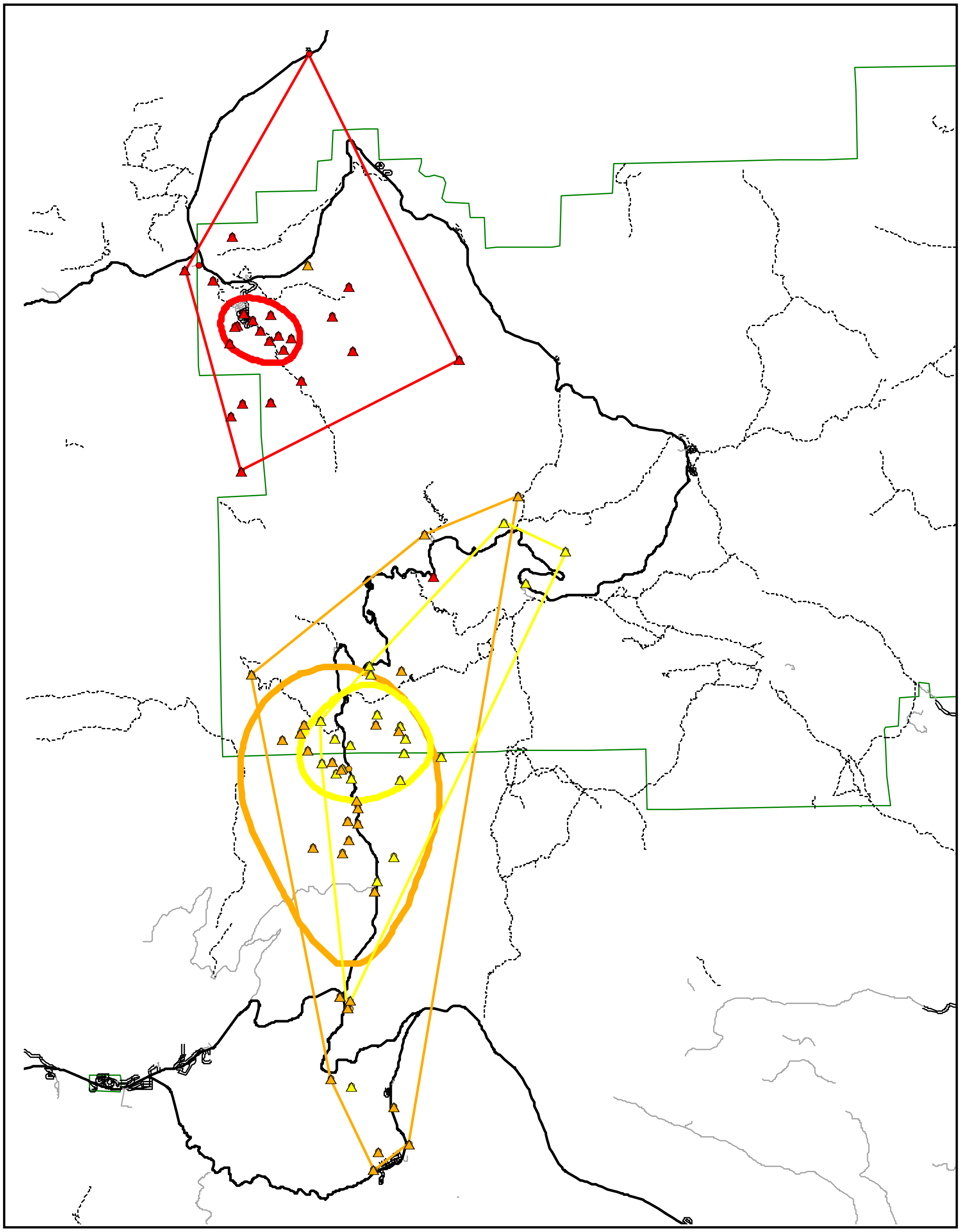


Figure 35: Summer 2002.

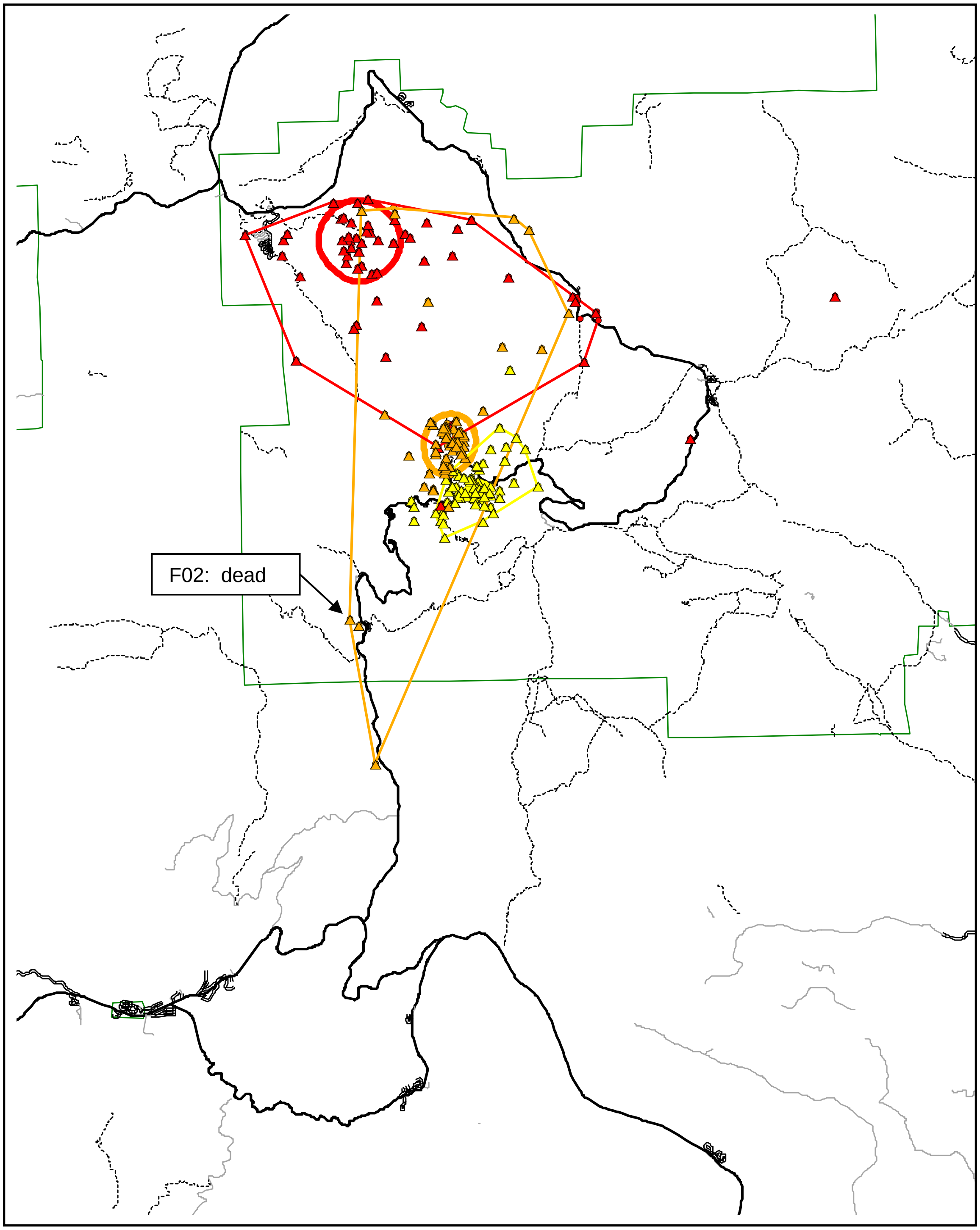
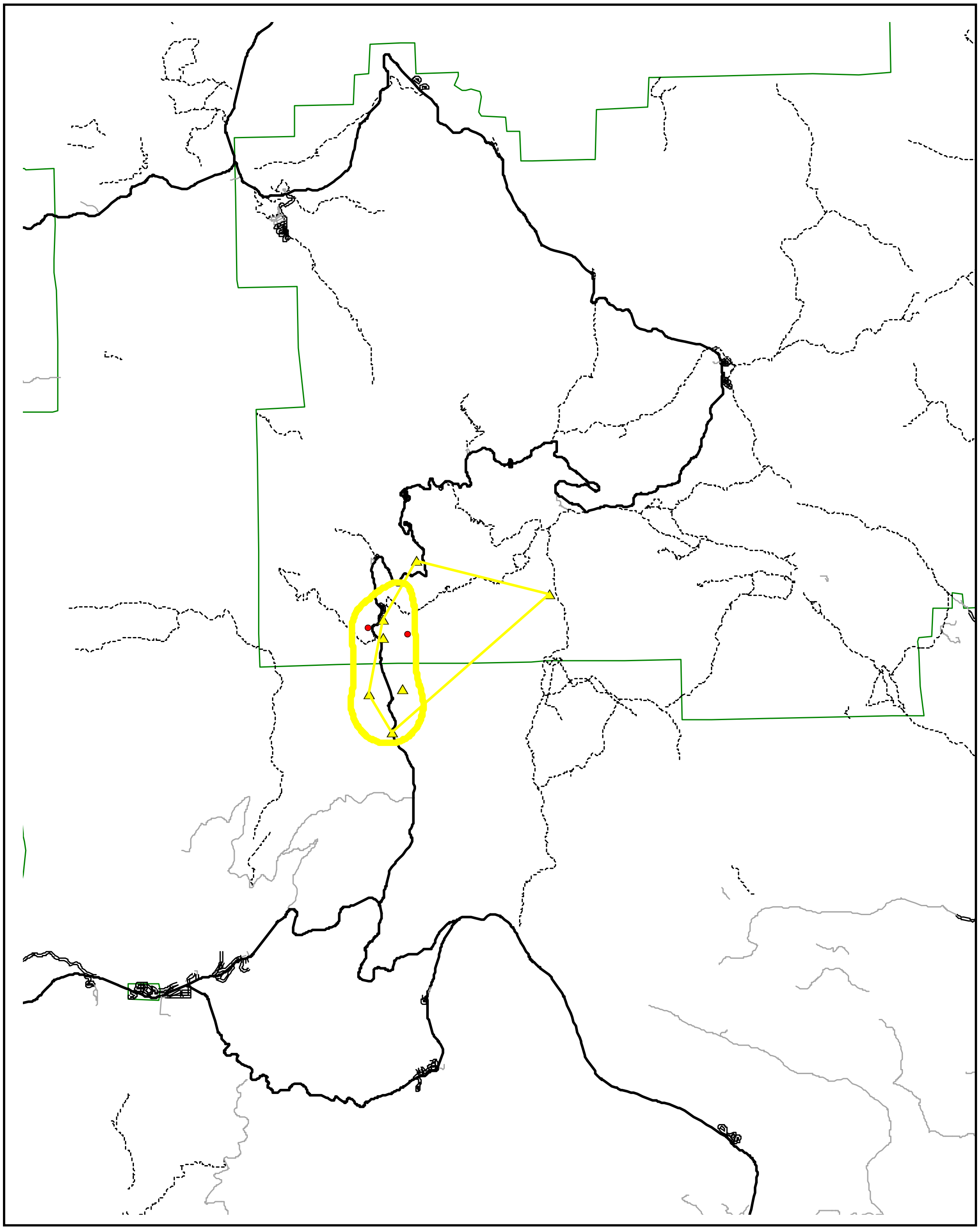


Figure 36: Winter 2003.



APPENDIX D

PARASITES OF LASSEN RED FOX

ECTOPARASITES

Captured red foxes that were not immediately released were given a cursory examination (1-2 min) for ectoparasites. The only ectoparasites observed during these examinations were fleas. Two specimens were collected, stored in 70% ethanol and later identified as *Odontopsyllus dentatus*.

FECAL PARASITES

A pair of very fresh scats was collected from 3 collared red foxes for fecal parasite analysis. All these defecation events were observed so the source fox was known, and the scat was collected within 10 minutes thereby minimizing the opportunity for environmental contamination. These scats were stored in plastic zipperlock baggies and refrigerated, as freezing might cause any protozoal cysts to rupture, impeding identification. Ben Sacks of UC Davis conducted a fecal floatation on these scats and identified the parasites therein (Table 33).

NECROPSY

Ben Sacks conducted a thorough parasite search during his necropsy of F04. He found no evidence of heartworm and there were no parasites in the colon or cecum. However, the small intestine contained 38 ascarids, probably *Toxascaris leonina,* which were collected and preserved in 70% ethanol.

Table 33: Fecal parasites of Lassen red fox.

Fox	Collection Date	Parasite Type	Parasite Species	Quantity
F01	18 January 2001	Lung fluke (trematode)	*Paragonimus* sp. (*kellicotti* ?)	2
		Tapeworm (cestode)	*Dipylidium caninum*	>100 *
	8 March 2001	Tapeworm (cestode)	*Dipylidium caninum*	some *
F03	February 2002	none found	--	--
	July 2002	Roundworm (nematode)	*Toxascaris* sp. (*leonina* ?)	1
F04	14 February 2001	Roundworm (nematode)	*Trichuris vulpes*	272
		Roundworm (nematode)	*Toxocara* sp. (*canis* ?)	16
		Roundworm (nematode)	*Toxascaris leonina*	2
	December 2001	Roundworm (nematode)	*Toxascaris leonina*	78

* Exact quantity could not be determined because *D. caninum* eggs were often bundled in sacs or packets, but were also sometimes free. Therefore, counting individual eggs was impractical. However, the second scat for F01 did not have nearly as many eggs as the first.

APPENDIX E

HISTORICAL TAXONOMY OF CALIFORNIA'S MOUNTAIN RED FOXES

The taxonomy of California's mountain red foxes has followed a circuitous, and almost circular, path. Prior to 1820, the red foxes of North America were not distinguished from those of Europe, *Canis* [= *Vulpes*] *vulpes*: (Linnaeus 1758); also sometimes referred to as *V. vulgaris* (e.g., Baird 1857). Desmarest (1820) argued that the New World red fox constituted a distinct species, *Canis* [= *Vulpes*] *fulvus*. The 3 color phases were identified as separate races or subspecies: *fulvus* for the red phase, *decussatus* for cross phase and *argentatus* for the black phase.

Baird (1857) argued that the red foxes of western North America were distinct from those of the east, and he assigned them the name *Vulpes macrourus*. The type specimen was collected from the Wasatch Mountains near the Great Salt Lake in Utah. Townsend (1887) appears to have collected the first red fox specimen in California. He used the older nomenclature for the black phase red fox that he collected in northern California in 1884, referring to it as *V. f. argentatus*. Although he reported collecting this specimen in March 1884 near Red Bluff (in Tehama County, adjacent to the Sacramento River), Grinnell et al. (1930) reviewed Townsend's field catalog and concluded that the fox had actually been captured near the east base of Lassen Peak in Lassen County in July. Townsend's original specimen has apparently been lost (Grinnell et al. 1930).

In his biological survey of Mount Shasta, Merriam (1899) referred to the red foxes there as *V. macrourus* Baird. However, the following year he described the red foxes of the Sierra Nevada (*V. necator*) and the Cascades (*V. cascadensis*) as distinct species (Merriam 1900). The type specimen of *V. necator* was collected in 1891 at 9500 ft (2900 m) elevation from Whitney Meadows near Mount Whitney, California. The type specimen of *V. cascadensis* was collected in 1898 at the base of Mount Adams, Washington. Merriam considered *V. necator* to be restricted to the Sierra Nevada Mountains of central and southern California, while *V. cascadensis* occurred throughout the Cascade Range of northern California, Oregon and Washington.

By 1929, the mountain red foxes were recognized as subspecies of the North American red fox, *V. fulva* (Seton 1929). Grinnell et al. (1930) disagreed with Merriam (1900) and considered the red fox of the Lassen region to be *V. f. necator*, not *V. f. cascadensis*, and they later observed (1937) that their specimens supported the recognition of only a single race of mountain red fox throughout California. Whether the state border represented an appropriate range limit for *V. f. necator* was not addressed. The current taxonomy arrived when Churcher (1959) demonstrated that the North American red fox was indeed conspecific with the Old World red fox, *V. vulpes*. The Sierra Nevada red fox therefore became known as *V. v. necator.*

It has been suggested, however, that red fox taxonomy in North America should be revised to no more than four subspecies, with the mountain red foxes comprising only one, *V. v. macroura* (Roest 1979). A final resolution of the taxonomy, presumably using molecular methods, remains to be conducted.