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# Sierra Nevada Red Fox (*Vulpes vulpes necator*)

## A Conservation Assessment

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# Sierra Nevada Red Fox (*Vulpes vulpes necator*): A Conservation Assessment

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# NOTES IN PROOF

- Genetic analyses by B. Sacks and others 2010 (Conservation Genetics 11:1523-1539) indicate that the Sacramento Valley red fox population is native to California and is closely related to the Sierra Nevada red fox. They designated the Sacramento Valley red fox as a new subspecies, *V. v. patwin*.

- In August 2010, as this document was going to press, biologists on the Humboldt-Toiyabe National Forest detected a red fox at an automatic camera station near the Sonora Pass along the border of Tuolomne and Mono Counties. Preliminary genetic analyses conducted at UC Davis indicate that the fox was a Sierra Nevada red fox. Further surveys and analyses are planned.

- The California Department of Fish and Game Region 1 Timber Harvest Program has established a Sierra Nevada red fox information portal, where many management-relevant documents can be downloaded as PDFs. See: https://r1.dfg.ca.gov/Portal/SierraNevadaRedFox/tabid/618/Default.aspx

# EXECUTIVE SUMMARY

This conservation assessment provides a science-based, comprehensive assessment of the status of the Sierra Nevada red fox (*Vulpes vulpes necator*) and its habitat. It identifies and evaluates key risk factors affecting viability and describes general Conservation Options. The current distribution, abundance and population trend for Sierra Nevada red fox are uncertain, but there is little evidence of increase or expansion. It is unclear whether this native mountain fox persists outside of the Lassen Peak region.

## *Summary of Key Findings*

**Historic Range and Population Densities**

- Throughout high elevations of the Sierra Nevada from Tulare County northward to Sierra County, and from Mount Shasta and Lassen Peak westward to the Trinity Mountains (Trinity County).
- Elevational range reportedly 1,200 to 3,600 m. Seldom sighted below 1,500 m and most often observed above 2,100 m.
- Occurred at low densities, even in areas of high relative abundance.

**Ecology**

- Little studied, as are mountain red fox populations in the Cascade and Rocky Mountains. One recent field study in the Lassen Peak region; most other accounts based on incidental observations.
- Small body size (average = 3.6 kg) and large seasonal home ranges (summer average = 2,300 ha).
- Human-associated mortality is fairly well described: trapping prior to the 1974 California prohibition, predator eradication programs associated with livestock or timber production, historic meadow over-grazing resulting in reduced prey populations, domestic dog-mediated disease vectors, and roadkill.
- Likely avoid coyotes (*Canis latrans*); niche overlap with marten (*Martes americana*) appears high.

**Habitat Relationships**

- Occupied habitats seem to be a composite typical of the high Sierra: high elevation barren, conifer and shrub habitats; montane meadows; subalpine woodlands and fell-fields.
- Seasonal elevational migration: summer habitat negatively associated with shrub and herbaceous cover; winter habitat 150-500 m lower and positively associated with forest cover comprised of large trees (>60 cm DBH) with >40% canopy closure.
- Den sites described as natural cavities in talus slopes or rockslides. May use earthen dens, boulder piles, or even the space beneath vacant cabins, as has been described for other mountain foxes.
- In winter, followed forested edge of openings, possibly avoiding areas where they would be exposed to attack by other carnivores. Ski tracks and other packed snow may facilitate winter travel.

**Potential Threats**

- Expansion of non-native lowland red foxes or coyotes into high elevation areas, resulting in increased competition and potential transmission of harmful diseases and parasites. Interbreeding with non-native red foxes may reduce genetic adaptation to local conditions.
- Development and recreation, resulting in increased exposure to humans, vehicles and pets, and possibly facilitating dispersal of non-native red foxes, coyotes and other competitors.
    - Habituation and begging habits may increase risk of mortality at roads, campgrounds, etc.
    - Fish poisoning disease mediated by stocking infected fish for recreational fisheries.
- Contact with rodenticides applied for vegetation or livestock management purposes.
- Climate change, resulting in a loss or restriction of their boreal environment or reduced snowfall.

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# INTRODUCTION

## *Purpose of this Assessment*

One goal of the Sierra Nevada Forest Plan Amendment (SNFPA) 2001 and 2004 Records of Decision was to protect and recover native Sierra Nevada red fox (*Vulpes vulpes necator*) populations in the Sierra Nevada (USDA Forest Service 2001 p. 14). To accomplish this goal, the ROD commits the U.S. Department of Agriculture (USDA) Forest Service to completing a conservation assessment for the Sierra Nevada red fox in cooperation with other federal, state, and local agencies, as well as Tribal governments. This conservation assessment synthesizes the best available scientific information and thought concerning habitat relationships, population status and trends, historical and current distributions, and key threats potentially affecting the distribution, abundance and persistence of the Sierra Nevada red fox. Biologists and resource managers from the Forest Service, US Department of the Interior (USDI) National Park Service, USDI Fish and Wildlife Service, US Geological Survey, University of California, and California Department of Fish and Game, along with private research scientists, worked cooperatively to develop this assessment. This conservation assessment provides a scientifically sound, comprehensive assessment of the status of the Sierra Nevada red fox population and its habitat. It identifies and evaluates key threats affecting viability and describes management considerations that could form the basis of a strategy to conserve and recover populations throughout the range of this species.

## *How the Document will be Updated*

This conservation assessment has been designed as a "living document" which will be periodically updated as relevant new information becomes available. All authors of this assessment, as well as biologists with a strong or vested interest in the Sierra Nevada red fox, will be encouraged to submit new publications or databases to either an ftp site, web site, or a designated document coordinator to be established specifically for this purpose. When sufficient new information is collected to warrant inclusion into the conservation assessment, it will be added as a dated addendum to the document's appendix. Should the new information significantly alter views established in the original conservation assessment, it (as well as all other addendum information) will be added to the body text as a new conservation assessment addition.

## *How Agency Biologists can use this Conservation Assessment*

Field biologists and managers are encouraged to use the information contained herein for project planning and analysis. In effects analyses, document the range of habitat associations in California, then focus on study results and data closest to the geographic location of the proposed project to evaluate effects of proposed management activities. Wherever possible, original literature should be reviewed and cited, rather than a summary document such as this assessment, except where such an assessment provides data or study comparisons to generate new information.

The National Environmental Policy Act of 1970 (NEPA) and implementing regulations provide specific direction for the procedure to incorporate information by reference into analyses. For example, it is not sufficient to state that all information contained in a document is incorporated. A summary of relevant data must be prepared and included in the project evaluation document.

Clearly list any assumptions and limitations associated with cited research to ensure proper contextual use of study inferences or conclusions. When doubt exists regarding proper interpretation of results, readers are encouraged to contact study authors directly, or discuss projects being planned with respected local Sierra Nevada red fox experts. When such contact results in a "personal communication" citation in an analysis document, it is wise to request review of any resultant text by the expert being cited to ensure accuracy and supportability.

## *Acknowledgements*

The authors would like to acknowledge the other members of the working group who provided their time and expertise toward developing this document: Reg Barrett and Tom Kucera of UC Berkeley, Rick Golightly of Humboldt State, Diane Macfarlane and Laurie Perrot of the Pacific Southwest Region of the USDA Forest Service, Mike Magnuson of Lassen Volcanic National Park, Tom Rickman of the Lassen National Forest, Ron Schlorff of the California Department of Fish and Game, and Jesse Wild of the US Fish and Wildlife Service. Keith Aubry of the USDA Forest Service, John Siperek of the California Department of Fish and Game, and David Graber of the National Park Service reviewed the draft manuscript and provided many useful comments. Ellen Jackowski of Tetra Tech EC made figure 1, Rick Schlexer of the USDA Forest Service made figure 3, and Kristi Fein of CDFG made figure 5. The authors would also like to thank Jonathan Arnold of Lassen Volcanic National Park, Les Chow of the US Geological Survey, and the numerous field biologists with the USDA Forest Service for providing red fox sighting records and other inventory data. Keith Slauson of the USDA Forest Service Pacific Southwest Research Station in Arcata graciously provided the cover photo.

# APPROACH

## *Organization of the Assessment*

The document is organized under the following key headings:

- **Description and Taxonomy**
- **Distribution and Population Density**
- **Ecology**
- **Conservation Status**
- **Potential Threats**
- **Conservation Options**
- **Inventory, Monitoring, and Research Needs**

Conservation considerations in the assessment could be used to launch a conservation strategy, provide guidance for field biologists as they evaluate potential effects of land and resource management projects, and identify habitat restoration opportunities during the landscape analysis process. Multiple agencies could use information from the assessment to begin a coordinated species conservation effort.

## Geographic Scope of the Assessment

The historical range of the Sierra Nevada red fox (*Vulpes vulpes necator*) included the Sierra Nevada, the southern Cascades in California, and the mountains of western Nevada (Grinnell and others 1937; Hall 1981). The current range is unknown. The extent of gene flow between *V. v. necator* and the mountain red fox of Washington and Oregon (the Cascade red fox, *V. v. cascadensis*) is also unknown. However, current taxonomy and management protections differentiate the mountain red fox of California from those in Washington and Oregon. Hence, the geographic scope for this assessment is the area encompassed by the species' historical range in California (*fig. 1*). This area includes the Sierra Nevada Framework Planning Area (SNFPA) composed of the Sierra Nevada Bioregion and Modoc Plateau, as well as the Shasta-Trinity and Lassen Peak areas that are outside the SNFPA but important, nonetheless, to the conservation of this species.

## Objectives

Objectives for this assessment include the following:

- Summarize current scientific knowledge and expert opinion about the status of the native red fox in the Sierra Nevada and southern Cascades in California.
- Summarize current information about the ecological conditions necessary for persistence of the species in the Sierra Nevada and southern Cascades in California.
- Identify and evaluate the relative importance of threats that may be affecting the species or its habitat.
- Develop options for species conservation, including the rationale for conservation considerations.
- Summarize existing research and identify key information gaps.

## Areas of Uncertainty

The ecology of mountain red foxes in North America is poorly known. Only three comprehensive ecological studies have been conducted: one in the Cascade Range of Washington and Oregon (Aubry 1983), one in Yellowstone National Park (Fuhrmann 1998), and one in the Lassen Peak region of northern California (Perrine 2005). Furthermore, few of the results from these studies have appeared in the peer-reviewed scientific literature. The paucity of targeted scientific research on these populations is a major factor complicating their effective management.

The majority of the scientific understanding of red fox ecology in North America is based upon research conducted in the eastern and midwestern United States (Aubry 1983) in profoundly different habitats than inhabited by the Sierra Nevada red fox. Some aspects of mountain red fox ecology may be significantly different from these other populations, but in the absence of local research, the results from these other populations represent the best available information on red fox ecology in North America. The information and conclusions in this document are based upon the best available ecological research. Information on montane populations is presented where available, and effort has been made to highlight areas of concern over the applicability of other information to the Sierra Nevada red fox.

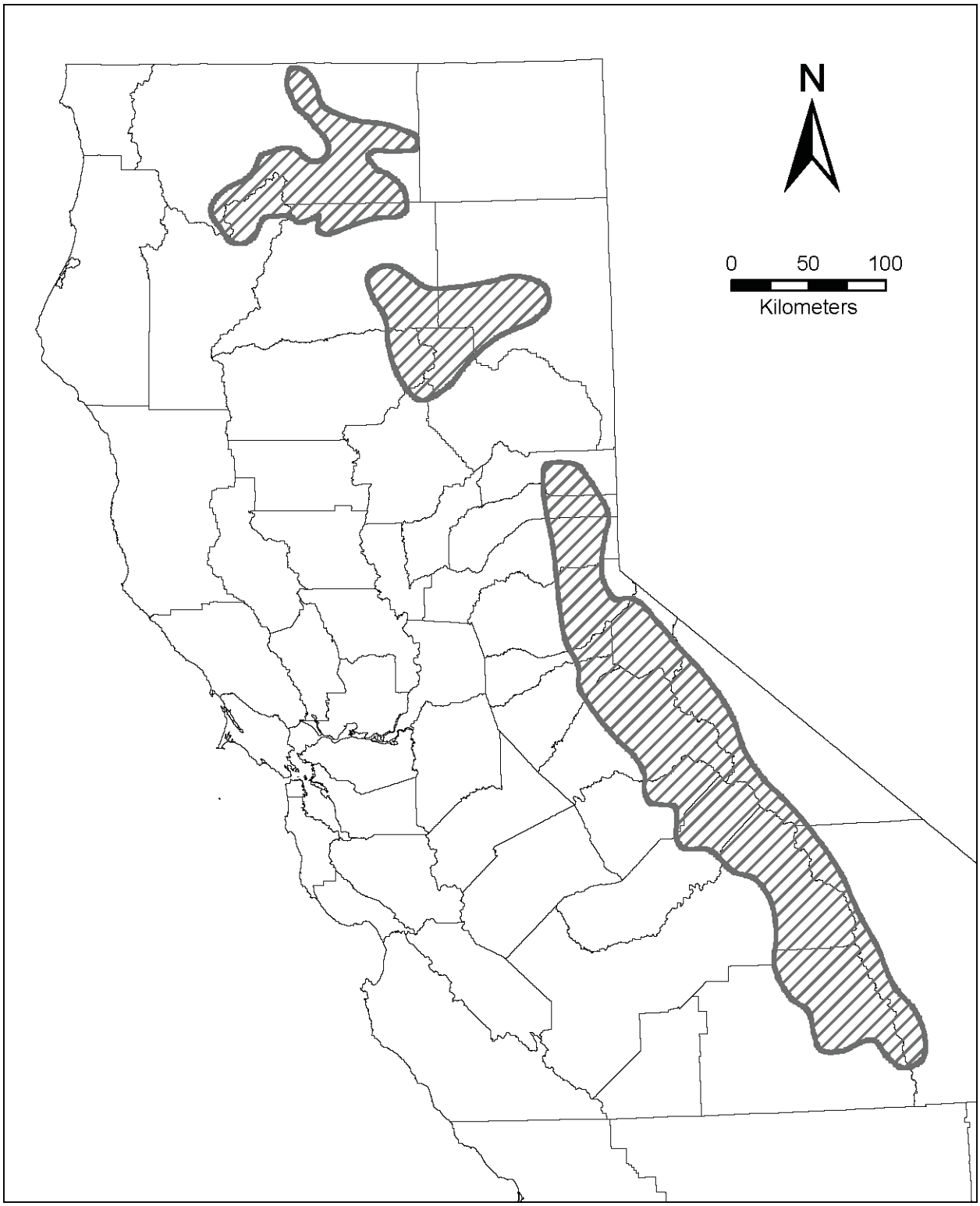


**Figure 1. Historical range of the Sierra Nevada red fox (*V. v. necator*) in California based on Grinnell and others (1937).**

# Description and Taxonomy

The red fox (*Vulpes vulpes*) is a small canid with an elongated snout, large ears, slender legs and body, and a large bushy tail with a prominent white tip (Larivière and Pasitschniak-Arts 1996). Three color morphs or phases have been documented: red, cross and silver/black. In the red phase, the upper body and tail are yellowish to reddish brown, the cheeks and underside of the throat and abdomen are white, and the lower extremities and ear tips are black. The cross phase is more grayish-brown, with dark guard hairs forming a line down the back and another across the shoulders. In the black or silver phase, the head, torso and tail are all black with occasional silver guard hairs. In all three color phases, the tail usually retains its white tip (Voigt 1987; Larivière and Pasitschniak-Arts 1996). These color morphs are determined genetically, but all three may occur within the same litter (Voigt 1987). In most populations, the red phase is the most common and the other two phases are rare. However, cross foxes may be more prevalent in mountainous areas (Grinnell and others 1937; Larivière and Pasitschniak-Arts 1996; Aubry 1997). Many mountain red foxes in the United States have a distinctive grayish-blonde pelage (Bailey 1931, 1936; Grinnell and others 1937; Aubry 1983; Crabtree 1993; Perrine 2001; Swanson and others 2005).

In North America, adult red foxes typically weigh between 3.5 and 7.0 kg (*table 1*), with an average of 4.5 to 5.4 kg for males and 4.1 to 4.5 kg for females (Ables 1975; Voigt 1987). Mountain red fox seem to be slightly smaller than their lowland counterparts, possibly due to reduced productivity in their montane environment. A trapper interviewed by Grinnell and others (1937) noted that the typical weight of Sierra Nevada red fox was about 4.2 kg for males and 3.3 kg for females. In the recent Lassen Peak study, the male fox weighed 4.0 kg and the four females averaged 3.5 kg (Perrine 2005). In the Cascades of Washington, the average weight of two adult males was 4.3 kg and two adult females was 3.3 kg (Aubry 1983). In most populations, male foxes are about 20% heavier than females (Voigt 1987).

The Sierra Nevada red fox, *V. v. necator*, is one of ten currently recognized red fox subspecies in North America (Hall 1981). It is one of three subspecies of "mountain red fox," along with the foxes of the Cascade Range (*V. v. cascadensis*) and the Rocky Mountains (*V. v. macroura*). These three subspecies are morphologically similar to each other and distinct from the other subspecies in North America (Roest 1977; Aubry 1983; Crabtree 1993). The mountain red foxes originated from the same source population, which was broadly distributed in the contiguous United States during the last glaciation but then retreated to boreal habitats in the western mountains after the glaciers receded (Aubry 1983; Aubry and others 2009). The other red fox populations in the United States arose from different lineages.

The taxonomy of California's mountain red foxes has followed a circuitous, and almost circular, path. Prior to 1820, North American red foxes were not taxonomically distinguished from those in 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 three color phases were identified as separate races or subspecies: *fulva* for the red phase, *decussatus* for the cross phase, and *argentatus* for the black phase. Baird (1857) claimed that red foxes in western North America were distinct from those of the east, and he assigned them to *V. macrourus*. Merriam (1899) used this designation for the red foxes inhabiting California's Mount Shasta, but revised it the following year, describing the Sierra Nevada red fox, *V. necator*, and the Cascade red fox, *V. cascadensis*, as distinct species (Merriam 1900). The type specimen of *V. necator* was collected in 1891 near Mount Whitney at 2,900 m elevation. Merriam considered the Sierra Nevada red fox to be restricted to the southern Sierra, while the Cascade red fox 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 and others (1930) considered the red fox of

the Lassen region of northern California to be *V. f. necator*, not *V. f. cascadensis*, and they later concluded that their specimens supported the recognition of only a single race of mountain red fox in California (Grinnell and others 1937). Whether the state border represented a biologically appropriate range limit for *V. f. necator* was not addressed. The current taxonomy arrived when Churcher (1959) showed that the North American red fox was indeed conspecific with the Old World red fox, *V. vulpes*. 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 subspecies: *V. v. macroura* (Roest 1979). A final resolution of the taxonomy, presumably using molecular methods, remains to be conducted.

In addition to the indigenous Sierra Nevada red fox, California is also home to multiple low elevation red fox populations of uncertain taxonomic status. Grinnell declined to provide a subspecies designation for the red foxes inhabiting the Sacramento Valley because he suspected that this population had likely been introduced to California by humans (Grinnell and others 1937). This conclusion was reinforced by Roest (1977), who found that red foxes from the Sacramento Valley were morphologically most similar to the Great Plains red fox (*V. v. regalis*). By the 1990s, the "valley fox" was no longer restricted to the Sacramento Valley but ranged throughout the entire Central Valley and the coastal regions from Marin to San Diego (Lewis and others 1999). A genetic analysis of lowland red foxes collected from the San Francisco Bay Area, Monterey County and near Los Angeles concluded that the populations in these areas likely arose from multiple introduction events from multiple source populations (Fitzpatrick 1999). However, a subsequent genetic analysis of lowland and montane red fox populations throughout California suggested that the situation may be more complicated, with the Sacramento Valley population possibly being native and closely related to the Sierra Nevada red fox and other western mountain subspecies, whereas the populations in the San Francisco Bay Area and southern California likely originated from outside of California and possibly outside of North America (Perrine and others 2007). Follow-up analyses are currently being conducted by a team led by Dr. Benjamin Sacks of UC Davis, and their findings will likely have profound impacts upon the taxonomic status and management of the various populations of lowland red fox in California. Range expansion by exotic red foxes and the implications for the conservation of the native Sierra Nevada red fox are discussed in more detail below.

**Table 1.** *Body measurements of red foxes.*

| Total Length (mm) | Mass, Ave. (kg) | Mass, Range (kg) | Sample Size | Location | Source |
|---|---|---|---|---|---|
| 993 | 3.9 | 3.6 - 4.0 | 2 subadult and 1 adult males | Sierra Nevada, CA | Grinnell and others 1937 [a] |
| 944 | 3.3 | 2.9 - 3.6 | 1 subadult and 2 adult females | | |
| 1,040 | 4.0 | NR | 1 male, possibly subadult | Lassen Peak / Mineral, CA | Perrine 2005 |
| 978 | 3.5 | 2.9 - 3.8 | 4 females, includes subadults | | |
| 1,070 | NR | 3.6 - 5.4 | 3 males | Mount Adams, WA | Bailey 1936 |
| NR | 4.25 | 4.0 - 4.5 | 2 adult males | Mt. Rainier, WA | Aubry 1983 |
| NR | 3.3 | 2.7 - 3.7 | 2 subadult and 2 adult females | | |
| 1,080 | NR | NR | 1 male | Liberty, NM | Bailey 1931 |
| 992 | NR | NR | 1 female | Taos Mountains, NM | |
| 1,015 | NR | 3.6 - 5.4 [b] | 1 subadult male | Wind River Mountains, WY | Bailey 1936 |
| NR | 4.0 | NR | not reported | Yellowstone National Park | Crabtree and Sheldon 1999 |
| NR | 4.5 | NR | 4 adults | Point Mugu, CA | Klope 1983 |
| NR | 3.7 | NR | 5 subadults | | |
| NR | 5.3 | 4.0 - 6.1 | 47 males | Tippecanoe County, IN | Hoffman and Kirkpatrick 1954 |
| NR | 4.2 | 3.3 - 5.7 | 52 females | | |
| 1,011 | 5.0 | 4.1 - 7.0 | 33 adult males | Illinois and Iowa | Storm and others 1976 |
| 954 | 4.0 | 3.0 - 4.7 | 35 adult females | | |
| 1,026 | 4.1 [c] | NR | 37 adult males | southern Ontario | Voigt 1987 |
| 973 | 3.4 [c] | NR | 37 adult females | | |
| NR | 3.1 | 2.9 - 3.3 | 21 males | Thumamah Reserve, Saudi Arabia | Macdonald and others 1999 |
| NR | 3.0 | 2.8 - 3.3 | 20 females | | |

NR = not reported. Unless otherwise noted, measurements at time of first capture.

[a] Grinnell and others (1937) also quoted a fur trapper who claimed that average weight for males and females was 4.2 and 3.3 kg, respectively.

[b] Bailey reported that this fox weighed "about 8 to 12 pounds."

[c] Skinned weight.

## Distribution and Population Density

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 extensive geographic range is largely a product of the unspecialized and adaptable nature of the red fox and its broad tolerances for many types of habitats and foods (Lloyd 1980). However, this characterization of the species contrasts starkly to that of the Sierra Nevada red fox and the other North American mountain subspecies, which are generally considered to have restricted distributions due to habitat or dietary specializations (Buskirk and Zielinski 2003).

Within their range, red fox population densities may vary by several orders of magnitude depending on the carrying capacity of their habitat. Densities may range from 1 fox per 30 ha in good habitat to 1 fox per 4,000 ha in poor habitat (Lloyd 1980). Higher densities, up to 1 fox per 3 ha, may occur in urban areas due to human-subsidized resource abundance (Voigt and Macdonald 1984; Voigt 1987). A wide variety of methods have been used to assess population densities, including standardized traplines, track counts, aerial census of dens, hunting and trapping harvest, bounty records, questionnaires, and sightings by rural mail carriers and school children (Larivière and Pasitschniak-Arts 1996).

Historically, the Sierra Nevada red fox occurred throughout the high elevations of the Sierra Nevada from Tulare County northward to Sierra County, and from Mount Shasta and Lassen Peak westward to the Trinity Mountains of Trinity County (Grinnell and others 1937). Within this range, Grinnell and others (1937) recognized three main population centers: the Shasta/Lassen region, the high Sierra near Mono Lake, and near Mount Whitney. Red foxes are apparently absent from the Coast Range (Grinnell and others 1937; Schempf and White 1977). Although the Sierra Nevada red fox seems to range from 1,200 to 3,600 m in elevation, it is seldom sighted below 1,500 m and is seen most often above 2,100 m (Grinnell and others 1937; Schempf and White 1977).

The current distribution and population status of the Sierra Nevada red fox are uncertain (CDFG 1996). In the decades following the publication of Grinnell and others (1937), the largest concentration of sightings in northern California was near Lassen Volcanic National Park, with more than one third of all collected records (Schempf and White 1977). The Lassen Peak region accounts for the only verified recent detections of mountain red fox (Kucera 1993 and 1995; Perrine and Arnold 2001; Perrine 2005). Carnivore surveys conducted in this area from 1992-2002 using baited camera stations detected red fox only in a small area within Lassen Volcanic National Park and the surrounding Lassen National Forest, at a median elevation of 2,000 m (range: 1,379-2,612 m) (*fig. 2*). A field ecology study of the Lassen red fox population was conducted from 1998-2002 (Perrine 2005) and the results are summarized throughout the "Ecology" section below. A genetic comparison of this population and other specimens collected throughout California concluded that the Lassen red foxes were indeed a remnant of the native Sierra Nevada red fox (Perrine and others 2007).

It is unclear whether the Sierra Nevada red fox persists outside of the Lassen Peak region. Although most National Forests within the historic range of the Sierra Nevada red fox have recently conducted carnivore surveys using trackplates and remotely-triggered cameras, none but the Lassen National Forest has detected red fox (*fig. 3*). A systematic survey (Zielinski and others 2005) of the entire Sierra Nevada and southern Cascade region of California, utilizing a combination of track plates and camera stations at each sample point, did not detect red fox anywhere within the historic range of the Sierra Nevada red fox (*fig. 4*). In Sequoia and Kings Canyon National Parks, a survey for marten (*Martes*

*americana*) and fisher (*M. pennanti*) using baited track plates and camera stations (Green 2006) and a survey for wolverine (*Gulo gulo*) using baited camera stations (Institute for Wildlife Studies 2006) both failed to detect red foxes. Similarly, a fisher survey using baited camera stations in Yosemite National Park in the early 1990s also detected no red foxes (Les Chow, U.S. Geological Survey, pers. comm.). Although these results are troubling, they may merely indicate that surveys targeting other carnivores, such as *Martes*, do a poor job of detecting red foxes. Since Schempf and White's 1977 summary and analysis, red fox sightings have been reported throughout much of the historic range of the Sierra Nevada red fox (*fig. 5*). Biologists at Yosemite National Park have received only ten red fox sighting reports since 1977, most of which occurred in or near Yosemite Valley (Les Chow, U.S. Geological Survey, pers. comm.). Unfortunately, sighting reports are notoriously inaccurate, and without a photograph or voucher specimen, it is impossible to confirm whether the sighting was of a red fox or some similar canid such as a gray fox or coyote. The last reliable sighting in the Sequoia National Park and the nearby Sequoia National Forest occurred in 1993 (David Graber, National Park Service, pers. comm.). A red fox was photographed in the winter of 1990-1991 at the Tioga Pass Resort (2,940 m) on the Inyo National Forest, just outside Yosemite National Park (Les Chow, U.S. Geological Survey, pers. comm.). According to Graber and Chow, the low number of sighting reports suggests that it is unlikely that significant red fox populations exist in Sequoia-Kings Canyon and Yosemite National Parks.

The Sierra Nevada red fox likely occurs at low population densities even within areas of high relative abundance. Grinnell and others (1937) reported that it was "not really numerous anywhere" and "its numbers are relatively small even in the most favorable territory." Trappers they interviewed believed that the red fox occurred at densities of about 1 per square mile (260 ha). Similarly, the density of Cascade red fox in Oregon is unclear (Verts and Carraway 1998). There is also some question as to whether the Sierra Nevada red fox is rare or just rarely seen. Grinnell and others (1937) considered it highly elusive, suggesting that tracks and scat may be the only evidence of its presence, while Schempf and White (1977) described it as "rare" throughout the Sierra Nevada. Similarly, an abundance of sightings is not necessarily indicative of a large local population. Most of the hundreds of red fox sightings reported in Lassen Volcanic National Park were due to three human-acclimated individuals (Perrine and Arnold 2001).

With both total range and population density unknown, no population estimate can be calculated for the Sierra Nevada red fox. If calculated, such an estimate would require impractically wide confidence intervals to incorporate all the necessary assumptions regarding the total range and the extent and density of occupied habitat.

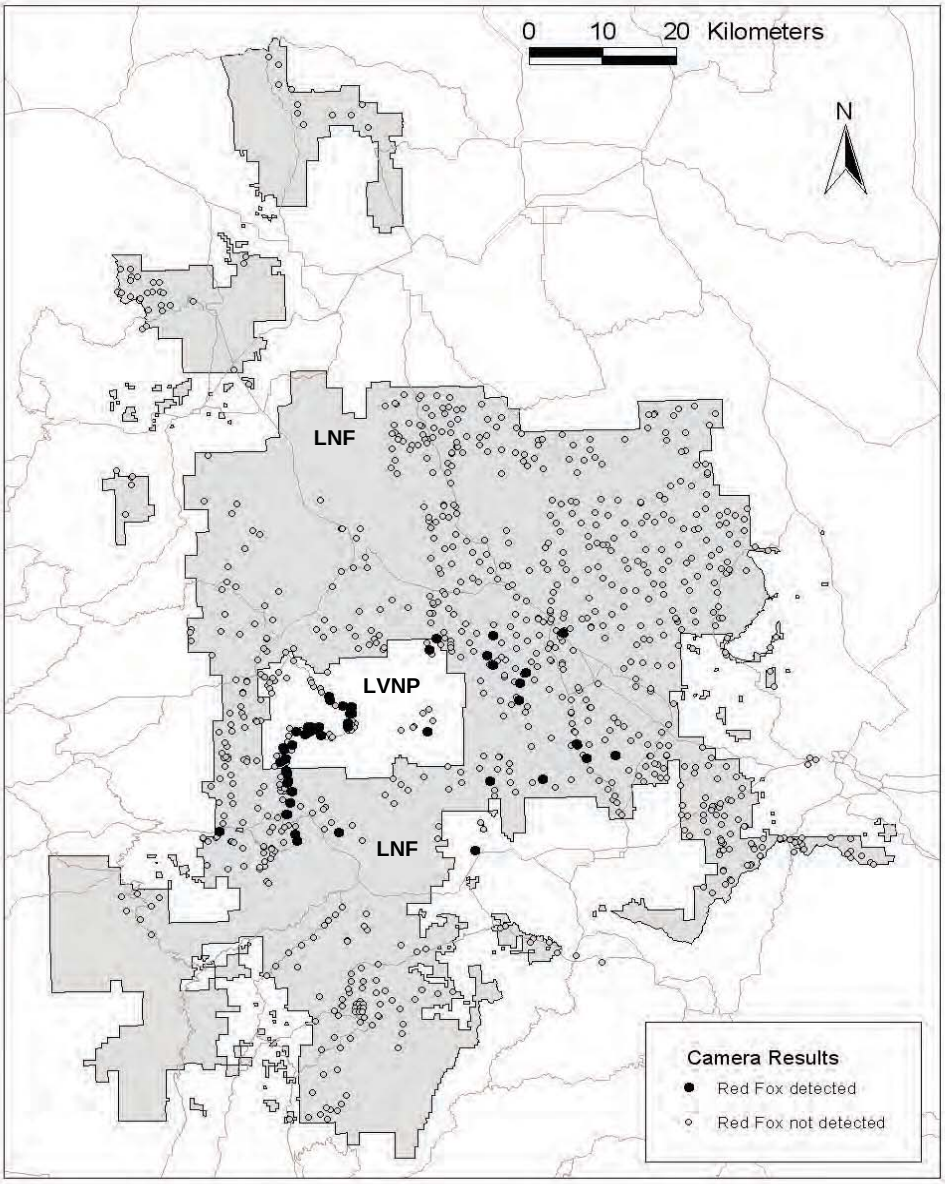


**Figure 2. Red fox detections and sampling effort by baited camera stations on the Lassen National Forest (LNF) and Lassen Volcanic National Park (LVNP), 1992-2002. Red foxes were detected by 53 of 998 camera stations. Red fox detections (dark circles) were concentrated in the highest elevations in the region, especially in the western portion of the park, near the town of Mineral just south of the park, and along the perimeter of the Caribou Wilderness east of the park. (Data from Perrine 2005.)**

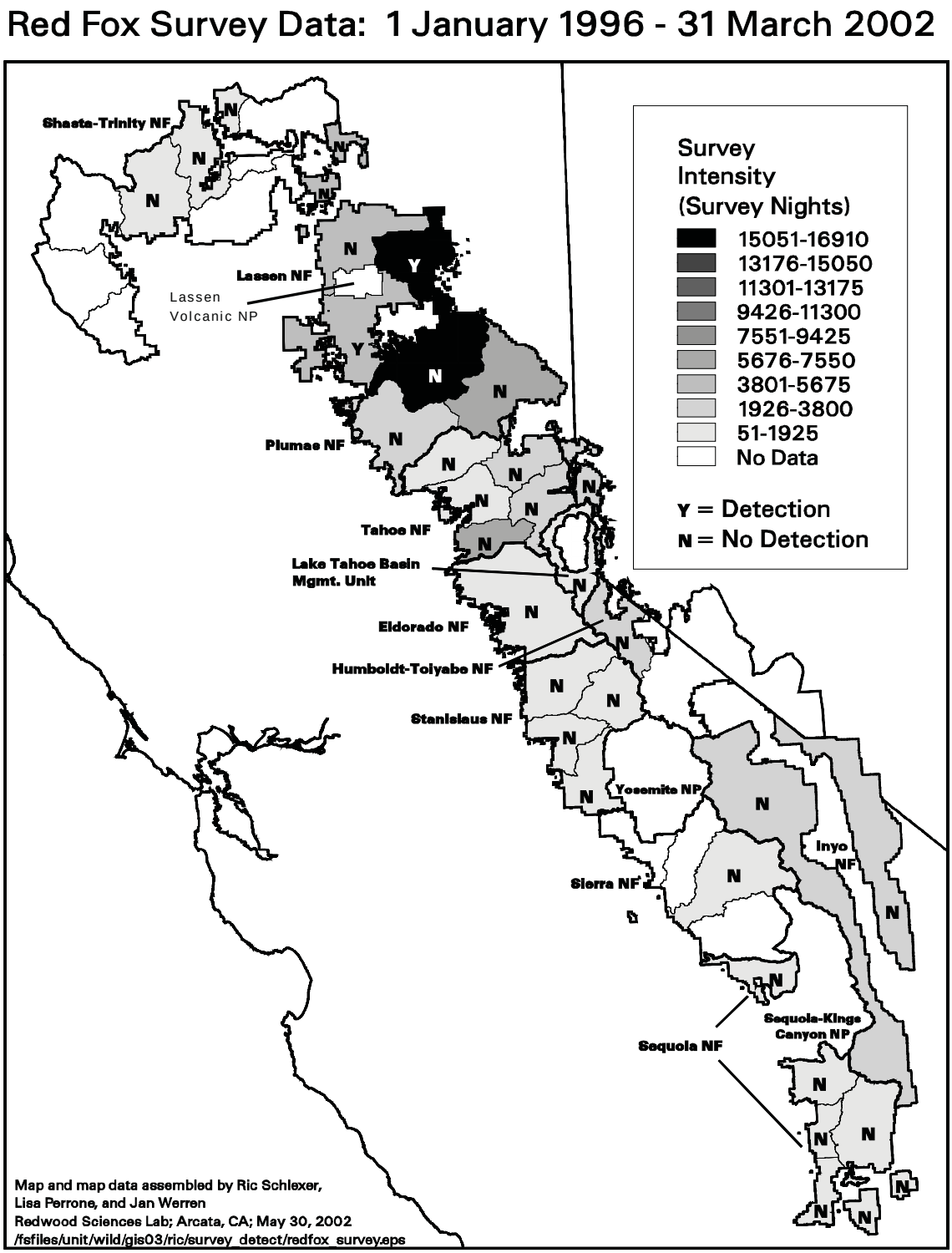


**Figure 3. Survey effort and occurrence of red fox in the Sierra Nevada and southern Cascades by National Forest. Carnivore surveys were conducted using sooted track plates and remotely-triggered cameras and may have targeted species other than red fox. Red foxes were detected only on the Lassen National Forest.**

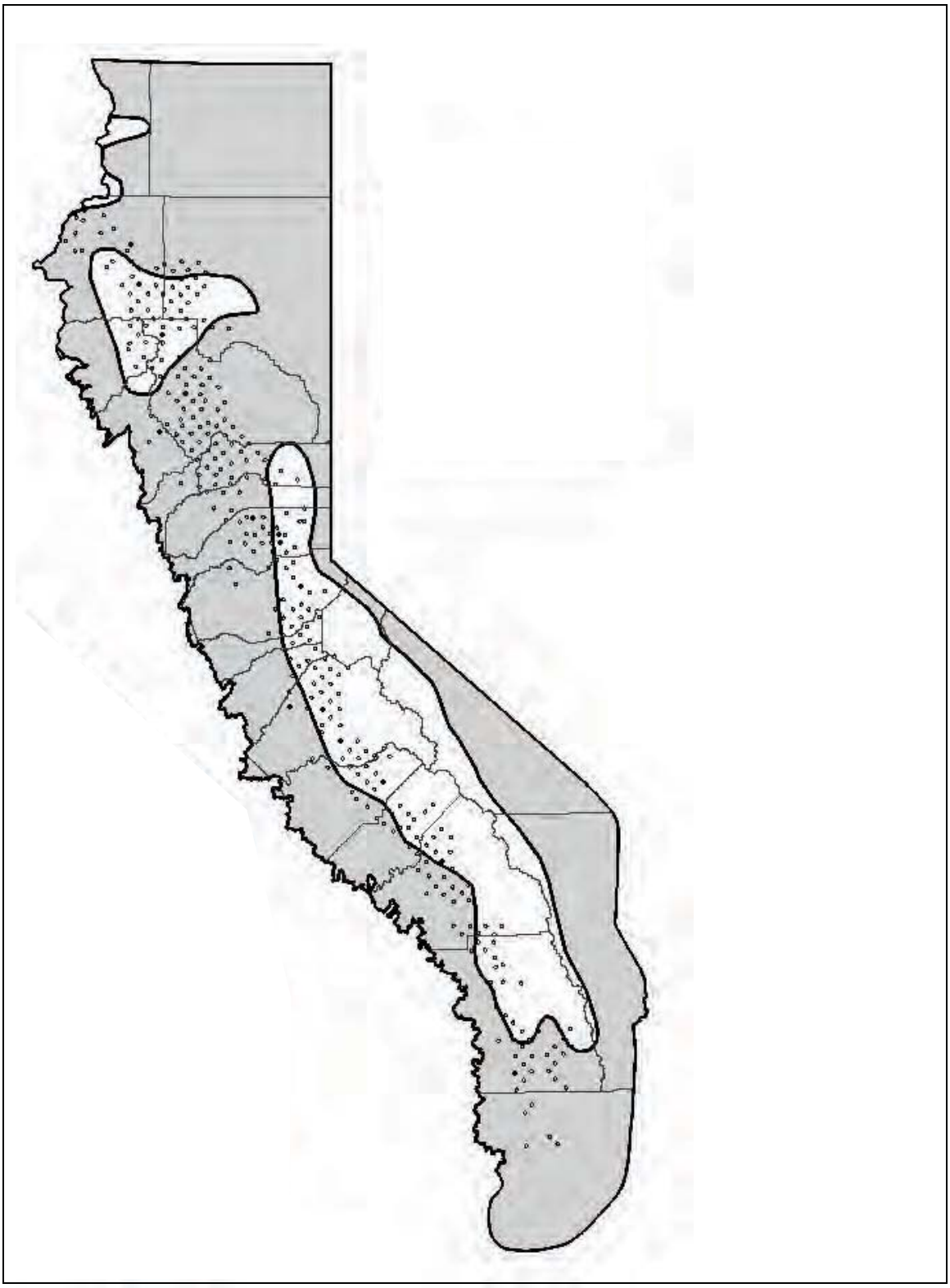

**Figure 4. Distribution of systematic carnivore survey locations (1996-2002) within the historical range (white area) of the Sierra Nevada red fox (*V. v. necator*). No red foxes were detected during these surveys. Each point represents a star-shaped array of 6 sooted track plates and 1-2 remotely-triggered cameras. (Data from Zielinski and others 2005.)**

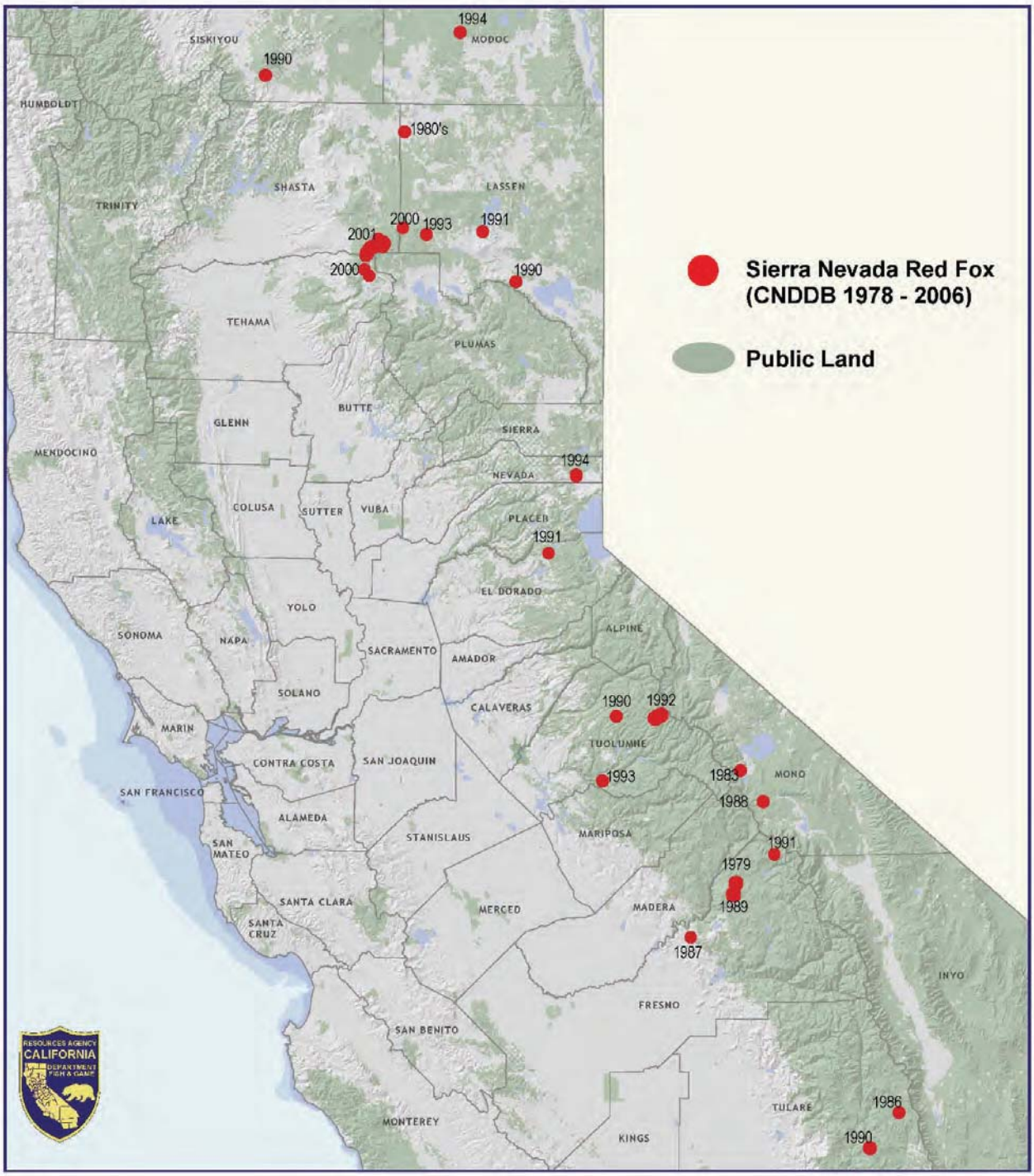


**Figure 5. Distribution of Sierra Nevada red fox sightings reported to California Department of Fish and Game since 1977.**

# ECOLOGY

The red fox is one of the world's most widespread and thoroughly studied carnivores (Lloyd 1980; Voigt 1987). Although numerous red fox studies have been conducted in North America, the vast majority have addressed populations in the eastern and midwestern regions. Consequently, little is known of the habitat requirements, activity patterns, food habits, reproductive ecology, population density, and other ecological characteristics of red foxes in the mountains of the western United States (Aubry 1983 and 1997). Published reports on these populations are largely limited to statewide or regional summaries of vertebrate natural history (e.g., Bailey 1931 and 1936; Grinnell and others 1937). Additional sources of information include trapping records, sighting reports, and reviews of museum specimens (Lewis and others 1995).

Targeted ecological investigations of mountain red fox populations in the United States are extremely sparse, with only three studies conducted to date: a PhD dissertation addressing the red fox of Washington and Oregon (Aubry 1983), an MS thesis on the red fox of the northern Yellowstone region (Fuhrmann 1998), and a PhD dissertation on the red fox of the Lassen Peak region of northern California (Perrine 2005). To date, virtually none of the results from these studies have appeared in the peer-reviewed scientific literature.

Overall, the characterization of the Sierra Nevada red fox as "the least well known furbearer in California" (Schempf and White 1977) remains true more than three decades later.

## *Population Ecology*

The red fox is predominantly monogamous (Lloyd 1980), although polygamy has been reported in a few instances (Voigt 1987). Females are monoestrous with mating occurring over several weeks in late winter and early spring, with the specific dates varying with latitude (Ables 1975; Storm and others 1976; Voigt 1987) and probably with elevation (Samuel and Nelson 1982). The proportion of non-breeding or barren females varies greatly among populations, ranging from less than 5% to greater than 45%, and is probably a function of population density, food supply, and mortality rate (Englund 1970; Harris 1979; Lloyd 1980; Voigt 1987). The gestation period is 51 to 53 days, with birth occurring from March through May (Voigt 1987). Estimates of litter sizes vary depending on whether live pups, embryos or placental scars are the unit of measure. Despite this, litter sizes are relatively consistent across published studies (*table 2*), with an average of five to six pups and a maximum of 12 (Ables 1975; Samuel and Nelson 1982; Larivière and Pasitschniak-Arts 1996). Litters larger than 12 pups probably represent communal denning by more than one female. The pups weigh 70 to 120 g at birth (Storm and Ables 1966).

The young are born in a sheltered den, usually an excavated burrow or protected cavity among boulders or beneath tree roots (Lloyd 1980). Red foxes may also use abandoned woodchuck / marmot (*Marmota* spp.) or badger (*Taxidea taxus*) burrows (Samuel and Nelson 1982). These dens may be used for many generations (Lloyd 1980). The pups remain in the den for their first month, and may be moved to other dens several times before they are six weeks old (Storm and others 1976). The pups are weaned by eight to 10 weeks and then may travel short distances from the den unaccompanied by a parent (Ables 1975; Storm and others 1976). By their twelfth week, the young foxes begin to explore their parents' home range during daylight. Their activity remains centered on the den site, and they remain with their

mother throughout the summer. Dispersal occurs in early fall when the pups are fully grown (Ables 1975; Storm and others 1976). Both males and females are capable of breeding their first winter (Ables 1975; Samuel and Nelson 1982), although their success rate may be lower than older adults (Lloyd 1980).

Little is known about the reproductive biology of the Sierra Nevada red fox or other mountain red foxes in North America. Snow tracking records (Grinnell and others 1937; Verts and Carraway 1998) suggest they are probably monogamous. In California, they likely breed in mid-February and give birth in early April. Grinnell and others (1937) reported that Sierra Nevada red fox litters averaged six pups and ranged from three to nine pups. The weight of evidence behind this conclusion is unclear although the range apparently reflects trappers' reports. Other sources indicate that litters of two to three pups may be more typical for mountain red foxes. Sighting records at Lassen Volcanic National Park include a single report of a mother fox and three pups near Hat Creek in August 1979, and the 1993 sightings from Yosemite National Park and the Sequoia National Forest were of a mother with two pups. An uncollared fox on Lassen Peak in 1999 raised only two pups. 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; necropsy of one of these females confirmed her nulliparity (Perrine 2005). In 1980, Aubry (1983) captured and radio-collared a family group consisting of an adult male, an adult female and two female pups. The following year one of these pups produced her own litter of three pups, at least one of which died by mid-June. Neither the other female pup nor her mother reproduced in 1981. None of seven adult female red foxes monitored by Meia and Weber (1993) in the Swiss Jura Mountains (1,000-1,300 m) bred, but one had reared pups just before the study began. Bailey (1931) estimated that mountain red fox in New Mexico had a *maximum* litter size of six pups, which is the *average* litter size in most other populations. In general, red fox reproductive output is strongly correlated with local food availability (Voigt 1987). It is possible that limited resources prevent mountain red foxes from achieving the reproductive output typical of populations in more productive environments. Whatever the cause, mountain red foxes appear to be at the lower range of typical litter size for the species.

Similarly, little data exist on the types of den structures used by Sierra Nevada red foxes. The den site of the only known reproducing female in the Lassen Peak study was never discovered or characterized because the fox was uncollared (Perrine 2005). Grinnell and others (1937) reported that Sierra Nevada red foxes did not use earthen dens, instead preferring natural cavities in rockslides or talus slopes; as above, this likely reflects reports from trappers. Bailey (1936) noted that Rocky Mountain red fox dens were located under rocks or in holes dug near rocky cover to provide refuge from coyotes. In New Mexico, Bailey (1931) noted a red fox den among the boulders above treeline, but also mentioned their "burrows," suggesting that earthen dens were common. In Washington, Cascade red foxes used earthen dens, some with multiple entrances, typically located in heavily timbered stands (Aubry 1983). Den entrances averaged 25x25 cm, with fans of hard-packed dirt extending outward. One Cascade fox also denned under a vacant cabin (Aubry 1983), which has also been reported among red fox in the Rocky Mountains (Dirk Van Vuren, UC Davis, pers. comm.). Sierra Nevada red fox likely use whatever structures are available to them, whether among rocks or in the ground (Aubry 1997), but to date no accounts of earthen burrows in the mountains of California are known.

**Table 2.** *Litter size estimates for red foxes.*

| # Pups Average | # Pups Range | Litters Examined | Den Type | Location | Source |
|---|---|---|---|---|---|
| 2.5 | 2 - 3 | 2 | 1 earthen,1 under cabin | Mount Rainier, WA | Aubry 1983 |
| 6 | 3 - 9 | NR | under boulders | Sierra Nevada, CA | Grinnell and others 1937 |
| 7 | 2 - 13 | 9 | not reported | Sacramento Valley, Colusa County, CA | Grinnell and others 1937 |
| 3.2 | NR | NR | Burrows | Point Mugu, Los Angeles County, CA | Klope 1983 |
| 3.6 | 1 - 9 | 12 | various; mostly burrows | Orange County, CA | Lewis and others 1993 |
| 6.8 [a] | 4 - 13 | 30 | NR | Tippecanoe County, IN | Hoffman and Kirkpatrick 1954 |
| 3.8 | 1 - 12 | 175 | Primarily burrows | Illinois | Storm and others 1976 |
| 3.5 | 1 - 10 | 384 | Primarily burrows | Iowa | Storm and others 1976 |
| 4.9 | NR | 210 | Burrows | Michigan | Switzenberg 1950 |
| 4.2 [a] | NR | 574 | NR | North Dakota | Allen 1983 |
| 5 | 3 - 7 | 10 | burrows and under buildings | central Alberta, Canada | Dekker 1983 |
| 4.7 | NR | 60 | NR | southern Sweden | von Schantz 1984 |
| 3.8 | NR | ~80 | NR | central Poland | Goszczynski 1989 |

NR = not reported.
[a] derived from embryo counts at necropsy.

## *Mortality Factors, Survivorship Rates, and Population Structure*

Human-associated factors such as trapping, hunting and road-kills account for a significant proportion of red fox mortality in many populations (Storm and others 1976; Samuel and Nelson 1982; Voigt 1987; Larivière and Pasitschniak-Arts 1996; Verts and Carraway 1998). Populations in the Midwest sustain an annual harvest of tens of thousands depending on the state (Lloyd 1980). One of Aubry's (1983) seven radio-collared Cascade red foxes was killed by a local trapper. Trapping and hunting likely had a negligible effect upon the Sierra Nevada red fox due to the low numbers taken each year. Grinnell and others (1937) estimated the total harvest to be about 21 individuals annually, and they did not consider this to be a threat to the population. From 1940 through 1959, only 135 red fox pelts were taken throughout California, with exotic red foxes from the lowland population comprising an increasing portion of the statewide harvest after 1950 (Gould 1980). After 1959, the average annual harvest from the mountains was only two foxes (Gray 1975). Despite the low harvest levels, state resource managers were concerned about any preventable sources of mortality upon a species thought to be in decline. In response to this concern, the California Legislature prohibited trapping and other non-scientific take of red fox throughout the state in 1974 (Gould 1980). The moratorium remains in effect today. It is unknown whether this moratorium had any substantive effect upon Sierra Nevada red fox population levels, but a similar prohibition has likely contributed to the persistence of mountain red fox in Yellowstone National Park (Buskirk 1999).

Like many other predators in the Sierra Nevada, red fox populations probably suffered from predator-eradication programs associated with livestock production (Grinnell and others 1937). Sheep ranchers routinely placed poison in dead sheep, killing thousands of predators and scavengers. In addition, over-grazing of mountain meadows by livestock likely harmed Sierra Nevada red fox indirectly by reducing the forage available for prey species (Grinnell and others 1937). Eliminating the use of poisons and reducing sheep allotments at high elevations in the Sierra undoubtedly benefited Sierra Nevada red fox conservation, although the absolute effects can only be surmised.

Sources of red fox mortality not directly associated with humans are poorly known (Ables 1975). Larger carnivores such as wolves, mountain lions, and domestic dogs may occasionally kill red foxes (Larivière and Pasitschniak-Arts 1996), but these events likely pose little population-level threat. A domestic dog killed one fox in the Lassen Park study (Perrine 2005). Golden eagles occasionally prey upon red foxes (e.g., Tjernberg 1981) and Grinnell and others (1937) considered them to be an important potential predator on the Sierra Nevada red fox. Bobcats may occasionally kill red foxes, especially juveniles or injured individuals (Grinnell and others 1937). Studies throughout North America have shown coyotes to be important competitors for red foxes, chasing them and occasionally killing them (Dekker 1983; Sargeant and Allen 1989). (See the "Community Interactions" section below for more detail.)

Diseases and parasites can also cause significant mortality in red fox populations. Rabies and distemper are the two diseases most commonly associated with red foxes (Ables 1975; Samuel and Nelson 1982; Nowak 1999). Other diseases include parvovirus, toxoplasmosis, canine hepatitis, tularemia, leptospirosis, and encephalitis, but these are not believed to control population densities (Voigt 1987). Many kinds of parasites, ranging from ticks and fleas to nematodes, trematodes, heartworms, and protozoans, have been documented in red foxes (Larivière and Pasitschniak-Arts 1996). Sarcoptic mange, caused by a mite infection, is usually fatal to red foxes (Samuel and Nelson 1982). In general, little is known about the effects of disease or parasites on mountain red foxes. Grinnell and others (1937) made no mention of parasites or disease of red fox in the Sierra Nevada. Trematodes,

cestodes and nematodes have been documented in Cascade and Sierra Nevada red foxes (Aubry 1983; Perrine 2005).

Although mortality rates, sex ratio, demographic structure and longevity have been examined in many red fox populations worldwide (Lloyd 1980), these data are derived almost exclusively from populations under heavy harvest pressure, which skew the results. For example, hunting and trapping typically take more males than females and more juveniles than older adults (Ables 1975; Lloyd 1980; Samuel and Nelson 1982). But more important than these biases, which may be corrected for, is the effect of such harvest pressure upon the population's overall demographic structure. According to Minta and others (1999: 341), "Human modification in the form of fur harvest, predator control, and hunting acts as a nonrandom, non-compensatory form of mortality, alters other demographic processes, and may disrupt social organization." Specifically, heavy hunting and trapping pressure decreases adult survival, shortens longevity, increases the proportion of young foxes in the age distribution, and decreases the male:female sex ratio (Lloyd 1980; Minta and others 1999). Therefore, demographic estimates derived from such populations cannot be assumed to extend to the Sierra Nevada red fox, which incurs no harvest pressure. No studies have calculated age-specific mortality rates, sex ratio, demographic structure, or longevity for Sierra Nevada, Cascade, or Rocky Mountain red foxes.

## Habitat Relationships

Worldwide, red foxes occur in a wide variety of habitats, including deserts, tundra, mountaintops, woodlots, meadows, agricultural fields, pastures, and urban areas (Lloyd 1980; Voigt 1987). Within these habitats, red foxes tend to select areas containing a mixture of vegetative types, structures and edges, and they avoid areas of unbroken or homogeneous vegetation (Ables 1975). Dense forests are apparently not widely used (Samuel and Nelson 1982), and shrub communities may be selected in some areas (Schofield 1960; Jones and Theberge 1982; Halpin and Bissonette 1988; Theberge and Wedeles 1989). Patterns of habitat selection may be complicated by weather conditions, prey availability, and interactions with competitors such as coyotes.

Little is known about habitat use or preference by the Sierra Nevada red fox other than their habitats seem to be those typical of the high Sierra. Grinnell and others (1937) reported that the Sierra Nevada red fox inhabited the Hudsonian and Canadian life zones, occurring above treeline, in mountain meadows and talus slopes, and in the subalpine woodlands of whitebark pine (*Pinus albicaulis*) and mountain hemlock (*Tsuga mertensiana*). In winter they descended to lower elevations (Grinnell and others 1937), presumably to red fir (*Abies magnifica*) and mixed conifer forests. Ingles (1965) described their habitats as the alpine fell-fields and the red fir and lodgepole pine (*P. contorta*) forests in the subalpine zone of the Sierra Nevada. Mountain red foxes in Oregon and New Mexico also occurred primarily in the Canadian life zone (Bailey 1931 and 1936). In Oregon, mountain red foxes were absent from areas of dense timber and brush to the west of the Cascade crest and from the sagebrush (*Artemisia* spp.) zones to the east (Bailey 1936). Mountain red fox likely forage for rodents in mountain meadows, openings in conifer stands, and among the talus slopes and exposed ridges above treeline (Bailey 1931; Grinnell and others 1937; Aubry 1983).

Perrine (2005) used a combination of baited camera stations and telemetry to determine habitat utilization by Sierra Nevada red foxes in the Lassen region. Habitat attributes at the scale of the individual camera station were not analyzed statistically due to concerns about independence among the cameras, but several trends were evident. The distribution of red fox detections appeared more restricted

than for marten: red foxes were detected at fewer camera stations (53 vs 132), at slightly higher elevations (2,000 m median, 1,379-2,612 m range vs 1,959 m median, 1,305-2,612 m range) across a smaller geographic area (935 $km^2$ vs 2,460 $km^2$ ; 95% Minimum Convex Polygon [MCP]), and in slightly fewer community types (9 vs 10 California Wildlife Habitat Relationships communities). Specifically, red foxes were detected in barren, conifer and shrub habitats at high elevations, but not in habitats of similar structure (e.g., sagebrush) at lower elevations. Multivariate analysis of 260 ha (1 $mi^2$) sampling units indicated that red fox detections were positively associated with elevation and highway extent (the latter likely due to sampling bias; see *fig. 2*) and negatively associated with the extent of shrub and herbaceous cover; in winter, detections were also positively associated with the extent of forest comprised of large trees (>60 cm DBH) with >40% canopy closure. In the summer, radio-collared red foxes (one male and three females) all selected barren habitats and avoided mid-elevation conifer, hardwood and herbaceous community types; shrub and high-elevation conifer communities tended to be used in proportion to their availability (but one fox selected shrub communities and another avoided high-elevation conifers). Winter habitat selection was not assessed due to uncertainty about the home range boundaries, but the winter home ranges were dominated by Sierran Mixed Conifer, Red Fir, Montane Chaparral and White Fir Forest California Wildlife Habitat Relationships (CWHR) communities. The collared foxes used a variety of structures as day rests. In summer, dense stands of young red fir (<5 m tall) were frequently used, as were spaces under large boulders amidst talus slopes, and open gaps among manzanita shrubs. In winter the foxes used cavities under fallen logs and trees, along with the hollows formed under the drooping lower boughs of snow-laden conifers. No day rests in earthen dens or dug-out cavities were found. Occupied day rest sites, ranked by frequency, were in barren, high-elevation conifer (Red Fir and Subalpine Conifer), mid-elevation conifer (White Fir, Lodgepole Pine and Sierran Mixed Conifer), and shrub (Montane Chaparral) communities in summer, and in mid-elevation conifer (Sierran Mixed Conifer and White Fir), shrub (Montane Chaparral) and Aspen communities in winter. These patterns reflect the seasonal elevation movement by the collared foxes, discussed in further detail below.

Aubry (1983) conducted a radio-telemetry study of the Cascade red fox at two sites near the northeast corner of Mount Rainier National Park in Washington. Both sites were in mountain hemlock woodlands and contained extensive subalpine meadows dominated by mountain bunchgrass (*Festuca viridula*). One additional study animal was captured in the open grand fir (*A. grandis*) forest near the town of Conconully. Aubry did not provide more detailed descriptions of the habitat types, or their relative use, within the home ranges of his animals.

Benson and others (2005) used snow tracks to infer the use of cover by red fox near Lassen Volcanic National Park. The foxes used open areas less and forest cover more than expected based on the availability of these habitat types. At clearings, the foxes tended to follow the forest side of the edge as opposed to moving straight into the openings. They also documented red foxes walking in ski and snowshoe tracks. These data suggest that the foxes may select areas where packed snow facilitates travel, and may avoid areas where they would be exposed to attack by other predators. Although sample sizes were low, this study represents the only published analysis of mountain red fox habitat use in California.

Sighting reports provide the only other information of habitat use by Sierra Nevada red fox. In the northern Sierra Nevada, sightings have been recorded about equally in fir and mixed conifer, with additional sightings in mixed pine and lodgepole pine. In the southern Sierra Nevada, reports were predominately from mixed conifer forests with additional sightings in lodgepole pine and fir (Schempf and White 1977). Red fox sightings on the Lassen National Forest in winter have been in mixed conifer and red fir forests above 1,500 m (Tom Rickman, Lassen National Forest, pers. comm.). Sightings in Lassen Volcanic National Park in 2000 and 2001 were concentrated in campgrounds, parking areas and along the main park road, reflecting the distribution of humans and 2-3 begging red foxes (Perrine and

Arnold 2001). Nevertheless, habitats for these areas included mixed conifer and red fir forests, mountain hemlock and whitebark pine woodlands, talus slopes and mountain meadows, suggesting that begging behavior did not change the foxes' principal habitat associations.

An important additional habitat attribute for Sierra Nevada red fox populations may be remoteness from human presence. Trappers interviewed by Grinnell and others (1937) considered the Sierra Nevada red fox to be the "wildest wild creature" with "greater fear of man and his scent than all the other fur bearers combined." Like the wolverine, the Sierra Nevada red fox may be extremely sensitive to human presence. If so, this would be a marked departure from the species' characteristics in other areas, where they have thrived in human-dominated habitats. However, nothing is known of how Sierra Nevada red foxes respond to increased human presence or disturbance. Such interactions may be complex and may depend upon other ecological factors. For example, in areas where competition with coyotes is important, human-dominated areas can provide important refugia for red foxes (Gosselink and others 2003). Human residences may also provide food and denning locations. Red foxes in the Lassen area of California clearly use roads as movement corridors to facilitate both daily and seasonal movements, with some individuals foraging along the roads as well (Perrine 2005). Several foxes in the Lassen area became quite acclimated to humans, posing problems at some campgrounds and parking areas (Perrine 2005).

In the absence of demographic data, habitat associations must be interpreted with care. Densely inhabited habitats may not be preferred or even sufficient to sustain their populations (Van Horne 1983; Pulliam 1988). In some areas, competition with coyotes has relegated red foxes to sub-optimal habitats (Harrison and others 1989; Fuller and Harrison 2006). Under such conditions, optimal habitats may appear unused and sink habitats may appear preferred. Habitat-specific survival and fecundity rates are necessary to accurately assess habitat relationships and requirements (Garshelis 2000). Unfortunately, such data are unavailable for mountain red foxes.

## *Home Range and Territoriality*

Globally, red fox home range sizes vary widely, from 10 ha to 3,400 ha (*table 3*), depending on habitat type and food availability (Ables 1975; Samuel and Nelson 1982; Voigt 1987). For example, red foxes in the urban areas of Bristol and Oxfordshire, UK, had among the smallest home ranges in the literature, 45 ha on average, 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 foxes in Orange County, California had average MCP home ranges of 427 ha (Lewis and others 1993). Family groups in Minnesota occupied areas that were ≤960 ha (Storm and others 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 and others 1989). Summer home ranges for red foxes 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 and others 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 and others 2001). Within a habitat, home ranges often increase in winter due to decreased prey availability or increased energetic demands associated with reproduction (Ables 1975; Aubry 1983). Breeding females may have smaller home ranges in the

weeks following parturition, when they remain in the den nursing the pups (Ables 1975; Samuel and Nelson 1982). Adult red foxes typically occupy the same home range for most of their life (Ables 1975).

Sierra Nevada red foxes in the Lassen Peak region had extremely large seasonal home ranges and a pronounced elevational migration. Perrine (2005) conducted radio-telemetry on five red foxes from 1998-2002, with individual animals tracked from three to 60 months. In the summer, the collared foxes (one male and three females) occupied the western half of Lassen Volcanic National Park and had an average home range size of 2,323 ha, with individual HRs ranging from 262 to 6,981 ha (95% MCP, based on >20 locations). Detection elevations ranged from 1,755 to 3,130 m, with an average of 2,416 m across the four foxes. In winter, the foxes descended to lower elevations, usually several km south of their summer ranges. Winter home ranges for five collared foxes (one male, four females) averaged 3,131 ha, with individual HRs ranging from 326 to 6,375 m. However, the true winter HR sizes may significantly larger, as telemetry was biased by the difficulty of accessing the higher elevations on foot due to the heavy snowfall in the area (Perrine 2005). Aerial telemetry locations were less biased, and indicated that winter HRs were 439 m lower than summer locations, on average. The descent to the winter range seemed to coincide with the advent of heavy snowfalls at high elevations. Grinnell and others (1937) reported a similar seasonal elevational movement for Sierra Nevada red foxes, with the winter range being 150-300 m lower than the summer range. Grinnell and Storer (1924: 77) described a captured red fox from Big Meadows, near Yosemite, which they speculated may have been driven to lower elevations by unusually severe winter weather. The large home ranges observed in the Lassen population are near the upper extreme of the values in the literature, and suggest that food, rest sites or other important resources occur at low densities or are widely dispersed even in summer. The elevational shift to lower elevations suggests that these resources may become unavailable once the heavy snows begin on the summer range. Together, these factors may limit the local population size to less than might otherwise be expected (Perrine 2005).

Aubry (1983) tracked a total of seven radio-collared Cascade red foxes during three summers and one winter. Summer home ranges (100% MCP, n=10) averaged 235 ha and ranged from 26 to 1,166 ha. Excluding the largest home range as a possible outlier, the revised average was 132 ha. Winter home ranges (n=3) averaged 193 ha and ranged from 91 to 308 ha. His study animals did not exhibit any seasonal elevation shifts in habitat use, although their home range size increased in winter. The HR values for Cascade red foxes are similar to the 200 ha average reported for red fox home ranges in Yellowstone National Park (Crabtree and Sheldon 1999), and for the 260 ha (1 $mi^2$) average estimated for Sierra Nevada red fox (Grinnell and others 1937). 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. Furthermore, Aubry conducted his telemetry during daylight, 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 and others 1981).

Foxes use urine and other scents to delineate the boundaries of their territories, and interlopers may be chased or attacked (Samuel and Nelson 1982; Voigt 1987). Ables (1975) questioned whether red fox exhibited territorial behavior, but noted that the existence of non-overlapping home ranges was powerful evidence. Voigt (1987) concluded that home ranges are defended as territories, but that substantial overlap also occurred. Such overlap is likely to be more extensive in populations with large home ranges, as individuals have reduced opportunity for border defense (Goszczynski 2002). Perrine (2005) did not conduct any analyses of home range overlap or discuss any interactions among neighboring foxes in the Lassen Peak population of Sierra Nevada red fox. The home ranges of the two foxes in Aubry's Yakima Park study area (in Mount Rainier National Park) overlapped substantially, but these individuals were never located near one another. Aubry also captured a family group of four foxes

(an adult male, a lactating female, and two juvenile females) in his Crystal Mountain study area (near Mt. Rainier). Their home ranges overlapped as well, and the overlap zone included the likely natal den.

## *Activity Patterns and Dispersal*

Red foxes are primarily nocturnal or crepuscular (Ables 1975; Voigt 1987). For example, foxes in Illinois became active up to two hours before dark and remained active until up to four hours after dawn (Storm 1965). Daytime foraging, however, is not uncommon, and may be more prominent during the winter (Ables 1975; Voigt 1987). A fox's travels during a typical day rarely exceed 10 km (Voigt 1987). Most areas within the home range are visited within a two-week period, with the fox often visiting the same area on several consecutive evenings (Voigt 1987). Telemetry and camera stations indicate that Sierra Nevada red foxes do little foraging during daylight hours, with most activity occurring between dusk and dawn (Perrine 2005). Similarly, Cascade red foxes were active throughout the day, with activity peaks in the early morning and late evening (Aubry 1983). Aubry did not conduct telemetry at night, so foraging behavior cannot be assessed. Daily movements by Sierra Nevada red foxes were comparable to those in most other populations: virtually all independent telemetry locations obtained less than 24 hours apart were within 10 km linear distance (Perrine 2005).

Information on the dispersal of mountain red foxes is extremely limited. Of the two juvenile females collared by Aubry (1983), one dispersed approximately 8 km before birthing a litter of pups, and the other remained near her original natal den. In general, young red foxes disperse between August and March, with the peak in October and November (Voigt 1987). Dispersal apparently occurs in "easy stages" rather than a tightly coordinated exodus (Ables 1975), and does not seem to be triggered by food limitations (Storm and others 1976). Juvenile males are more likely to disperse than females and generally travel two to three times as far (20-30 km for males vs 10-15 for females; Ables 1975; Storm and others 1976; Lloyd 1980; Voigt 1987). Foxes not dispersing their first season likely do so the following year (Storm and others 1976). Since dispersing individuals must cross occupied home ranges, dispersal distance is positively correlated with home range size. Therefore, poorer habitats are associated with longer dispersal distances (Voigt 1987). Distances may vary widely even within the same habitat type or population, and may range from 2 to 400 km (Ables 1975; Lloyd 1980). Dispersal distances greater than 200 km for males and 100 km for females have been documented in the Midwest (Storm and others 1976). One subadult male marked in Wisconsin was recovered nearly 400 km away in Indiana the following year, but this was considered exceptional (Ables 1965). Most recoveries of marked juveniles are within 16 km of their birthplace; however, such recoveries may underestimate dispersal distance because the individuals may not have reached their final destination at the time of capture (Ables 1975).

**Table 3.** *Home range sizes (in ha) estimated for red foxes. (MCP = minimum convex polygon.)*

| Average | Range (ha) | Method | Comments | Location | Source |
|---|---|---|---|---|---|
| 191 | 132 – 282 | seasonal 95% MCP | 2 males | Mount Rainier, WA | Aubry 1983 |
| 125 [a] | 26 – 308 | | 4 females | | |
| 311 | 104 - 440 | NR | 2 females, 1 male | Point Mugu, Los Angeles County, CA | Klope 1983 |
| 435 | NR | MCP | 11 adult males | Orange County, CA | Lewis and others 1993 |
| 415 | NR | | 8 adult females | | |
| 197 [b] | 116 - 353 | seasonal MCP | 7 adult females, 2 adult males | Jura Mountains, Switzerland | Weber and Meia 1996 |
| 852 | NR | 95% MCP | 31 adults | Thumamah Reserve, Saudi Arabia | Macdonald and others 1999 |
| 131 | 63 - 270 | MCP | 9 males | Jervis Bay, New South Wales, Australia | Meek and Saunders 2000 |
| 132 | 60 - 210 | | 5 females | | |
| 124 | 19 - 233 | 95% MCP | 3 males, 2 females | Maremma Natural Park, Italy | Cavallini and Lovari 1994 |
| 1,611 | 277 - 3420 | MCP | 4 males, 3 females | Northwestern British Columbia, Canada | Jones and Theberge 1982 |
| 141 [c] | 71 - 220 | MCP | 2 males, 5 females | Madison, WI | Ables 1969 |
| 1,990 | NR | MCP | 4 adults | western Maine | Major and Sherburne 1987 |
| 503 [d] | 224 - 1087 | seasonal 95% adaptive kernel | 9 adults, summer | east-central Illinois | Gosselink and others 2003 |
| 1,404 [d] | 246 - 3179 | | 8 adults, winter | | |
| 1,470 | 600 - 2750 | annual MCP | 3 males, 3 females | eastern Maine | Harrison and others 1989 |
| 1,190 [e] | 330 - 2120 | annual MCP | 15 families | North Dakota | Sargeant and others 1987 |

NOTE: Home range size can vary widely depending on the method used.
[a] not including 1 female on a different study site with a summer home range of 1,165.5 ha.
[b] not including 1 female with a home range of 3,383 ha.
[c] not including 1 male with a home range of 931 ha.
[d] median.
[e] family home ranges

## Food Habits

Probably no facet of red fox ecology has been more thoroughly studied than their food habits. More than a hundred studies have been conducted on red fox dietary patterns throughout a wide range of countries and habitats (Ables 1975; Lockie 1977). The overall result is a general characterization of red foxes as opportunistic predators and scavengers that eat a wide variety of foods depending on their seasonal availability. Small and medium-sized mammals usually dominate the diet, with birds, insects, invertebrates, fruit, carrion, garbage and other foods important seasonally (Ables 1975; Lloyd 1980; Samuel and Nelson 1982; Larivière and Pasitschniak-Arts 1996; Verts and Carraway 1998; Nowak 1999). Food preferences independent of availability are poorly known, except that red foxes appear to prefer voles (*Microtus* spp.) and avoid shrews and moles (Macdonald 1977; Lloyd 1980).

Grinnell and others (1937) documented mice (probably *Peromyscus* sp. or *Microtus* sp.), bushy-tailed woodrats *(Neotoma cinerea*), Douglas squirrels (*Tamiasciurus douglasii*), Belding's ground squirrels (*Spermophilus beldingi*), chipmunks (*Tamias* sp.), and white-tailed jackrabbits (*Lepus townsendii*) in Sierra Nevada red fox scats. Additionally, they observed or found evidence of red foxes hunting golden-mantled ground squirrels (*S. lateralis*), voles (*Microtus* sp.) and snowshoe hares (*L. americanus*), and noted that the foxes likely also consumed hairy woodpeckers (*Picoides villosus*), Williamson's sapsuckers (*Sphyrapicus thyroideus*), Clark's nutcrackers (*Nucifraga columbiana*), mountain chickadees (*Poecile gambeli*), blue grouse (*Dendragapus obscurus*), flying squirrels (*Glaucomys sabrinus*), pikas (*Ochotona princeps*), and weasels (*Mustela* spp.), and scavenged livestock carcasses.

The diet of foxes in the Lassen region was dominated by rodents year-round, with pocket gophers (*Thomomys monticola*), mice (*Peromyscus* sp.), voles (*Microtus* sp.) and ground squirrels (*Spermophilus* sp.) being particularly prominent (Perrine 2005). Mule deer (*Odocoileus hemionus*) carrion was also frequently consumed, particularly in winter, and insectivore remains were more common than in most other studies. Arthropods were prevalent in summer scats and manzanita (*Arctostaphylos nevadensis*) berries were common in autumn, and birds and garbage were taken incidentally throughout the year. Lagomorph remains were virtually absent from the scats of Lassen red foxes, marten, and coyotes, suggesting that local populations may be low.

Aubry (1983) found that Cascade red foxes in Washington had a summer diet consisting of pocket gophers (*Thomomys talpoides*), red-backed voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), and other rodents, along with fruit, insects, birds, grass, and garbage. Their winter diet was narrower, consisting largely of snowshoe hares, red-backed voles, pocket gophers, and other mammals, with some birds and garbage taken opportunistically.

Pocket gophers clearly seem to be an important food for mountain red foxes. Bailey (1931 and 1936) also noted that pocket gophers were common in mountain red fox scats from both New Mexico and Oregon. The fact that gophers were prominent in the Cascade red fox diet but not abundant in the study site led Aubry (1983) to suggest that the foxes might be specialists on this particular prey. In Lassen, gophers seemed to be widespread throughout the foxes' summer range, so it was unclear whether they were being taken disproportionate to their availability (Perrine 2005). However, the importance of gophers as a summer and autumn food, their inaccessibility once heavy snows begin, and the apparent paucity of snowshoe hares and other lagomorphs may be factors behind the seasonal elevational movements of the Lassen red foxes (Perrine 2005).

## Community Interactions

As noted in the "Mortality Factors" section above, Sierra Nevada red foxes may be chased, attacked, or killed by a variety of other species, including golden eagles, bobcats, mountain lions, and coyotes (Grinnell and others 1937). Of these species, coyotes likely have the most significant impact on red fox distribution and abundance, due to their role as both a predator and a competitor. Antagonism by coyotes toward red fox has been documented in numerous populations throughout North America. Red foxes appear to minimize such interactions by avoiding areas occupied by coyotes (Dekker 1983; Voigt and Earle 1983; Major and Sherburne 1987; Sargeant and others 1987; Harrison and others 1989; Gosselink and others 2003). Bailey (1936) noted that Cascade red foxes were found primarily in areas where coyotes were uncommon, and that the red foxes lived and bred near rocky areas that provided retreats and cover from coyotes. Likewise, Aubry (1983) hypothesized that predation by and competition with coyotes might partially explain the distribution of Cascade foxes and their failure to expand their range. Perrine (2005) used baited camera stations to assess the overlap between Sierra Nevada red foxes and coyotes in the Lassen region. Aside from a general trend of more coyote detections at lower elevations and more red fox detections at higher elevations, his results were inconclusive; camera stations are a poor method of detecting coyotes because territory-holding individuals may detect and avoid them (Sequin and others 2003). In Yellowstone National Park, red fox home ranges did not coincide with coyote core areas, and red foxes were active at night while coyotes were primarily diurnal or crepuscular (Fuhrmann 1998; Crabtree and Sheldon 1999). The reintroduction of wolves (*Canis lupus*) to Yellowstone may benefit red foxes by reducing coyote populations (Fuhrmann 1998). Coyotes occur throughout the historical range of the Sierra Nevada red fox (Zeiner and others 1990), although their use of high-elevation habitats is poorly studied. In most populations, interference competition by coyotes causes fine-scale resource partitioning between the two canid species, not extirpation of the red fox population (Crabtree and Sheldon 1999). In areas with an elevational gradient, such partitioning can result in elevational stratification, with coyotes at lower elevations restricting the red foxes to the higher elevations (Dekker 1989; Fuller and Harrison 2006). However, the presence of coyotes and other large carnivores may not be exclusively detrimental to red foxes. In particular, red foxes may benefit from scavenging carcasses of prey killed by larger carnivores, especially during winter (Buskirk 1999).

Competitive interactions with smaller carnivores are more difficult to address. Gray foxes (*Urocyon cinereoargenteus*) may dominate red foxes in some areas (Voigt 1987), but gray foxes do not seem to be common at the elevations occupied by the Sierra Nevada red fox. Nevertheless, dispersing gray foxes could possibly transfer diseases or parasites into the Sierra Nevada red fox population. Bobcats are not generally considered a major competitor with red foxes (Major and Sherburne 1987). Marten likely have the most extensive range overlap with the Sierra Nevada red fox (Grinnell and others 1937; Zeiner and others 1990; Kucera and others 1995), potentially leading to competitive interactions between these species. In Europe and Scandinavia, red foxes have significant habitat and dietary overlap with stone martens (*Martes foina*) and pine martens (*M. martes*) (Serafini and Lovari 1993; Padial and others 2002). Occasional predation of martens by red foxes, and increases in pine marten numbers following a decline in red foxes, suggest that these species may have competitive interactions (Lindstrom and others 1995; Overskaug 2000). Avoidance of red foxes has been hypothesized to have a major influence upon marten habitat utilization (Drew and Bissonette 1997). However, little research has been conducted on competitive interactions between red fox and marten in North America despite the overlap in their ranges. In the Lassen region, red foxes and martens had extensive overlap in their habitat utilization, activity time and diet, but there was no evidence of competitive exclusion and the resources they shared did not appear to be limiting (Perrine 2005).

# CONSERVATION STATUS

In 1974, the California state legislature prohibited trapping and other non-scientific take of red foxes throughout the state due to concern over apparent declines of the native mountain population (Gould 1980). The Sierra Nevada red fox was listed as a State Threatened species in 1980. It is not listed under the federal Endangered Species Act but is considered a Sensitive Species by the Pacific Southwest Region of the USDA Forest Service**.** The California Department of Fish and Game has classified it as "extremely endangered," with <6 viable occurrences or <1,000 individuals or <2,000 acres (810 hectares) of occupied habitat (CDFG 2004). No estimates of population size or trend are available.

Perrine and others (2007) conducted a genetic comparison of nine specimens from the Lassen Peak population (collected from 1998-2002) and 22 museum specimens from throughout the historic range of the Sierra Nevada red fox (collected from 1911-1941). The individuals in the modern Lassen population had only one mitochondrial DNA haplotype, although an additional four haplotypes were present in the historic specimens. This result suggests that the Lassen foxes comprise a small, isolated remnant population that has lost much of its genetic diversity. Follow-up analyses are underway to see if nuclear markers show a similar pattern. These analyses are hindered by the lack of any additional modern specimens from the historic range of the Sierra Nevada red fox.

The Sierra Nevada red fox is the only major population of red foxes in North America that is of conservation concern due to apparently declining populations (Nowak 1999). The actual trend is unknown, due largely to the difficulty in surveying such a rare species in such inhospitable terrain. Grinnell and others (1937) believed that the population was naturally dynamic, with some portions increasing while others decreased. Trappers they interviewed believed that the Sierra Nevada red fox was increasing locally. However, 40 years later, Schempf and White (1977) concluded that the Sierra Nevada red fox was at best maintaining low population levels, and was perhaps declining. Of the six furbearers they reviewed (red fox, wolverine, fisher, river otter [*Lutra canadensis*], marten, and ringtail [*Bassariscus astutus*]), only the red fox did not seem to be increasing in abundance. Trends since 1977, however, are unknown.

The relatively low number and localized distribution of recent Sierra Nevada red fox sightings suggests a small, restricted, and possibly declining population (Schempf and White 1977; CDFG 1996). A recent assessment concluded that the Sierra Nevada red fox "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).

# POTENTIAL THREATS

A threat is a factor that adversely affects individuals, populations, habitat, prey or other essential resources. Such factors may be of anthropogenic or non-anthropogenic origin. The paucity of available data on Sierra Nevada red fox ecology makes threats difficult to assess and prevents cause-and-effect relationships from being documented. Likewise, the ecological factors that may limit Sierra Nevada red fox distribution, fecundity, and survival are unknown. In fact, the absence of reliable data upon which to base management decisions has itself been described as a threat to the population (CDFG 1987). Therefore, this threat assessment is largely speculative, and additional research is needed to assess the relative importance of the potential threats listed below.

## *Non-native Red Fox*

One of the greatest threats to the Sierra Nevada red fox may be the non-native red fox, also known as the lowland or valley fox. Low-elevation red foxes in California were first recorded from the northern Sacramento Valley, where they occurred from Sutter County north to Shasta County at elevations below 100 m (Grinnell and others 1937). Grinnell and others (1937) surmised that this population likely had been "planted there by man" prior to 1890, but expressed no concern about their possible impacts upon the native Sierra Nevada red fox, as the lowland population was "very restricted [and] evidently wholly cut off from the population of the Sierra Nevada." In subsequent decades, however, the range of the lowland red foxes increased dramatically. By the 1990s, valley foxes had been documented in at least 36 counties in California (Lewis and others 1993). In addition to the Sacramento Valley, their current range includes virtually the entire area between the San Francisco Bay and San Diego, extending eastward through the San Joaquin Valley to the Sierra Nevada foothills (Lewis and others 1999). Red foxes escaping from commercial fur farms may have contributed to the sudden expansion of the valley fox range. 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 and others 1999). While most of these farms were at lower elevations, several were located within the historical range of the Sierra Nevada red fox, and others were within dispersal distance (Lewis and others 1995). These factors have raised concerns that the lowland red fox may have invaded the historic range of the Sierra Nevada red fox (Lewis and others 1995, 1999). These concerns are compounded by the fact that morphological characteristics alone cannot reliably diagnose an individual red fox as native or exotic (Roest 1977).

A recent genetic analysis (Perrine and others 2007) found no evidence that exotic red foxes had invaded the Lassen Peak population. The Lassen population had the same mitochondrial haplotype that was most abundant in museum specimens collected prior to 1940 throughout the range of the Sierra Nevada red fox. This haplotype was absent from the lowland populations in the San Francisco Bay Area and southern California, suggesting little genetic contact. Surprisingly, these lowland populations were also quite different from the red foxes in the Sacramento Valley, which were more similar to the modern and historic mountain specimens. Although the Sacramento Valley population shared haplotypes with the montane populations, differences in haplotype frequencies indicated little gene flow. These results indicate that the dramatic range increase in the lowland red fox since the 1950s was not due to expansion of the Sacramento Valley population. This finding is consistent with Fitzpatrick's (1999) genetic analysis of specimens collected from near San Francisco, Monterey and Los Angeles, which concluded that these populations had originated from multiple anthropogenic introductions from multiple source populations. The rapid range expansion of red foxes in southern California is consistent with their exotic origins (Lewis and others 1999). It remains unclear whether they have expanded into the Sierra, but the threat cannot be discounted.

Exotic red foxes could have a number of detrimental effects upon the native Sierra Nevada red fox (Lewis and others 1995). Interbreeding could cause genetic swamping of the native, locally-adapted genotype, producing hybrids of reduced fitness. Also, the exotic red fox might simply exclude or out-compete the native fox, or transmit harmful diseases and parasites to the native Sierra Nevada red fox (Lewis and others 1995). On the other hand, exotic red foxes may not be able to persist in the extreme habitats of the Sierra Nevada and Cascade Range, especially in competition with a locally-adapted native genotype. Aubry (1984) hypothesized that physiological or behavioral limitations restricted introduced foxes to lower elevations in Washington and similarly restricted the native Cascade red foxes to the higher elevations.

## *Development and Recreation*

Road construction and increased human settlement in the Sierra Nevada might facilitate the dispersal of non-native red foxes into the historic range of the Sierra Nevada red fox, by providing access to areas previously unavailable to the exotic foxes. Although Sierra Nevada red foxes use roads and areas of packed snow as travel corridors, these features may also facilitate the expansion of coyotes and exotic red foxes into Sierra Nevada red fox habitat. In Washington, a band of dense forest on the west side of the Cascades separates the introduced and native fox populations (Aubry 1983 and 1984). Conversion of these forested habitats might ultimately be detrimental to the native red fox, as it might favor coyotes and exotic red foxes, both of which are potential competitors. Although the tolerance of Sierra Nevada red fox to the presence of humans is a topic of debate, it is clear that the non-native red foxes thrive in human-altered environments (Lewis and others 1999; Kamler and Ballard 2002). In addition, development within the range of Sierra Nevada red fox poses a threat to the species through an increased risk of predation from domestic pets, disease transmission, automobile collisions and other human-wildlife conflicts.

Risks from recreation are primarily associated with developments such as ski areas, snow parks, campgrounds, and picnic areas. In campgrounds without bear boxes, where campers' food and trash are more accessible, red foxes can develop begging habits and thereby increase the possibility for conflict with humans. Red foxes are intelligent and can quickly become acclimated to human handouts. They may be particularly susceptible in mountainous regions where natural productivity is low and winter food is scarce. Begging foxes have been a periodic problem in Lassen Volcanic National Park and the adjacent Lassen National Forest (Perrine and Arnold 2001; Perrine 2005). One of Aubry's study animals became a beggar at a town near his study site (Aubry 1983) and begging foxes have been reported from subalpine parks in Hokkaido, Japan (Tsukada 1997) and New South Wales, Australia (Bubela and others 1998). Domestic dogs in recreation areas may also have an impact on Sierra Nevada red foxes by chasing or harming them or by transmitting diseases such as canine distemper, rabies, and sarcoptic mange (Ables 1975; Samuel and Nelson 1982; Lewis and others 1993). Educating the public to avoid interactions with wildlife and to properly control their dogs could reduce these threats but cannot eliminate them entirely. Fortunately, these threats are unlikely to affect entire red fox populations, although virulent diseases could have a major impact, especially on a small population with reduced genetic diversity.

Fish stocking for recreation may represent another threat. *Neorickettsia helminthoeca* is a rickettsial organism present in some trout and salmon stocks. Consumption of infected fish can cause salmon poisoning disease (SPD), which is typically fatal for dogs, foxes and other canids (Gorham and Foreyt 1990). The rickettsial infection is known to occur in wild populations of salmonid fish in northern California, Oregon and Washington, but may be spread beyond these areas via translocations from infected hatchery populations (Hedrick and others 1990; Mack and others 1990). The trematode host of *N. helmintoeca* has been detected in at least three state hatcheries and four private farms in northern California, and rickettsia-infected fish from at least one of these sites were used to stock portions of the Truckee River Basin (Hedrick and others 1990). Red foxes could be exposed to SPD by scavenging offal from recreational fishing or due to the failure of aerial stocking to hit the targeted lake. Additionally, dead salmonids from hatcheries have been used as bait for photographic surveys of wild carnivores in some areas (Tom Rickman, Lassen National Forest, pers. comm.). Because of the documented occurrence of infected salmonids in both natural and hatchery fish populations within the range of Sierra Nevada red fox, and the high mortality rate of SPD in canids, further investigation of this potential threat, including possible routes of infection, seems warranted.

## *Forest Management and Livestock Grazing*

It is difficult to evaluate the potential impacts that past and present forest management practices have had on the Sierra Nevada red fox, as little information exists on their habitat associations and movement patterns. The available information suggests that Sierra Nevada red foxes require a composite of habitat types including open forest, meadows, and subalpine fell fields. Clearly, conservation and recovery of the Sierra Nevada red fox will require the retention of sufficient habitat for red fox and their prey, along with sufficient habitat connectivity throughout its range. Forest management practices, including fire suppression activities and livestock grazing, may have significant impacts on habitat suitability and connectivity for the Sierra Nevada red fox and its prey.

Grinnell and others (1937) considered the overgrazing of alpine meadows by sheep to be "the greatest menace to the productivity" of the Sierra Nevada red fox, due to the reduction of forage available for prey species, ostensibly grassland species such as meadow voles (*Microtus* sp.). Similarly, decades of fire suppression in the Sierra Nevada have allowed tree cover to encroach on meadow and riparian areas, reducing herbaceous cover for prey and reducing meadow extent. The direct impacts upon the Sierra Nevada red fox are unclear, however. Current livestock grazing does not occur at the intensity of the past (Ratliff 1985; Menke and others 1996), and some rodent populations (e.g., pocket gophers and Belding ground squirrel) may actually increase due to grazing practices (Ratliff 1985). Furthermore, increasing the amount of tree cover in meadow habitats can increase the number of chipmunks and tree squirrels using these habitats (Cain 2001). Consequently, livestock grazing and fire suppression may simply shift prey abundance from meadow voles to gophers and squirrels, all of which may be important components of the red fox diet (Bailey 1931 and 1936; Grinnell and others 1937; Aubry 1983; Perrine 2005). The extent to which the Sierra Nevada red fox can adapt to such shifts in prey abundance is unknown.

Sierra Nevada red foxes likely occupy elevations higher than most commercial timber extraction activities. However, they descend to mid-elevation forested areas in winter (Grinnell and others 1937; Perrine 2005). Reduction in forest density and canopy coverage could result in local increases in prey species such as *Microtus*, *Peromyscus* and *Thomomys*, possibly benefiting red foxes. However, as mentioned above, such structural changes could also cause increased use by coyotes and facilitate invasion by lowland red foxes, resulting in threats to the Sierra Nevada red fox. Snow tracks of Sierra Nevada red fox in the Lassen area indicated that they avoided openings in the forests, perhaps to minimize interactions with potential predators or competitors (Benson and others 2005).

The use of toxins such as strychnine in grazing and forest management practices could harm Sierra Nevada red foxes by reducing prey populations and by the risk of secondary exposure to the toxins themselves. The widespread and indiscriminant use of strychnine to control predator populations on grazing lands has largely been outlawed, especially in California. However, rodenticides are still widely used on public and private lands to protect vegetation and livestock and to control plague. The most widely used chemicals appear to be strychnine, used for pocket gopher control, and diphacinone, used to control ground squirrel and chipmunk populations primarily in response to plague outbreaks in human recreation areas (Dave Bakke, USDA Forest Service, pers. comm.). Historically, the widespread above-ground application of strychnine for rodent control caused extensive mortality of non-target species, including canids (Linsdale 1931 and 1932). Application of strychnine occurs on an average of several thousand acres per year out of the 21 million acres managed by the Forest Service in California, and diphacinone use is relatively rare, occurring in one to two campgrounds a year (Dave Bakke, USDA Forest Service, pers. comm.). Current laws and regulations for controlling pocket gophers with

strychnine are designed to minimize non-target species mortality by applying the toxin underground, monitoring the treatment area and removing rodent carcasses on the surface. However, even underground treatment for pocket gophers can cause reduction in local ground squirrel populations, and strychnine may remain in the gastrointestinal tracts of affected ground squirrels (Anthony and others 1984). Therefore, a risk of secondary poisoning remains should predators or scavengers consume a sufficiently large number of poisoned animals. Sierra Nevada red foxes may face a higher risk than other predators or scavengers (e.g., birds) as pocket gophers are an important food year-round (Perrine 2005). Furthermore, they routinely dig gophers out of their burrows, making it likely that they would also be able to access poisoned carcasses and residual traces of bait belowground. The risk may be higher with the use of anticoagulant rodenticides such as diphacinone. As a first-generation anti-coagulant, diphacinone has relatively low toxicity to rodents and requires multiple applications to ensure effective treatment. These baits typically are applied aboveground, and evidence suggests that secondary poisonings are possible if a predator consumes the gastrointestinal tract or cheek pouches of poisoned rodents (Mendenhall and Pank 1980; Hegdal and others 1981; Littrell 1990). These treatments are usually applied at recreation sites such as campgrounds, which may increase the exposure to human-habituated red foxes. Although the risk of poisoning may be low, especially if appropriate precautions are taken and if standard protocols are closely followed, further investigation of the possible impacts of rodenticides may be warranted given the importance of pocket gophers and ground squirrels as red fox prey.

## *Climate Change*

The available evidence agrees that all three western mountain red fox subspecies are closely associated with boreal and subalpine habitats at high elevations (Bailey 1931 and 1936; Grinnell and others 1937; Schempf and White 1977; Aubry 1983; Fuhrmann 1998; Swanson and others 2005; Perrine 2005). Aubry (1983) hypothesized that these three subspecies were adapted to the boreal conditions that were widespread in the contiguous United States during the last glaciation, and then became isolated in mountainous regions when the glaciers retreated (Aubry and others 2009). Whether due to physiological or behavioral limitations, or to other mechanisms which remain unclear, these montane subspecies do not show the wide range of habitat tolerances that is more commonly associated with the red fox (Aubry 1984; Buskirk and Zielinski 2003). As an apparently obligate inhabitant of boreal and subalpine communities, the Sierra Nevada red fox may be strongly affected by climate change. Such effects include the direct effects of temperature, precipitation and habitat structure, as well as the cascading ecological interactions that may occur within these high-elevation communities.

Over the past century, average temperatures in alpine regions have increased 0.3 to 0.6°C, resulting in dramatic glacial retreat (Oerlemans 1994). This warming trend is expected to continue due to the increasing concentration of carbon dioxide and other greenhouse gases in the atmosphere. These gases are expected to double well before the year 2100, with estimated increases of between 1.4 and 5.8°C in global mean temperature (IPCC 2001). In California, temperature increases would be highest in the higher elevations of the Sierra Nevada, with a projected increase in average annual temperature of 3.8°C (Snyder and others 2002). The temperature increase would likely be accompanied by a dramatic decrease in snow accumulation at high elevations. Weather station records from the western US indicate that these trends have already commenced, with increasing winter and spring temperatures causing precipitation to fall as rain rather than snow (Knowles and others 2006). In the Great Basin, a 3°C increase in annual temperature would raise the lower limit of the boreal zone 500 m and cause a 62% reduction in boreal habitat (McDonald and Brown 1992; Moen and others 2004). A similar calculation for the Sierra Nevada would suggest a 50% reduction in boreal habitat based on elevational gradients alone,

and an even greater reduction given the amount of rockland and icefield habitats found above 2,750 m. Such warming could facilitate the movement of coyotes, bobcats, and lowland red foxes into habitats currently occupied by mountain red fox, possibly resulting in increased competition and predation rates and increased risk of competitive exclusion and disease transmission.

Currently, too little research has been conducted on the Sierra Nevada red fox to identify the specializations or limitations that restrict them to boreal environments. However, the extinction of a number of boreomontane-adapted animals during the last climatic warming (e.g., noble marten [*Martes nobilis*]; Grayson 1984 and 1987), or their elimination from mountain ranges south of their current distribution (e.g., mountain goats [*Oreamnos americanus*] in the Sierra Nevada and hoary marmot [*Marmota caligata*] in the southern Cascades; Hoffmann and Taber 1967), suggests that climate change may pose a very real threat to the Sierra Nevada red fox. While the Sierra Nevada red fox may have survived the 1.5°C higher average temperature of the last climatic warming (the altithermal of 6,000 yrs ago), it may not survive the much greater temperature increase projected for the next 100 years.

### *Trapping*

Red fox trapping has been banned in California since 1974. Furthermore, the state passage of Proposition 4 in 1998 prohibited the use of all body-gripping traps for commercial purposes. Therefore, trapping likely has a minimal impact upon Sierra Nevada red foxes. However, due to the apparent low densities and isolated nature of Sierra Nevada red fox populations, incidental trapping or poaching could represent a threat, albeit small, to local populations.

### *Summary of Potential Threats*

The factors likely to affect the distribution and persistence of Sierra Nevada red fox include climate change, conversion of habitat by human development, and expansion of coyotes and exotic red foxes into high-elevation areas. Recreation, including the effects of salmon poisoning and plague control activities, may represent a threat to individuals through increased risk of harm from interactions with people and pets, from disease transmission, and from contact with rodenticides, but the severity of this threat is not currently known. As noted above, the general lack of basic ecological information for this species makes the identification and analysis of threats a largely speculative exercise, and ultimately poses a risk to the effective management of the Sierra Nevada red fox and its habitat.

## CONSERVATION CONSIDERATIONS

This section identifies considerations or opportunities that may assist in the conservation of the Sierra Nevada red fox in California. Developing management considerations for this species is challenging due to the paucity of knowledge about its distribution and ecology. The isolated nature of Sierra Nevada red fox populations suggests that incidental detections may occur rarely. However, until additional rigorous, focused research or systematic monitoring can be conducted, the slow accumulation of incidental detections or samples from researchers or managers conducting other projects may be the only practical way to acquire information.

Because of the urgent need to document the distribution of this species, the most efficient way to proceed may be to make minor adjustments to the field protocols for ongoing surveys for other species such as marten, fisher and wolverine (see details below). These modifications could be implemented in the historic range of the Sierra Nevada red fox and in habitat types similar to those in which red foxes have been documented in the Lassen region.

Vegetation management in Sierra Nevada red fox habitat should include activities that maintain or restore the health of montane meadows and the prey species they support. Because of the seasonal elevational movements of this species (Grinnell and others 1937; Perrine 2005), the availability and maintenance of movement corridors from upper elevation areas to the mixed conifer zone will be important.

Although the sensitivity of Sierra Nevada red fox to human presence is debatable, the negative impacts of direct human-wildlife interactions are not. Red foxes are intelligent and adaptable, and can quickly become acclimated to humans. Accounts of red foxes scavenging at houses, campgrounds and parking lots, and even directly approaching humans and vehicles during daytime, have been documented in the Lassen region (Perrine and Arnold 2001; Perrine 2005) and for other mountain fox populations (Aubry 1983; Tsukada 1997; Bubela and others 1998). Increased exposure to humans, vehicles, and pets entail additional risks to red foxes. Provision of educational materials on red fox and the importance of minimizing direct contact with red foxes may be helpful in reducing undesirable behaviors on the part of foxes and minimize their exposure to disease. Availability of bear-proof garbage cans and food storage lockers in campgrounds, particularly in areas used during the winter, may help curb red fox scavenging in these areas.

In the Lassen region, radio-collared red foxes were highly mobile, with large home ranges and extensive daily and seasonal movements, and they routinely crossed administrative boundaries during the course of normal foraging behavior (Perrine 2005). Successful management of these foxes will therefore require coordination and cooperation among multiple agencies and stakeholders, including the USDA Forest Service, the National Park Service, California Department of Fish and Game, California Department of Forestry and Fire Prevention, and private forests and landowners.

# INVENTORY, MONITORING, AND RESEARCH NEEDS

Woefully little information exists on the distribution and ecology of mountain red fox in California. The paucity of basic scientific information makes the development of a defensible conservation strategy for Sierra Nevada red fox extremely challenging. Of greatest urgency is the determination of the species' current distribution in California. Such occurrence data can be used to further clarify habitat relationships and to identify focal locations for more intensive research efforts. This suggests a two-pronged research approach: a thorough survey of the historical range to identify local populations, using methods with a high probability of detecting red foxes; followed by intensive study of these populations. Such a pattern has already been applied, to a limited extent, in the Lassen region (Perrine 2005).

Documenting the current distribution of Sierra Nevada red fox throughout its historical range is essential. The collection of anecdotal sighting reports, although important, is insufficient to reliably document what proportion of Sierra Nevada red fox historical range remains occupied. Methods to detect forest-associated carnivores have been well developed over the past decade (e.g., Zielinski and Kucera 1995). These methods consist primarily of sooted track plates, remote camera systems, and snow

tracking. However, only baited camera stations have been demonstrated to reliably and unambiguously detect mountain red fox (Perrine 2005). Camera stations established to detect marten, fisher or wolverine may not detect red foxes if the bait or sensor is positioned >1 m above the ground or snow level, because red foxes seldom climb trees. In addition, seasonal movements such as those documented in the Lassen region (Perrine 2005) suggest that monitoring exclusively in summer will not fully reflect the species' distribution or habitat use. Although winter surveys would likely be more challenging, the probability of detection would likely be higher given the scarcity of food resources. Surveys conducted specifically to detect red foxes, using methods and protocols known to detect red foxes, are the most reliable method to document their current distribution. Snow track surveys (Halfpenny and others 1995) by trained observers may also be an efficient way to assess whether red foxes occur in an area. However, obtaining definitive results from snow tracks may be more difficult than with camera stations. Scat surveys with specially-trained dogs (e.g., Smith and others 2003) could also be used to inventory local areas, with the added benefit that the feces could provide genetic samples (see below) and dietary information. A thorough evaluation of the range of potential inventory methods and their relative benefits needs to be conducted so that resources can be allocated efficiently.

In addition to providing occurrence data, distribution surveys may be used to develop broad-scale habitat relationships for the Sierra Nevada red fox. This information could then be used to evaluate management alternatives relative to the distribution and abundance of habitat utilized by the red foxes. Additionally, if individuals can be differentiated, such as by DNA or unique markings, an index of local population density could be calculated. Ideally, detection surveys would incorporate methods to obtain non-invasive genetic samples, such as through hair snags or the collection of feces. Genetic samples are essential for quantifying the extent of gene flow among local populations of Sierra Nevada red fox and among mountain fox populations in California, Nevada, Oregon, and Washington. Documenting, quantifying, and understanding the genetic structure of mountain red fox populations, and the factors affecting their connectivity and persistence are essential for successful management. Genetic samples also are needed to document whether exotic red foxes have expanded into the historical range of the Sierra Nevada red fox, especially in the southern portion of its range. Since exotic and native red foxes are morphologically similar, genetic markers need to be identified to reliably differentiate the two groups (Roest 1977; Lewis and others 1995; Aubry 1997; Perrine et al 2007).

Ultimately, successful conservation will require identifying and addressing limiting factors, with particular emphasis on reproduction and mortality. Inventory methods such as cameras and snow tracks can document habitat use, but they provide little insight into survival and fecundity (other than detecting pups in an area). Information on habitat associations in the absence of demographic data may be misleading, as densely populated habitats may not be the most suitable (Van Horne 1983; Pulliam 1988). Assessing individual fitness requires individually marked and monitored animals. Identifying sources of mortality that are directly linked to human activities would also be particularly important. Additional information needs include fine-scale documentation of habitat use, especially habitats used for natal dens, seasonal changes in habitat use, and elevational movement patterns. This information is important but will be more difficult to collect than presence-absence data because it requires the use of intensive techniques such as radio-telemetry and mark-recapture. Clearly, such intensive local studies would also be an additional source of genetic data, which would be essential for determining the extent of genetic variability within local populations.

Developing both extensive and intensive data-gathering efforts focused on Sierra Nevada red fox offers the best combination of information to inform management and conservation efforts. Extensive surveys can provide occurrence and broad-scale habitat associations and may provide genetic samples necessary for describing the genetic structure of red fox populations. Collaboration among local, state

and federal entities would facilitate the compilation of genetic material. Such entities obviously include the land management agencies listed above, but should also include other agencies that may have the opportunity to collect specimens, such as the California Highway Patrol, California Department of Transportation, state and federal Wildlife Services agents, local animal control officers, and academic or agency biologists operating at high elevations in the Sierra Nevada and Cascades in California. Coordination of these efforts would likely require the establishment of a central contact or clearing house, which would also compile the resulting specimens and data. Genetic information may also be obtained from intensive studies involving mark-recapture or radio-telemetry techniques through the collection of tissue, hair, or scat from captured animals. Intensive studies would offer insights into reproduction, survival, diet, and fine-scale habitat use and may help identify significant mortality factors and important habitat elements. These data are essential for the development of a comprehensive conservation strategy for the Sierra Nevada red fox in California.

# LITERATURE CITED

Ables, E. D. 1965. **An exceptional fox movement.** Journal of Mammalogy 46: 102.

Ables, E. D. 1969. **Home range studies of red foxes (*Vulpes vulpes*).** Journal of Mammalogy 50: 108-120.

Ables, E. D. 1975. **Ecology of the red fox in North America.** In: Fox, M. W., ed. The wild canids: their systematics, behavioral ecology and evolution. New York: Van Nostrand Reinhold Company; 216-236.

Allen, S. H. 1983. **Comparison of red fox litter sizes determined from count of embryos and placental scars.** Journal of Wildlife Management 47: 860-863.

Anthony, R. M.; Lindsey, G. D.; Evans, J. 1984. **Hazards to golden-mantled ground squirrels and associated secondary hazard potential from strychnine for forest pocket gophers.** In: Proceedings of the Eleventh Vertebrate Pest Conference; 1984 March 6-8; Sacramento, CA; 25-31.

Aubry, K. B. 1983. **The Cascade red fox: Distribution, morphology, zoogeography and ecology.** Seattle: University of Washington; 151 p. Ph.D. dissertation.

Aubry, K. B. 1984. **The recent history and present distribution of the red fox in Washington.** Northwest Science 58: 69-79.

Aubry, K. B. 1997. **The Sierra Nevada red fox (*Vulpes vulpes necator*).** In: Harris, J. E.; Ogan, C. V., eds. Mesocarnivores of northern California: biology, management and survey techniques. 1997 August 12-17; Humboldt State University, Arcata, CA. The Wildlife Society, California North Coast Chapter; 47-53.

Aubry, K. B.; Statham, M. J.; Sacks, B. N.; Perrine, J. D.; Wisely, S. M.. 2009. **Phylogeography of the North American red fox: vicariance in Pleistocene forest refugia.** Molecular Ecology 18: 2668-2686.

Bailey, V. 1931. **Mammals of New Mexico.** Washington, D.C.: US Department of Agriculture, Bureau of Biological Survey; 296-298.

Bailey, V. 1936. **The mammals and life zones of Oregon.** North American Fauna No. 55. Washington, D.C.: U.S. Department of Agriculture, Bureau of Biological Survey; 281-285.

Baird, S. F. 1857. **Mammals: General report upon the zoology of the several Pacific railroad routes.** Washington, D.C.: Reports, explorations and surveys for railroad routes from the Mississippi to the Pacific Ocean; 121-133.

Benson, J. F; Perrine, J. D.; Golightly, R. T.; Barrett, R. H. 2005. **Use of cover and response to cover type edges by female Sierra Nevada red foxes.** Western North American Naturalist 65: 127-130.

Bubela, T. M.; Dickman, C. R.; Newsome, A. E. 1998. **Diet and winter foraging behaviour of the red fox (*Vulpes vulpes*) in alpine and subalpine New South Wales.** Australian Mammalogy 20: 321-330.

Buskirk, S. W. 1999. **Mesocarnivores of Yellowstone.** In: Clark, T. W.; Curlee, A. P.; Minta, S. C.; Karieva, P. M., eds. Carnivores in ecosystems: The Yellowstone experience. New Haven: Yale University Press; 165-187.

Buskirk, S. W.; Zielinski, W. J. 2003. **Small and mid-sized carnivores.** In: Zabel, C. J.; Anthony, R. G., eds. Mammal community dynamics: Management and conservation in the coniferous forests of western North America. Cambridge: Cambridge University Press; 207-249.

Cain, J.W. 2001. **Nest success of yellow warblers (*Dendroica petechia*) and willow flycatchers (*Empidonax traillii*) in relation to predator activity in montane meadows of the central Sierra Nevada, California.** Sacramento: California State University, Sacramento; 209 p. M.S. thesis.

Cavallini, P.; Lovari, S. 1994. **Home range, habitat selection and activity of the red fox in a Mediterranean coastal ecotone.** Acta Theriologica 39: 279-287.

CDFG. 1987. **Sierra Nevada red fox: Five-year status report.** Sacramento: California Department of Fish and Game; 6 p.

CDFG. 1996. **The status of rare, threatened and endangered animals and plants of California.** Sacramento: California Department of Fish and Game, p. 17.

CDFG. 2004. **Special animals.** Sacramento: California Department of Fish and Game. 48 p.

Churcher, C. S. 1959. **The specific status of the New World red fox.** Journal of Mammalogy 40: 513-520.

Crabtree, R. L. 1993. **Gray ghost of the Beartooth.** Yellowstone Science. Spring: 13-16.

Crabtree, R. L.; Sheldon, J. W. 1999. **Coyotes and canid coexistence in Yellowstone.** In: Clark, T. W.; Curlee, A. P.; Minta, S. C.; Karieva, P. M., eds. Carnivores in ecosystems: The Yellowstone experience. New Haven: Yale University Press; 127-163.

Dekker, D. 1983. **Denning and foraging habits of red foxes, *Vulpes vulpes*, and their interactions with coyotes, *Canis latrans*, in central Alberta, 1972-1981.** Canadian Field-Naturalist 97: 303-306.

Dekker, D. 1989. **Population fluctuations and spatial relationships among wolves, *Canis lupus*, coyotes, *Canis latrans*, and red foxes, *Vulpes vulpes*, in Jasper National Park, Alberta.** Canadian Field-Naturalist 103: 261-264.

Desmarest, A. G. 1820. **Mammalogie ou description des espèces de mammifères.** Paris, France.

Drew, G. S.; Bissonette, J. A. 1997. **Winter activity patterns of American martens (*Martes americana*): Rejection of the hypothesis of thermal-cost minimization.** Canadian Journal of Zoology 75: 812-816.

Englund, J. 1970. **Some aspects of reproduction and mortality rates in Swedish foxes (*Vulpes vulpes*), 1961-63 and 1966-69.** Viltrevy 8:1-82.

Fitzpatrick, B. M. 1999. **Genetic founder effects and admixture in California's non-native red foxes.** Arcata: Humboldt State University; 52 p. M.A. thesis.

Fuhrmann, R. T. 1998. **Distribution, morphology, and habitat use of the red fox in the northern Yellowstone ecosystem.** Bozeman: Montana State University; 78 p. M.S. thesis.

Fuller, A. K.; Harrison, D. J. 2006. **Ecology of red foxes and niche relationships with coyotes on Mount Desert Island, Maine.** Orono, ME: Department of Wildlife Ecology, University of Maine. Final contract report to Acadia National Park and USDI National Park Service Northeast Region. 41 p.

Garshelis, D. L. 2000. **Delusions in habitat evaluation: Measuring use, selection and importance.** In: Boitani, L.; Fuller, T. K., eds. Research techniques in animal ecology. New York: Columbia University Press; 111-164.

Gorham, J. R.; Foreyt, W. J. 1990. **Salmon poisoning disease.** In: Greene, C. E., ed. Infectious diseases of the dog and cat. Philadelphia: W.B. Saunders; 397-403.

Gosselink, T. E.; Van Deelen, T. R.; Warner, R. E.; Joselyn, M. G. 2003. **Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois.** Journal of Wildlife Management 67: 90-103.

Goszczynski, J. 1989. **Spatial distribution of red foxes *Vulpes vulpes* in winter.** Acta Theriologica 34: 361-372.

Goszczynski, J. 2002. **Home range in red fox: territoriality diminishes with increasing area.** Acta Theriologica 47 (Suppl. 1): 103-114.

Gould, G. I. 1980. **Status of the red fox in California.** Sacramento: California Department of Fish and Game, Nongame Wildlife Investigations, Job I-8. 3 p.

Gray, R. L. 1975. **Sacramento Valley red fox survey.** Sacramento: California Department of Fish and Game, Nongame Wildlife Investigations, Job II-1.2; 5 p.

Grayson, D. K. 1984. **Time of extinction and nature of adaptation of the noble marten, *Martes nobilis*.** In: Genoways, H. H.; Dawson, M. R., eds. Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Publication 8. Pittsburgh: Carnegie Museum of Natural History; 233-240.

Grayson, D. K. 1987. **The biogeographic history of small mammals in the Great Basin: observations on the last 20,000 years.** Journal of Mammalogy 68: 359-375.

Green, R. 2006. **Distribution and habitat associations of forest carnivores and an evaluation of the California Wildlife Habitat Relationships model for American marten in Sequoia and Kings Canyon National Parks.** Arcata: Humboldt State University; 90 p. M.S. thesis.

Grinnell, J.; Storer, T. 1924. **Animal life in the Yosemite.** Berkeley: University of California Press; 752 p.

Grinnell, J.; Dixon, J.; Linsdale, L. 1930. **Vertebrate natural history of a section of northern California through the Lassen Peak region.** Berkeley: University of California Press; 594 p.

Grinnell, J.; Dixon, J.; Linsdale, L. 1937. **Fur-bearing mammals of California.** Berkeley: University of California Press; 777 p.

Halfpenny, J. C.; Thompson, R. W.; Morse, S. C.; Holden, T.; Rezendes, P. 1995. **Snow Tracking.** In: Zielinski, W. J.; Kucera, T. E., eds. American marten, fisher, lynx and wolverine: Survey methods for their detection. PSW-GTR-157. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 91-163.

Hall, E. R. 1981. **Mammals of North America.** New York: John Wiley and Sons. 1181 p.

Halpin, M. A.; Bissonette, J. A. 1988. **Influence of snow depth on prey availability and habitat use by red fox.** Canadian Journal of Zoology 66: 587-592.

Harris, S. 1979. **Age-related fertility and productivity in red foxes, *Vulpes vulpes*, in suburban London.** Journal of Zoology (London) 184: 195-199.

Harris, S. 1980. **Home ranges and patterns of distribution of foxes (*Vulpes vulpes*) in an urban area, as revealed by radio tracking.** In Amlaner, C. J.; Macdonald, D. W., eds. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press; 685-690.

Harrison, D. J.; Bissonette, J. A.; Sherburne, J. A. 1989. **Spatial relationships between coyotes and red foxes in eastern Maine.** Journal of Wildlife Management 53: 181-185.

Hedrick, R. P.; Arnandi, A.; Manzer, D. 1990. ***Nanophyetus salmincola*: The trematode vector of *Neorickettsia helmintheca*.** California Veterinarian, July/August: 18-22.

Hegdal, P. L.; Gatz, T.A.; Fite, E. C. 1981. **Secondary effects of rodenticides on mammalian predators.** In: Chapman, J.A.; Pursley, D., eds. Proceedings of the First Worldwide Furbearer Conference; 1980 August 3-11; Frostburg, Maryland: Worldwide Furbearer Conference Inc.; 1781-1793.

Heptner, V. G.; Naumov, N. P.; Yurgenson, P. B.; Sludskii, A. A.; Chirkova, A. F.; Bannikov, A. G., eds. 1998 (English translation). **Mammals of the Soviet Union: Vol. II, Part 1a: Sirenia and Carnivora**. Enfield, NH: Science Publishers, Inc.; 520-537.

Hoffman, R. A.; Kirkpatrick, C. M. 1954. **Red fox weights and reproduction in Tippecanoe County, Indiana.** Journal of Mammalogy 35: 504-509.

Hoffmann, R. S.; Taber, R. D. 1967. **Origin and history of Holarctic tundra ecosystems, with special reference to their vertebrate faunas.** In: Wright, H. E.; Osburn, W. H., eds. Arctic and alpine environments. Bloomington: Indiana University Press; 143-170.

Ingles, L. G. 1965. **Mammals of the Pacific States.** Stanford: Stanford University Press; 506 p.

Institute for Wildlife Studies. 2006. **2006 winter wolverine survey in Sequoia and Kings Canyon National Parks.** Unpublished report, available at: http://www.iws.org

IPCC (Intergovernmental Panel on Climate Change) 2001. **Climate Change 2001 - Impacts, Adaptation, and Vulnerability.** Cambridge: Cambridge University Press; 1032 p.

Jones, D. M.; Theberge, J. B. 1982. **Summer home range and habitat utilization of the red fox (*Vulpes vulpes*) in a tundra habitat, northwest British Columbia.** Canadian Journal of Zoology 60: 807-812.

Kamler, J. F.; Ballard, W. B. 2002. **A review of native and nonnative red foxes in North America.** Wildlife Society Bulletin 30: 370-379.

Kernohan, B. J.; Gitzen, R. A.; Millspaugh, J. J. 2001. **Analysis of animal space use and movements.** In: Millspaugh, J. J.; Marzluff, J. M., eds. Radio tracking and animal populations. New York: Academic Press; 125-166

Klope, M. W. 1983. **The ecology of the red fox (*Vulpes vulpes*) at the Pacific Missile Test Center: A progress report, March 1982-October 1983.** In: Proceedings of the Mugu Lagoon / San Nicholas Island ecological research symposium; 1983 October 21-22; 196-201.

Knowles, N.; Dettinger, M. D.; Cayan, D. R. 2006. **Trends in snowfall versus rainfall in the western United States.** Journal of Climate 19: 4545-4559.

Kucera, T. E. 1993. **The Sierra Nevada red fox.** Outdoor California. October-November: 4-5.

Kucera, T. E. 1995. **Recent photograph of a Sierra Nevada red fox.** California Fish & Game 81: 43-44.

Kucera, T. E.; Zielinski, W. J.; Barrett, R. H. 1995. **Current distribution of the American marten, *Martes americana*, in California.** California Fish & Game 81: 96-103.

Larivière, S., and M. Pasitschniak-Arts. 1996. ***Vulpes vulpes*.** Mammalian Species 537: 1-11.

Lewis, J. C.; Sallee, K. L.; Golightly, R. T. 1993. **Introduced red fox in California.** Arcata, CA: Department of Wildlife, Humboldt State University. 70 p. California Department of Fish and Game, Nongame Bird and Mammal Report 93-10.

Lewis, J. C.; Golightly, R. T.; Jurek, R. M. 1995. **Introduction of non-native red foxes in California: Implications for the Sierra Nevada red fox.** Transactions of the Western Section of The Wildlife Society 31: 29-32.

Lewis, J. C.; Sallee, K. L.; Golightly, R. T. 1999. **Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California.** American Midland Naturalist 142: 372-381.

Lindstrom, E. R.; Brainerd, S. M.; Helldin, J. O.; Overskaug, K. 1995. **Pine marten - red fox interactions: A case of intraguild predation?** Annales Zoologici Fennici 32: 123-130.

Linnaeus, C. 1758. **Systema naturae**, 10th ed. Stockholm: Laurentii Salvii.

Linsdale, J. M. 1931. **Facts concerning the use of thallium in California to poison rodents—its destructiveness to game birds, song birds and other valuable wildlife.** Condor 33: 92–106.

Linsdale, J. M. 1932. **Further facts concerning losses to wild animal life through pest control in California.** Condor 34: 121–135.

Littrell, E. E. 1990. **Effects of field vertebrate pest control on nontarget wildlife.** Proceedings of the Fourteenth Vertebrate Pest Conference; 1990 March 6-8; Sacramento, CA; 59-61.

Lloyd, H. G. 1980. **The red fox.** London: B. T. Batsford; 320 p.

Lockie, J. D. 1977. **Studying carnivores.** Mammal Review 7: 3-5.

Macdonald, D. W. 1977. **On food preference in the red fox.** Mammal Review 7: 7-23.

Macdonald, D. W.; Courtenay, O.; Forbes, S.; Mathews, F. 1999. **The red fox (*Vulpes vulpes*) in Saudi Arabia: Loose-knit groupings in the absence of territoriality.** Journal of Zoology (London) 249: 383-391.

Mack, R. E.; Bercovitch, M. G.; Ling, G. V.; Lobingier, R. T.; Melli, A. C. 1990. **Salmon poisoning disease complex in dogs – a review of 45 cases.** California Veterinarian, July/August, 42-45.

Major, J. T.; Sherburne, J. A. 1987. **Interspecific relationships of coyotes, bobcats, and red foxes in western Maine.** Journal of Wildlife Management 51: 606-616.

McDonald, K. A.; Brown, J. H. 1992. **Using montane mammals to model extinctions due to global change.** Conservation Biology 6: 409-415.

Meek, P. D.; Saunders, G. 2000. **Home range and movement of foxes (*Vulpes vulpes*) in coastal New South Wales, Australia.** Wildlife Research 27: 663-668.

Meia, J. S.; Weber, K. M. 1993. **Choice of resting sites by female foxes *Vulpes vulpes* in a mountainous habitat.** Acta Theriologica 38: 81-91.

Mendenhall, V. M.; Pank, L. F. 1980. **Secondary poisoning of owls.** Journal of Wildlife Management 8: 311-315.

Menke, J.; Davis, C.; Beesley, P. 1996. **Rangeland assessment.** In: Sierra Nevada Ecosystem Project: Final report to Congress, Vol. III, Assessments, commissioned reports, and background information. Davis: Centers for Water and Wildland Resources, University of California; 901-972.

Merriam, C. H. 1899. **Results of a biological survey of Mount Shasta, California.** North American Fauna 16. Washington, D.C.: Division of Biological Survey, US Department of Agriculture; 179 p.

Merriam, C. H. 1900. **Preliminary revision of the North American red foxes.** Proceedings of the Washington Academy of Sciences 2: 661-676.

Minta, S. C.; Karieva, P. M.; Curlee, A. P. 1999. **Carnivore research and conservation: Learning from history and theory.** In: Clark, T. W.; Curlee, A. P.; Minta, S. C.; Karieva, P. M., eds. Carnivores in ecosystems: The Yellowstone experience. New Haven: Yale University Press; 323-404.

Moen, J.; Aune, K.; Edenius, L.; Angerbjörn, A. 2004. **Potential effects of climate change on treeline position in the Swedish mountains.** Ecology and Society 9(1): 16.

Nowak, R. N. 1999. **Walker's Mammals of the World** (6th edition, vol. 1). Baltimore: Johns Hopkins University Press; 636-639.

Oerlemans, J. 1994. **Quantifying global warming from the retreat of glaciers.** Science 264: 243-245.

Overskaug, K. 2000. **Pine marten *Martes martes* versus red fox *Vulpes vulpes* in Norway; An inter-specific relationship?** Lutra 43: 215-221.

Padial, J. M.; Avila, E.; Gil-Sanchez, J. M. 2002. **Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats.** Mammalian Biology 67: 137-146.

Perrine, J. D. 2001. **The Sierra Nevada red fox: Mysterious hunter of the mountains.** Outdoor California March-April: 28-31.

Perrine, J. D. 2005. **Ecology of red fox (*Vulpes vulpes*) in the Lassen Peak region of California, USA.** Berkeley: University of California; 236 p. Ph.D. dissertation.

Perrine, J. D.; Arnold, J. F. 2001. **A new wildlife sighting reporting and database system for Lassen Volcanic National Park.** Transactions of the Western Section of The Wildlife Society 37: 8-15.

Perrine, J. D.; Pollinger, J. P.; Sacks, B. N.; Barrett, R. H.; Wayne, R. K. 2007. **Genetic evidence for the persistence of the critically endangered Sierra Nevada red fox in California.** Conservation Genetics 8: 1083-1095.

Pulliam, H. R. 1988. **Sources, sinks and population regulation.** American Naturalist 132:652-661.

Ratliff, R. D. 1985. **Meadows in the Sierra Nevada of California: state of knowledge.** GTR-PSW-84. Albany, CA: Pacific Southwest Experiment Station, Forest Service, U.S. Department of Agriculture; 52 p.

Roest, A. I. 1977. **Taxonomic status of the red fox in California.** San Luis Obispo: California Polytechnic State University. Available from California Department of Fish and Game, Job II-1.3.

Roest, A. I. 1979. **Subspecies of North American red foxes (*Vulpes vulpes*).** Unpublished manuscript presented at the 59th Annual Meeting of the American Society of Mammalogists, 1979 June 17-21, Oregon State University, Corvallis, OR; 8 p.

Samuel, D. E.; Nelson, B. B. 1982. **Foxes.** In: Chapman, J. A.; Feldhamer, G. A., eds. Wild mammals of North America: biology, management and economics. Baltimore: Johns Hopkins Univ. Press; 475-489.

Sargeant, A. B.; Allen, S. H. 1989. **Observed interactions between coyotes and red foxes.** Journal of Mammalogy 70: 631-633.

Sargeant, A. B.; Allen, S. H.; Hastings, J. O. 1987. **Spatial relations between sympatric coyotes and red foxes in North Dakota.** Journal of Wildlife Management 51: 285-293.

Schempf, P. F.; White, M. 1977. **Status of six furbearer populations in the mountains of northern California.** Berkeley: Department of Forestry and Conservation, and Museum of Vertebrate Zoology, University of California. 51 p. Published by the U. S. Department of Agriculture, Forest Service, California Region.

Schofield, R. D. 1960. **A thousand miles of fox trails in Michigan's ruffed grouse range.** Journal of Wildlife Management 24: 432-434.

Serafini, P.; Lovari, S. 1993. **Food habits and trophic niche overlap of the red fox and the stone marten in a Mediterranean rural area.** Acta Theriologica 38: 233-244.

Seton, E. T. 1929. **Lives of game animals. Volume I, Part 2: Cats, wolves, and foxes.** Garden City, NY: Doubleday, Doran and Company; 467-552**.**

Sequin, E. S.; Jaeger, M. M.; Brussard, P. F.; Barrett, R. H. 2003. **Wariness of coyotes to camera traps relative to social status and territory boundaries.** Canadian Journal of Zoology 81: 2015-2025.

Smith, D. A.; Ralls, K.; Hurt, A.; Adams, B.; Parker, M.; Davenport, B.; Smith, M. C.; Maldonado, J. E. 2003. **Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes (*Vulpes macrotis mutica*).** Animal Conservation 6: 339-346.

Smith, G. J.; Cary, J. R.; Rongstad, O. J. 1981. **Sampling strategies for radio-tracking coyotes.** Wildlife Society Bulletin 9: 88-93.

Snyder, M. A.; Bell, J. L.; Sloan, L. C.; Duffy, P. B.; Govindasamy, B. 2002. **Climate responses to a doubling of atmospheric carbon dioxide for a climatically vulnerable region.** Geophysical Research Letters 29: 1514; 4 p.

Storm, G. L. 1965. **Movements and activities of foxes as determined by radio-tracking.** Journal of Wildlife Management 29: 1-13.

Storm, G. L.; Ables, E. D. 1966. **Notes on newborn and full-term wild red foxes.** Journal of Mammalogy 47: 116-118.

Storm, G. L.; Andrews, R. D.; Phillips, R. L.; Bishop, R. A.; Siniff, D. B.; Tester, J. R. 1976. **Morphology, reproduction, dispersal, and mortality of midwestern red fox populations.** Wildlife Monographs 49: 1-82.

Swanson, B. J.; Furhmann, R. T.; Crabtree, R. L. 2005. **Elevational isolation of red fox populations in the Greater Yellowstone Ecosystem.** Conservation Genetics 6: 123-131.

Switzenberg, D. F. 1950. **Breeding productivity in Michigan red foxes.** Journal of Mammalogy 31: 194-195.

Theberge, J. B.; Wedeles, C. H. R. 1989. **Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon.** Canadian Journal of Zoology 67: 1285-1290.

Tjernberg, M. 1981. **Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden.** Holarctic Ecology 4: 12-19.

Tsukada, H. 1997. **A division between foraging range and territory related to food distribution in the red fox.** Journal of Ethology 15: 27-37.

USDA Forest Service. 2001. **Sierra Nevada Forest Plan Amendment Final Environmental Impact Statement and Record of Decision.** Vallejo, CA: Pacific Southwest and Intermountain Regions, Forest Service, US Department of Agriculture.

USDA Forest Service. 2004. **Sierra Nevada Forest Plan Amendment Final Supplemental Environmental Impact Statement and Record of Decision.** Vallejo, CA: Pacific Southwest and Intermountain Regions, Forest Service, US Department of Agriculture.

Van Horne, B. 1983. **Density as a misleading indicator of habitat quality.** Journal of Wildlife Management 47: 893-901.

Verts, B. J.; Carraway, L. N. 1998. **Land mammals of Oregon.** Berkeley: University of California Press; 369-373.

Voigt, D. R. 1987. **Red fox.** In: Novak, M.; Baker, J. A.; Obbare, M. E., eds. Wild furbearer management and conservation in North America. Ontario: Ontario Ministry of Natural Resources; 379-392.

Voigt, D. R.; Earle, B. D. 1983. **Avoidance of coyotes by red fox families.** Journal of Wildlife Management 47: 852-857.

Voigt, D. R.; Macdonald, D. W. 1984. **Variation in the spatial and social behavior of the red fox (*Vulpes vulpes*).** Acta Zoologica Fennica 171: 261-266.

Voigt, D. R.; Tinline, R. R. 1980. **Strategies for analyzing radio tracking data.** In: In Amlaner, C. J.; Macdonald, D. W., eds. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press; 387-404.

Von Schantz, T. 1984. **Nonbreeders in the red fox *Vulpes vulpes*: a case of resource surplus.** Oikos 42: 59-65.

Weber, K. M.; Meia, J. S. 1996. **Habitat use by the red fox *Vulpes vulpes* in a mountainous area.** Ethology Ecology and Evolution 8: 223-232.

Zeiner, D. C.; Laudenslayer, W. F.; Mayer, K. E.; White, M., eds. 1990. **California's Wildlife: Volume III: Mammals.** Sacramento: California Department of Fish and Game; 407 p.

Zielinski, W. J.; Kucera, T. E. 1995. **American marten, fisher, lynx and wolverine: Survey methods for their detection.** PSW-GTR-157. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 163 p.

Zielinski, W. J.; Truex, R. L.; Schlexer, F. V.; Campbell, L. A.; Carroll, C. 2005. **Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA.** Journal of Biogeography 32: 1385-1407.

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