Distribution, morphology, and habitat use of the red fox in the northern Yellowstone ecosystem
by Robert Todd Fuhrmann

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
The distribution, morphology, and habitat use of the red fox (Vulpes vulpes) was examined in the northern Yellowstone ecosystem during the winters of 1994-1995 and 1995-1996. National Park Service sighting records were examined to indicate the overall abundance of red foxes within Yellowstone National Park.

Morphological and genetic samples were collected on live-captured and dead foxes to identify the presence and distribution of potential red fox subspecies across an elevational gradient. In the examination of morphological measurements on 22 red foxes captured at elevations of 1350-3350 m, shorter tail length at higher elevations was the only significant parameter. Other parameters indicated trends of beneficial adaptations to climatically harsh environments at high elevations. At elevations above 2300 m, there was a significant higher frequency of observations of a light gray coat color. It appeared through genetic analysis that the population of foxes above 2100 m was genetically isolated from lower elevations. This occurred without a geographic barrier between subpopulations.

By snow tracking foxes using GPS and GIS technology, the habitat use compared to availability in a coyote-dominated canid assemblage was determined. Habitat characteristics were measured at 699 habitat points, 75 forage sites, and 9 bed sites along 77 km of fox tracks. Foxes were distributed across the study area and in a wide range of forest cover types and habitat components. In all categories, foxes selected (use significantly greater than availability) habitat that was <25 m from an ecotone. They preferred mesic meadows and spruce-fir habitats at low angle slopes with a wide range of aspects. Sagebrush communities were also frequently used. Foxes foraged in mesic meadows, sagebrush communities, and spruce-fir forests close to ecotones. Below 2100 m, foxes were more general in their use of habitat compared with availability and foraged in mesic meadows and sagebrush. Above 2100 m foxes preferred spruce-fir forests and mesic meadows were also used extensively. Foxes foraged in mesic meadows and spruce-fir and older lodgepole pine forests above 2100 m.

Conclusions indicated that red fox populations were contiguous across the study area and were classified as a forest carnivore. Foxes above 2100 m used different habitats, were genetically isolated, had a different color morph, and were to some degree different in body size.

# DISTRIBUTION, MORPHOLOGY, AND HABITAT USE OF THE RED FOX IN THE NORTHERN YELLOWSTONE ECOSYSTEM

by

Robert Todd Fuhrmann

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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# APPROVAL

of a thesis submitted by

Robert Todd Fuhrmann

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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To Jeanne Johnson who stood by my side through all of the ups and downs of this project (and not just the skiing). I couldn't have done it without you rafiki.

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# ABSTRACT

The distribution, morphology, and habitat use of the red fox (*Vulpes vulpes*) was examined in the northern Yellowstone ecosystem during the winters of 1994-1995 and 1995-1996. National Park Service sighting records were examined to indicate the overall abundance of red foxes within Yellowstone National Park.

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By snow tracking foxes using GPS and GIS technology, the habitat use compared to availability in a coyote-dominated canid assemblage was determined. Habitat characteristics were measured at 699 habitat points, 75 forage sites, and 9 bed sites along 77 km of fox tracks. Foxes were distributed across the study area and in a wide range of forest cover types and habitat components. In all categories, foxes selected (use significantly greater than availability) habitat that was <25 m from an ecotone. They preferred mesic meadows and spruce-fir habitats at low angle slopes with a wide range of aspects. Sagebrush communities were also frequently used. Foxes foraged in mesic meadows, sagebrush communities, and spruce-fir forests close to ecotones. Below 2100 m, foxes were more general in their use of habitat compared with availability and foraged in mesic meadows and sagebrush. Above 2100 m foxes preferred spruce-fir forests and mesic meadows were also used extensively. Foxes foraged in mesic meadows and spruce-fir and older lodgepole pine forests above 2100 m.

Conclusions indicated that red fox populations were contiguous across the study area and were classified as a forest carnivore. Foxes above 2100 m used different habitats, were genetically isolated, had a different color morph, and were to some degree different in body size.

# CHAPTER 1

# INTRODUCTION

Sighting records from Yellowstone National Park indicate that red foxes have an unusual variety of coat colors and have undergone several population fluctuations. From 1881 to 1900, sighting records indicated that foxes were observed relatively frequently (Varley and Brewster 1992). According to Yellowstone's second superintendent, P. W. Norris, foxes were "...numerous and of various colors, the red, grey, black and the cross varieties (most valuable of all) predominating in the order named" (Norris 1881). This level of detail is impressive as are the sightings themselves because today many long-time residents (e.g., M. Kolence, pers. comm.) of the area say they have never seen a fox in their travels in and around Yellowstone.

Shortly after the turn of the century, reports of red foxes became sporadic, and sightings were uncommon. Although these sightings were scarce and were from many different areas of the Park (Figure 1.1), accounts consistently reported lighter and gray colored foxes, especially at higher elevations. Fox sightings remained infrequent until the late 1980's. The increase that occurred around 1986 was most likely the result of increased interest rather than an actual increase in population. Two events, an official rare mammal sighting program begun in 1986 and an intensive coyote study initiated in 1989, marked the beginning of a period in which the number of red fox sightings steadily grew. Since then,

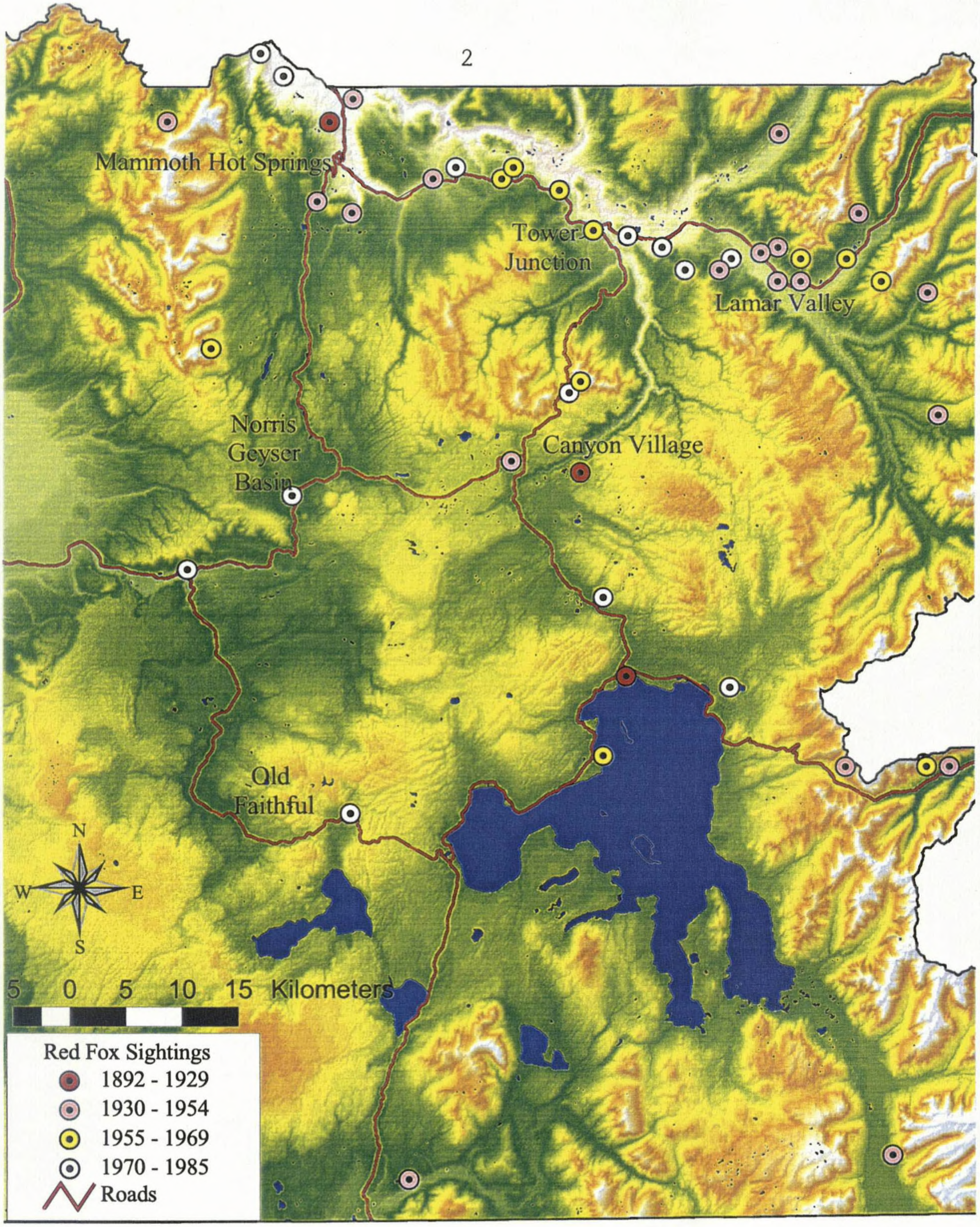


Figure 1.1. Red fox sightings in Yellowstone National Park from 1892-1985.

red foxes have been reported throughout the Greater Yellowstone Ecosystem in all months of the year in areas ranging from riparian communities at low elevations (1500 m) to alpine tundra at elevations exceeding 3000 m (Figure 1.2). During February and March 1993, I routinely observed at least 7 individual foxes in the Lamar Valley alone.

Due to the complete lack of knowledge regarding red fox in the northern Yellowstone ecosystem, I initiated this study to determine which subspecies of red foxes occur in this region and to describe their habitat use patterns. This thesis is divided into 2 chapters that reflect these objectives.

## Biogeographic Background of Red Fox

During Lewis and Clark's expedition up the Missouri River heading to the west coast in 1804-1806, many species of plants and animals were catalogued. In the upper Missouri drainage, they reportedly identified a "great-tailed fox" which they presumed to be the Rocky Mountain red fox (*V. v. macroura*) (Cutright 1969). This sighting probably came from north central Montana near the Missouri River. In addition, Audubon notes that a fox similar to what Lewis and Clark described was collected from a trapper before 1850 on the Upper Missouri River (no reference Audubon 1989). This fox was mostly gray and had a rather large tail. This fox was also presumably collected in central or eastern Montana.

Interestingly, Hoffman et al. (1969) indicates that prior to the 1950's, the only red fox that inhabited Montana (*V. v. macroura*) was in the higher elevation forests (e.g., Yellowstone National Park) yet absent from low elevation valleys in Montana. These foxes were restricted only to mountainous areas of extreme western and southwestern parts of the

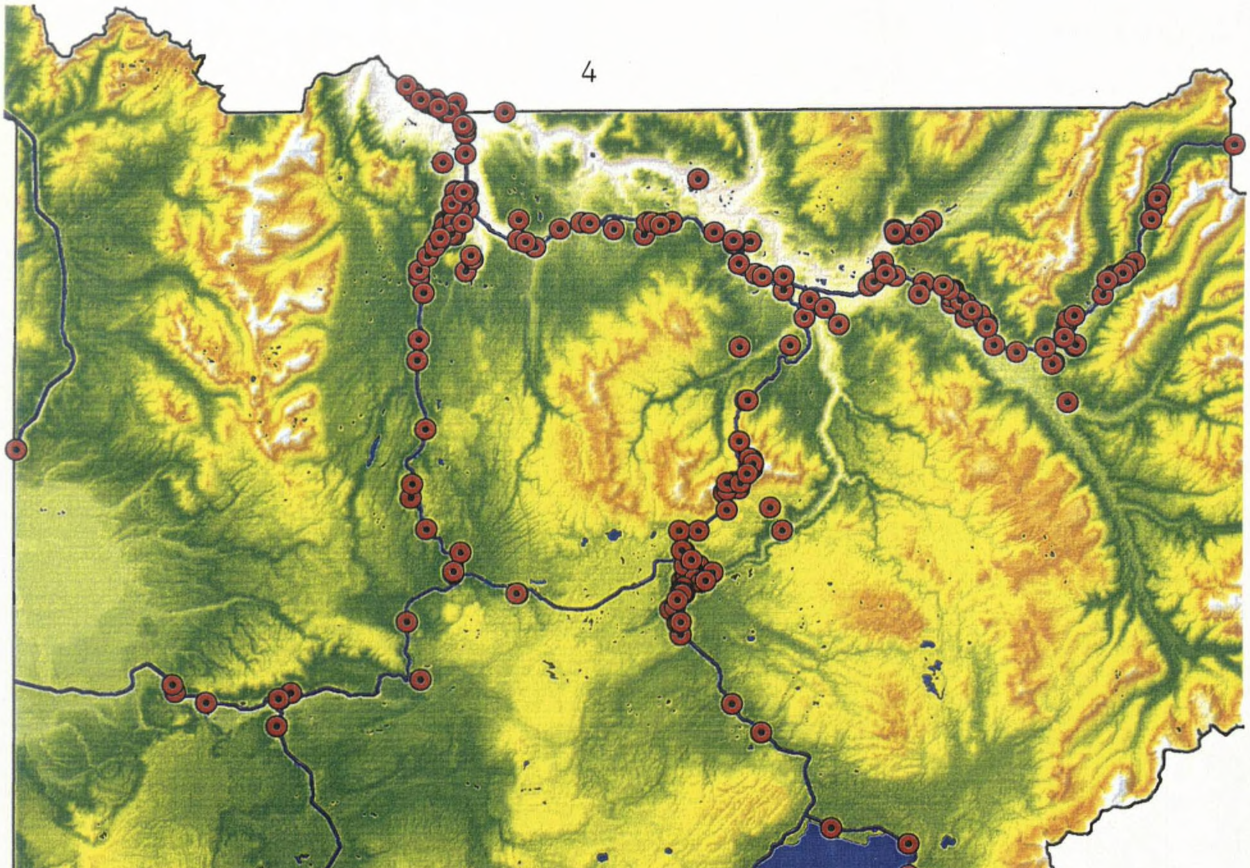


Figure 1.2. Red fox sightings in Yellowstone National Park from 1986 to 1996.

state. The discrepancies between Lewis and Clark and Audubon and Hoffman raises an interesting question. Were red fox present in central and eastern Montana prior to the 1950's? It appears as though red foxes were present during the early 1800's in this region but might have disappeared between that period and the 1950's. One possibility is that through predator eradication programs, foxes on the plains of eastern Montana were extirpated.

After 1950, red foxes were commonly seen in lowland and agricultural areas, especially throughout eastern and central Montana. These foxes could have repopulated the area from at least two sources. They could be mountain fox or the introduced variety from Europe brought into the eastern U.S. in the 18th century. European red foxes were brought to this country for fox hunts, but many escaped the jaws of the hounds or fur farms, and successfully adapted to their new environment. Prior to the 1800's, red fox distribution, west of the Mississippi River, was limited to the mountainous regions of the western United States possibly including central and maybe eastern Montana as well. The extent of the European red fox's expansion has been attributed, in part, to the widespread habitat changes brought on by agricultural development (Sheldon 1992). It is believed that the European red fox now inhabits agricultural and human-disturbed habitat at lower elevations while the red fox endemic to North America still resides in the high-elevation montane/alpine zones of the Rocky, Sierra, and Cascade Mountain ranges and boreal forests of Canada, Alaska, and the northern Great Lakes states (Crabtree 1993).

The origin of the red fox inhabiting central and eastern Montana is unclear. If these foxes are *V. v. macroura,* they could have descended from the montane habitats back to the plains following the conclusion of the large scale predator eradication programs. Conversely, the European red fox (*V. v. fulva*) could have migrated from the surrounding region to fill the niche of *V. v. macroura*. In addition, it is unknown where the dividing line is between these two subspecies or if an integrade zone exists. Further research is needed to obtain an answer to this complex question.

The endemic red foxes inhabiting isolated mountain ranges of the lower 48 states are possible relics from the Wisconsin glaciation (Aubry 1983). If this hypothesis is true, the mountain foxes are not well adapted to low elevation grasslands under current climatic conditions and mix of competing predators (Merriam 1900, Brooks 1936, Aubry 1983). The high elevation red fox, adapted to alpine tundra and subalpine forests, has survived in the higher elevations of the Greater Yellowstone Ecosystem (Yellowstone and Grand Teton National Parks and the seven surrounding national forests) since the Wisconsin glaciation. More information is needed to validate the historic distribution of red fox within the Greater Yellowstone Ecosystem.

I collected morphological measurements on live-trapped and dead foxes to identify the presence and distribution of red fox subspecies in the northern Yellowstone ecosystem.

## Habitat Use Patterns

Yellowstone has had only 2 canid predators, foxes and coyotes (*Canis latrans*), for the past 70 years. In 1995, wolves (*C. lupus*) were reintroduced. This reintroduction will likely have major impacts on the other canids in the system. A review of 16 separate studies of sympatric coyote and red fox populations indicated that coyotes have a tremendous negative impact on fox populations (Crabtree and Sheldon in press.). In fact, red fox survival is primarily a function of avoiding fatal encounters with coyotes while attempting to secure, or defend access to, prey. To avoid this, foxes may have to survive in between and on the periphery of the territories of the coyotes (Harrison et al. 1989, Sargeant et al. 1987). In Yellowstone, track surveys and remote cameras demonstrated that 90% of known fox locations occurred on the periphery of or in between coyote territories in the northern range (Gehman et al. 1997).

Wolves are known to kill coyotes and may exclude them from core areas of pack ranges (Murie 1944, Berg and Cheness 1978, Pacquet 1989, and Crabtree and Sheldon 1996). How reduced coyote numbers in a 3-canid system will influence fox habitat use is unknown. There is clear evidence of temporal and spatial partitioning between sympatric canids (Johnson et al. 1996). Temporal segregation may or may not be effective in reducing interference competition. It can reduce competition for food only if different activity patterns result in access to different prey populations (Pianka 1974) or if food resources are renewed within the period of temporal segregation (Litvaitis 1992). Spatial segregation works only where the smaller species can effectively limit its contact with the larger species. The smaller canid usually avoids the larger, but foxes and wolves may be ecologically separated enough that foxes will be ignored by wolves.

I used snow tracking, global positioning system (GPS) spatial technology, and geographic information system (GIS) data layers to describe habitat use by foxes in a coyote dominated canid assemblage. This will provide a replicable baseline against which changes in foxes habitat use can be assessed as wolf populations grow.

# CHAPTER 2

# MORPHOLOGY OF THE RED FOX IN THE NORTHERN YELLOWSTONE AREA

## Introduction

The red fox (*Vulpes vulpes fulva)* has been studied extensively in the Midwestern United States (Sergeant et al. 1987, Ables 1975, Storm et al. 1976, Pils and Martin 1978). Since the mid 1700's when the European red fox was introduced for fox hunts, this subspecies has spread across much of the U.S. and has likely interbred with native red foxes throughout their range except possibly at high elevations (Aubry 1983). Three surviving subspecies of high elevation foxes, collectively know as mountain foxes, are extant and thought to be indigenous to the western mountain states. These subspecies are restricted to the Cascade Mountains (*V. v. cascadensis*), Sierra Mountains (*V. v. necator*), and Rocky Mountains (*V. v. macroura*). Very little scientific information is available on distribution, ecological parameters, and genetic purity of these subspecies.

Previous to my work, the only study conducted on any of these three subspecies was by Aubry (1983) in the Cascade Mountains. Currently the Sierra red fox is being investigated in northern California (Kucera, pers. comm.). Other studies have examined the potential differences between subpopulations of the introduced European red fox (Butler 1945, Hattingh 1956, Storm el at. 1976).

The mountain subspecies of red foxes are possible relics from the Wisconsin glaciation (Aubry 1983). One theory suggests that these foxes, adapted to colder climatic conditions and habitats, migrated elevationally following the retreating edge of the glacial ice sheets along with their cold adapted prey base. As the foxes moved, they became isolated in the higher elevations of the western mountain ranges. This high elevation movement did occur in other montane and subalpine species such as the brown lemming in southern Alberta (Pielou 1991). Historically, Yellowstone National Park, with an average elevation of more than 2100 m, has harbored populations of red foxes, and these are likely to be the subspecies *V. v. macroura* (Varley and Brewster 1992).

Another proposed theory is that during the last few thousand years of the Wisconsin glaciation, the continental ice sheet was broken by an ice-free corridor. This corridor extended from Beringia south through Canada and down the Rocky Mountain eastern front (Pielou 1991), close to the present Beartooth Plateau of Montana and Wyoming. By using this corridor, red foxes (*V. v. abietorum*) from the northern refugium could have dispersed south much faster than was previously thought (Crabtree 1993). Although the mountain fox of the Beartooth Plateau appears within the presumed range of *V. v. macroura*, it may be more closely related to the red fox of the northern boreal forests (*V. v. abietorum*). The northern Yellowstone region could also be a hybrid zone between a more northern red fox and the southern Rocky Mountain red fox. After the last ice age and the introduction of the European red fox, the mountain foxes were climatically, and possibly competitively, excluded from the lower elevations (Merriam 1900, Brooks 1936, Aubry 1983).

Subspecies are recognized based on geographic segregation, behavioral differences, and morphological and/or genetic differences. Aubry (1983) concluded that the Cascade Mountain fox was ecologically, morphologically, and genetically distinct from European red foxes at nearby lower elevations. He noted that the Cascade fox was probably unable to expand its distribution due to adaptations to high altitude and cold habitats and, consequently, had little opportunity to interbreed with foxes of European stock. He also found that the Cascade Mountain fox had different parasite assemblages than lowland foxes which is further evidence supporting allopatric populations. This could be similar for foxes living in the high elevation areas surrounding and including Yellowstone Park.

The historical and present sighting records of foxes in Yellowstone and the Beartooth Plateau reveal that a large percentage of foxes observed at high elevations (>2400 m) were reported to be a light gray color phase. A number of phenotypic studies have been conducted on red fox color morphs (Butler 1945, Johnson and Hersteinsson 1993). Five morphs have been identified: red, smokey red, cross, black, and amber/cream coat colors (Swanson 1993). In general, European foxes vary in the extent and pattern of black hairs within a red coat and in the degree of silvering; however, gray or cream morphs are rarely reported. It is not known if the apparent differences in color between low and high elevation foxes indicate genetic or habitat use segregation. The frequency and consistency of coat color segregation are unknown, but if other morphological characteristics follow coat color, there is the possibility of subspeciation.

Due to potential separation of fox populations between lower and higher elevations, there could be differences in various morphometric measurements due to adaptations to climatic conditions. The highest elevations on the Beartooth Plateau, within the study area, are above 2700 m which is higher than any previous record of the mountain fox (Aubry 1983). Aubry determined that the Cascade foxes were smaller than the lowland foxes in a habitat that did not have the sustained harsh winter conditions of the Beartooth Plateau. The Beartooth Plateau is a southern displaced tundra habitat that is the largest of its kind in the lower 48 states. Species inhabiting this area might have thicker coats and be more robust and larger overall with shorter extremities according to Bergman's and Allen's rule (Pianka 1988). Although these two rules have been discredited in some cases (McNab 1971), I examined trends in measurements to determine if there might be either phenotypic or genotypic differences between low and high elevation foxes that were consistent with predictions according to beneficial adaptations of these rules.

In this study, I took a series of body measurements in foxes taken from lower and higher elevations. In addition, I collected tissue samples that were analyzed (B. Swanson) to determine if there were genetic differences that mirrored phenotypic differences between low and high elevation foxes.

## Materials And Methods

### Study Area

Figure 2.1 depicts the fox collection sites in the northern Yellowstone study area. I attempted to collect specimens across all major elevation and habitat zones in an area extending from Livingston, MT (1350 m) to the Beartooth Plateau, MT and WY (up to 3350 m). I divided the area into 3 regions defined by elevation and macro habitat type classifications: (1) Mammoth Hot Springs, WY (1902 m) to the Pebble Creek, WY drainage

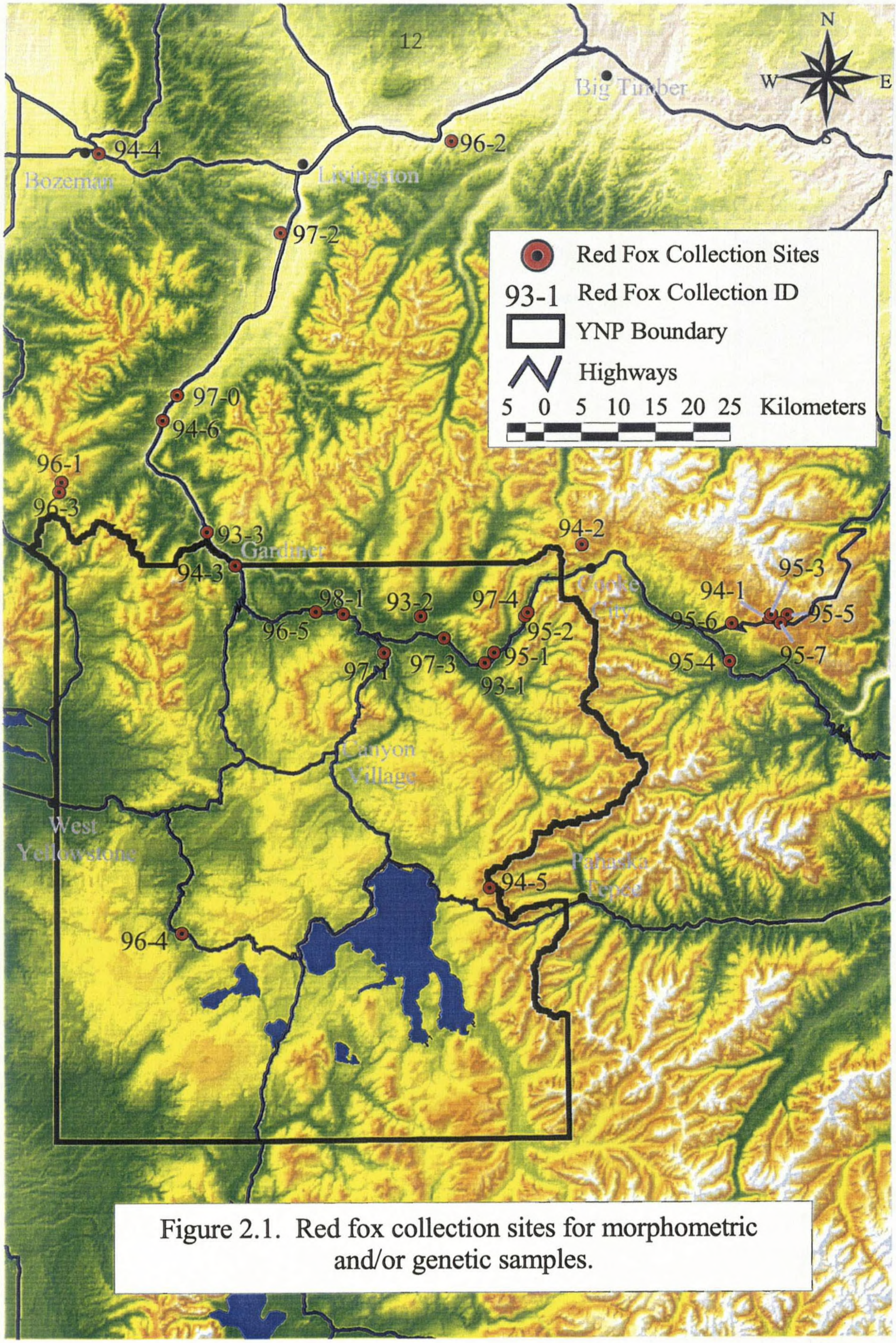


Figure 2.1. Red fox collection sites for morphometric and/or genetic samples.

(2100 m) in Yellowstone National Park which is a combination of meadows and forests; (2) the high elevation region from Pebble Creek to Beartooth Plateau which contains subalpine forests and tundra-like terrain above tree line; and (3) low elevation valleys used for agriculture and grazing characterized by grassland and sagebrush steppe between Livingston and Gardiner, MT (1609 m).

## Trapping

To examine the potential morphometric and genetic differences between foxes throughout the study area, collection of foxes was necessary. Live-trapping, collecting road-killed foxes, and data from foxes killed by local trappers were used to collect tissue and morphologic information. Live-trapping took place when the opportunity arose with no formal trap lines established. In the winter months, box traps were placed in areas where foxes had either been observed or where there was a high density of fox tracks. I designed plywood box traps with trap doors triggered by pulling a piece of bait inside the box. Wood traps instead of wire traps were used to protect the foxes from the winter weather. Traps were checked at least twice a day and more if the temperatures were below 0°C. In seasons other than winter, padded offset leg-hold traps were used in areas that foxes frequented.

When a fox was trapped, the animal was removed from the box or leg-hold trap using a noose pole. The fox was then hobbled by tying the legs together and further constrained with a muzzle. The fox was anesthetized if it was struggling or if inexperienced people were directly involved with the capture. A combination of Ketamine and Rompin were used in a 10:1 ratio. One ml of this mixture would sedate the fox for approximately 45 minutes which was enough time to process the animal. The following morphologic measurements were recorded: head length, head girth, neck girth, body length, tail length, hind foot length, ear length, and weight (Appendix). Each fox was given at least one colored and numbered ear tag. Before inserting the ear tag, a leather punch was used to extract a tissue sample from the ear at the location of the tag attachment. Blood samples were also taken when feasible to examine blood chemistry and antibody profiles. Blood samples, and whole carcasses in some cases, were sent to the University of Wyoming for analysis.

Tissue samples were sent to Brad Swanson, Purdue University, for microsatellite amplification and visualization analysis (e.g. Lade et al. 1996). Tissue samples were digested in 400 µl of 1x TNE, 50 µl of 10% SDS and 40 µl of Proteinase K followed by an overnight incubation at 55°C. All DNA was extracted via the phenol-chloroform method. The first extraction was done in 500 µl of buffered phenol, followed by a second extraction in 500 µl of phenol-chloroform-isoamyl alcohol mixture (25:24:1), and a third extraction in 500 µl of chloroform. Precipitation was done first in 100 µl of 100% EtOH followed by a precipitation in 100 µl of 70% EtOH. DNA was stored in 1x TE.

Microsatellite amplification utilized canid primers 123, 155, 172, 204, 213, 246, 442, and 671 (Research Genetics, Montgomery, AL). One primer was end-labeled $\gamma S_{35}$ (Amersham) via a $T_4$ polynucleotide kinase catalyzed reaction (Sambrook et al. 1994). This primer was then used in a 50 µl reaction. The reaction mixture consisted of 33.7 µl of sterile distilled water, 5 µl of each primer, 0.3 µl of Taq, and 1 µl of whole genomic DNA at a concentration of 50 ng/µl. Each sample was run for 30 cycles consisting of 45 seconds at 95°C, 40 seconds at 52°C, and 45 seconds at 72°C. At the end of the 30 cycles a 3-minute extension period of 72°C was performed. Seven µl of each sample, mixed with 2 µl of loading dye, were loaded on a 4% polyacrylamide gel and visualized on autorad film. An M13 sequence was run with each gel to allow for accurate sizing and between gel comparisons of alleles.

The analysis was performed using the $R_{st}$ statistics developed by Slatkin (1995) specifically for microsatellites and analogous to the traditional $F_{st}$ developed by Wright (1951). $R_{st}$ is a ratio based estimator of the variance in the difference in allele size (number of repeat units) between populations, $R_{st} = (S_T - S_W) / S_W$ where ST is the total variance in allele size over all subpopulations, and SW is twice the variance of allele size within a subpopulation, averaged over all subpopulations. Multiple loci were incorporated by averaging the variance estimates of each locus to produce the estimates of $S_T$ and $S_W$, producing the overall estimate of $R_{st}$. Significance was determined by performing 100 bootstraps, and determining the percentage of bootstrap $R_{st}$ values that the observed value exceeded.

Red fox carcasses obtained from collisions with vehicles were collected along road sides throughout the study area. Because red foxes are a fur-bearing species in portions of the study area outside the park, fur trappers were contacted to in order to collect additional samples. Data from foxes caught and killed by trappers were collected similarly to that of a live-trapped fox except when the fox had already been skinned. Measurements from road killed foxes were only taken when it was deemed that neither the cause of the accident nor time since death influenced the measurements.

I used an elevation of 2100 m as the dividing line between high and low elevation categories based on habitat, coat color, and potential genetic differences between the red foxes. Sites >2100 m are very different in habitat and snow characteristics than sites below this elevation. Sites >2100 m where foxes were collected were in the subalpine forest habitat type while <2100 m the habitat was montane forests or large open meadows. Although generally, the subalpine forest is limited to elevations above 2300 m in this region, the 2100-2300 m samples along Soda Butte Creek, WY were considered to be part of the high-elevation sample because subalpine forests persisted due to a cold air drainage basin.

### Historical Records and Sightings

All historical red fox sightings were extracted from the database of mammal sightings in Yellowstone National Park. For each sighting, the date, Universal Transverse Mercator (UTM) coordinates, elevation, and coat color, if described, were extracted. The frequency of the light gray coat color was collected based on elevation.

### Analysis

To examine the difference between high elevation and low elevation fox morphology, statistical significance ($p \leq 0.10$) was determined through an analysis of covariance (ANCOVA). Alternate analysis approaches such as scaling measurements to body length and using a 3-factor ANOVA including elevation as a third factor (2 levels <2100 m and >2100 m) were also used and produced similar results. Only ANCOVA, therefore, was included in my results section. Age and gender can confound the variability in the data; therefore, they were entered as independent variables. Elevation was entered as a covariate, and the dependent variables were the morphometric measurements. Chi-square analysis was employed to test whether trends (larger size and smaller extremities at high elevation) in morphometric measurements were significant. STATISTICA 5.1 software (StatSoft, Tulsa, OK) was used to conduct statistical tests. Graphic representation was created in Excel 97 or Quattro Pro 7.

## Results

Analysis of Park records suggests that the lighter gray phenotype occurs most frequently at higher elevations (Figure 2.2). It was determined that the frequency of the lighter color morphs drastically increases above 2300 m, which is the approximate boundary between lower montane forests and higher subalpine forests. There was a significant difference ($t=-9.15$, $p<0.0001$) in the average elevation of the sightings for the typical red morph (1876 ±174.4 m) compared with the lighter gray phenotype (2346 ±351.3 m) (Fuhrmann and Swanson, unpub. data).

Morphometric measurements were collected from 22 foxes across the west-east elevational gradient of northern Yellowstone (Figure 2.1). Not all measurements were taken from each fox since some features on some foxes were distorted by trauma, fur removal, or post-mortem deterioration. Tissue samples for DNA analysis were collected from an additional 6 dead foxes. Eleven foxes were live trapped; 11 were killed on roads; 3 were trapped for fur; one was killed for Park management reasons; 1 climbed into a wolf pen and was killed; and 1 died of unknown causes.

Analysis of covariance indicated that the age classes (adult and juvenile) had no

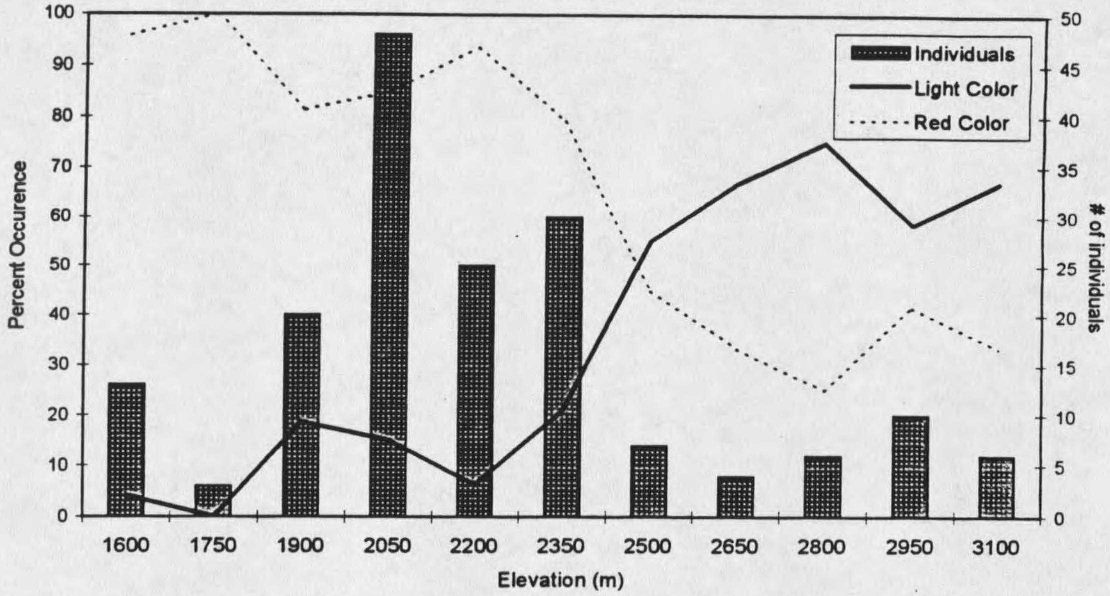


Figure 2.2. Coat color frequency in Yellowstone National Park by elevation. Solid line depicts the lighter coat colors, dashed line indicates red coat color, and bars represent number of sightings at each elevation (N=168). (Used with permission from B. Swanson.)

effect on any of the morphometric parameters. The juvenile foxes I measured were close to if not equal to the size of adult foxes. The ANCOVA, therefore, omitted age and used gender as the only independent variable. Elevation remained as the covariate. Weight (p=0.060), neck girth (p=0.055), chest maximum (p=0.063), and chest minimum (p=0.076) differed significantly between sexes. Overall, the male and female foxes were similar in size with the males being slightly heavier and having a larger girth circumference.

None of the variables were significantly related to the covariate in the ANCOVA (Table 2.1) except for tail length (p=0.057). With more samples there may be significant differences in morphometrics between the foxes found at the lower elevations and those at higher elevations. There may also be some biological significance in the differences.

Trends following Bergman's and Allen's rules (i.e. positive relationships between circumference measurements and elevation and negative relationships between extremity size and elevation) were tested using a Fisher exact test to indicate if they were distributed in a

Table 2.1. Results of ANCOVA with gender as an independent variable by elevation for captured foxes.

| | F-statistic | r | p-value |
|---|---|---|---|
| Weight | 0.183 | 0.118 | 0.676 |
| Head Length | 0.596 | 0.202 | 0.453 |
| Body Length | 0.260 | 0.130 | 0.618 |
| Tail Length | 4.26 | 0.470 | 0.057 |
| Hind Foot Length | 1.47 | 0.308 | 0.245 |
| Head Girth | 0.199 | 0.133 | 0.664 |
| Neck Girth | 0.016 | 0.034 | 0.901 |
| Chest maximum | 0.553 | 0.229 | 0.474 |
| Chest minimum | 0.178 | 0.139 | 0.683 |
| Ear Length | 0.172 | 0.130 | 0.687 |

manner different than chance (Table 2.2). Results indicated that 8 out of 8 trends were in the direction predicted by Bergman's and Allen's rules according to beneficial adaptations at the higher elevation environment (p=0.039). Biological significance of this test may be marginal since some variables are interrelated.

Through analysis of the genetic samples, 5 of the 8 microsatellites amplified with sufficient specificity to be of use in the analysis: primer 442, 204, 671, 155, and 172 (Table 2.3). Only locus 442 from the lower elevation showed deviation ($p<0.01$) from Hardy-Weinberg equilibrium; all other loci from both populations failed to reject Hardy-Weinberg equilibrium ($p>0.05$). The lower elevation population had 17 alleles not found in the subalpine population, while the subalpine population had 6 alleles not found in the lower elevation population. A Mann-Whitney U test indicated that, at $\alpha=0.1$, there was a significantly ($U=5.0$, $p=0.1$) greater number of alleles in the lower elevation population than in the subalpine population.

Table 2.2. Correlations of morphometrics to elevation.

| | Weight | Head Length | Body Length | Tail Length | Foot Length | Head Girth | Neck Girth | Chest Max | Chest Min | Ear Length |
|---|---|---|---|---|---|---|---|---|---|---|
| Elevation | 0.088 | 0.207 | -0.117 | -0.421 | 0.338 | 0.134 | 0.094 | 0.371 | 0.044 | -0.218 |
| | N=17 | N=19 | N=20 | N=20 | N=19 | N=16 | N=19 | N=14 | N=13 | N=16 |
| | p=0.738 | p=0.395 | p=0.622 | p=0.065 | p=0.157 | p=0.620 | p=0.703 | p=0.192 | p=0.886 | p=0.418 |

Table 2.3. Results from the microsatellite analysis of red fox from the northern Yellowstone ecosystem comparing fox populations at high and low elevations.

| | Primer | | | | | |
|---|---|---|---|---|---|---|
| | 155 | 172 | 204 | 442 | 671 | $\bar{x}$ |
| N high elevation | 13 | 13 | 12 | 13 | 12 | |
| N low elevation | 8 | 8 | 8 | 8 | 8 | |
| No. alleles | 7 | 6 | 10 | 12 | 8 | 8.6 |
| Size Range | 124-136 | 114-129 | 125-187 | 126-156 | 124-170 | |
| Heterozygosity | 0.476 | 0.723 | 0.90 | 0.42 | 0.41 | 0.586 |
| $R_{st}$ | 0.002 | -0.090 | 0.082* | 0.141** | 0.282** | 0.14** |

*=p<0.05, **=p<0.01

$R_{st}$ estimates were calculated at each locus and overall (Table 2.3). Estimates of population subdivision varied considerably across the loci, from an indication of extensive population subdivision between the low and high elevation populations at primer 671 ($R_{st}$=0.282), to effectively no subdivision at primer 155 ($R_{st}$=0.002) and 172 ($R_{st}$=-0.09). The overall estimate of population subdivision, $R_{st}$=0.14 (Table 2.3), was significant based on 1000 bootstrap replications (p<0.01) and were exchanging an average of 0.76 individuals per generation based on Slatkin's (1995) equation (Fuhrmann and Swanson unpub. data). Foxes collected < 5 km apart but at different elevations could potentially have more allele differences than foxes collected >50 km apart. This is very intriguing since there is no geographic barrier within this elevational gradient.

Only 6 blood and carcass samples were analyzed (Table 2.4) so I was unable to make comparisons between parasites or diseases at different elevations. More samples are needed to conduct statistically sound tests.

Table 2.4. Wildlife disease monitoring program results for tests performed.

| **Fox ID** | **Date** | **Results of Tests** |
|---|---|---|
| 92-1 Washburn Overlook 8555 ft | 7-7-92 | Nothing unusual; No rabies |
| 94-4 Bozeman on ramp 4800 ft | 8-29-94 | Nematodes in stomach; *Ascarid* sp. |
| 94-5 Sedge Bay 8000 ft | 9-20-94 | No evidence of significant infectious disease |
| 94-6 Paradise Valley 4900 ft | 7-94 | Nematodes and *Capillaria hepatica* (insignificant infection);Multi-focal verminous hepatitis |
| 96-3 Tom Miner Basin 9850 ft | 2-1-96 | Mild multifocal myositis; *Sarcocystis*-like protozoal cysts in muscle fibers; nematode in small intestine; Not clinically significant |
| 96-4 Old Faithful 7360 ft | 6-25-96 | *Sarcocystis* sp. (protozoal cysts)-not significant; No evidence of an infectious disease in the tissues; No rabies or distemper |

## Discussion

Some evidence suggests that there are genetic, phenotypic, and potentially morphometric differences between red foxes above and below 2100 m in the Yellowstone region. The foxes at higher elevations may have adapted to colder climatic conditions and generally have lighter color morphs (gray or creamy). Although red foxes are contiguously distributed throughout the study area from Livingston, MT to the Beartooth Plateau, there appears to be 2 genetically isolated populations.

By examining 21 tissue samples collected from trapped and road-killed red foxes there appears to be 2 genetically distinct populations of red foxes separated by elevation, inhabiting the northern Yellowstone ecosystem. Interestingly, there is no distinct geographic barrier separating them, however, very limited gene flow occurs between these elevational zones. The fox subpopulations show a degree of division ($R_{st}$=0.14) comparable to that found between island and mainland red fox populations ($R_{st}$=0.15) in Australia which shows that they have been isolated ($M_R$=0.76) (Lade et al. 1996). Through further analysis of tissue samples already collected on this study, more questions may be answered about the genetic separation of these subpopulations.

With no geographic barrier separating low and high elevation foxes, it might be assumed that the higher elevation foxes might disperse to lower elevations and establish home ranges in the less harsh lower environments or vice versa. However, the limited gene flow indicates low dispersal in either direction. In general, canids are thought to interbreed extensively (Sheldon 1992). There are wolf-dog hybrids, coyote-dog hybrids, and the red wolf is thought to be a combination of gray wolf and coyote (Sheldon 1992). Sympatric coyotes and wolves in Ontario appear to be morphologically converging in body weight and length over the last 40 years (Schmitz and Lavigne 1987). It is unusual then that there is such limited gene flow between subpopulations above and below 2100 m.

The lighter gray coat color common at high elevations has not previously been described in the literature. It is unknown if the apparent differences in color between low and high elevation foxes indicate genetic or habitat use segregation, but some trappers (e.g. Martin Kolence, pers. comm.) do not remember any foxes in the low country around Livingston, MT prior to World War II. Hoffman (1969) states that prior to the 1950's, the red fox seemed to be rare in most parts of Montana and restricted only to mountainous areas of extreme western and southwestern parts of the state. If these sources describe range extension by European red foxes accurately, interbreeding may not yet have swamped the gene pool of the high elevation foxes in the northern Yellowstone ecosystem.

Foxes in the Yellowstone area have adapted to survive in harsh winter conditions at high elevations. They exploit higher elevations more than coyotes, which may be a spatial competition avoidance mechanism since there are few if any coyote territories above 2100 m (Gehman et al. 1997, Crabtree and Sheldon in press.). In addition, foxes seem to be better adapted to hunt in deep snow than coyotes. Foxes have large feet in proportion to body size when compared to coyotes. An adult coyote weighs about 13.5 kg (30 lbs) in Yellowstone which is 3 times as large as an adult fox (4.6 kg or 10.1 lbs.) but its track size is not 3 times as large as a fox's. The large feet and long track length allows foxes to stay on top of the snow like a snowshoe thus keeping them from sinking.

Morphologic divergence is another possible test of population isolation, depending on the amount of time the populations have been segregated and the extent to which characteristics are plastic (phenotype). Although the morphometric data do not indicate that there is a statistically significant difference along the elevational gradient found within the study area, high elevation foxes living in harsher environments did tend to have larger bodies and smaller ears than low elevation foxes. This is consistent with Bergman's and Allen's rules, but may or may not have biological significance. An interesting story unfolds through examination of the correlations of elevation and each variable (Table 2.2).

A variable which did not fit Allen's rule is hindfoot length. The trend indicated that foxes at higher elevations may have larger hind feet than at lower elevations. Foxes at higher elevations have to withstand significantly deeper, less dense snow, and longer periods of it; therefore, the hind feet should be longer and larger to act like a snowshoe and reduce foot loading (lower kg/cm$^2$). With the small sample size, this appears to be the case. Most of the foxes I observed at high elevations had small toe pads (~3 mm wide x ~10 mm long) and an abundance of fur covering all of the pads in their entirety including the heel pad. This amount of fur and small pads was never observed at low elevations. This could potentially keep their paws from forming ice crystals while traveling in deep, less dense snow. In addition, abundant fur on the feet (as in lynx) decreases foot loading and increases the snowshoe effect.

Due to the small sample size and lack of genetic information from other fox populations, I was unable to determine the taxonomic origin of the foxes at higher elevations in Yellowstone National Park and the Beartooth Plateau. Light colors are not the only unusual color morph in Yellowstone. A red fox was hit by a vehicle between Mammoth Hot Springs and Tower Junction that was about 60% black. When asked about this dark color many wildlife biologists in Yellowstone and other agencies had never seen or heard of anything like it. Since this is the first study of the Rocky Mountain subspecies *(V. v. macroura)*, further research is needed to compare the 2 subpopulations of foxes studied to other regions such as the grasslands of eastern Montana or central Wyoming and other parts of the Rocky Mountains. In addition, the high elevation foxes should also be compared with the red fox inhabiting northern Canada and Alaska (*V. v. abietorum*). This would assist in deciphering the question of the origin of these high elevation foxes. If either of the two theories on the origin of these foxes is valid, an isolated fox subspecies existed at one time both climatically and by habitat characteristics at higher elevations and could still remain today in the alpine regions in the Greater Yellowstone Ecosystem.

# CHAPTER 3

## WINTER HABITAT USE BY THE RED FOX IN THE NORTHERN YELLOWSTONE AREA

### Introduction

Coyotes (*Canis latrans*) (Crabtree and Sheldon in press.), bears (*Ursus arctos* and less intensively *U. americanus*) (Knight and Eberhart 1992), mountain lions (*Felis concolor*) (Murphy 1998), and pine martens (*Martes americana*) (Fager 1991, Kujala 1993, Coffin 1994, Sherburne and Bissonette 1994) have been studied extensively in the Yellowstone ecosystem. In contrast, red foxes (*Vulpes vulpes*) have had little attention despite the possible occurrence of 2 unique subspecies within the ecosystem (Chapter 2). Until this study, there had been no research on red foxes in the Yellowstone region.

The larger vertebrate predators have been the focus of debate for predator communities in the Yellowstone ecosystem because they are difficult to study and generate controversy when management options are explored (Knight and Eberhart 1992, Murphy 1998). Also, populations of large carnivores are vulnerable to human activities in most ecosystems. Their position at the top of the food chain, low population densities, large size, and high potential for negative interactions with humans make them easy targets for extirpation. The relative vulnerability of smaller predators and the impact changes that populations of large predators may have on smaller predators (Soule 1988) are unknown in the Yellowstone ecosystem.

Red foxes (*V.v. fulva*) have been studied extensively in the Midwestern United States (Sergeant et al. 1987, Ables 1975, Storm et al. 1976, Pils and Martin 1978). This subspecies was introduced from Europe for fox hunts and fur farms. Since the mid 1700's, this subspecies has spread across much of the U.S. and has interbred with native red foxes throughout their range except possibly at high elevations. Three surviving subspecies of high elevation foxes, collectively know as mountain foxes, are extant and thought to be indigenous to the western mountain states. These subspecies are restricted to the Cascade Mountains (*V. v. cascadensis*), Sierra Mountains (*V. v. necator*), and Rocky Mountains (*V. v. macroura*). Very little scientific information is available on distribution, ecological parameters, and genetic purity of these subspecies. The only study conducted on any of these three subspecies, until this one, was in the Cascade Mountains (Aubry 1983).

Red foxes in Yellowstone have remained a mystery for many years due in part to their elusive, nocturnal behavior. The National Park Service maintains the red fox along with the bobcat, mountain lion, wolverine, and other mammals on its "rare animal sighting form" (Branch of Natural Resources, Yellowstone National Park 1986) which indicates that little is known about the foxes, and more information is needed to better understand their ecology and distribution.

The taxonomic status of foxes in the northern Yellowstone ecosystem is an unanswered question, and the potential differences between habitat use by potentially different subspecies is completely unknown. The habitat structure of Yellowstone is not typical for the European lowland red fox. European foxes in the U.S. typically inhabit lowland forests, agricultural lands, and grassland areas. Yellowstone, however, contains mostly montane and alpine habitats. If the high proportion of sightings of light colored foxes at high elevations in the Yellowstone area (Chapter 2) represent a mountain subspecies, habitat use at high elevations may be different from that at lower elevations. The comparative rarity of coyotes at higher elevations (Crabtree and Sheldon in press.), may also be reflected in different habitat use at high and low elevations.

I investigated winter habitat use by red foxes in the northern Yellowstone ecosystem using tracks in the snow. I had 3 objectives: first, I attempted to classify important habitat components that are either preferred or avoided by foxes. The components I measured were forest cover type, escape cover, distance to ecotone, slope, aspect, and elevation. Second, I examined the difference in habitat use by foxes at high and low elevational zones. Third, I attempted to determine if habitat use patterns differed throughout the winter.

## Methodology

### Study Area

The core study area was located between Mammoth Hot Springs, WY (1900 m) and the Beartooth Plateau, MT and WY (3350 m) east of Cooke City, MT (2,250 m) (Figure 3.1). This included the northern ¼ of Yellowstone National Park and portions of the Gallatin and Shoshone National Forests. Vegetation types inside of Yellowstone consisted of lodgepole pine, Douglas-fir, and some spruce-fir forests; grassland, upland sage, sage-grassland, riparian, mesic meadow, and mesic shrub-meadow (Despain 1990). In the higher elevations near Cooke City and in the Beartooth Plateau, the habitat types consisted of

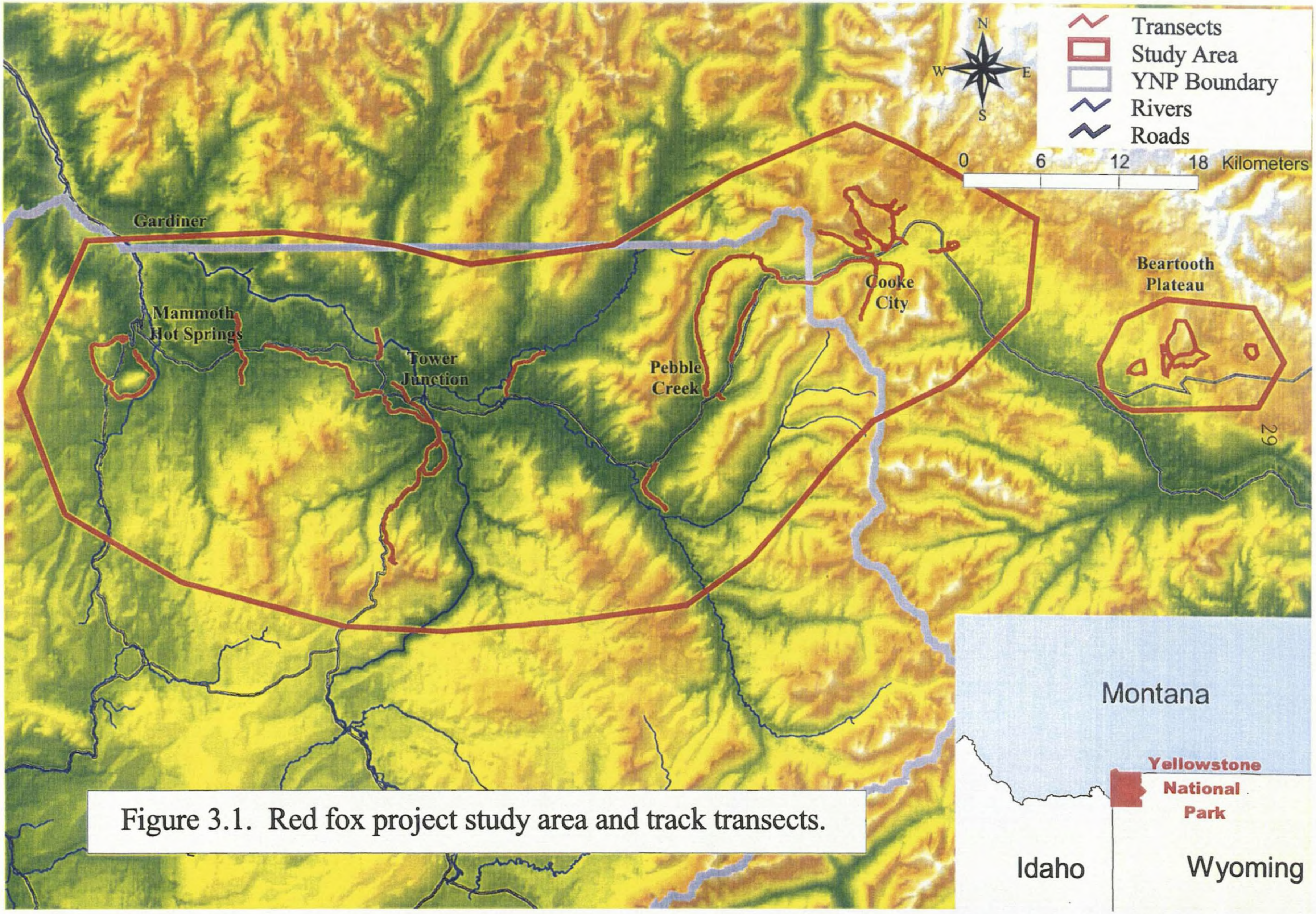


Figure 3.1. Red fox project study area and track transects.

montane and subalpine forests of Engelmann spruce, subalpine fir, lodgepole pine, and whitebark pine, as well as tundra and open mesic meadows (US DOI and US DOA 1997). Average precipitation, mostly in the form of snow, varies from 50 cm at lower elevations to over 150 cm per year at high elevations.

This study included 2 winter field seasons: January through early April 1995 and November 1995 to early April 1996. These winters were separated into 3 temporal divisions. Field data from the early winter period, November 4 to December 22, was collected only in the second winter. The second temporal section was midwinter, January 1 through February 22. Late winter ran from February 23 to April 4 each winter. These divisions were chosen because, early, middle, and late winter may correspond to different snow pack and weather conditions which, in turn, could affect forage and travel strategies of fox. Generally, there is more snow in late winter which may make it more difficult for fox to forage for small mammals compared with early winter when there is less snow and foraging may be easier.

## Snow-tracking Transects

Habitat use is a trajectory through 4 dimensional space (3 geographic coordinates and a time dimension) (White and Garrott 1990). Snow tracking is a method to determine habitat utilization along this trajectory excluding the time dimension. This method was employed to compare habitat use to availability along transects delineated within the study area. The transects I established provided samples of major habitat types and elevation zones within the study area. Low elevation transects were placed along ski trails in Yellowstone Park. High elevation transects were located along National Forest trails along Highway 212.

Twenty-five transects were traversed either with cross-country skis or snowshoes at least once, sometimes twice, during each of the 5 temporal periods, except where otherwise noted (Table 3.1). Two additional transects were sampled once the second winter, and the road corridor from Mammoth to Cooke City was periodically monitored for fox activity during both years. Transects were placed along trails because of easy access in the winter on skis and snowshoes (the term skis will be used hereafter), safety concerns, and consistency in replication of data collection among temporal collection periods.

Snow tracking provides accurate, detailed information on movement and behavior patterns of an animal with minimal researcher impact. The research animal is rarely disturbed. For species that are nocturnal and secretive, direct observation is very difficult. Snow tracking eliminates this problem. This method allows data to be collected on a microhabitat scale and provides information on several aspects of habitat use including foraging sites, resting sites, and scent marks. It does not provide information on how long the animal spends along the route (Singleton 1995). In contrast, radio-telemetry does not allow such small scale information to be collected on a species. With radio tracking, the animal is only tracked when the researcher is in the field collecting data and results in a "connect the dots" representation of movement patterns. Snow tracking provides a continuous sample of habitat utilization.

## <u>Tracking</u>

Global positioning system (GPS) units (Motorola LGT-1000) were used to collect, store, and geo-reference data on fox tracks observed along the transects. Transects monitored on any given day were chosen on the basis of time and logistics. This allowed

Table 3.1. Snow tracking transects with number of track sets per temporal period.

| TRANSECT | Elevation (m) | Period 1 Jan-Feb 95 | Period 2 Mar-Apr 95 | Period 3 Nov-Dec 95 | Period 4 Jan-Feb 96 | Period 5 Mar-Apr 96 |
|---|---|---|---|---|---|---|
| Snow Pass Trail | 2100 | 2 | 4 |  | 0 | 4 |
| Bunsen Peak Road | 2070 | 2 | 5 |  | 1 | 2 |
| Blacktail Deer Creek | 2010 | 2 | 2 |  | 0 |  |
| Frog Rock Road | 2070 | 1 | 2 | 0 | 1 |  |
| Blacktail Plateau Drive | 2130 | 2 | 1 | 1 | 0 | 0 |
| Hellroaring Creek Trail | 1860 | 1 | 1 |  | 0 | 1 |
| Lost Lake Trail | 2010 | 0 | 4 | 1 | 1 |  |
| Tower Junction Loop | 2040 | 3 | 3 |  | 0 | 3 |
| Mt. Washburn | 2700 | 0 | 4 |  | 1 | 1 |
| Yancey's Hole Trail | 1880 | 1 | 1 |  | 0 | 1 |
| Slough Creek Trail | 1920 | 2 | 4 | 0 | 1 | 1 |
| Lamar River Trail | 2040 | 1 | 1 | 0 | 1 |  |
| Pebble Creek Trail | 2250 | 2 | 1 | 1 | 1 | 2 |
| Baronette Ski Trail | 2130 | 3 | 4 | 2 | 0 | 0 |
| Bannock Trail | 2220 | 3 | 5 | 6 | 3 | 2 |
| Republic Creek Trail | 2460 |  |  | 1 | 1 | 0 |
| Woody Creek Trail | 2430 | 1 | 3 | 0 | 0 | 1 |
| Sheep Basin Trail | 2430 |  | 0 | 3 | 0 |  |
| Miller Creek Drainage | 2610 | 0 | 2 | 2 | 2 | 2 |
| Fisher Creek Drainage | 2700 | 0 | 2 | 0 | 2 | 3 |
| Lady of the Lake Trail | 2640 | 1 | 2 | 2 | 0 |  |
| Kersey Lake Trail | 2400 | 0 | 2 | 1 |  | 2 |
| Clay Butte Area | 2700 |  | 9 | 2 | 1 |  |
| Island Lake Area | 2850 |  | 2 |  | 1 |  |
| Road Corridor | 1860-2250 | 4 | 0 | 3 | 2 | 0 |
| Paradise Valley | 1350-1560 | Trapping | Records |  |  |  |

"0" indicates transect was skied but no tracks were found and a blank depicts the transect was not skied.

transects to be repeated each season and to not bias the data. When I began a transect, I systematically searched for tracks on either side of the trail. To avoid potential bias, the direction the transects were skied was reversed each time. If a transect started at the road and ended 8 km out on a trail, tracks along that transect were collected starting from the road one time. The next time I would ski to the end of the transect and begin tracking on the way back.

The transects were spatially distributed to avoid biases due to collecting many samples within one fox's home range. Fox home ranges average between 2-5 km$^2$ (Herstensson and Macdonald 1982), and most of my transects were separated >5 km.

When a set of fox tracks was located, the GPS unit was activated and Universal Transverse Mercator (UTM) coordinates were logged onto a memory card. A track set is defined as a set of fox tracks found along one of the ski trail transects and then followed. The track set was backtracked first to not disturb the fox and bias its behavior. If time permitted, the track set was also forward tracked.

Track sets were followed over distances ranging from 150 m to 1.5 km. Every track set included at least two measurements of habitat characteristics referred to as "habitat points" collected approximately every 150 m. A 150-m increment between collection points on a track set was chosen in order to assess small scale habitat use by red foxes throughout the region. Different limiting factors determined how long a specific track set was followed. Some track sets were lost due to tracks of other animals. During some tracking sessions, the GPS unit and the handheld computer would malfunction or undergo battery failure. At times, tracking was discontinued because the fox traveled into areas which were unsafe for researchers. The unsafe conditions included areas with high avalanche danger (i.e, steep slopes), ice that was not stable enough for a human, or movement into the middle of a bison herd.

Each GPS unit included a microprocessor that ran Geolink software (GeoResearch Inc., Billings, MT) used to collect various types of data utilizing pre-programmed function keys. Table 3.2 specifies the different variables that were pre-programmed on the GPS unit and their descriptions. In addition to these variables, a comments section was used to enter explanatory material.

Habitat characteristics were entered on Hewlett-Packard handheld computers at habitat points, forage sites, and bed sites (Table 3.2). A resident Lotus 1-2-3 spreadsheet was used to record these data. The cover types used were from Despain (1990) and were classified into different successional forest cover types (Table 3.3). Due to snow cover, non-forested habitats that required ground stratum species differentiation were combined into broader categories. Distance to edge was determined as the distance from the track set to the next major change in habitat structure such as an open meadow, sagebrush, or forest stand.

The LGT-1000 GPS memory card containing the data was downloaded onto a personal Toshiba T-1910 laptop computer. GPS base station files were used to differentially post-correct GPS field files. Once corrected, these data were estimated to have an accuracy of <2 m. The following base stations were used: Montana State University, Bozeman, MT; Idaho National Environmental Engineering Laboratories (INEEL), Pocatello, ID; and a base station established at my home in Gardiner, MT near the major study area. The first 2 base stations utilized Trimble Navigator hardware (Trimble, Sunnyvale, CA). To convert these

Table 3.2. Parameters measured along the track sets for the GPS and the handheld computer (HP).

| Variable Name | Description |
|---|---|
| Gait Type (GPS) | Traveling mode |
| walk | 4 feet registering in snow |
| trot | Direct register with hind foot entering same spot as front foot |
| run | 4 feet registering in long strides |
| Snow Type (GPS+HP) | |
| powder | Fresh snow or snow that has not melted then frozen |
| packed | Usually found on a snowmobile or ski trail |
| crust | Snow that has melted and then frozen or wind blown areas |
| wet | Occurs when ambient temperature is above 0°C |
| Number of Tracks together (GPS) | Minimum number of foxes that were traveling on the same corridor |
| Scent Mark (GPS) | |
| Type | What type of scent mark was it |
| urine | Urination mark |
| scat | Defecation |
| scratch | Snow or ground with scratch marks |
| combination | Any combination of the above |
| Sex I.D. | Depending on trajectory of urine hole in the snow the possible sex was recorded |
| Foraging Type (GPS) | The way the fox foraged |
| nose cone | Fox stuck just it's muzzle in the snow |
| pounce | Definitive jump into the snow |
| chase | Where a fox ran attempting to catch something |
| dig | Noticeable dig in the snow |
| carrion | Leg bone, antler, or other portion of a carcass |
| 150 m habitat point (GPS) | Location where habitat information was collected on the HP |
| Bed Site (GPS) | Location where a fox lay down. Noticed by an iced over patch in snow with possible fragments of fox fur stuck in snow. |
| Cover Type (HP) | Dominant class recorded based on Despain (1990); See Table 3-3 |
| Distance to Edge (HP) | Distance (m) from point to next major division in habitat types |
| Slope (HP) | Degrees of pitch; clinometer or visual estimate of a 10 m radius around point |
| Aspect (HP) | Compass bearing from handheld compass in direction of runoff; examining 10 m radius around point |
| Snow Depth (HP) | Measured in 5 cm increments using demarcated ski |

Table 3.3. Forest cover type descriptions (Despain 1990).

| Forest Cover Type | Description |
|---|---|
| xeric | Non-forested areas that have dry and arid conditions |
| mesic | Non-forested areas that have moist conditions |
| asp | Aspen groves with minimal understory in winter |
| rock | Exposed rock with little or no soil or vegetation |
| wb | Climax whitebark pine stands; may contain a few Engelmann spruce, subalpine fir, or lodgepole pine; most common above 2580 m |
| df | Climax Douglas-fir stands; lodgepole pine may be a component |
| lp | Climax lodgepole pine stands; some whitebark pine; understory always has lodgepole seedlings |
| lp1 | Very dense stands of small diameter lodgepole pine; understory of small trees is nonexistent; usually 50-150 years old |
| df1 | Young Douglas fir stands with numerous small, dead branches along tree trunks from ground to crown |
| df2 | Closed-canopy stands dominated by Douglas-fir; similar to lp2 |
| wb2 | Closed-canopy stands dominated by whitebark pine; similar to lp2 |
| lp2 | Closed-canopy stands dominated by lodgepole pine; understory of Engelmann spruce and subalpine fir seedlings and saplings up to 2.5 m.; usually 150-300 years old |
| wb0 | Recently burned whitebark pine; herbaceous vegetation may be abundant |
| sf | Climax stands dominated by Engelmann spruce and subalpine fir in canopy and understory; lodgepole or whitebark pine may be significant |
| lp3 | Lodgepole pine canopy quite ragged, containing some Engelmann spruce, subalpine<br>fir, and whitebark pine; understory consists of small to large seedlings and saplings; usually over 300 years old |
| sb | Sagebrush areas which provide a lot of cover |
| df0 | Post-disturbance stands with Douglas-fir dominant small trees |
| lp0 | Recently burned forests where lodgepole pine expected to colonize or has done so already; usually 0-40 years old |
| sf0 | Lots of small spruce and fir trees with branches to the ground |

files to a usable format, Pathfinder (Trimble Software, Sunnyvale, CA) software was used. A compatible Motorola base station was used in Gardiner so no conversions were needed. These post-corrected files were all examined and edited using GeoLink Data Manager software (GeoResearch, Billings, MT). Each file was then converted to an ArcInfo (ESRI, Redlands, CA) format. Using Yellowstone National Park's Geographic Information System (GIS) lab, all of the files were finally converted to an ArcView software format for use with the GIS at Yellowstone.

## GIS Analysis

Habitat availability was determined from Yellowstone's GIS layers and defined as a 500-m buffer on either side of a snow tracking transect. This distance was chosen because it included approximately 95% of the track sets followed. To have individual measures of habitat availability for statistical analyses, a randomly placed, systematic grid was overlain on a habitat map of Yellowstone in order to estimate habitat parameters at the gridpoints. These gridpoints were spaced at 1-km intervals which insured spatial independence. The total number of gridpoints was 181 compared with 175 total track sets. For each of these gridpoints, the same habitat parameters were measured in order to compare used to available data sets.

A forest cover type GIS layer, extracted from the Cumulative Effects Model (CEM) layer for grizzly bears for the Greater Yellowstone Ecosystem which is the most accurate habitat layer in existence for the region, was used to quantify forest cover type availability for the buffer on the transects. An overlay of a 7 ½ minute quadrangle map, a burned and unburned sagebrush layer, and a "burned forest" layer were used to quantify other habitat characteristics. Distance to edge was calculated by measuring the distance from a grid point to the next closest habitat boundary. Elevation, slope, and aspect were extracted through using a USGS DEM layer.

### Fox Tracks

Fox tracks were distinguished from coyote tracks by using a formula developed from data previously collected by J. Halfpenny (pers. comm.), a concurrent study on medium-sized carnivores (Gehman et. al 1997), and measurement data I collected. Red fox tracks were defined as any set of tracks with an intergroup length of less than 12 inches (30 cm), a straddle of less then 5 inches (12.5 cm), and a track length of less than 3 inches (7.5 cm) (Figure 3.2). This was called the "12-5-3 rule". The intergroup distance is the measurement from the track group (location where a hind foot directly registers on top of a front foot) on the left to the next track group on the right of the track set. To be accurate, these measurements were taken in at least three locations along a track set and all criteria had be met. This method excluded small coyotes and potentially a few large foxes.

Of the fox tracks that were measured, the interdigital length, straddle, and track length had a mean of the following: 11.6 (29.5), 3.7 (9.4), and 2.6 (6.6) inches (cm), respectively. These measurements correspond to the "12-5-3" rule. Straddle came up consistently as the measurement that most accurately discriminated fox from coyote tracks.

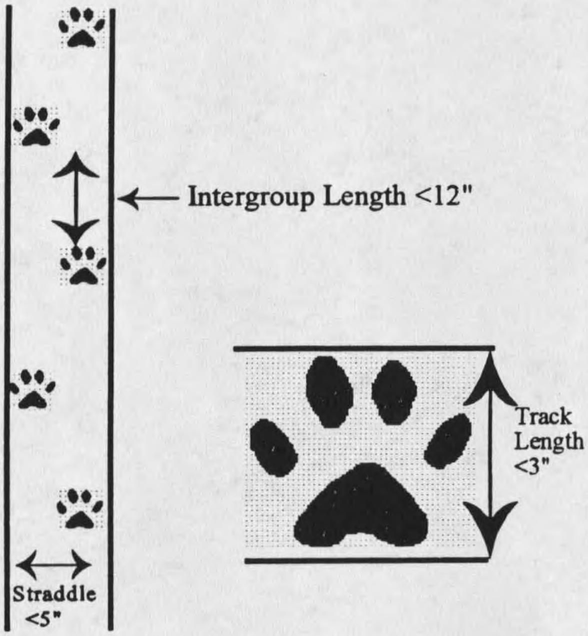


**Figure 3.2. Measurements used in determining fox tracks compared to coyote tracks(not to scale).**

Statistical Analysis

To ensure independence and avoid pseudo-replication, the data from each habitat point along a track set were averaged. Forest cover types along a track set were condensed to one sample by taking the most prevalent cover and classifying that track set with that cover type. Means for all other variables were derived and comparisons were made for each track set.

Since forest cover type is a categorical parameter, the computer program *HabUse* (A. Wood, unpub.) was utilized, to evaluate use and availability, using the Neu et al. (1974) statistical method. A chi-square value and Bonferroni confidence interval were calculated to compare use and availability for each forest cover type.

To examine the use compared with what was available for escape cover, distance to edge, slope, and aspect, data were rank-transformed. Since the data were not normally distributed and were highly skewed, a nonparametric approach was needed (Conover and Iman 1981). A Median test was, therefore, implemented. From this, a chi-squared statistic and a p-value were computed. The forest cover types were transformed to a horizontal obscurity index prior to being ranked into escape cover. This horizontal obscurity was ordered from most to least open from the perspective of a fox since escape cover is important to a fox (Ables 1975, Sheldon 1992). Table 3.3 lists escape cover types in order of lowest to highest rank.

A discriminate function analysis (DFA) was used to differentiate between fox habitat use and the available habitat characteristics and to determine which set of variables contributed most to the best model for separating use and availability. Variables with an alpha significance level > 0.10 were eliminated in the DFA. STATISTICA 5.1 software (StatSoft, Tulsa, OK) was used to run the statistical tests. Graphic representation was created in Excel 97 or Quattro Pro 7.

## Results

Approximately 186 km of trails per winter were skied, usually twice, to look for the presence of fox tracks. On all transects, fox tracks were present at least once in nearly every season (Table 3.1). Transects traversed a wide range of elevations (1900-3350 m).

To examine whether the points spaced at 1-km intervals, used to define availability over the whole study area, were representative of the 500 m buffer on either side of the transects, forest cover types from each subset were compared. The proportions of cover types calculated based on the 1-km points were similar compared to the proportions of cover types within the buffered transects (Figure 3.3) except for sagebrush which was under sampled. Forest cover type proportions in the buffered transects were similar to proportions in the entire study area.

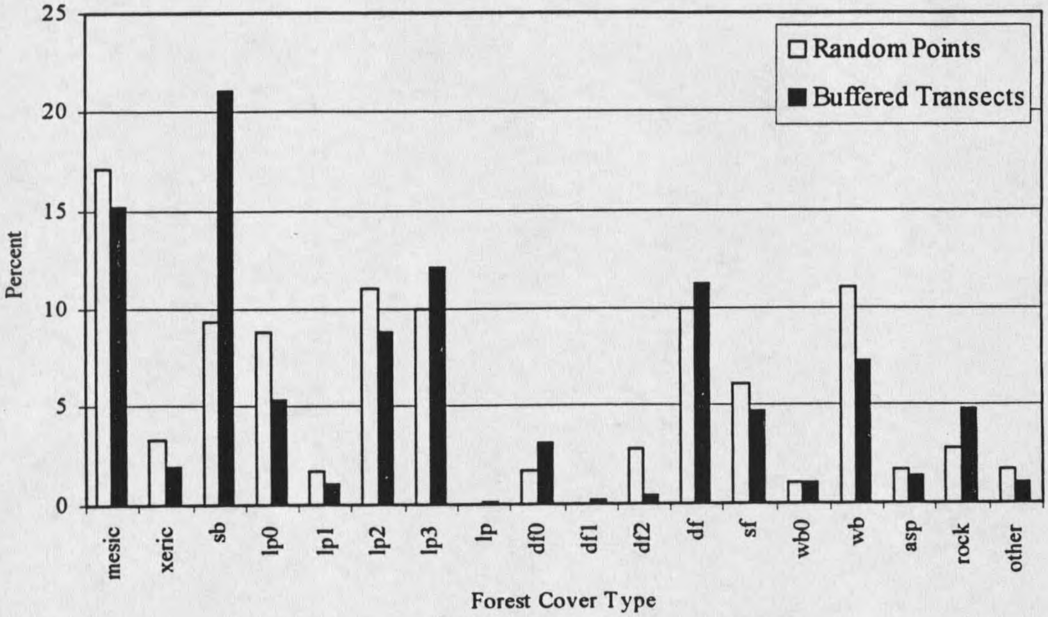


Figure 3.3. Comparison of 1-km random points and the 500 m buffered transects.

## Track Set Analysis

Thirty-seven and 26 km of tracks in 145 independent segments were followed and post corrected on the GPS in the winters of 1994-5 and 1995-6, respectively (Figure 3.4). Another, 14 km of fox track sets (30 track sets) which were not accurately located using GPS were usable based on habitat characteristics collected on the handheld computers. Habitat

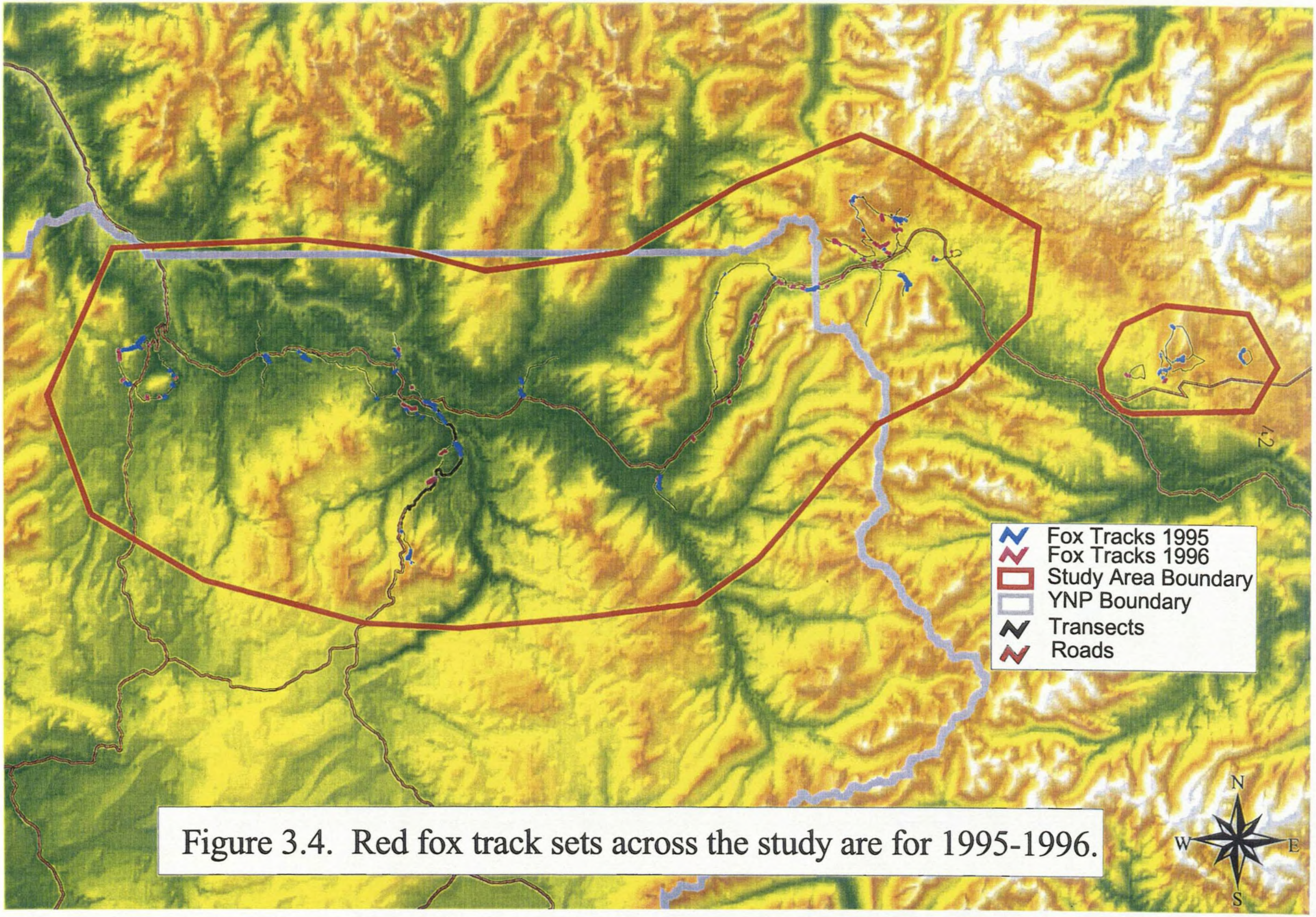


Figure 3.4. Red fox track sets across the study are for 1995-1996.

characteristics were measured at 699 habitat points, 75 forage sites, and 9 bed sites along 175 track sets. Due to the small sample of bed sites, no analysis was completed. Also, due to faulty conversions of the attribute data to the GIS no analysis of the scent marks occurred.

Habitat Use vs. Availability for Track Sets

Red foxes traveled in areas close to edges of major changes in vertical vegetation on low angle slopes covering a wide range of aspects and elevations. Use of several forest cover types significantly differed from proportions available (Figure 3.5). Mesic meadows and spruce-fir were preferentially used by foxes ($p<0.05$) and xeric, lp0, wb0, wb, sf0, and asp were avoided ($p<0.05$). Fifty-four percent of locations were in 2 types, mesic meadows and spruce-fir forests. Sagebrush was the third most frequently used cover type (12%) but was not used significantly more frequently than expected (9%).

Red foxes used escape cover (rank-transformed forest cover types) ($p=0.009$) (Figure 3.6), distance to edge ($p<0.001$), slope ($p<0.001$), and elevation ($p=0.006$) in proportions significantly different than proportions available (Table 3.4). Use of aspect was not significantly different than expected ($p=0.874$).

Red foxes tended to travel near ecotones (the edge of major habitat types). Foxes used areas <25 m away from the ecotone 50% of the time (Figure 3.7). Distances >125 m only accounted for 11% of the used sites. Foxes used elevation classes in proportion to availability (Figure 3.8).

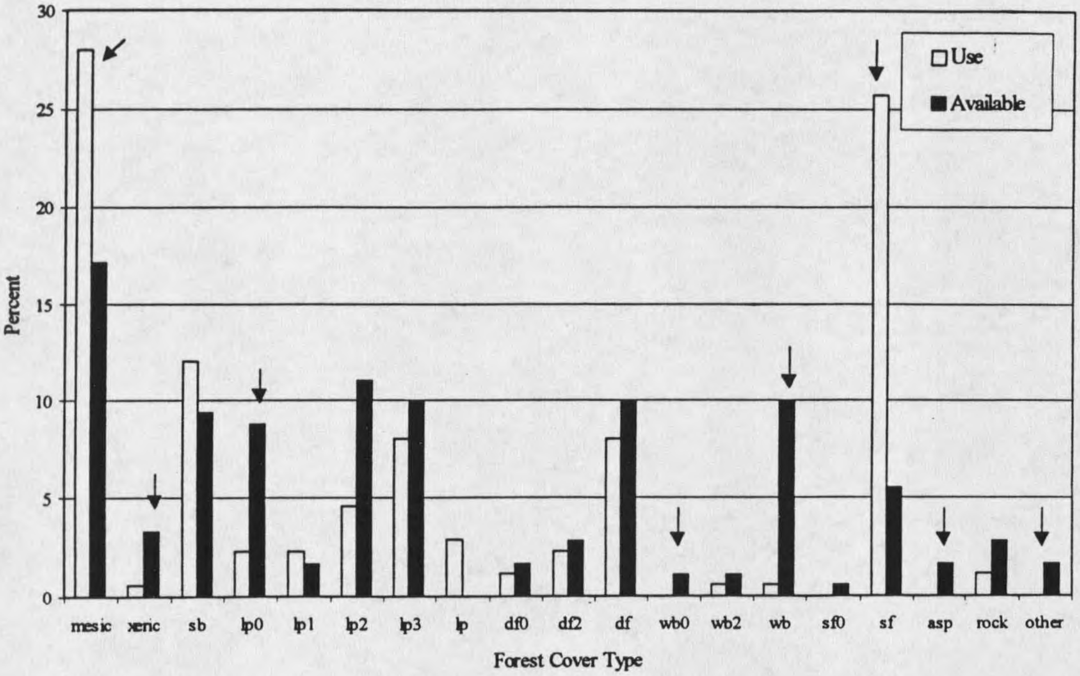


Figure 3.5. Habitat use vs. availability for forest cover types.
Arrow indicates a significant difference at p<0.05.

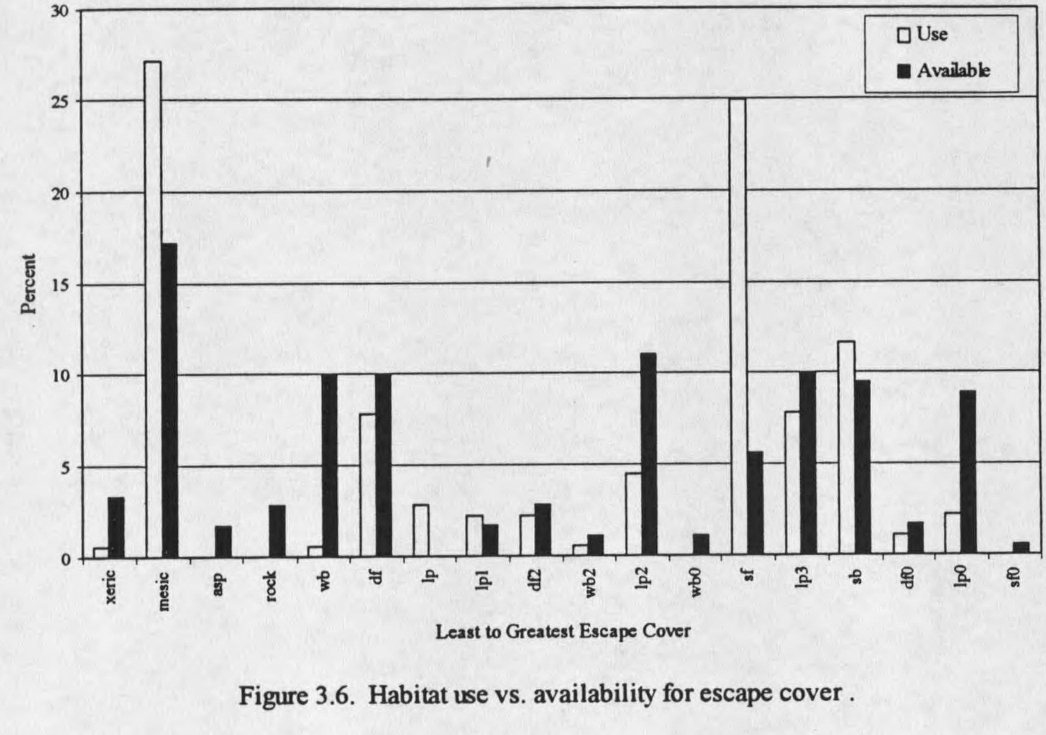


Figure 3.6. Habitat use vs. availability for escape cover .

Table 3.4. Median test statistics for habitat use vs. availability.

| | Use vs. Availability | | Use vs. Availability >2100 m | | Use vs. Availability <2100 m | | Use >2100 m vs. Use <2100 m | |
|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value |
| Escape Cover | 6.79 | 0.009 | 5.64 | 0.018 | 1.24 | 0.266 | 8.85 | 0.003 |
| Dist. to Edge | 40.14 | 0.000 | 47.27 | 0.000 | 1.25 | 0.263 | 5.85 | 0.016 |
| Slope | 20.47 | 0.000 | 27.58 | 0.000 | 0.010 | 0.920 | 1.13 | 0.288 |
| Aspect | 0.025 | 0.874 | 2.64 | 0.104 | 1.25 | 0.264 | 16.92 | 0.000 |
| Elevation | 7.68 | 0.006 | 4.52 | 0.034 | 0.042 | 0.838 | N/A | N/A |

| | Use vs. Availability | | Use vs. Availability >2100 m | | Use vs. Availability <2100 m | | Use >2100 m vs. Use <2100 m | |
|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value | $\chi^2$ stat. | p-value |
| Escape Cover | 5.32 | 0.021 | 5.80 | 0.016 | 0.565 | 0.452 | 1.29 | 0.256 |
| Dist. to Edge | 22.82 | 0.000 | 30.89 | 0.000 | 0.492 | 0.483 | 9.62 | 0.002 |
| Slope | 0.42 | 0.517 | 2.60 | 0.107 | 0.030 | 0.863 | 0.162 | 0.687 |
| Aspect | 1.64 | 0.201 | 2.60 | 0.107 | 2.05 | 0.153 | 12.71 | 0.0004 |
| Elevation | 13.19 | 0.0003 | 1.57 | 0.210 | 2.11 | 0.146 | N/A | N/A |

Foxes used steep slopes less frequently than expected (Figure 3.9). This relationship may be biased since the transects were located along established trails which in general were not very steep. Although some fox tracks were followed from trails to steeper slopes, I abandoned the tracks if they moved into terrain with high avalanche potential. Foxes used different aspects in proportion to availability (Figure 3.10).

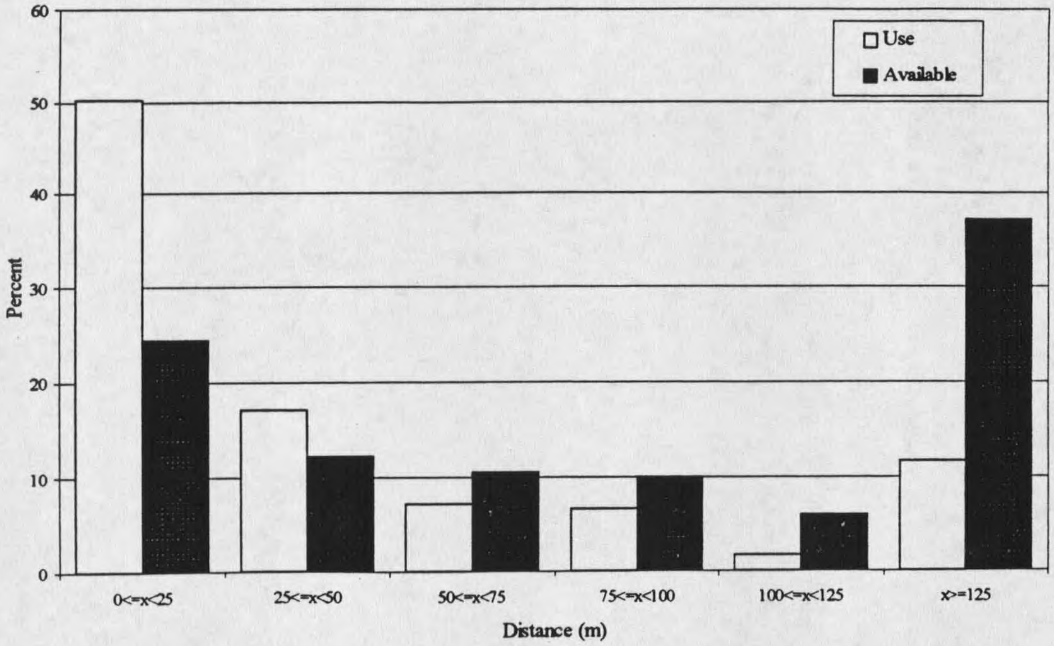


Figure 3.7. Habitat use vs. availability for distance to ecotone.

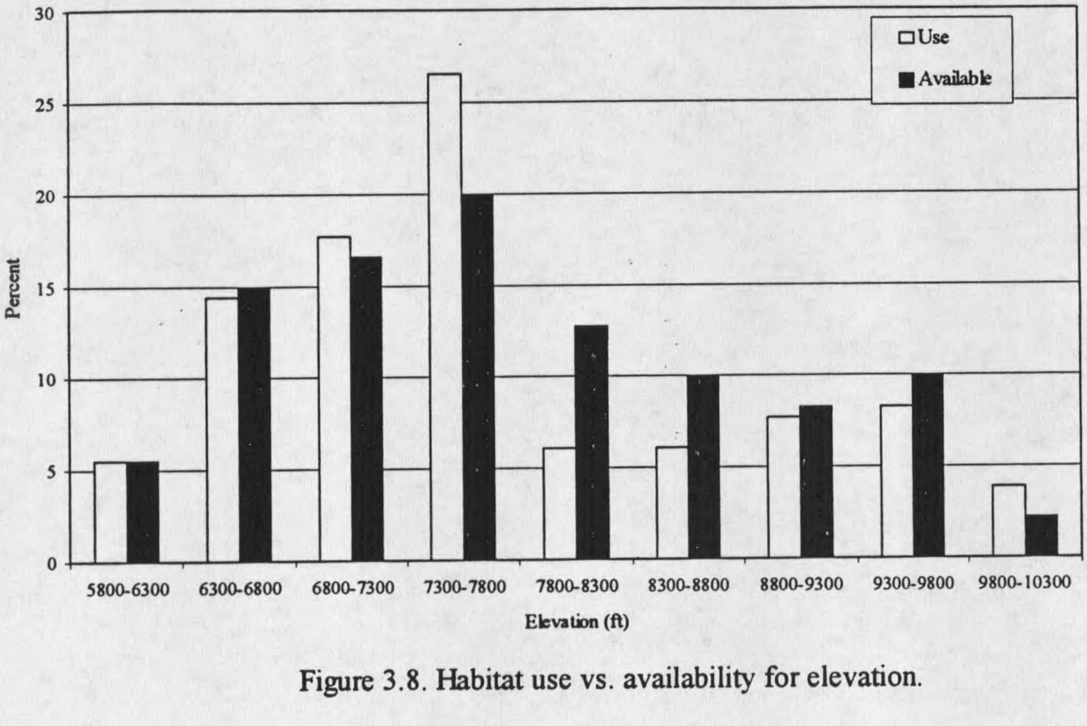


Figure 3.8. Habitat use vs. availability for elevation.

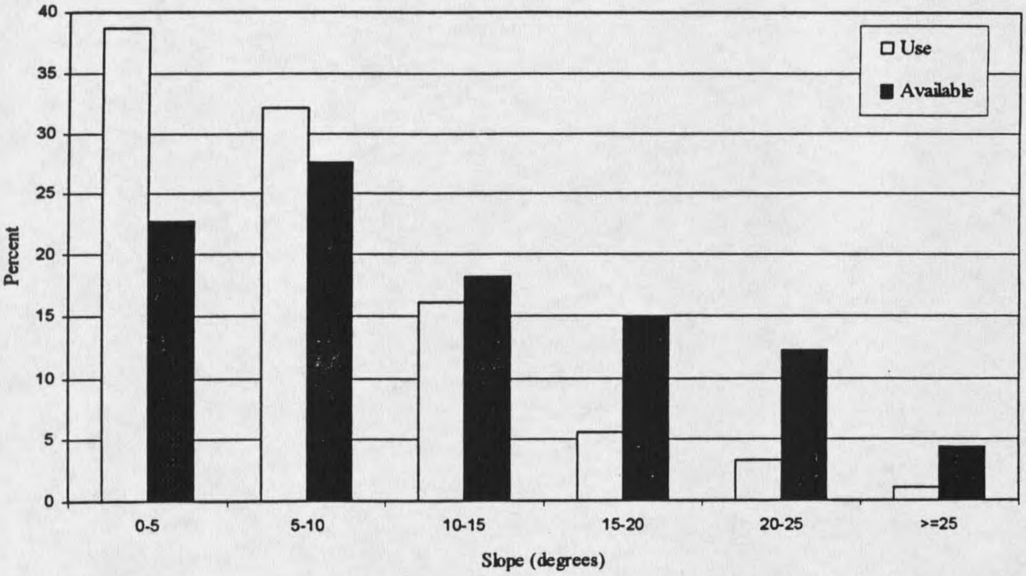


Figure 3.9. Habitat use vs. availability for slope.

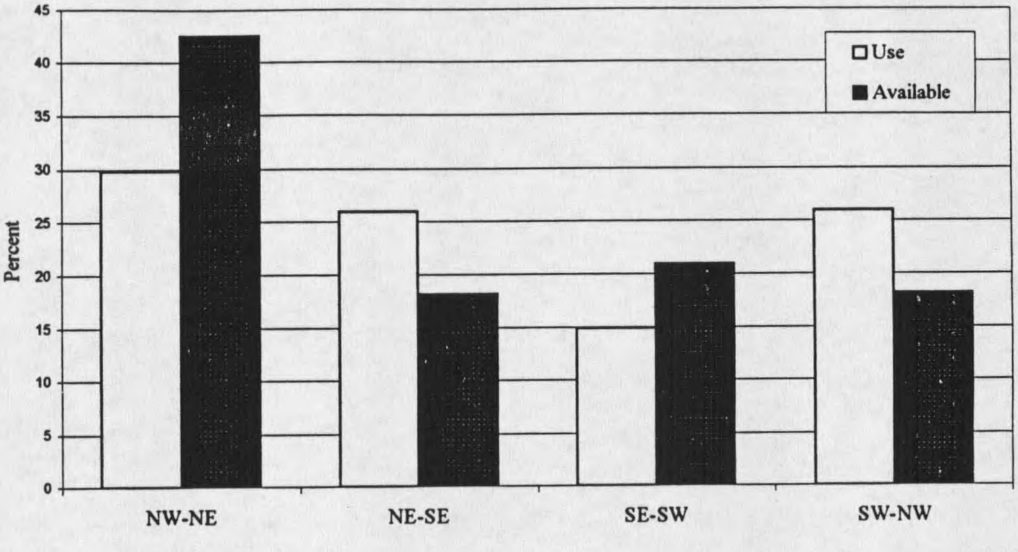


Figure 3.10. Habitat use vs. availability for aspect.

Three of the 5 habitat parameters included in the multivariate DFA were significant, and the DFA indicated that the predictive value of the combined variables was high (Wilk's $\lambda=0.811$, $p<0.0001$) (Table 3.5). Escape cover, distance to edge, and slope were the best joint predictors in discriminating between fox locations and the random points used for habitat availability.

Figure 3.5. Discriminate function analysis for habitat use vs. availability (* indicates best predictors for the model).

| | Use vs. Availability | | Use vs. Availability >2100 m | | Use vs Availability <2100 m | | Use >2100 m vs. Use <2100 m | |
|---|---|---|---|---|---|---|---|---|
| | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value |
| OVERALL | 0.811 | <0.0001 | 0.710 | <0.0001 | 1.0 | -- | 0.867 | <0.0001 |
| Escape Cover | 0.816* | 0.175 | 0.718* | 0.104 | 0.998 | 0.659 | 0.883* | 0.077 |
| Dist. to Edge | 0.914* | <0.0001 | 0.854* | <0.0001 | 0.997 | 0.624 | 0.875* | 0.191 |
| Slope | 0.871* | <0.0001 | 0.792* | <0.0001 | 0.995 | 0.498 | 0.863 | 0.414 |
| Aspect | 0.810 | 0.371 | 0.709 | 0.486 | 0.999 | 0.947 | 0.965* | <0.0001 |
| Elevation | 0.810 | 0.435 | 0.710 | 0.788 | 0.999 | 0.951 | N/A | N/A |

| | Forage Sites vs. Availability | | Forage vs. Avail. >2100 m | | Forage vs. Avail. <2100 m | | Forage >2100 m vs. Forage <2100 m | |
|---|---|---|---|---|---|---|---|---|
| | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value | Wilk's $\lambda$ | p-value |
| OVERALL | 0.837 | <0.0001 | 0.740 | <0.0001 | 0.932 | 0.064 | 0.743 | <0.0001 |
| Escape Cover | 0.849* | 0.068 | 0.766* | 0.016 | 0.925 | 0.453 | 0.741 | 0.702 |
| Dist. to Edge | 0.969* | <0.0001 | 0.954* | <0.0001 | 0.930 | 0.706 | 0.796* | 0.025 |
| Slope | 0.846* | 0.119 | 0.748* | 0.170 | 0.931 | 0.827 | 0.740 | 0.596 |
| Aspect | 0.842* | 0.243 | 0.740 | 0.810 | 0.974* | 0.064 | 0.897* | <0.0001 |
| Elevation | 0.825 | 0.406 | 0.738 | 0.540 | 0.948* | 0.245 | N/A | N/A |

I was unable to calculate distribution of snow depths across the study area; however, I was able to compare snow depths along track sets to the snow depth collected at Tower Ranger Station (Figures 3.11 and 3.12). Due to the difference in snow depths east of Yellowstone, the track set snow depths were only plotted from Mammoth Hot Springs to the Northeast Entrance of Yellowstone in order to compare them to Tower snow depths. In general, foxes appeared to travel in snow depths representative of those on the northern range. This was corroborated by visual inspection of 77 km of fox track sets. Red fox rarely sank >10 cm in snow of any consistency.

### Forage Point Use vs. Availability

In general, foxes foraged in habitat types proportionate to where they traveled. Foraging red foxes used mostly mesic meadows, sagebrush communities, and spruce-fir forests, spent most of their time close to ecotones, and on slopes <10°. Sixty percent of foraging locations were on aspects between NW and NE. Forage sites occurred in forest cover types in proportion to availability (Figure 3.13). Use of mesic meadows (27%), sagebrush (15%), and spruce-fir forest (15%) cover types was not significantly different than availability. Foxes apparently selected against lp1, lp2 , whitebark pine, and aspen stands in foraging ($p<0.05$).

Foxes significantly preferred greater escape cover ($p=0.021$), foraging with a short distance to edge ($p<0.0001$), and middle elevations ($p=0.0003$) at foraging sites compared to availability (Table 3.4). I found no significant selection or avoidance for slope steepness.

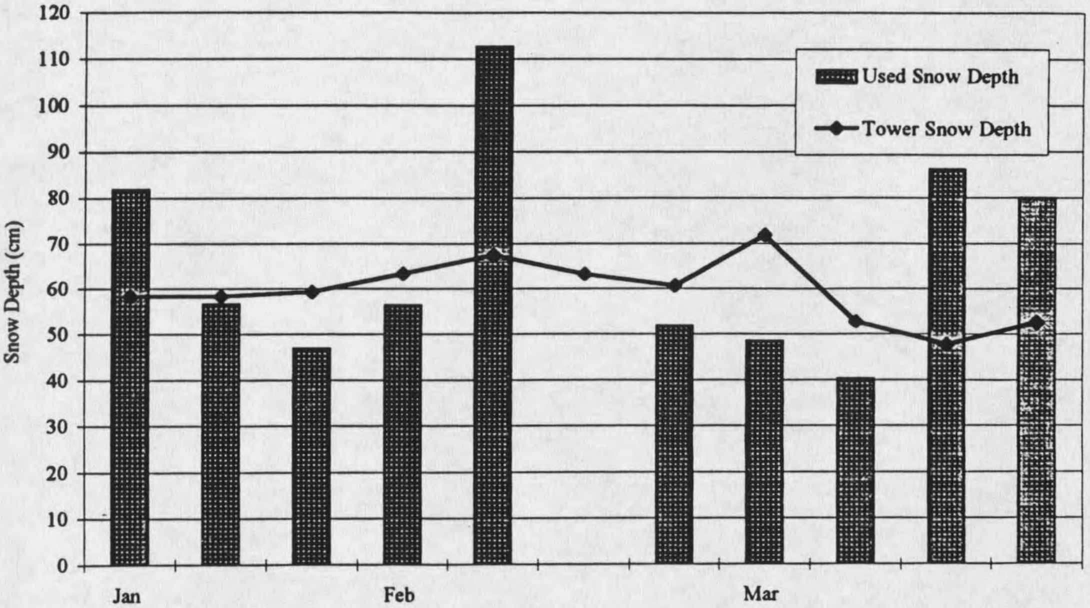


Figure 3.11. Snow depths for 1995 by week. Bars indicate depths along track sets between Mammoth Hot Springs and the Northeast Entrance and line indicates depth at Tower Ranger Station.

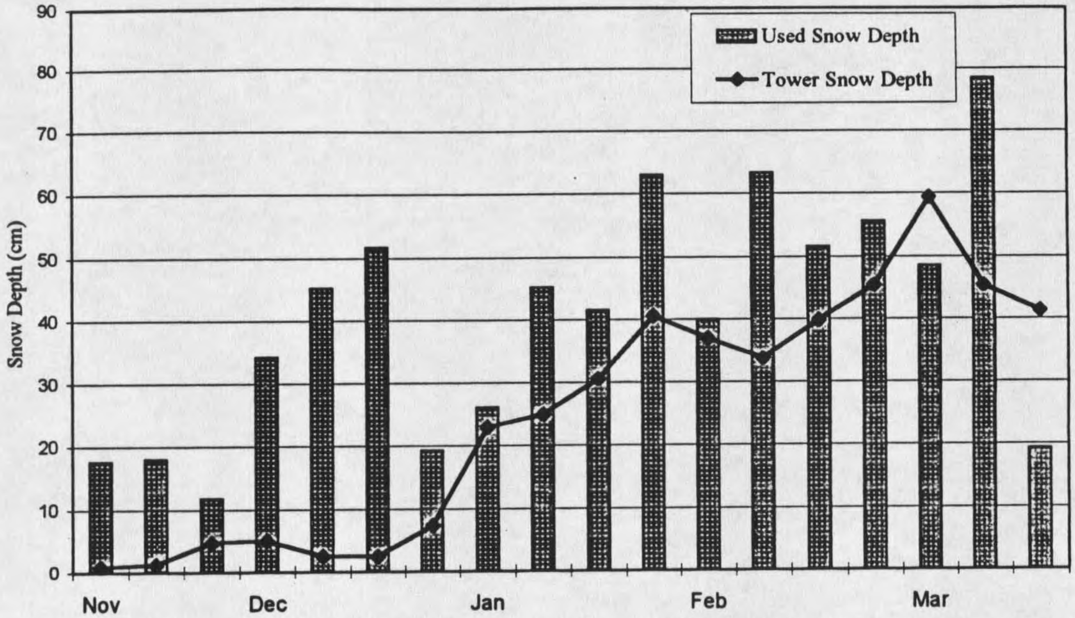


Figure 3.12. Snow depths for 1995-96 by week. Bars indicate depths along track sets between Mammoth Hot Springs and the Northeast Entrance and line indicates depth at Tower Ranger Station.

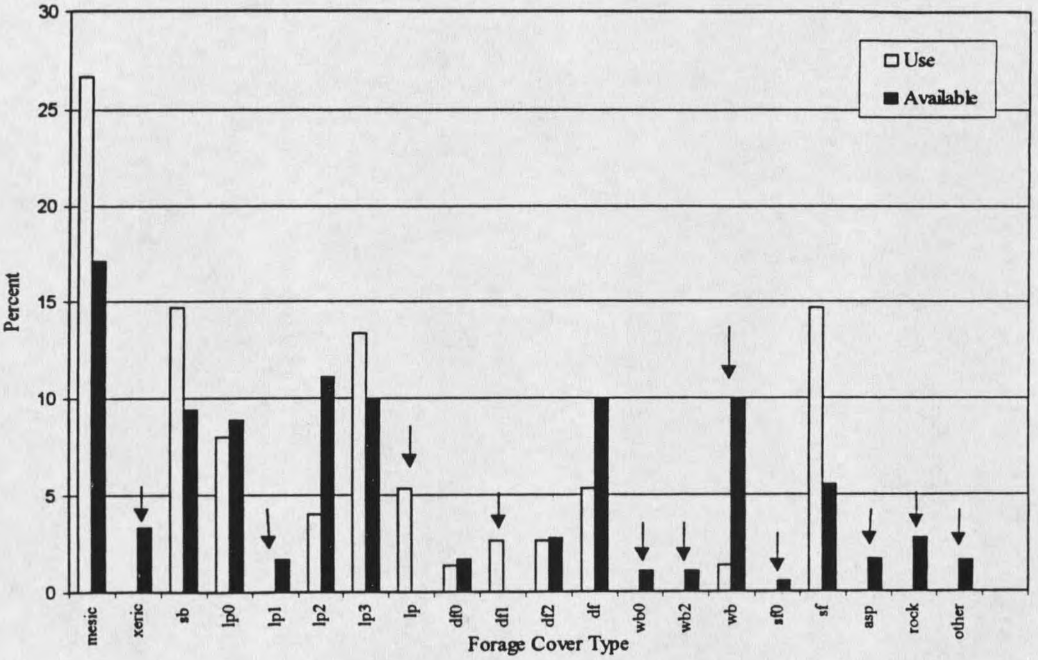


Figure 3.13. Forage point use vs. availability for forest cover types.
Arrow indicate significant difference ($p<0.05$).

This indicated that foxes were using steeper slopes more frequently for foraging than for traveling . Foxes foraged most often (29%) in the 10-15° category while they only use this category as travel routes 16% of the time.

Four of the 5 habitat parameters included in the DFA for forage sites were significant, and the best model indicated that the predictive value of the combined variables was high (Wilk's $\lambda$=0.837, $p<0.0001$) (Table 3.5). Escape cover, distance to edge, slope, and aspect were the best predictors for separating forage points from random points.

Habitat Use vs. Availability Above and Below 2100 m

When track sets were divided into 2 elevation zones, below and above 2100m, a more complex view of habitat selection was apparent. This elevation was selected due to the differences in habitat and snow characteristics as well as the coat color, genetic, and to some degree the morphometric differences in the foxes (Chapter 2) between these two zones.

For tracks observed below 2100 m, foxes were more general in their use of the habitat. Mesic meadows, sagebrush, and stands of Douglas-fir, were used most frequently, but not significantly more than expected while older stands of lodgepole and spruce-fir were used significantly more than expected (Figure 3.14). Foxes avoided lp0, wb2, wb, and aspen ($p<0.05$). They were most often observed on slopes < 10° with an aspect usually between SW to NW, but no habitat variable was used in proportions different than those available (Table 3.4). The DFA indicated that there was no combination of predictors that distinguished fox locations at elevations <2100 m (Wilk's $\lambda=1.0$) (Table 3.5).

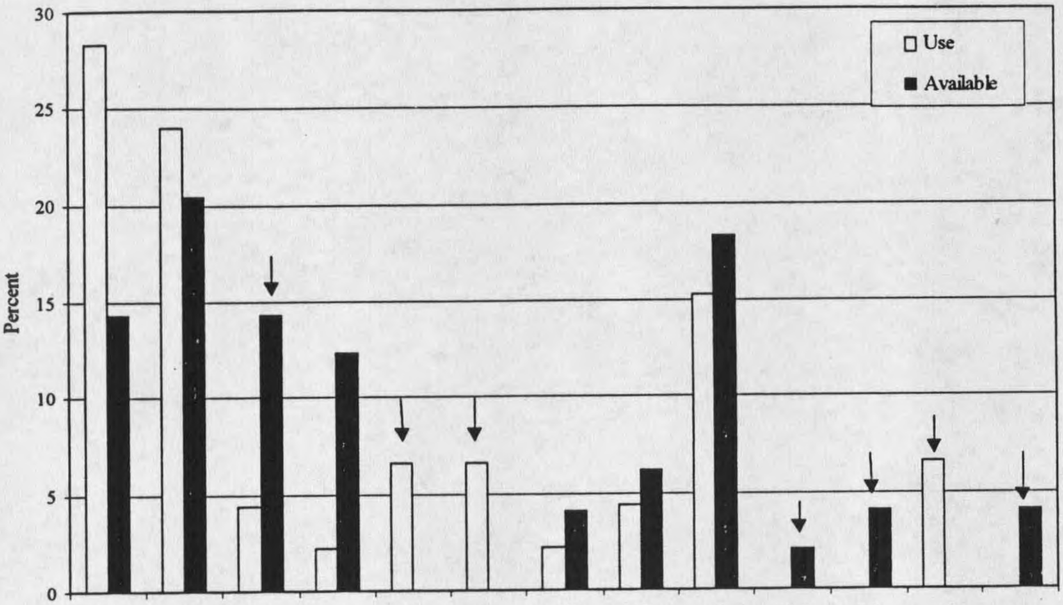


Figure 3.14. Habitat use vs. availability below 2100 m.
Arrow indicates a significant difference ($p<0.05$).

Above 2100 m, red foxes utilized mostly forested habitats with some open areas, but travel was mostly restricted to the edges of these meadows. In general, foxes frequented low angle slopes with aspects from NE to SE. Spruce-fir forest cover type was preferred while xeric, lp0, wb0, wb, sf0, aspen were avoided ($p<0.05$) (Figure 3.15). Spruce-fir and mesic meadow cover types made up over 55% of the cover types used. Median tests indicated that the use of escape cover ($p=0.018$), distance to edge ($p<0.0001$), slope ($p<0.0001$), and elevation ($p=0.034$) were significantly different than expected based on availability. Aspect was used in proportion to availability (Table 3.4). The DFA indicated that escape cover, distance to edge, and slope above 2100 m were the best predictors of the used habitat compared to what was available (Wilk's $\lambda=0.710$, $p<0.0001$) (Table 3.5).

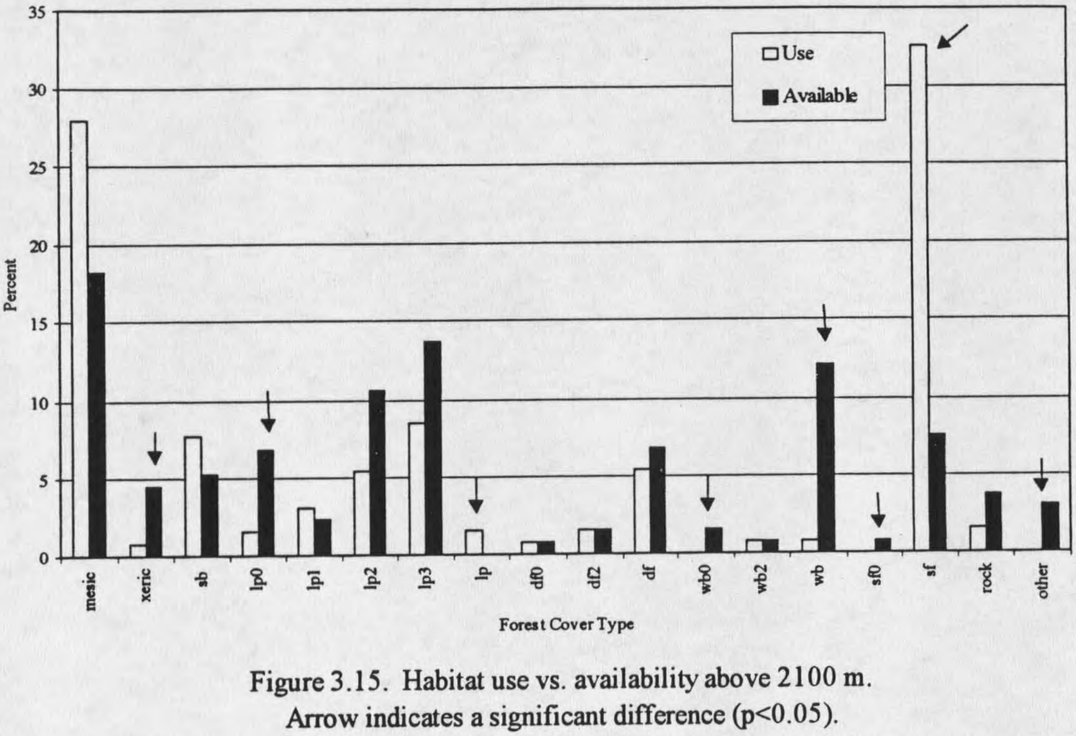


Figure 3.15. Habitat use vs. availability above 2100 m.
Arrow indicates a significant difference ($p<0.05$).

Along track sets above and below 2100 m, there was a marked difference in habitat characteristics. In both areas foxes used mesic cover types similarly whereas foxes used significantly more sagebrush at lower elevations and spruce-fir at high elevations (Figure 3.16). Escape cover (p=0.003), distance to edge (p=0.016), and aspect (p<0.0001) were significantly different above and below 2100 m (Table 3.4). The DFA indicated escape cover, distance to edge, and aspect as the best variables to separate tracks above and below 2100 m (Wilk's $\lambda$=0.867, p<0.0001) (Table 3.5).

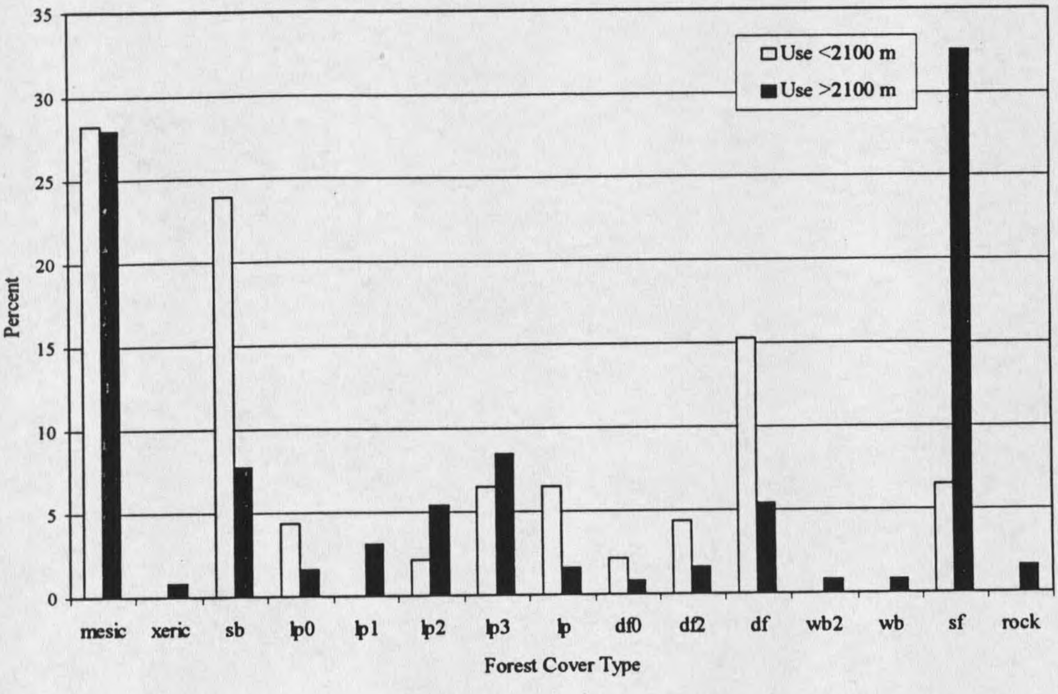


Figure 3.16. Comparison of habitat use below and above 2100 m.

<u>Forage Sites Below and Above 2100 m</u>

Below 2100 m, red foxes foraged mostly in the productive open meadows and sagebrush sites over a wide range of slopes. Aspects were almost entirely between W to N.

Habitat use at forage sites of red foxes was in proportion to what was available (Table 3.4), although mesic meadows and sagebrush areas comprised the majority (57%) of the forage sites (Figure 3.17). The DFA identified aspect and elevation as most important in differentiating forage sites from random points (Wilk's λ=0.932, p=0.064) (Table 3.5).

Above 2100 m, red foxes foraged in both open and forested areas close to ecotones in areas with slopes <10° with a wide array of aspects. Forage sites were found primarily in mesic, sf, and lp3 (69%) forest cover types (Figure 3.18) and close to changes in vertical habitat structure. Escape cover (p=0.016) and distance to edge (p<0.0001) were significantly different from expected (Table 3.4). Slope and aspect differed when compared to what was available for forage sites but was marginally not significant (p=0.107). From the results of the DFA, the best predictors to differentiate the forage point habitat use pattern from availability above 2100 m were escape cover, distance to edge, and slope (Table 3.5).

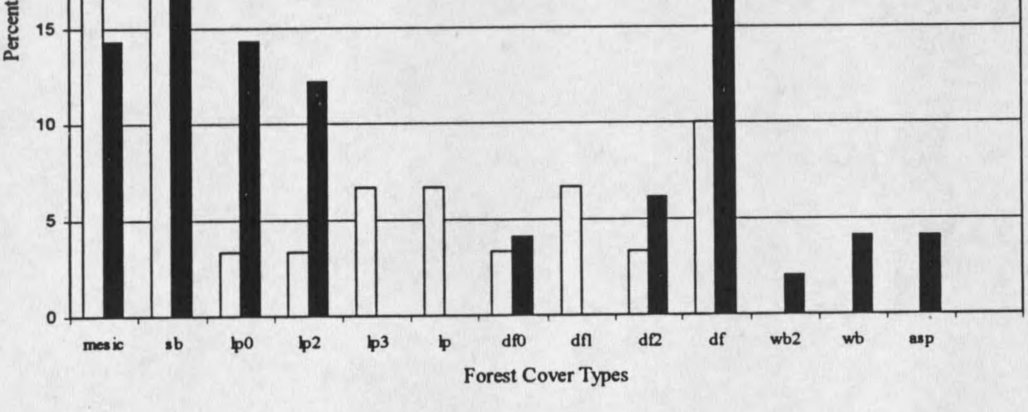


Figure 3.17. Forage point use vs. availability for forest cover types below 2100 m.

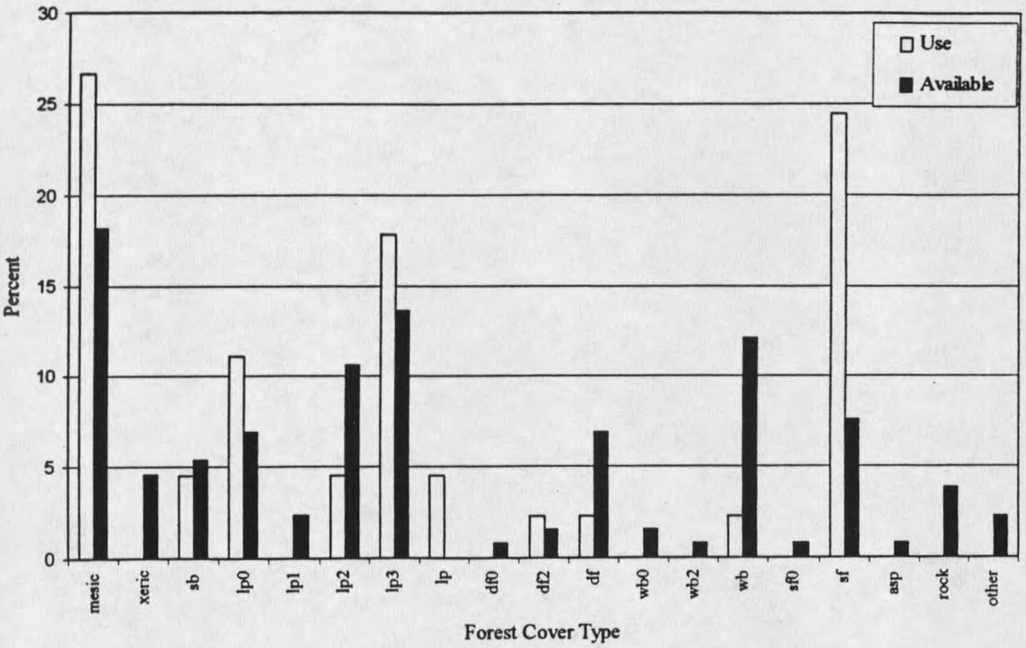


Figure 3.18. Forage point use vs. availability for forst cover type above 2100 m.

The predictive value of the model was high (Wilk's $\lambda$=0.740, p<0.0001). Due to the small sample size of 30 forage points below 2100 m and 44 forage points above 2100 m with 13 and 19 habitat types, respectively, statistical comparisons were not made across the forest cover types.

When forage sites above 2100 m were compared directly to sites below 2100 m, distance to edge and aspect were significantly different (p=0.002, p=0.0004, respectively). The mesic cover type was used at forage sites the same above and below 2100 m (27%). Sagebrush was used 30% of the time below 2100 m compared with 4% of the time above 2100 m. Lp3 and sf were used in 39.5% of forage sites above 2100 m (17.5% and 22% respectively) compared with only 7% and no use below 2100 m (Figure 3.19). In multivariate analysis, the predictors that exemplified the difference between the forage sites above and below 2100 m were distance to edge and aspect. They had a high predictive value (Wilk's $\lambda$=0.743, p<0.0001) (Table 3.5).

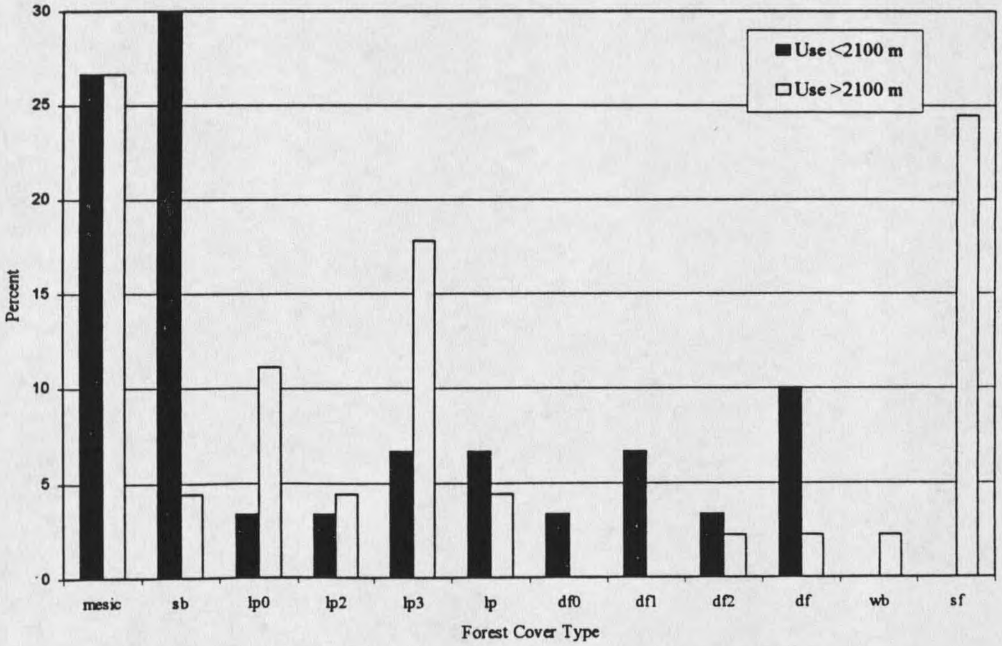


Figure 3.19. Forage point forest cover type use below and above 2100 m.

## Seasonal Differences in Habitat Use vs. Availability

Over the winter, there may be changes in the use of habitat components by red foxes. Data were collected in November and December in only 1 year. The November and December 1995 data were not significantly different (p>0.10) from the January to February 1996 data and were pooled and classified as early winter. Distribution of track sets in early winter of the first and second year statistically differed, so they could not be pooled for seasonal analysis. The late winter periods in both years, however, were not statistically different. The differences in the 2 early winters are likely due to differences in snow densities and depths between the two years. Late winter is a time when snows usually become consolidated, therefore, easier for a fox to travel on top.

Statistical differences between early and late winter were pronounced in both winters. All 5 habitat parameters were important in differentiating early and late winters in both years. The predictive value of the combined parameters was high (Wilk's $\lambda=0.934$, $p<0.083$ for year 1); (Wilk's $=0.786$, $p<0.005$ for year 2).

## Discussion

### Habitat Use of Red Fox

Despite a wide range of elevations and habitats, red foxes are contiguous in distribution across the northern Yellowstone region. Fox tracks were located at all elevations from 1350 to 3000 m. Frequent sightings in areas that were not formally examined for fox tracks, such as Paradise Valley between Livingston, MT (1350 m) and Gardiner, MT (1585 m), further demonstrates the contiguous distribution of fox throughout the northern Yellowstone ecosystem. Although red foxes were found to inhabit almost every habitat type in the study area, their use patterns (preference and avoidance) of specific habitat components differed by elevation and by season.

Prior to this study, little was known about fox habitat use in this area. My study suggests that northern Yellowstone red foxes above 2100 m are best classified as a forest carnivore and those below are more general in their habitat use. They appeared to select montane and subalpine forests as did the mountain red foxes in the Cascade and Sierra Ranges

(Aubry 1983). In Yellowstone, foxes preferred habitats that were close to the edge of a major structural change in vegetation. Sagebrush and older growth forests were important for foxes for escape cover because they provided a high degree of visual security. Over 87% of the distance to edge measurements were <125 m from an ecotone, and 50% of the track sets were <25 m from an ecotone. Red foxes frequenting open habitats below 2100 m are often chased (Gese et al. 1996), and occasionally killed by, coyotes (Sargeant and Allen 1989).

Foxes selected gentle slopes and flat areas. This may have given them greater access to prey such as vole species, but it more importantly may have served to conserve energy in deep snow. Foxes would usually contour around a steep area if their other choice was to climb it.

I observed distinct differences between foxes followed at low and high elevations. Above 2100 m foxes used subalpine/montane forests in preference to open areas. Below 2100 m, they showed less selection for old growth even when its reduced availability was considered.

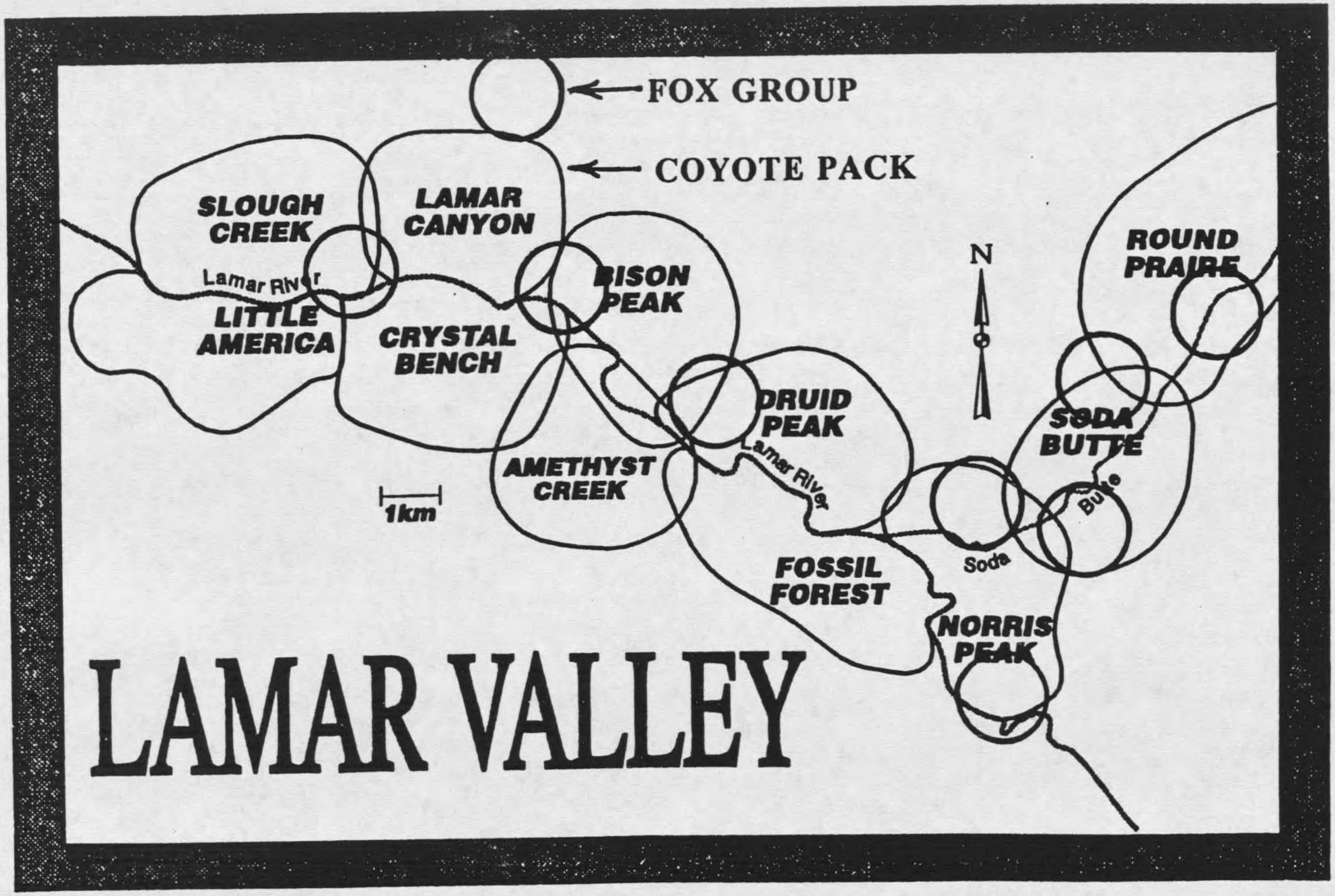
The habitat differences could be due to preferences by two subspecies. Mountain foxes are reported to prefer subalpine forests and European red foxes to prefer more open cover types (Aubry 1983), or other factors may be different between these two elevational zones. One such factor could be the lack of coyotes above 2100 m. From 16 studies conducted on red fox and coyote interactions, it has been shown that foxes tend to avoid coyotes both spatially and temporally when there is an overlap in their niches (e.g. Dekker 1983, Voight and Earle 1983, Sargeant and Allen 1989, Gese et al. 1996). Crabtree and

Sheldon (1996) and Gese et al. (1996) report similar trends in northern Yellowstone.

Below 2100 m in Yellowstone, red foxes survive by occupying areas between coyote territories where they are sympatric (Figure 3.20) (Fuhrmann et al. 1995). The coyote study in Yellowstone (Crabtree and Sheldon, in press.) and my personal observations suggest that coyotes do not have defended territories above 2100 m and are absent from high elevations during winter. In contrast, foxes and their tracks were regularly seen at the higher elevations. Coyotes, therefore, are unlikely to account for differences in habitat use above and below 2100 m since foxes at higher elevations tended to the more secure forested types more frequently than low elevation foxes that had to contend with coyotes.

Below 2100 m, foxes frequently used open and sagebrush areas but had to avoid coyotes at the same time. They accomplished this by strong temporal avoidance (nocturnal behavior) and spatial avoidance (use of areas outside coyote core areas). Below 2100 m, the main habitats used by fox were mesic meadows and sagebrush (52%). The sagebrush offered cover that effectively hid foxes from coyotes. Foxes also used older growth Douglas-fir, spruce-fir, and lodgepole pine stands which provided protective cover. When using open cover types at low elevations, foxes remained close to escape cover. The distance to edge for a fox traveling in a meadow, also supports this conclusion. Foxes tended to stay close to ecotones while in open areas (mesic meadows) compared to when they traveled in sagebrush and forested areas. Mean measure of distance to edge was higher in sagebrush than in forested or open types, potentially indicating that it provides the most protective cover for the foxes.

Above 2100 m, where coyotes were rare, I assumed foxes would be more likely to



**The 2 km² circle depicts the locations of resident red fox (based on sightings, tracks, and photos) in relation to known coyote packs in Lamar Valley, Yellowstone National Park.**

Figure 3.20. Distribution of resident fox and coyote groups in the Lamar Valley of Yellowstone National Park.

venture farther into and spend more time in open areas. Instead, red foxes utilized heavier forest cover and had lower mean distances to edge than below 2100 m. Due to the decreased densities of coyotes at the higher elevations, it is assumed that foxes would spend more time in open areas to catch small mammals. At these higher elevations, however, foxes are utilizing the edge of open mesic habitats 27% and spruce-fir forests 30% of the time. I do not know if the habitat use differences were related to sub-specific differences or to prey availability differences at different elevations. The differences in habitat use of low and high elevation foxes, however, could be associated with differences in genotypes and phenotypes I observed.

### Forage Sites

Due to the larger quantity of available sagebrush habitat below 2100 m, which provided excellent hiding cover and a prey base dominated by voles (*Microtis* spp.), mice (*Peromyscus* spp.), and pocket gophers (*Thonomys* spp.) (Johnson and Crabtree, in press), foxes foraged in sagebrush at a much higher rate than above 2100 m where sagebrush was less available. Above 2100 m, foxes foraged heavily in the sf and lp3 habitats. Snowshoe hares *(Lepus americanus)* and red-backed voles (*Clethrionomys gapperi*) are probably major prey in spruce-fir and in older growth lodgepole pine habitat types at high elevations. Further studies are needed to determine exactly what foxes were seeking in both of these areas.

Because foxes forage almost exclusively on small mammals (Sheldon 1992), it is not surprising that foxes use mesic meadows extensively. Mesic meadows harbor the densest populations of voles in northern Yellowstone (Johnson and Crabtree in press). At the same time, however, red foxes feeding heavily on small mammals might result in competition with coyotes. Foxes evidently avoided coyotes in these meadows by foraging at night. Data from remote camera bait stations (Gehman et al. 1997) demonstrated that foxes are almost exclusively active at these bait stations between 6 p.m. to 6 a.m., and no activity occurs during the day. In contrast, coyotes are more active in the day at these locations (Figure 3.21) (Fuhrmann et al. 1995). Similar activity patterns of red fox have been noted in other studies (Ables 1975, Travaini et al. 1993).

Coyotes and foxes have a nearly complete overlap in diet except where coyotes are utilizing larger prey species such as elk or deer (Major and Sherburne 1987, Sargeant 1987). Red foxes generally utilize a larger number of prey species than coyotes, and Therberge and Wedeles (1989) report red fox persistence due to a more elastic and broader food niche than the coyote's. Typically when a complete overlap in diet is found, there is a high degree of spatial and/or temporal segregation (Green and Flinders 1981, Therberge and Wedeles 1989).

### Seasonal Differences

Early and late winter in the study area differed significantly in amount and consistency of snow. Late winter typically has deeper, denser snow and forms a settled base which supports the weight of a red fox. Early winter can be more unpredictable in terms of snow level and consistency. The two late winter periods were more similar due to a more typical pattern in dense, late winter snow characteristics which converge regardless of snow depth.

The difference in snow densities and carrion availability (Gese et al. 1996b) between the beginning and end of winter may affect foraging strategies of foxes. In early winter,

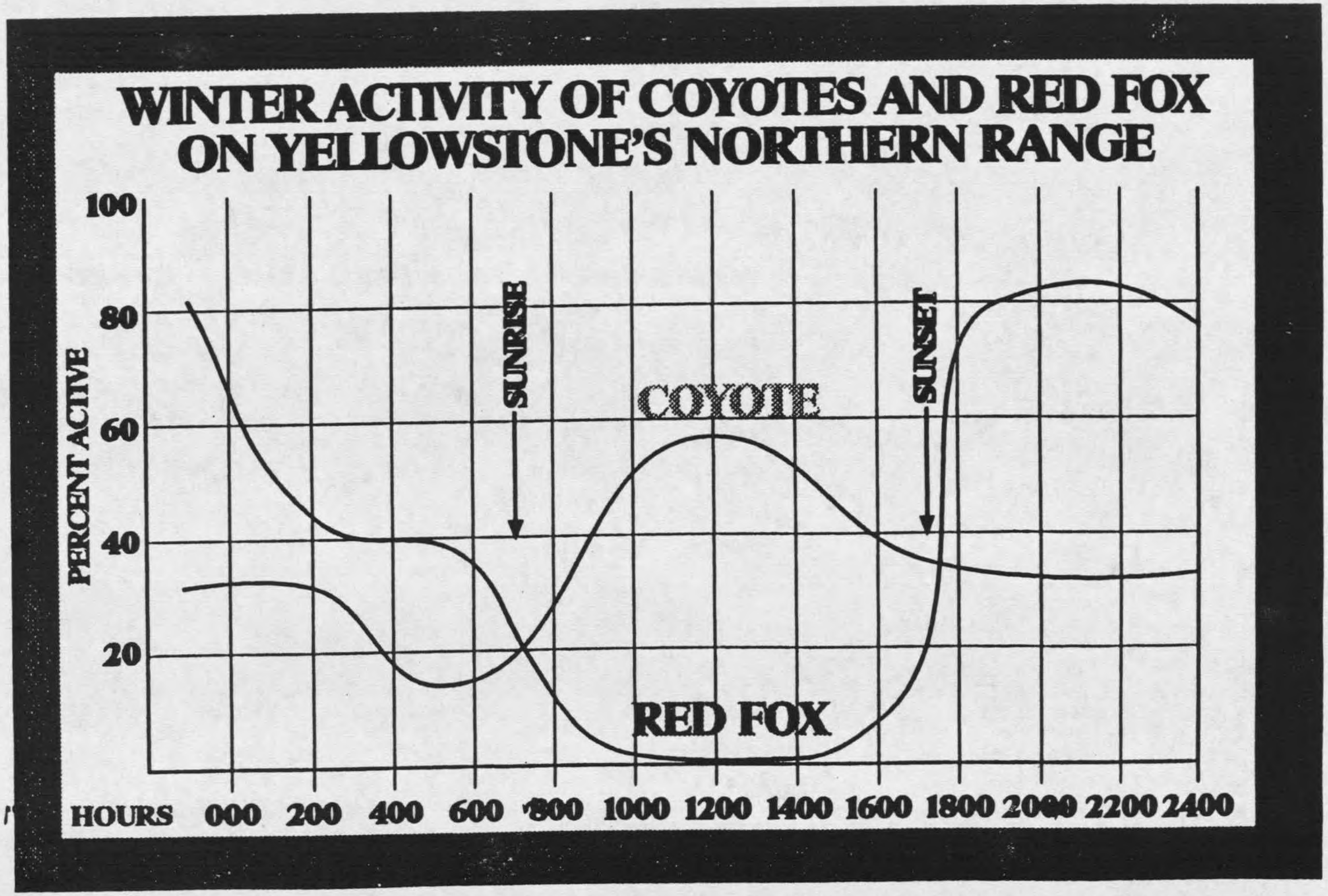


Figure 3.21. Winter activity of red fox and coyotes in the northern Yellowstone ecosystem. Data collected from remote camera stations using bait.

foxes should concentrate on small mammals which are relatively easy to catch when the snow is unconsolidated, and they can "pounce" through the snow relatively easily. As winter progresses, it is more difficult for a fox to break through the layers of snow to gain access to small mammals. At this time, foxes may turn more to scavenging from carcasses left by larger predators or excavate and consume cached food (observed 11 out of 75 time at forage points in this study).

Snow consistency probably had little impact on the ability of foxes to travel. Foxes rarely sank more then a few cm in the snow. The only time they appeared to avoid travel was immediately after or during a large snow storm. The feet of a fox act like snowshoes and keep them on top of the snow. Given the heavily furred pads of these foxes, I calculated the foot loading (0.39 kg/cm$^2$) to be roughly the same as that of a lynx (0.41 kg/cm$^2$). Energy expenditure increases dramatically if a red fox is not able to stay on top of the snow.

### Wolf Effects

The reintroduction of wolves (*Canis lupus*) in 1995 and 1996 to Yellowstone National Park increased interest in research related to the role of predators in community organization, diversity, and stability within the Park (Crabtree 1996, Murphy 1998). My habitat use data described fox habitat use in a system missing the top canid predator. In other ecosystems, ecologists have identified significant direct and indirect effects on community dynamics because of a decrease in predators (Abrams 1987, Martin et al. 1989). Terborgh (1988) maintains that the removal of a few large vertebrate predators in South American ecosystems may lead to major changes in community stability and species diversity at all trophic levels.

New studies have shown that the absence of the wolves in Yellowstone National Park for the past 70 years affected community stability and species diversity (Murphy 1998, Crabtree and Sheldon in press.).

Coyotes may have forced red foxes into a more limited or at least different habitat use pattern than they would have in the presence of wolves. Data are available for the past 9 years on coyote territories in the Lamar Valley and Blacktail Plateau of Yellowstone (Crabtree and Sheldon in press.). In these areas, red fox sightings have been concentrated on the edges of the coyotes' territories. A similar pattern has been reported in other studies examining the interaction between these two species (Ables 1975, Harrison et al. 1989, Major and Sherburne 1987, Voight and Earle 1983, Sargeant et al. 1987, Dekker 1983). Since 1995, many coyotes have been killed or displaced by the wolves. Due to less competition for space and food, foxes seemed to fill in behind the missing coyotes. In one area of the Lamar Valley where there were 4 contiguous coyote territories containing 25-30 coyotes prior to wolf reintroduction, there are now no coyote packs. In this same location, a high concentration of fox sightings were reported compared to what was documented in the few years prior (pers. obs.). This indicates that wolves can have an indirect affect on the occurrence and distribution of red fox. Future studies will be able to compare habitat use patterns with what I observed to determine if red foxes habitat use also shifts.

# CHAPTER 4

# CONCLUSION

Red foxes have been observed in Yellowstone since it was created as a national park and probably longer. There has been, however, a lack of information on foxes and no formal research has occurred on foxes in this region. It is true that more funding is usually available for the charasmatic megafauna or a species that may potentially aid humans, but there is a need to study all parts of an ecosystem to understand it better.

Due to the nocturnal behavior, habitat use, and relatively low densities of the red fox, some employees and visitors have never seen a fox in Yellowstone. This brings up the question then of whether sighting records should be used as a tool for abundance estimates, monitoring, and management decisions. Over long periods of time, sighting records will give an example of some species' presence or absence and possibly indicate major trends over several decades. Beyond that, sighting records are biased and can be misleading. Examining the recent sighting records of red fox in Yellowstone (Figure 1.2), it is obvious that most of the sightings are found along the road corridor since this is where most people concentrate in Yellowstone. Sighting records do serve a function but only to give a baseline measure of what species are present, and they should not be used to determine habitat use, population estimates, trends, or management decisions. The lynx was recently not listed as an endangered species because not enough information was available. This could mean that there are not enough individuals left to study and trying to conduct research on them would be close to impossible. The red fox in Yellowstone has been listed as a rare animal in the park because there was a lack of information on their distribution. Through this research, the red fox has now been found to essentially inhabit every habitat in northern Yellowstone and has a wide distribution throughout the rest of the park. Hopefully this project will be an impetus for future studies on other species which have not been examined thoroughly in Yellowstone as well as other regions.

Snow tracking results determined that foxes in the winter in Yellowstone inhabit areas in between coyote territories. These areas tend to be in habitats that contain abundant cover such as spruce-fir forests or sagebrush communities. When foxes are using open habitats, they are foraging and traveling close to escape cover. Generally, and specifically above 2100 m, red foxes in the Yellowstone area are a forest species and mainly inhabit montane and subalpine forest edges.

By examining the results of the habitat use and availability and morphometric statistical tests, it appears that foxes above 2100 m differ genetically, use different habitats, are to some degree different in their body size, and have different color morphs compared with foxes below 2100 m. Even though the specific morphometrics were not statistically significant, there were significant trends that suggest morphology was different between the two elevational zones.

Above 2100 m, foxes traveled through spruce-fir forests extensively and stayed closer to the edge of major vegetation structure changes more frequently than below 2100 m. The morphology of the foxes above 2100 m was somewhat more robust with larger circumferences and shorter extremities compared with below 2100 m. At higher elevations there is also a trend of more lighter color foxes (gray or cream).

Due to the differences in coat color, habitat use, and less significantly morphology, it appears that there is something unique about the foxes at higher elevations. My study was unable to determine the exact cause of this uniqueness, so further research is needed.

## Further Research Needs

This study demonstrated that 2 subspecies of fox may occupy the northern Yellowstone ecosystem and provided a pre-wolf baseline on habitat use patterns for low and high elevation foxes, but more research is needed. Several questions regarding the origin and taxonomic differences of red fox in the Yellowstone area remain unanswered. To better understand the differences in the potential subpopulations of foxes across an elevational gradient in the northern Yellowstone area, measurements and tissue samples from additional foxes are needed. To be able to differentiate the red fox throughout this region, these samples should also be compared with foxes that inhabit the region surrounding the study area at both lower elevations and similar elevations. This will better elucidate potential genetic differences and further examine possible genetic isolation between populations or subspecies.

A variety of factors influence habitat and forage selection. One of the most prevalent factors faced by the red fox population of the northern Yellowstone ecosystem is the interaction with sympatric canids which could affect the ways fox utilize areas available to them. Although in my second field season, 2 packs of wolves used part of the Lamar Valley, I did not notice changes in the coyote density. Due to only slight differences in coyote behavior in response to the wolves during this second field season, and extrapolating this to the red fox, my habitat use data, therefore, are a valid baseline against which changes in habitat use due to the impacts of wolves on coyotes can be compared. I hope that someone takes advantage of the opportunity to examine the indirect effects of the wolves on the foxes. It will be interesting, therefore, to reexamine the red fox distribution and habitat use after wolves have fully established themselves in northern Yellowstone.

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# APPENDIX

## Red Fox Morphometric Records

| FOX ID | LOCATION | Elev. (m) | SEX | Age (~yrs) | WEIGHT (lbs) | HEAD LENGTH (cm) | BODY LENGTH (cm) | TAIL LENGTH (cm) | HIND FOO LENGTH (cm) | HEAD GIRTH (cm) | NECK GIRTH (cm) | CHEST MAX (cm) | CHEST MIN (cm) | EAR LENGTH (cm) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 93-1 | Hitching Post | 2040 | F | 4-5 | 10 | 16.5 | 50 | 46.5 | 17 | 26 | 22.5 | 38 | 26 | 12 |
| 93-2 | Slough Creek | 1895 | M | 2-3 | 10 | 16.5 | 54 | 47 | 17 |  | 21 | 34 | 29 | 12 |
| 93-3 | Maiden Basin | 1560 | M | 2-3 dead |  | 16.5 | 55 | 42 | 16.5 | 25.5 | 21 |  |  | 10.5 |
| 94-1 | Top of World | 2805 | M | 1 | 11.5 | 16.1 | 50.4 | 43.5 | 17.2 |  | 22.2 | 40 | 33 |  |
| 94-2 | Daisy Pass | 2940 | M | 3 | 11.22 | 17 | 42 | 36 | 17 | 29 | 23 | 43 | 27 | 11 |
| 94-3 | S. Gard. School | 1620 |  | Juv-dead |  |  |  |  |  |  |  |  |  |  |
| 94-4 | Bozeman on-ramp | 1440 |  | Adult-dead |  |  |  |  |  |  |  |  |  |  |
| 94-5 | Sedge Bay | 2400 | M | Adult-dead | 8 | 16 | 33 | 47 | 17 | 26 | 24 |  |  | 9.5 |
| 94-6 | Point of Rocks | 1470 |  | Juv-dead |  |  |  |  |  |  |  |  |  |  |
| 95-1 | S.B. Wolf Pen | 2080 |  | dead |  |  |  |  |  |  |  |  |  |  |
| 95-2 | Lower Baronette | 2115 | M | 3-4 |  |  | 47.5 | 45 | 16 |  |  |  |  |  |
| 95-3 | Island Lake | 2860 | M | 6-7 | 12 | 18 | 47 | 47 | 17 | 29 | 27 | 42 | 40 |  |
| 95-4 | Painter's Store | 1950 | F | 1 |  | 17.7 | 49.5 | 43 | 16.5 | 25.5 | 17 | 31 | 28 | 10.5 |
| 95-5 | Long Lake area | 2915 | F | 1-2 | 9.7 | 16 | 51 | 38 | 16.75 | 24.5 | 19 | 34 | 28 |  |
| 95-6 | Road Camp | 2615 | F | 1-2 | 10.1 | 16 | 45 | 40 | 16.75 | 25 | 19 | 34 | 26 | 9 |
| 95-7 | Chain Lakes | 2855 | F | 2-3 | 8.7 | 16.5 | 50 | 43 | 17.5 | 23 | 16.5 | 31 | 24 | 10.5 |
| 96-1 | Tom Miner | 2960 | M |  | 10.5 |  |  |  |  |  |  |  |  |  |
| 96-2 | Springdale | 1260 | F |  | 11 |  |  |  |  |  |  |  |  |  |
| 96-3 | Tom Miner | 2960 | M | adult | 10 | 17 | 58 | 42 |  | 28 | 20 | 36 | 29 | 11 |
| 96-4 | Old Faithful | 2210 | M | 3-4 | 10.8 | 16.5 | 53 | 45 | 16.5 | 16 | 22 |  |  | 10 |
| 96-5 | Frog Rock | 2085 | F | 5-8 | 8.47 | 16 | 45 | 39 | 16 | 24.5 | 22.5 | 33.5 | 29.5 | 11.5 |
| 97-0 | Paradise Valley | 1480 |  |  |  |  |  |  |  |  |  |  |  |  |
| 97-1 | Tower Falls | 1935 | M | ~3 | 11.55 | 16.5 | 53 | 49 | 17 | 27.5 | 20.5 | 36 | 33 | 12 |
| 97-2 | Paradise Valley | 1400 | F | 3-4 |  | 15.5 | 52 | 46 | 17 | 26 | 20 | 34.5 | 29.5 | 11 |
| 97-3 | Fisherman's PO | 1990 | F | 2-3 | 9.9 | 17 | 43 | 42 | 16.5 | 26 | 22 | 36 |  | 9 |
| 97-4 | Lower Baronette | 2110 |  | 5-6 |  | 17.5 | 51 | 46 | 16 | 27 | 23 |  |  | 12 |
| 98-1 | Hellroaring Pullout | 2055 | F | 3-4 | 8.25 | 13.5 | 38 | 44 | 15 |  | 19 |  |  | 11 |