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THE CASCADE RED FOX: DISTRIBUTION, MORPHOLOGY, ZOOGEOGRAPHY AND ECOLOGY

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THE CASCADE RED FOX: DISTRIBUTION, MORPHOLOGY, ZOOGEOGRAPHY AND ECOLOGY

by

Keith Baker Aubry

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

Doctor of Philosophy

University of Washington

1983

Approved by Richard D Taber
(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree College of Forest Resources

Date May 26, 1983

Doctoral Dissertation

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Date May 27, 1983

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INTRODUCTION

The indigenous red fox of the north-western United States, _Vulpes vulpes cascadensis_, known commonly as the Cascade red fox, is a rare, secretive animal whose distribution is restricted to habitat near timberline in the Cascade Mountains of Oregon, Washington and British Columbia (Bailey, 1936a; Dalquest, 1948). Because of the remoteness of its preferred habitat, its historically low population numbers, and its fear of human contact, this fox is rarely encountered. Only a few are taken each year by fur-trappers.

The Cascade red fox is one of three recognized subspecies of the red fox that are restricted to habitat at high elevations in the mountains of the western United States. The Sierra Nevada red fox, _V. v. necator_, occupies the Sierra Nevada Range in California and the Rocky Mountain red fox, _V. v. macroura_, is found throughout the Rocky Mountains (Hall, 1981). These three varieties of 'mountain' foxes are ecologically and morphologically (Roest, 1977) distinct from the more common indigenous red foxes of the northern boreal regions and those of the eastern United States, which were probably introduced.

In the Pacific Northwest there were no lowland red foxes in aboriginal times, but populations of red foxes are now known to occur in disturbed habitat at low elevations in the Puget Sound Basin of Washington and British Columbia, the Columbia Basin of eastern Washington and the Willamette and Malheur river valleys of Oregon. Prior to this study, no distribution maps depicting their geographic ranges had been constructed, however, nor had their taxonomic relationships to indigenous populations in this region been investigated. Given the well-known adaptability of red foxes and their capacity for long-range dispersal (Ables, 1965), the possibility existed that lowland foxes had extended their distribution into mountainous regions, and hybridized with Cascade populations.

Red foxes colonized North America from Asia during the Illinoian glaciation (Kurtén and Anderson, 1981), yet prior to the present study, no comprehensive analysis of their Quaternary history and zoogeography had been attempted. It was not known how red foxes colonized the western mountains, nor why they occupied such an ecologically and geographically restricted range.

The red fox is one of the more intensively studied carnivores in North America, by virtue of its long-standing economic importance as a furbearer and a competitor for game and domestic livestock; yet most of this research has been conducted on those populations occupying the mid-western and eastern United States. Aside from the present study, no comprehensive field study of the Cascade, Sierra Nevada or Rocky Mountain red foxes has ever been conducted, so nothing has been known of the habitat requirements, activity patterns, winter ecology, reproductive ecology or food habits of these unique populations of red foxes.

Objectives

The objectives of this study are divisible into four major sections which are included here as Chapters 1 to 4.

1) To substantiate historical reports of the introduction of red foxes into Washington and document when, where and how these introductions occurred; construct a reliable distribution map for indigenous and introduced populations of red foxes in Washington and describe the habitats occupied by each population.

2) To extend these findings to British Columbia and Oregon, where Cascade and introduced populations reportedly also occur; construct a distribution map for the red fox in the Pacific Northwest and test the appropriateness of the distributional boundaries drawn with a morphometric analysis of the cranial and dental characteristics of contemporary specimens.

3) To reconstruct the Quaternary history of red foxes in North America and develop a zoogeographic hypothesis to explain present distributional patterns in the Pacific Northwest.

4) To describe the ecology of a representative population of the Cascade red fox and compare these findings with results from studies conducted in other regions of North America.

Because Chapters 1 to 3 were written to stand on their own as potentially publishable manuscripts; methods, results, and discussion sections are presented separately within each chapter. A summary of results found and conclusions regarding their significance is presented at the end of the dissertation.

Scientific and common names for mammals follow Jones, et al. (1982), and those for plants follow Hitchcock and Cronquist (1978).

CHAPTER 1

RECENT HISTORY AND PRESENT DISTRIBUTION IN WASHINGTON

In the State of Washington, fur-trapping is a widespread recreational and economic activity. One hundred or more red foxes, *Vulpes vulpes*, may be harvested annually, the great majority of which are from areas at low elevations in the western portion of the State (Wash. State Dept. Game, 1976-1980). Standard works, which presented detailed distributional information for red foxes in Washington (Dalquest, 1948; Ingles, 1965; Hall, 1981), referred only to the indigenous Cascade red fox, *V. v. cascadensis*. This variety was reportedly restricted to mountainous regions. No consideration was given to populations occurring at low elevations. The presence of an introduced 'lowland' red fox in the Puget Sound region, however, has long been recognized by residents and by personnel of the Washington State Department of Game. A comprehensive evaluation of the distribution of red foxes in Washington is needed, given the importance of introduced red foxes as furbearers and the possibility of their competing and interbreeding with native Cascade foxes.

In the western United States, indigenous populations of the red fox occupy subalpine meadow and parkland habitats. The Cascade red fox is found in the Cascade Mountains of Oregon, Washington and southern British Columbia; the Sierra

Nevada red fox, V. v. necator, in the Sierra Nevada Range of California; and the Rocky Mountain red fox, V. v. macroura, in the Rocky Mountains from New Mexico to Montana and the southern Canadian Rockies, and west to Idaho and the Blue Mountains of Oregon (Bailey, 1936a). During the early 1900's, when western areas of the continent were being settled, populations of red foxes became established in valleys at low elevations, and along coastal areas. In Oregon, red foxes are also found near the north-western coast (Bailey, 1936b; Maser, et al., 1981) and in the Willamette Valley, west of the Cascades (Livezey and Evenden, 1943; Maser, et al., 1981). According to Ingles (1965) these lowland populations were the result of introductions from the southern United States. Grinnell, et al. (1937) reported that the population of red foxes in the Sacramento Valley of northern California was geographically isolated from the population in the Sierra Nevada, and that red foxes were probably introduced sometime prior to 1900, although the circumstances of the introduction could not be determined. Recent work (Gray, 1977) indicated that the Sacramento Valley population had significantly expanded its range since that time. In a review of the distribution of red foxes in Idaho, Fichter and Williams (1967) documented their presence in habitats previously unoccupied by the species, such as cultivated areas, cool deserts of the foothills, and the Snake River Plain. This range-expansion was largely attributed to downslope movement by Rocky Mountain foxes, but they did not exclude the possibility that these populations had resulted from accidental introductions. Fox-farms were present in southern Idaho in the early part of this century, and the authors documented several instances of individuals escaping from such farms.

Available information on the lowland red fox in Washington is limited, and appears not to have been based on documented records. Lauckhart (1970) claimed that two races of red fox were present: a rare, indigenous high mountain form and a common, introduced lowland form whose ranges were separated by uninhabited expanses of forested foothills and mountains. Larrison (1970) assigned the lowland red fox to the subspecies _fulva_ of the eastern United States and claimed that it had been introduced into the Kitsap Peninsula in Puget Sound, farmlands south of the Olympic Peninsula, and the north-eastern Puget Sound region. It is now, reportedly, found in nearly all lowland areas of western Washington. Lauckhart (1972) asserted that the Eastern red fox began to appear in the Skagit Valley of the north-eastern Puget Sound region sometime in the 1920's. The source of this population was believed to have been red foxes brought into the area by hound hunters, but he further speculated that escaped animals from private fur-farms might have accelerated the spread of this population.

METHODS AND MATERIALS

During three winter trapping seasons (1978 to 1980), all registered trappers in Washington were contacted by mail. They were asked to provide detailed reports of all previous sightings or trappings of red foxes, and to include any information regarding the introduction of red foxes into Washington. Over the three-year period, an average of about 1900 trappers from all areas of the State were contacted each year. I received 153, 38 and 74 replies for the years 1978, 1979 and 1980, respectively. Local trappers are probably better-informed about red foxes in Washington than any other sizeable group of people, they are distributed throughout the State, and many have lived and trapped in this region for most of the century. I therefore believed that they could be relied on to accurately identify red foxes, and would be a valuable source of information on the history of red foxes in Washington.

Records of the Washington State Dept. of Game, National Park Service and U.S. Forest Service were searched for pertinent information. All museums in the United States and Canada that potentially contained red fox material from Washington (Choate and Genoways, 1975) were either visited or contacted by mail to obtain locality-records of specimens.

All records that could be located on a map to an area less than one township in extent were used. These were plotted on a 1:500,000 scale USGS map of Washington. Areal, elevational and ecological information was used to delineate boundaries around populations of red foxes. West of the Cascade Crest, red foxes occurred either in relatively undisturbed habitats in mountainous regions, or at lower elevations in areas of human settlement. A wide, uninhabited zone of dense forest separated the populations in these two areas, and boundaries around each were easily drawn. Because forested habitats differ east of the Crest, no such 'buffer zone' exists there. Nevertheless, eastern records were also either from relatively unsettled, forested areas at high elevations or from mostly non-forested areas at lower elevations near towns or along river valleys and highways. Therefore, east of the Cascade Crest, records were assigned to introduced populations if a source of introduction in the area was documented, and if the records were from areas of human activity at low elevations. Records were assigned to the Cascade population if they occurred in the less-disturbed forested habitats at higher elevations.

RESULTS AND DISCUSSION

History of Introductions

Introductions of red foxes, both intentional and accidental, are shown in Fig. 1. Mr. Floyd G. Squires, a long-term resident of Bow, Washington in western Skagit Co., has spoken to many 'old timers' in the area, and informed me that in "1909, two females and one male were imported from the State of Illinois...each vixen produced a litter of pups which were raised and released that fall. Shortly after the release of the pups, both females escaped from the enclosure. The male was released the following day". The next spring, one of the females was observed denning on a nearby ridge. According to the 'old timers', red foxes did not occur in Skagit Co. at that time, and were introduced for hunting with hounds by settlers who came from the south-eastern United States, and missed having red foxes around. He further stated that "about 1915,...between five and eight fox were released on the south side of Alger Mountain [in north-western Skagit Co.]. These fox...were also from the State of Illinois". The last record was confirmed by M. Splane of Sedro Wooley, Washington, who was interviewed by Scheffer (1939) and reportedly "believes fox [were] introduced 25 years ago by Dave and Don Henry on Butler's knob [near Alger Mountain]". In addition,

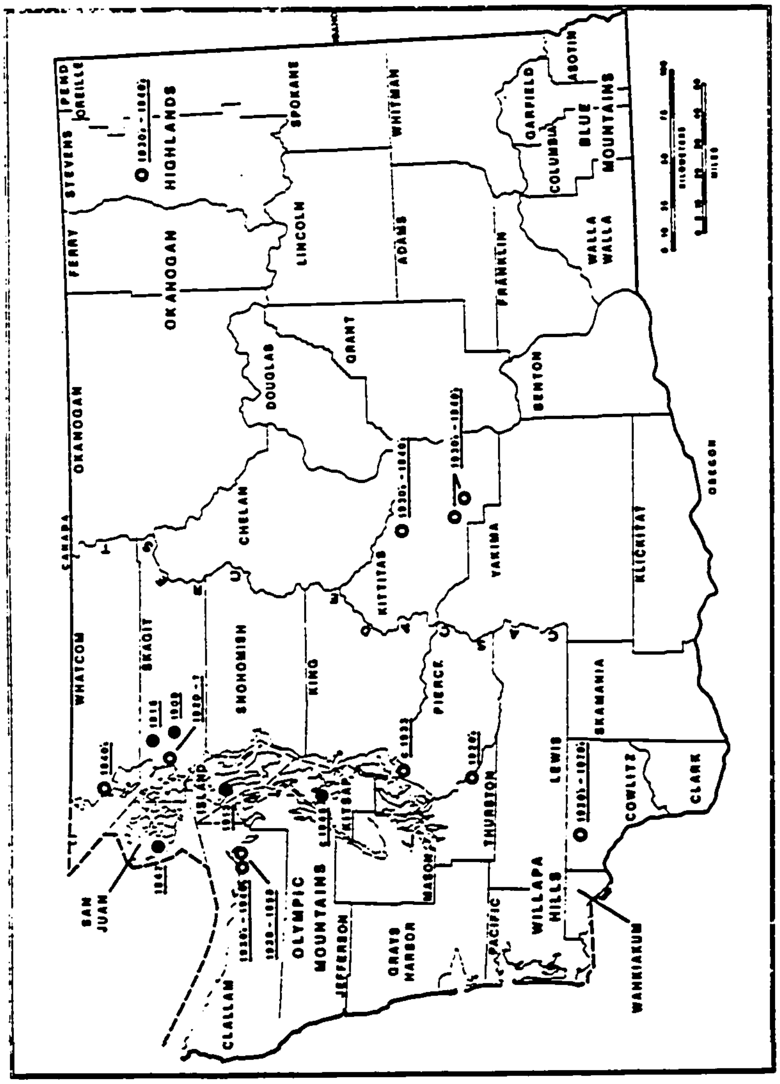

Figure 1. Dates and locations of fox-farms (circled stars) and points of introduction of red foxes (solid circles) in Washington.

according to Brooks (1930) in a report on the larger mammals of the Mt. Baker National Forest, which covered much of Whatcom, Skagit and Snohomish Counties, red foxes were "absolutely unknown up to about 1910. Now common".

Subsequent introductions were apparently made on two of the larger islands in Puget Sound. Mr. Squires reported that "in 1912 or 1914, five of the original stocking were live-trapped and released on Whidbey Island [in Island Co.]. Prior to this time, it is reported that there were no fox on this island... . Subsequent trappings and releases were made on San Juan Island [in San Juan Co.]". Schoen (1972) reported that red foxes were introduced on San Juan Island in an attempt to control an irruptive population of European rabbits, Oryctolagus cuniculus. A man named Osburn, who was the Extension Agent for San Juan Co., informed him that a pair of red foxes was introduced in 1947, and that others were brought in during the following years. In 1972, red foxes were apparently nearing extinction on the Island. Trapping records of the State Dept. of Game further illuminate that situation (Table 1). One red fox was taken from San Juan Co. in 1942, and two in 1947. These probably represent animals remaining from the original stocking. From 1948 to 1959, no foxes were harvested from the Island. After that, presumably when the population began to build up again after the second introduction, foxes were trapped in

Table 1. Harvest records of red foxes in Washington west of the Cascade Crest, as reported by licensed trappers between 1938 and 1980. Data from Washington State Dept. of Game, expressed in 5-yr. blocks.

COUNTY	1938 to 1942	1943 to 1947	1948 to 1952	1953 to 1957	1958 to 1962	1963 to 1967	1968 to 1972	1973 to 1977	1978 to 1980	TOTAL
Whatcom	77	115	26	32	70	7	83	17	3	505
Skagit	115	291	30	84	64	82	73	53	15	807
Snohomish	31	78	28	58	74	85	25	10	1	390
King	1	4	1	1	2	4	14	20	7	54
Lewis	7	2	1	3	38	16	7	15	1	90
Skamania	1	0	0	0	0	0	5	3	0	9
Clark	0	0	2	2	0	1	0	5	3	13
Cowlitz	0	0	0	2	2	0	12	13	3	32
Wahkiakum	0	1	0	0	1	0	1	0	0	3
Pacific	0	0	0	0	1	0	14	0	0	15
Grays Harbor	0	1	0	5	17	16	25	4	3	71
Thurston	1	19	20	15	4	9	40	22	17	155
Mason	0	0	3	1	5	27	14	35	13	98
Kitsap	0	0	3	0	5	34	53	94	33	222
Jefferson	0	0	0	0	0	0	0	25	63	88
Clallam	0	0	0	5	6	27	5	48	23	114
Island	0	0	0	2	23	33	20	285	46	409
San Juan	1	2	0	0	5	26	143	0	0	177

increasing numbers until in 1968, 1969 and 1970 there were 25, 83 and 35 animals harvested, respectively. None has been reported after that. Whether red foxes are extinct on San Juan Island, or simply at the low end of a population cycle, is not known.

Mr. Andy Rogers of Seabeck, Washington in Kitsap Co., a trapper of over 40 years' experience, informed me that "foxes were unheard of [in Kitsap Co.] until they began to be sighted...shortly after World War II. Some years ago, in a conversation with Bill Glud of Brownsville, I learned that he and Russell Root of Fernwood...had released foxes here thinking they might be good game for hound hunting". He was not told, however, where these foxes had originated.

The escape or release of red foxes from fur-farms has also been an important mechanism of introduction. Mr. Squires stated that "in 1920, a fox-farm was started at Bay View Ridge [in western Skagit Co.]. The population being comprised of both...blue and silver [foxes]. Some of these escaped and it is reported that they may have mated with the already established population of [introduced] red fox". Mr. Bill Hoffman of Concrete, Washington, a retired employee of the State Dept. of Game, informed me that in the early 1950's, he trapped a silver fox that had a brand on it, indicating that it had escaped from a fur-farm. He believed this animal came from a farm that had operated in the 1940's near Ferndale in western Whatcom Co. Presumably, when fur prices significantly declined in the early 1950's, the animals at this farm were simply turned loose. During this period, the average pelt-price for red foxes in Washington dropped to a low of $0.65 (Fig. 2), which no doubt rendered fox-farming uneconomical.

The presence of a fur-farm in the southern Puget Sound region in the 1930's, is indicated by a museum specimen that was obtained from a silver fox-farm near Tacoma in western Pierce Co., in December of 1933 (Mus. Nat. Hist., Univ. Puget Sound, specimen no. 522). In addition, Sid Hayes of Twisp, Washington, a native of Yelm in eastern Thurston Co., reported that "a neighbor...Roy Shearer...raised red fox. About 1920 or 1922, a bunch of his foxes dug under [the] fence. Before that time, I'd never [seen] a fox in Washington...or spoke to anyone who had. I do know that they became quite plentiful in the coast area after that...". John and Stuart Keatley of Castle Rock, Washington, ran a silver fox-farm just above the mouth of the Toutle River in Cowlitz Co. from the 1930's to the 1970's. According to one of the owners, however, none of their animals ever escaped.

The only records of fox-farms on the Olympic Peninsula occurred in north-eastern Clallam Co. Mr. Dowell Hilt, of Port Angeles, Washington, a retired mink rancher, reported

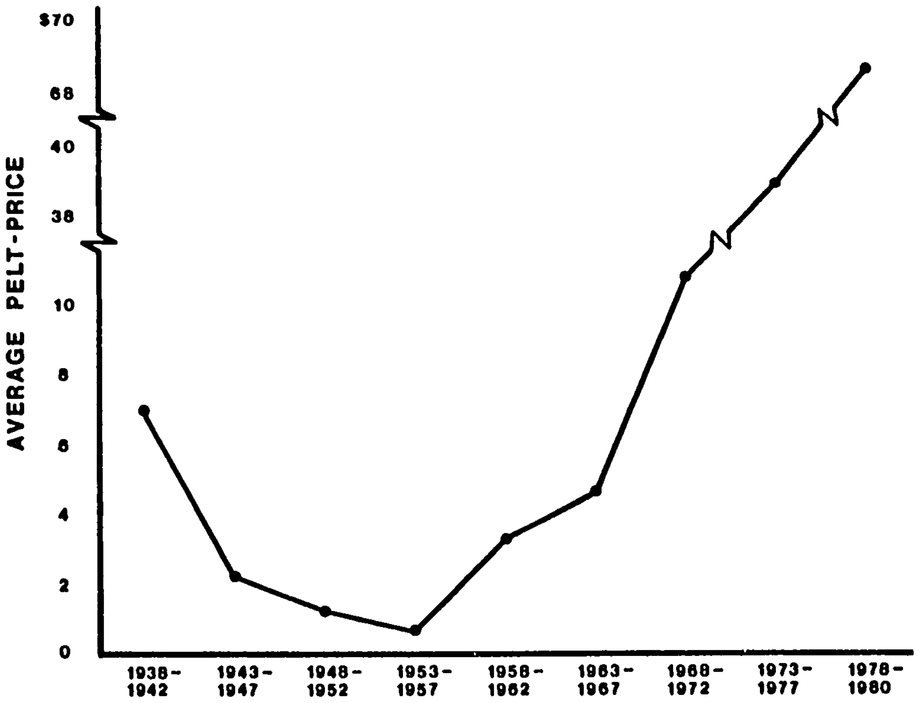

Figure 2. Average pelt-price for red fox in Washington between 1938 and 1980. No data available for 1942, 1943 1945 or 1950. Data from Washington State Dept. of Game.

that there were two fox-farms in this region. One was a farm at McDonald Creek that raised silver fox breeders in the 1930's and 1940's. According to Mr. Hilt, these foxes were worth thousands of dollars at the time, and it is unlikely that any escaped or were released. The other was operated by Mr. Milo Rice on the Dungeness River from about 1938 to 1958. He raised several color phases including red, platinum, silver and gray (probably cross). They escaped frequently, and he reportedly also let many go. According to Mr. Hilt, wild foxes were not present before this farm began operating. State trapping records (Table 1), and historical reports support this assertion. Red foxes were not trapped in Clallam Co. until 1955. In Jefferson Co., which is situated south and east of Clallam Co., however, red foxes were not reported by trappers until 1974. This indicates that red foxes did not colonize the northern Olympic Peninsula from the mainland to the south, where they had been common for some time, but that they originated in Clallam Co., and subsequently moved into the coastal areas of eastern Jefferson Co. Scheffer (1949) conducted a survey of mammals on the Olympic Peninsula in the late 1940's and reported that red foxes did not occur there. By the early 1950's, that situation was apparently unchanged (Johnson and Johnson, 1952).

Fox-farms were also in operation on the east side of the Cascades. According to Mr. Russell Thompson of Thorp, Washington, a former Federal trapper and employee of the State Dept. of Game, there were three fox-farms that operated in Kittitas Co. in the 1930's and 1940's. One was in the northern part of the County near Liberty in the foothills of the Wenatchee Mountains, the other two were in the vicinity of Ellensburg in southern Kittitas Co. C. E. McFarland, who was interviewed by Scheffer (1938), reported "there are a few [red foxes] between Cashmere and Leavenworth [in southern Chelan Co.], mostly blacks. Silvers occasionally escape from farms".

Mr. Bob Lynds of Colville, Washington in Stevens Co., reported that a fox-farm was operated four miles north of Colville in the 1930's and 1940's by a man named Mottler. In 1942, Mr. Lynds trapped two tame silver foxes that had escaped from the fur-farm. Upon contacting Mr. Mottler, he learned that a few foxes escaped every year. According to Mr. Lynds, whose father and grandfather began trapping north-eastern Washington before 1900, there were no red foxes in that area before this farm came into operation.

The average pelt-price for red foxes in Washington has risen sharply since the late 1960's (Fig. 2). Apparently, this increase has once again stimulated interest in fox-farming. I am aware of three farms currently operating in the State: at Cle Elum in central Kittitas Co., since 1981; in the Cathcart area of south-western Snohomish Co., since 1977; and at Graham in western Pierce Co., during the last few years. There is no indication that any foxes have escaped or been released from these farms.

Present Distribution

Distribution records of red foxes in Washington, which include State and Federal records, museum specimen localities and records gathered from correspondence with trappers, are shown in Fig. 3. All records are included, except for the area contained within Mt. Rainier National Park. There are over 140 sight-records from the Park dating back to 1897. Consequently, I have only indicated those records that represent different areas where foxes have been sighted. It is noteworthy that only three of these records came from the north or west side of the mountain, and of these, only one was made since 1970.

On the basis of these records, geographic ranges were drawn for existing populations of red foxes (Fig. 3). A widely distributed population of introduced red foxes occurs throughout the lowlands west of the Cascade Mountains. These foxes inhabit farmlands, the coastal areas of Puget Sound and the Strait of Juan de Fuca, and developed river valleys in the western foothills of the Cascade Mountains.

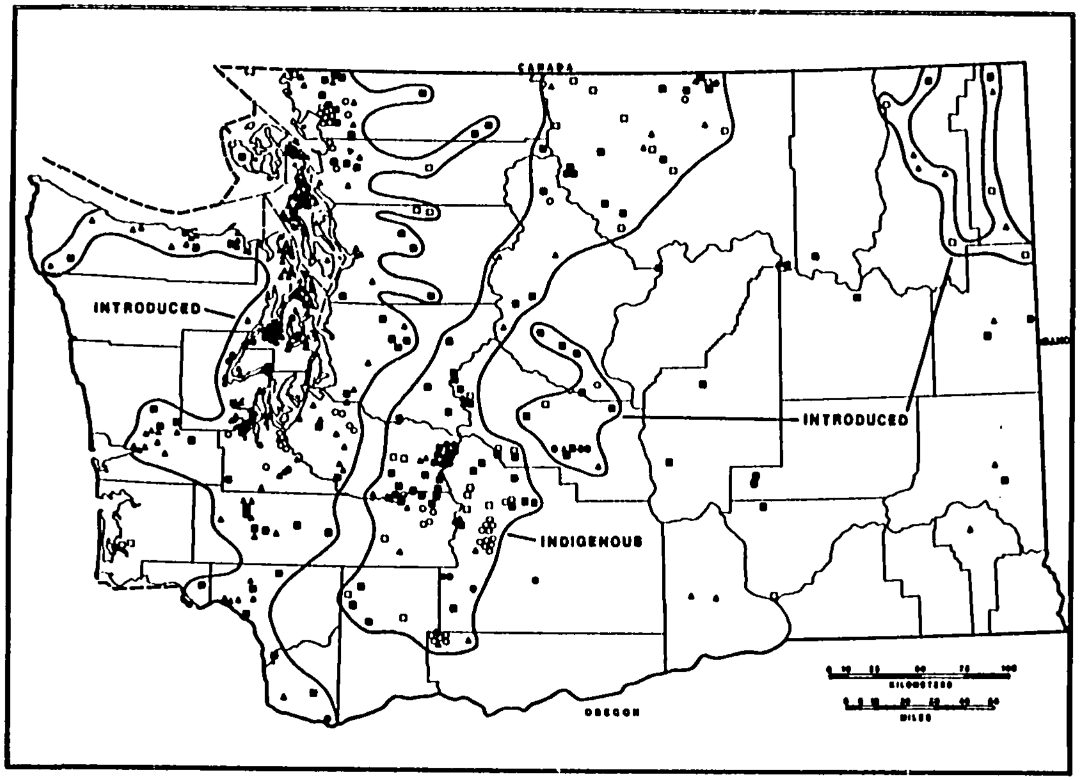

Figure 3. Distribution records and geographic ranges for indigenous and introduced populations of red foxes in Washington. Squares represent sight-reports; triangles, trapping reports; and circles, locality-records of museum specimens. Hollow symbols indicate records dated prior to 1970.

Areas that are apparently unsuitable for introduced red foxes in western Washington include: the dense forests of the Cascades, the Willapa Hills in south-western Washington, the outer coast zone, and the forests and subalpine meadows of the Olympic Mountains.

The range of the Cascade red fox differs somewhat from that shown on distribution maps published previously (Booth, 1947; Dalquest, 1948; U.S. Army Corps of Engineers, 1974). Because of the presence of high mountains in central and eastern Whatcom Co., most notably Mt. Baker, this area has been included within the range of the Cascade fox. This region, however, is cut off from the main Cascade chain by the deep valley of the Skagit River, and no records of red foxes from high elevations have been reported from this area. Presumably, this river acts as a barrier to the movements of Cascade foxes and, as a result, the only red foxes present are introduced animals that have moved into the area along river valleys and highways. In addition, the eastern boundary of the range of the Cascade fox has typically been drawn to include portions of the Columbia Basin to accomodate distribution records that are in fact representative of introduced populations.

In the southern end of their range, Cascade foxes inhabit extensive areas west of the Cascade Crest. Appropriate habitat on two volcanoes, Mt. St. Helens in north-western Skamania Co., and Mt. Rainier, account for these distribution records. Unlike the situation in the Mt. Baker area, there is no barrier to the movement of Cascade foxes beween these areas and the meadows near the Cascade Crest.

Since most records of lowland red foxes were gathered during the course of this study, it is not possible to determine whether range expansion or contraction has occurred for introduced foxes in recent years. Many historical records for the Cascade fox exist, however, and these are indicated by hollow symbols in Fig. 3. Comparing these records with those dated since 1970 (indicated by solid symbols), it is evident that no significant changes in distribution have occurred in recent years. Cascade foxes were present on the slopes of Mt. St. Helens, but their population status following the May, 1980 eruption is unknown.

At mid-elevations, the western slope of the Cascades is characterized by dense, wet forests dominated by western hemlock, Tsuga heterophylla, and Douglas fir, Pseudotsuga menzeisii, with a lush understory (Franklin and Dyrness, 1973). This habitat appears to be unsuitable for both the Cascade and lowland populations, probably because red foxes are cursorial predators favoring open meadows for hunting small rodents, their principal prey (Bailey, 1936b).

Consequently, west of the Cascade Crest, introduced and indigenous populations of red foxes are separated by a belt of dense coniferous forest. Red foxes would be capable of crossing this uninhabited zone, because these forests do not present a physical barrier to their movements. Introduced foxes have not colonized the subalpine meadows of the Olympic Mountains, even in the absence of competition from native foxes. This indicates that introduced red foxes are restricted to habitat at low elevations by physiological or behavioral limitations, and provides strong evidence that introduced red foxes have not invaded the meadows at upper elevations in the western Cascades, and interbred with native foxes. Apparently, such limitations have also operated to restrict indigenous red foxes to habitat at high elevations.

Cascade red foxes clearly favor the eastern slope of the Cascade Range. At mid-elevations, annual precipitation is much lower than on the west side, the forests are much drier and the understory less dense. Dominant forest species are principally grand fir, _Abies grandis_, and ponderosa pine, _Pinus ponderosa_ (Franklin and Dyrness, 1973). Because the east-side forests are open, they probably provide enough space for these cursorial predators to effectively exploit available prey, whereas the dense forests at similar elevations on the western slope do not.

The red fox is reportedly absent from the Columbia Basin east of the Cascades (Dalquest, 1948; Larrison, 1970). Information gathered from trappers, however, indicates that foxes are infrequently found in this region. The river valleys and populated areas of central Kittitas and southern Chelan Counties appear to support a sizeable population that is presumably derived from foxes that escaped from fur-farms in the 1930's and 1940's. The other, scattered reports from the Columbia Basin probably represent wandering or dispersing individuals, because the great majority of trappers from those areas have never reported sighting or trapping a red fox.

On the east side of the Cascades, unlike the west, no wide buffer zone of uninhabited forest separates indigenous and introduced populations of red foxes. Consequently, these populations are nearly parapatric in Chelan and Kittitas Counties, and it is here that hybridization would most likely occur. Assessment of this possibility, however, must await the collection of an adequate series of specimens.

The presence of red foxes in the highlands of north-eastern Washington has long been recognized. This population has been assigned to both the Rocky Mountain (Dalquest, 1948), and Cascade (Booth, 1947) subspecies. All records, however, were from developed sites at low elevations along river valleys. A game-mammal census conducted in 1925 on the Colville National Forest in north-eastern Washington made no mention of red foxes (Anonymous, 1925). A similar census five years later, estimated a population of five foxes (Anonymous, 1931). These facts, along with the information provided by Mr. Lynds on the introduction of farm foxes into this area, provide strong evidence that this population is descended from introduced animals.

The Blue Mountains in south-eastern Washington have consistently been included within the range of the Rocky Mountain red fox (Booth, 1947; Dalquest, 1948; Hall, 1981). In 1923, a red fox was collected from the Blue Mountains of Washington (Nat. Mus. Natur. Hist., specimen no. 244010), although no specific collecting-locality was recorded. This specimen constitutes the only evidence that indigenous red foxes occur in south-eastern Washington. The one other record of a red fox from this area came from a ploughed field at the base of the Blue Mountains in Garfield Co. (Fig. 3). Numerous trappers, many of whom have trapped for decades, consistently reported that red foxes do not occur in the Blue Mountains. As shown in Table 2, red foxes have not been reported by trappers in any of the four counties which encompass the Blue Mountains (Asotin, Garfield, Columbia and Walla Walla). It is evident that these were

Table 2. Harvest records of red foxes in Washington east of the Cascade Crest, as reported by licensed trappers between 1938 and 1980. Data from Washington State Dept. of Game, expressed in 5-yr. blocks.

COUNTY	1938 to 1942	1943 to 1947	1948 to 1952	1953 to 1957	1958 to 1962	1963 to 1967	1968 to 1972	1973 to 1977	1978 to 1980	TOTAL
Asotin	0	0	0	0	0	0	0	0	0	0
Garfield	0	0	0	0	0	0	0	0	0	0
Columbia	0	0	0	0	0	0	0	0	0	0
Walla Walla	0	0	0	0	0	0	0	0	0	0
Benton	12	0	0	0	0	0	0	1	1	14
Franklin	0	0	0	0	0	0	0	0	0	0
Douglas	0	0	0	0	1	0	0	0	0	1
Grant	0	0	0	0	0	0	1	0	0	1
Adams	0	0	0	0	0	0	1	0	0	1
Whitman	0	0	0	0	0	0	2	0	0	2
Lincoln	0	0	0	0	0	0	0	0	0	0
Spokane	0	1	0	0	0	2	1	0	0	4
Pend Oreille	0	2	0	0	0	0	0	6	1	9
Stevens	0	0	0	0	0	0	0	0	0	0
Ferry	2	0	0	0	0	0	0	0	0	2
Okanogan	6	4	5	2	0	1	1	0	0	19
Chelan	5	2	0	0	0	1	0	0	0	8
Kittitas	17	3	4	2	5	21	37	21	8	118
Yakima	16	12	0	0	1	0	5	0	1	35
Klickitat	8	10	0	0	4	0	0	1	0	23

wandering individuals that were not from an established local population.

Because the geographic origins of the introduced red fox in Washington are largely unknown and probably diverse, assignment of these populations to established subspecies is unwarrented. It is doubtful also that anything significant can be gained by granting unique subspecific status to introduced populations of red foxes in Washington. Recognition of the fact that they are not indigenous would seem sufficient.

CHAPTER 2

DISTRIBUTION AND MORPHOLOGY IN THE PACIFIC NORTHWEST

The geographic distribution of the Cascade red fox includes the Cascade Mountains of southern British Columbia, Washington and Oregon (Bailey, 1936a; Hall, 1981), where it is restricted to subalpine meadows at high elevations. Throughout this region, however, populations of red foxes also occur at low elevations in habitats that are uncharacteristic for the subspecies. In Chapter 1, I argued that in Washington, red foxes occurring in the Puget Sound lowlands, the Columbia Basin and the north-eastern Okanogan Highlands are descended from introduced animals that were intentionally released for hunting purposes or had escaped from fur-farms in the early part of this century. Additionally, introduced red foxes were found to be restricted to habitat at low elevations near areas of human disturbance, while indigenous red foxes were confined to the less-disturbed meadows and parklands near the Crest of the Cascade Range and to the dry, open forests on its eastern slope. Neither form was found to occur in densely-forested habitat at mid-elevations west of the Cascade Crest.

The purpose of this chapter is to 1) extend my analysis of the distribution of red foxes in Washington to include indigenous and introduced populations of red foxes in British Columbia and Oregon, and 2) to test the appropriateness of the geographic ranges here defined using a multivariate analysis of cranial and dental morphology.

DISTRIBUTION IN BRITISH COLUMBIA AND OREGON

In British Columbia, where the red fox of western Canada, *V. v. abietorum*, the Rocky Mountain red fox, *V. v. macroura*, and the Cascade red fox, *V. v. cascadensis*, are reportedly parapatric (Hall, 1981), considerable confusion exists as to where distributional boundaries should be drawn. Bailey (1936a) depicted the range of *cascadensis* to extend only slightly above the south-central border of British Columbia, while *abietorum* occupied the northern portion of the Province and the south-central Interior Plateau between the Coast Mountains to the west and the Rocky Mountains to the east. Later workers (Cowan and Guiguet, 1965; Hall, 1981), maintained that records of red foxes from the eastern slope of the Coast Mountains in the Interior Plateau, and those from the Puget Sound lowlands near the mouth of the Fraser River, represent the northern extension of the range of *cascadensis*. Cowan and Guiguet (1965) also included south-central and south-eastern British Columbia within the range of *cascadensis*. The latter region, however, was considered by Hall (1981) and Bailey (1936a) to represent the northern extension of the range of macroura.

Cowan and Guiguet (1965) considered the range of abietorum to include all of northern and central British Columbia, except the coastal mainland near Queen Charlotte Island. Most of south-central British Columbia was considered to be an area in which the taxonomic status of red foxes was unknown. They believed it extremely likely that escaped fur-farm animals had confused the systematic status of red foxes in populated areas of the Province. Hall (1981), however, assigned red fox specimens from that region to abietorum.

In Oregon, distributional limits for subspecies of red foxes are similarly unclear. Bailey (1936a) in his revision of the North American red foxes, limited the range of cascadensis in Oregon to rocky areas at high elevations in the Cascade Mountains. In a monograph on the mammals of Oregon published the same year, Bailey (1936b) extended the range of cascadensis to include the north-western coastal region. This extension was based on historical reports of red foxes occurring at Fort Dalles (The Dalles) by Suckley and Gibbs in 1855, near the mouth of the Columbia River by Lewis and Clark in 1805 and near Tillamook on the coast by Fisher in 1897.

Fort Dalles was located near sea level on the Columbia River just east of the Columbia Gorge, which separates the Cascade Mountains of Washington and Oregon, and it was well below the elevational range of the Cascade red fox. Bailey (1936b) stated that Fort Dalles was a trading post where "large numbers of [red fox] skins...were...brought in... . Suckley examined 25 pelts in the possession of a trader and claimed that "on the Columbia, well dried, good skins can be readily purchased for 25 cents apiece..." (Suckley and Cooper, 1860). According to the notes of William Clark, "the silver fox is an animal very rare, even in the country he inhabits. We have seen nothing but the skins of this animal, and those were in the possession of the natives of the woody country below the Columbia falls, which makes us conjecture it to be an inhabitant of that country, exclusively" (Coues, 1893). This is the only reference made to red foxes in Oregon by Lewis and Clark. The information contained in these reports do not indicate that red foxes actually inhabited the localities where their pelts were seen or purchased. Because no other historical records of the occurrance of red foxes in this region were found, it is likely that these reports and the specimens seen by Fisher on the coast represent red foxes that were brought to these areas from the mountains by natives or white fur-trappers.

Livezey and Evenden (1943) described the den of a red fox which they found near Corvallis in the central Willamette Valley of western Oregon. They attributed the den to cascadensis, but its location in an oak woodland at low elevation makes this assumption doubtful. According to Graf (1947), no evidence of red foxes had ever been reported in the central Willamette Valley before 1940; and Bailey (1936b) made no mention of red foxes occurring there prior to that time. In the early 1940's, however, red foxes appeared in the area, and by 1945, one trapper reported taking 11 foxes near Albany (Graf, 1947), which is about 20 km northeast of the den described Livezey and Evenden (1943).

Ingles (1965) claimed that red foxes were native to Oregon in the forests at upper elevations of the Cascade Mountains, and that they were widely and firmly established in many counties in north-western Oregon as the result of introductions from the southern United States. In his accompanying distribution map, however, he made no distiction between indigenous and introduced populations of red foxes.

Maser, et al. (1981), reported that in western Oregon, red foxes were found along the northern Coast and in the Willamette Valley, as well as in the high Cascades. They speculated that the red fox may expand its range with the continued clearcutting of the Coast Range forests, but did not comment on the possibility that the populations at low elevations resulted from the introduction of red foxes into Oregon. According to Mace (1979), indigenous red foxes are now extinct in Oregon. He claimed that they once occurred in the northern Coast Range and in the Cascade, Blue and Wallowa Mountains, but have disappeared with human settlement of the region. All red foxes now present in Oregon were reported to be the descendents of animals introduced for hunting purposes in the Willamette Valley.

METHODS AND MATERIALS

Museums in the United States and Canada listed as potentially containing red fox specimens from the Pacific Northwest (Choate and Genoways, 1975), were visited or contacted by mail. Two hundred and sixty-seven specimens were available from museums. A list of these museums and the number of red fox specimens from the Pacific Northwest contained in each is included as Appendix A.

All collection sites were plotted on a 1:2,500,000 scale map of British Columbia, Washington and Oregon. Because all specimen-locations from Washington were depicted in Fig. 3, only localities for specimens from Washington used in the taxonomic analyses are indicated here.

Distributional boundaries for indigenous and introduced populations of red foxes in Washington were also taken from Fig. 3. Distributional boundaries for indigenous and introduced populations of red foxes in British Columbia and Oregon were drawn on the basis of habitat characteristics of the collection sites of museum specimens, and the known distributional limitations of indigenous and introduced red foxes in this region (Aubry, 1983).

A morphometric analysis based on cranial and dental measurements was then conducted to test the appropriateness of the distributional boundaries drawn. Only cranial and dental characters were used because pelage differences are not useful in distinguishing subspecies of the red fox in North America, due to the high degree of variability in fur color within populations (Churcher, 1957), and because the skulls of red foxes were better represented in museums than other specimen materials. Fifteen measurements were taken with a vernier caliper to the nearest tenth of a millimeter on a series of 127 adult crania. Skulls were judged to be adult if the basioccipital-basisphenoid suture was closed (Churcher, 1960). The measurements included:

1) <u>Total length</u>: From anteriormost point on premaxilla to posteriormost point on occipital crest.
2) <u>Condylobasal length</u>: From anteriormost point on premaxilla to posteriormost point on occipital condyles.

3) Zygomatic breadth: Greatest distance across zygomatic arches.

4) Palatal length: From anteriormost point of posterior edge of palatine to posteriormost point of alveolus of first incisor.

5) Post-palatal length: From anteriormost point of posterior edge of palatine to anteriormost edge of foramen magnum.

6) Palatal width: Width of palatine at the medial projection of the first molar.

7) Braincase bredth: Greatest distance across braincase.

8) Interorbital breadth: Least distance dorsally between orbits.

9) Post-orbital breadth: Least distance dorsally at constriction just posterior to the post-orbital processes.

10) Lyre breadth: Distance across temporal ridges at frontal-parietal suture.

11) Auditory bulla breadth: Greatest distance across auditory bulla.

12) Rostral breadth: Greatest distance across lateral sides of canine alveoli.

13) Maxillary tooth row: From anteriormost edge of canine to posteriormost edge of second molar.

14) Length of first molar: Greatest distance across long axis of first molar.

15) Length of fourth premolar: Greatest distance across long axis of fourth premolar.

Discriminant function analyses were then performed on various subsets of the available data, using the Biomedical Computer Program BMDP7M (Dixon and Brown, 1979). The usefullness of this technique for addressing problems in canid taxonomy is well established (e.g., Jolicoeur, 1959; Lawrence and Bossert, 1967; Rohwer and Kilgore, 1973; and Waithman and Roest, 1977), and detailed treatments of the theoretical and statistical basis of discriminant analysis can be found in these sources. A sexual dimorphism was found for the measurements taken in accordance with the findings of Churcher (1960). This enabled me to sex specimens with over 90% accuracy using discriminant analysis. Dummy variables were assigned to each sex and then included as a covariate in the discriminant functions to enable the sexes to be combined in a single analysis. Analyses were also conducted on males and females separately. Only specimens with complete measurements were used, as sample sizes were relatively small and missing values could not be estimated with confidence. Discriminant analyses were run in a stepwise fashion to include only those variables that contributed significantly to the discrimination (Partial F > 4.0).

RESULTS AND DISCUSSION

Distribution

In British Columbia, museum records of red foxes were from the northern boreal regions, the Interior Plateau and its surrounding foothills or the Puget Sound lowlands

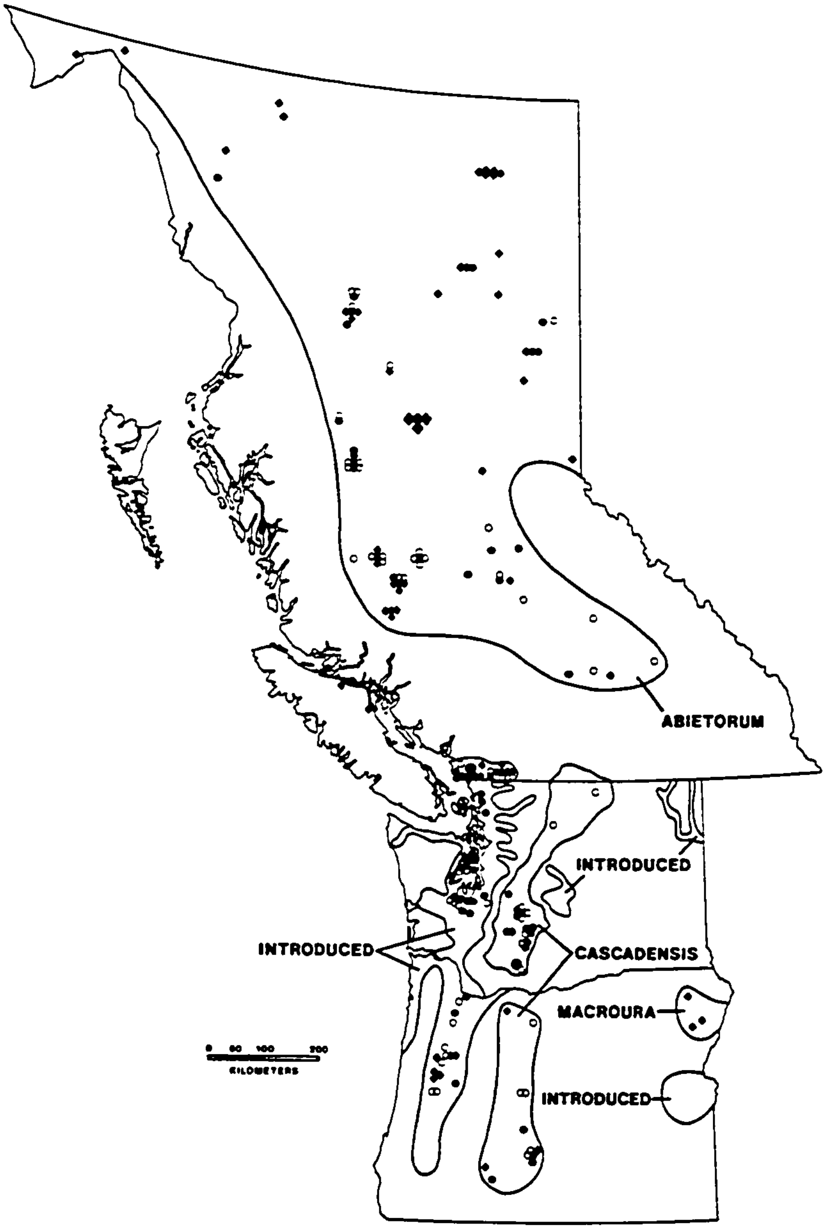

Figure 4. Museum specimen localities and distributional ranges of indigenous and introduced populations of red foxes in the Pacific Northwest. Solid circles represent adult male specimens, and open circles represent adult female specimens used in the morphometric analyses. Diamonds represent specimens not used in the analyses. Small symbols indicate one specimen, large symbols, five.

(Fig. 4). Museum records from the Interior Plateau are widely separated from those near Puget Sound and in the Cascades of Washington, yet are nearly continuous with museum records from northern areas of the Province. All specimens of red foxes from the Interior Plateau northward were assigned to abietorum. Foxes occurring in the Puget Sound lowlands of British Columbia are probably descended from red foxes introduced into western Washington (Aubry, 1983). No museum specimens from British Columbia were found that could be assigned to cascadensis, but on the basis of available favorable habitat, the range of cascadensis was drawn to include the northernmost portion of the Cascade Mountains in southern British Columbia. No specimens were found that would support assertions (Bailey, 1936a; Hall, 1981) that macroura occupies south-eastern British Columbia. Museum records of red foxes from the north-eastern coast of Vancouver Island indicate the presence of introduced foxes, but their distributional range is not known.

In Oregon, museum records were either from the high elevations of the Cascade Range and its eastern foothills, the Willamette Valley or the Wallowa Mountains in eastern Oregon. In accordance with my similar findings in Washingon, cascadensis clearly favors the drier, more open forests on the eastern slope of the Cascades over the wetter, denser forests on the western side. Because of this, the population of red foxes in the Willamette Valley is widely separated from the population in the Cascades. From habitat characteristics and the lack of historical records of the occurrence of red foxes there, the population in the Willamette Valley is considered to have been introduced.

Oregon State trapping records provided additional information on the distribution and history of red foxes (Oregon Dept. of Fish and Wildlife, 1946-1980). In the central Willamette Valley, red foxes have been reported in large numbers by trappers since the mid-1940's. In the northern parts of the Valley, red foxes have been trapped in appreciable numbers only since the early 1960's, and in the southern counties, it is only since the early 1970's that red foxes have been an important component of the yearly fur harvest. This indicates that red foxes were originally introduced into the central regions of the Valley, and have only recently colonized the northern and southern portions. State records also indicated the recent presence of red foxes in low numbers along the northern coast, in accordance with the findings of Maser, et al. (1981).

In the Cascade Mountains, the geographic distribution of red foxes cannot be easily determined. No museum specimen from that area post-dates 1939. State trapping records from counties which encompass the east slope of the

Cascades provided some insight into the distribution of red foxes. Only one trapping report and one museum specimen have been recorded from the eastern Cascade slope in northern Oregon. In southern Oregon, red foxes have consistently been reported in small numbers east of the Crest. Forests dominated by ponderosa pine attain their maximum extent in the southern counties (Franklin and Dyrness, 1973). As in Washington, indigenous red foxes find favorable conditions in these dry, open forests and are apparently still extant there, as well as in the meadows and parklands at high elevations.

In the Wallowa Mountains of north-eastern Oregon, three specimens, classified as macroura, were collected in 1923, 1924 and 1930. The lack of recent specimens or trapping-reports casts considerable doubt on the continued existance of indigenous red foxes in eastern Oregon.

Reports of trappers harvesting red foxes in large numbers in the Malheur River Valley near the Idaho border only in the last ten years, indicate the recent establishment of red foxes in that region. Both Mace (1979) and Maser, et al. (1981) reported the presence of red foxes there. The recent colonization of the Snake River Plain and cultivated areas of southern Idaho by red foxes has been documented by Fichter and Williams (1967), who suggested that these populations may have resulted from the accidental introduction of red foxes. The east-central Oregon population is most likely a westward extension of introduced populations currently inhabiting southern Idaho.

Morphometrics

cascadensis vs. Introduced Forms

The Columbia River forms the northern boundary of the distributional range of the gray fox, *Urocyon cinereoargenteus*, in Oregon. This river would therefore be expected to present a similar barrier to the movements of red foxes between Washington and Oregon. Since Cascade red foxes are restricted to habitat at high elevations, the low elevations in the Columbia Gorge would also restrict gene flow between the populations of Cascade foxes in Washington and Oregon. For these reasons, and because introduced populations in these regions are probably derived from diverse source populations, red foxes from Washington and Oregon were analyzed separately.

The discriminant analysis between introduced foxes and *cascadensis* from Washington, combining both sexes, was highly significant although a complete separation was not achieved (Fig, 5, Table 3). One likely source for the red foxes introduced into western Washington was Illinois (subspecies *fulva*). Merriam (1900) noted, that in cranial and dental characteristics, *cascadensis* was most similar to

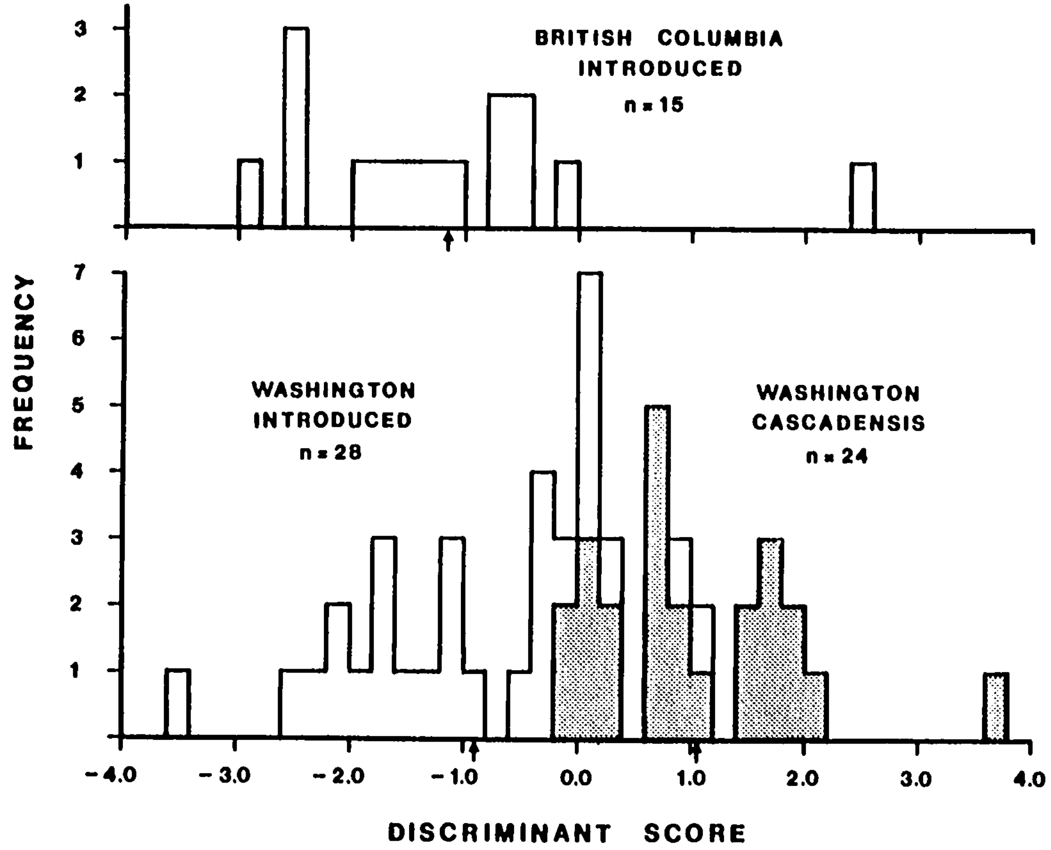

Figure 5. Lower graph: histogram of discriminant scores for introduced specimens from Washington (open bars) and cascadensis from Washington (stippled bars). Upper graph: histogram of discriminant scores for introduced specimens from British Columbia when included in the analysis as unknowns. Both sexes were used, and group means are indicated by arrows.

Table 3. Discriminant function computed for introduced red foxes from Washington vs. *cascadensis* from Washington. Both sexes were used.

Variable		Partial F	Character Coefficients
15	Length of 4th premolar	14.571	1.70800
10	Post-orbital breadth	7.525	-0.44717
7	Braincase breadth	6.627	0.40529
13	Rostral breadth	5.141	-0.50695
14	Length of 1st molar	4.691	-1.27646
Constant for males			-6.94515
Constant for females			-6.23615

Overall F = 7.313; d.f. = 6; P < .001

fulva. Consequently, the differences between the two groups might not be expected to be strong.

When specimens from the Puget Sound lowlands of British Columbia are classified, on the basis of the resulting discriminant function (upper graph, Fig. 5; Table 3), they fall almost completely within the range of the introduced population. Red foxes from the south-western corner of British Columbia are clearly not Cascade foxes, but belong to the introduced population of red foxes found throughout western Washington.

Similar analysis between introduced foxes and _cascadensis_ from Oregon again show a statistically significant separation (Fig. 6, Table 4). This provides additional evidence that red foxes in the Willamette Valley are descended from introduced animals.

abietorum vs. Washington cascadensis vs. Oregon cascadensis

Having identified introduced populations of red foxes in the Pacific Northwest, it was then possible to examine the relationships between indigenous populations in this region. In particular, since it is extremely unlikely that gene flow is occurring between populations of Cascade foxes in Washington and Oregon, the appropriateness of placing these two populations within a single subspecies must be evaluated.

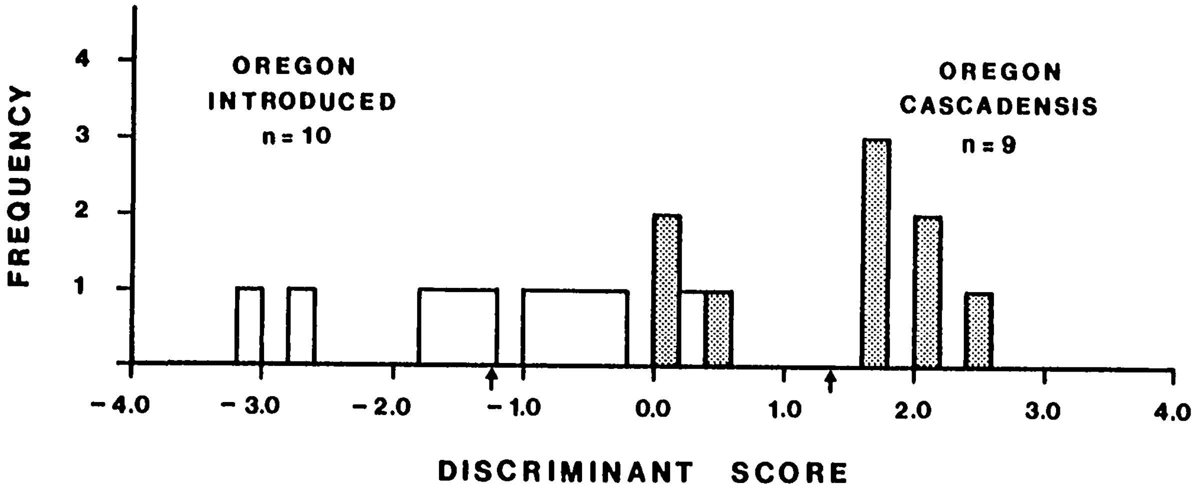

Figure 6. Histogram of discriminant scores for introduced specimens from Oregon (open bars) and *cascadensis* from Oregon (stippled bars). Both sexes were used, and group means are indicated by arrows.

Table 4. Discriminant function computed for introduced red foxes from Oregon vs. _cascadensis_ from Oregon. Both sexes were used.

Variable	Partial F	Character Coefficients
3 Zygomatic breadth	26.976	-0.69177
7 Braincase breadth	8.501	0.77505
Constant for males		13.23934
Constant for females		11.67944

Overall F = 9.550; d.f. = 3; P < .001

The results of a discriminant analysis between *abietorum*, Washington *cascadensis* and Oregon *cascadensis*, combining both sexes, is shown in the upper graph in Fig. 7. The overlap which resulted between the groups was extensive, and provided no basis for distinguishing one population from another. When females were analyzed separately (lower graph, Fig. 7), the separation achieved was even poorer, resulting in an almost complete overlap between *abietorum* and the two *cascadensis* groups. Because only one variable contributed significantly to the discrimination, only the first canonical variable could be derived.

When males were analyzed separately, a complete separation was achieved between *abietorum* and both *cascadensis* groups, while a complete overlap between Washington and Oregon *cascadensis* resulted (Fig. 8, Table 5). It is only by using the males that *abietorum* can be distinguished from *cascadensis*, whereas the two *cascadensis* populations cannot be differentiated.

A strong similarity between Cascade foxes in Washington and Oregon was noted by Merriam (1900), and convinced him to place them within a single taxon. Similar montane habitat in the Cascade Mountains of Washington and Oregon has presumably operated to maintain the morphological similarity between these forms. Thus, they can be viewed as ecotypes due not to the continued exchange of genetic material, but

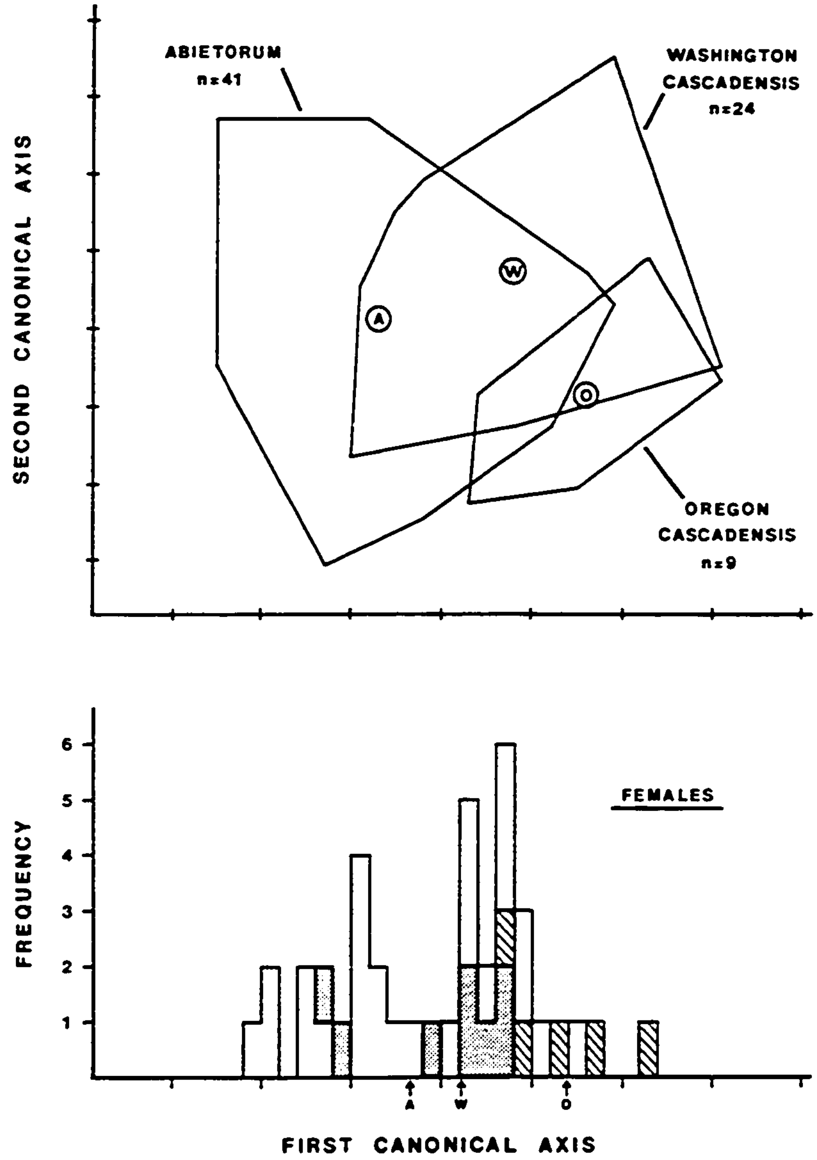

Figure 7. Upper graph: outline of outermost points from graph of discriminant scores for *abietorum*, *cascadensis* from Washington and *cascadensis* from Oregon. Both sexes were used, and circled symbols indicate group means. Lower graph: histogram of discriminant scores for *abietorum* (open bars); *cascadensis* from Washington (stippled bars) and *cascadensis* from Oregon (cross-hatched bars). Females only were used, and arrows indicate group means.

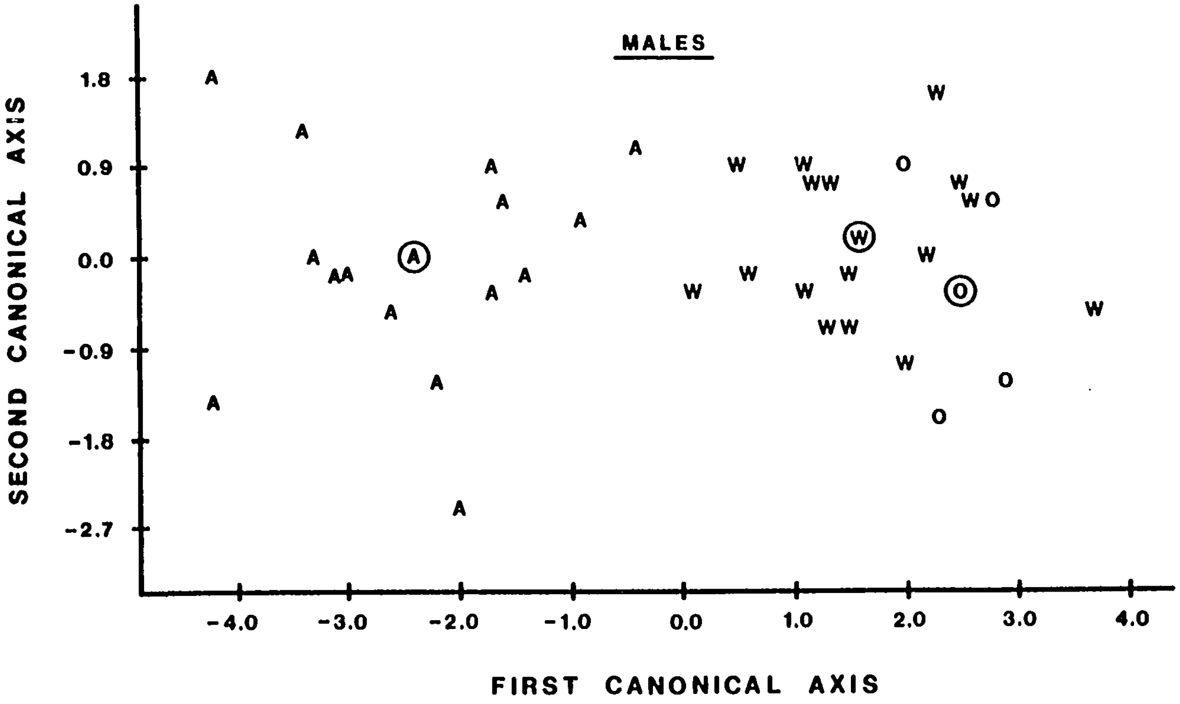

Figure 8. Graph of discriminant scores for *abietorum* (A's), *cascadensis* from Washington (W's) and *cascadensis* from Oregon (O's). Males only were used, and circled symbols indicate group means.

Table 5. Discriminant function computed for *abietorum* from British Columbia vs. *cascadensis* from Washington vs. *cascadensis* from Oregon. Males only were used.

Variable	Partial F	Character Coefficients (X) First Canonical Axis	 (Y) Second Canonical Axis
6 Palatal width	20.586	-1.04439	0.50536
15 L. 4th premolar	10.671	1.04439	1.34479
4 Palatal length	5.421	-0.29094	-0.15865
14 L. 1st molar	4.079	-1.51399	-1.08056
Constant		29.23310	-4.88126

Overall F = 10.334; d.f. = 8; P < .001

rather to a common origin and similar environmental influences.

Male *abietorum*, however, are distinctly different from male *cascadensis* (Fig. 8). *Abietorum* occupies boreal and sub-boreal habitats, and does not occur in the high mountains. Clearly, in terms of both morphology and preferred habitat, these populations of red foxes represent separate subspecies. The southernmost specimens from British Columbia are somewhat unique in that they occur in areas of human settlement in habitats characterized by dry forests of ponderosa pine and Douglas fir, whereas those to the immediate northwest occupy the aspen parklands. In light of Cowan and Guiguet's (1965) caveat that introduced animals may have confused the taxonomy of red foxes in this region, caution should be exercised before assigning specimens from this area to *abietorum*. However, inasmuch as no information is available on the introduction of red foxes into British Columbia, and since the one specimen from that region (Fig. 4) included in the discriminant analysis was very similar in size and shape to other *abietorum* skulls, these specimens have been tentatively assigned to that subspecies.

Abietorum males are larger than *cascadensis* males for all measurements taken except lyre breadth and post-orbital breadth (Tables 6 and 7). Females are larger than males for

Table 6. Means standard deviations and mean differences of 15 cranial and dental measurements taken on adult male and female specimens of V. v. abietorum. Sample sizes are in parentheses, measurements in millimeters.

	V. v. abietorum				
	Males (15)		Females (26)		Diff. Between
Measurement	Mean	S.D.	Mean	S.D.	Means
Total length	150.7	5.16	140.2	4.60	10.5
Condylobasal length	145.5	4.62	135.9	4.08	9.6
Zygomatic breadth	78.2	3.35	73.1	2.71	5.1
Palatal length	72.0	2.49	67.6	2.60	4.4
Post-palatal length	64.2	2.34	59.4	2.05	4.8
Palatal width	19.3	1.12	17.1	1.31	2.2
Braincase breadth	48.9	1.37	48.3	1.11	0.6
Interorbital breadth	28.0	1.78	26.3	1.24	1.7
Post-orbital breadth	23.2	1.81	23.4	1.19	-0.2
Lyre breadth	7.9	2.84	9.6	2.22	-1.7
Auditory bulla breadth	41.6	1.86	39.0	1.54	2.6
Rostral breadth	24.2	1.19	23.1	1.07	1.1
Maxillary tooth row	68.3	2.70	63.5	2.26	4.8
Length of first molar	13.2	0.57	13.0	0.43	0.2
Length of fourth premolar	15.5	0.67	15.3	0.52	0.2

Table 7. Means, standard deviations and mean differences of 15 cranial and dental measurements taken on adult male and female specimens of V. v. cascadensis. Sample sizes are in parentheses, measurements in millimeters.

	V. v. cascadensis				
	Males (20)		Females (13)		Diff. Between
Measurement	Mean	S.D.	Mean	S.D.	Means
Total length	143.2	3.60	137.9	4.79	5.3
Condylobasal length	137.4	3.62	132.0	4.22	5.4
Zygomatic breadth	73.2	3.26	70.5	2.68	2.7
Palatal length	67.6	2.08	65.5	2.23	2.1
Post-palatal length	61.3	2.02	58.0	2.64	3.3
Palatal width	17.1	0.91	16.7	0.89	0.4
Braincase breadth	48.1	0.96	48.0	1.61	0.1
Interorbital breadth	26.0	1.34	25.1	1.18	0.9
Post-orbital breadth	22.8	1.15	23.8	1.79	-1.0
Lyre breadth	9.3	2.26	11.9	3.39	-2.6
Auditory bulla breadth	39.2	1.37	38.9	1.26	0.3
Rostral breadth	22.5	1.06	21.9	0.92	0.6
Maxillary tooth row	64.6	2.03	62.5	2.35	2.1
Length of first molar	12.7	0.42	12.5	0.50	0.2
Length of fourth premolar	15.4	0.58	14.7	0.51	0.7

lyre breadth and post-orbital breadth in both subspecies. A slightly lesser tendency for saggital crest formation in female red foxes as compared to males (Churcher, 1957), probably accounts for their wider lyre breadths. As the mean differences show (Tables 6 and 7), the relative differences between male and female *abietorum* are greater than those betweeen male and female *cascadensis* for most of the measurements. One possible explanation for the larger relative differences between male and female *abietorum* is that sexual selection is operating more strongly on *abietorum* than on *cascadensis* males. This leads to the prediction that *abietorum* is more polygynous than *cascadensis*. Both monogamous and polygynous social groupings have been reported for the red fox in Europe (Macdonald, 1980). Sheldon (1949, 1950) speculated that observations of two females with separate litters occupying the same den in New York represented polygynous matings and Martin and Pils (1974) described a communal den in Wisconsin which they interpreted to represent a polygynous social unit. It may prove fruitful for ecologists studying red foxes in British Columbia to be aware of the possibility of polygyny. The reasons for variation in social behavior among red foxes are believed to be related to habitat (Macdonald, 1980), but the ecological factors which may favor one social system over another are not known.

The identification of red fox specimens of unknown taxonomic affinity from the Pacific Northwest is difficult and may require the application of a multivariate analysis of cranial and dental morphology. Characteristics of habitat and physiography are critical factors determining the distributional extent of populations of red foxes from this region. Introduced and indigenous red foxes were restricted in the range of habitats they successfully occupied, and there was no indication that these populations intergraded geographically. It is therefore proposed that specimens from localities occurring within the geographic ranges depicted here, including those currently contained within museums, be assigned accordingly. Specimens from areas outside of these ranges should be classified on the basis of the discriminant functions presented here, if possible, but otherwise be identified by characteristics of habitat and elevation. Introduced red foxes occupy generally non-forested habitat at low elevations in areas of human disturbance. Indigenous red foxes in Washington and Oregon (cascadensis) occupy sub-alpine meadows and parklands at high elevations and the open forests on the eastern slope of the Cascade Mountains. Indigenous red foxes in British Columbia (abietorum) occupy the boreal and sub-boreal regions in the north and the aspen parklands and dry forests in the south.

CHAPTER 3

QUATERNARY ZOOGEOGRAPHY IN NORTH AMERICA

PLEISTOCENE HISTORY AND DISTRIBUTION

The oldest known fossils of the red fox in North America were found in central Alaska, and date from the penultimate or Illinoian glaciation of the Pleistocene (Péwé and Hopkins, 1967). A specimen found in southern Alberta has been attributed to the Sangamon interglacial period (Churcher, 1970). All other Pleistocene fossils of this species were found in deposits of Wisconsinian age, either in the unglaciated regions of central Alaska and the Yukon or in the continental United States, south of the margin of glacial ice (Fig. 9).

These records suggest that red foxes colonized North America during the Illinoian glacial period by way of the Beringian land bridge (see also Kurtén and Anderson, 1981). Following the retreat of Illinoian glaciers, red foxes moved south during the Sangamon interglacial at least as far as southern Alberta. Although an ice-free corridor apparently existed in the Yukon Territory, north-eastern British Columbia and northern Alberta in mid-Wisconsin time (Hopkins, 1967), by the late Wisconsin, North American red foxes were divided into two refugial populations: one in the Beringian region to the north and the other in the

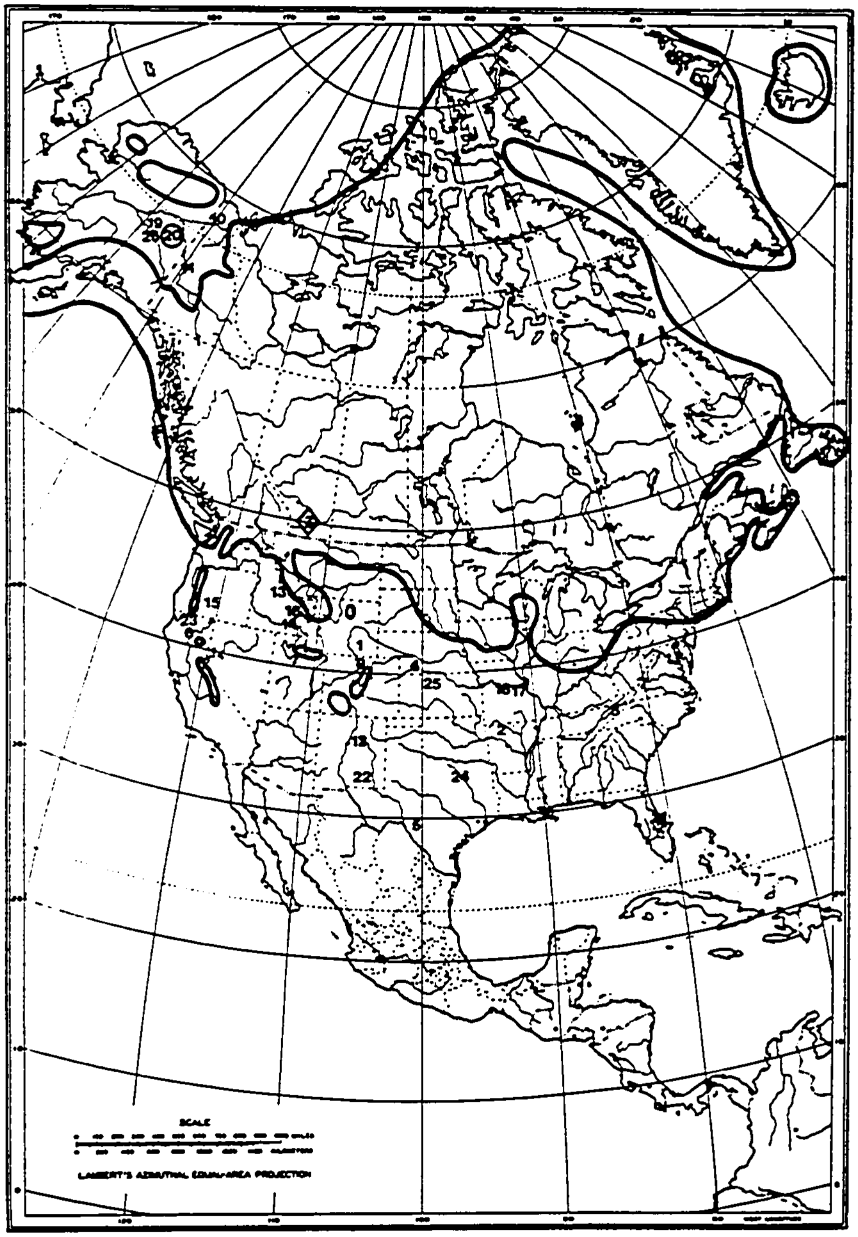

Figure 9. Geographical distribution of Wisconsin glacial ice and Pleistocene fossil localities of the red fox in North America. The circled record is of Illinoian age, the one indicated with a diamond is of Sangamonian age and all other records are of Wisconsinian age. The source for each record is referenced by number in the Literature Cited section.

unglaciated areas south of the ice sheets.

Published Wisconsinian records for the red fox in Beringia have existed only since the mid-1970's (Péwé, 1975; Harington, 1977). Before these fossils were described, Macpherson (1965) speculated that all modern populations of the red fox in North America were derived from a southern refugial population because he believed that red foxes did not survive the Wisconsin glaciation in Beringia. The fossil record clearly demonstrates the inaccuracy of this interpretation (Fig. 9). Red foxes did not become extinct in Beringia during Wisconsin time, nor are there ecological or zoogeographical rationales for explaining such an event. Red foxes colonized North America during the preceding glacial phase, which was of greater severity than the Wisconsin glaciation (Hopkins, 1967), and were therefore clearly capable of surviving in a periglacial environment. During most of Wisconsin time Alaska was a biogeographic province of Siberia rather than North America (Hopkins, 1967). Thus, even if red foxes did become extinct in Alaska in the early Wisconsin period, due to adverse climatic changes, colonization from Asia would have again taken place once the Beringian land bridge was reestablished.

HOLOCENE DISTRIBUTION

The zoogeographical history of the red fox in North America is complicated by the fact that European red foxes were introduced into the eastern coastal regions of the United States in the mid-1700's (Churcher, 1959), and subsequently transplanted within North America, especially in the West (Grinnell, et al., 1937; Ingles, 1965; Aubry, 1983). Zoogeographical analyses must therefore proceed from a consideration of the distribution of red foxes before the advent of European settlement, rather than from present-day distributional patterns.

Churcher (1959) examined the historical literature and concluded that red foxes were native to North America north of latitude 40° or 45° N in the east. South of this region, dense tracts of hardwood forest did not provide suitable habitat for the red fox, but did favor the occurance of the gray fox. Extant populations of the red fox in the eastern United States were presumed by Churcher to have been derived from the spread of red foxes introduced by European settlers (and possibly the immigration of indigenous foxes from the north) into this region following the alteration of habitat brought about by human land-use practices. Archaeological evidence supports this conclusion. According to Guilday, et al. (1978), "Only gray fox remains occur in late Pleistocene archaeological sites from Pennsylvania on south in eastern North America. The red fox appears to have been absent from the eastern forests during most of Holocene times...".

In the West, red foxes were introduced and have become established in a number of disturbed areas at low elevations. I have shown in Chapter 1 and elsewhere (Aubry, 1983) that several populations of red foxes currently extant in Washington were derived from individuals that were either intentionally introduced or escaped from fur-farms. I argued in Chapter 2 that populations of red foxes in south-western British Columbia, Oregon, and probably southern Idaho, have been similarly introduced; and in California, the presence of introduced red foxes in the Sacramento Valley has long been recognized (Grinnell, et al., 1937; Ingles, 1965). Indigenous red foxes in the western United States are confined to the meadows and open forests at high elevations in the Cascade, Sierra Nevada and Rocky Mountains.

The hypothetical distribution of red foxes in North America prior to colonization by Europeans, is shown in Figure 10. Red foxes occupied essentially two regions: the tundra and boreal forests of Canada and Alaska, and the alpine and sub-alpine meadows and parklands in the western mountains. Similar conclusions regarding the Holocene distribution of red foxes were reached by Churcher (1959)

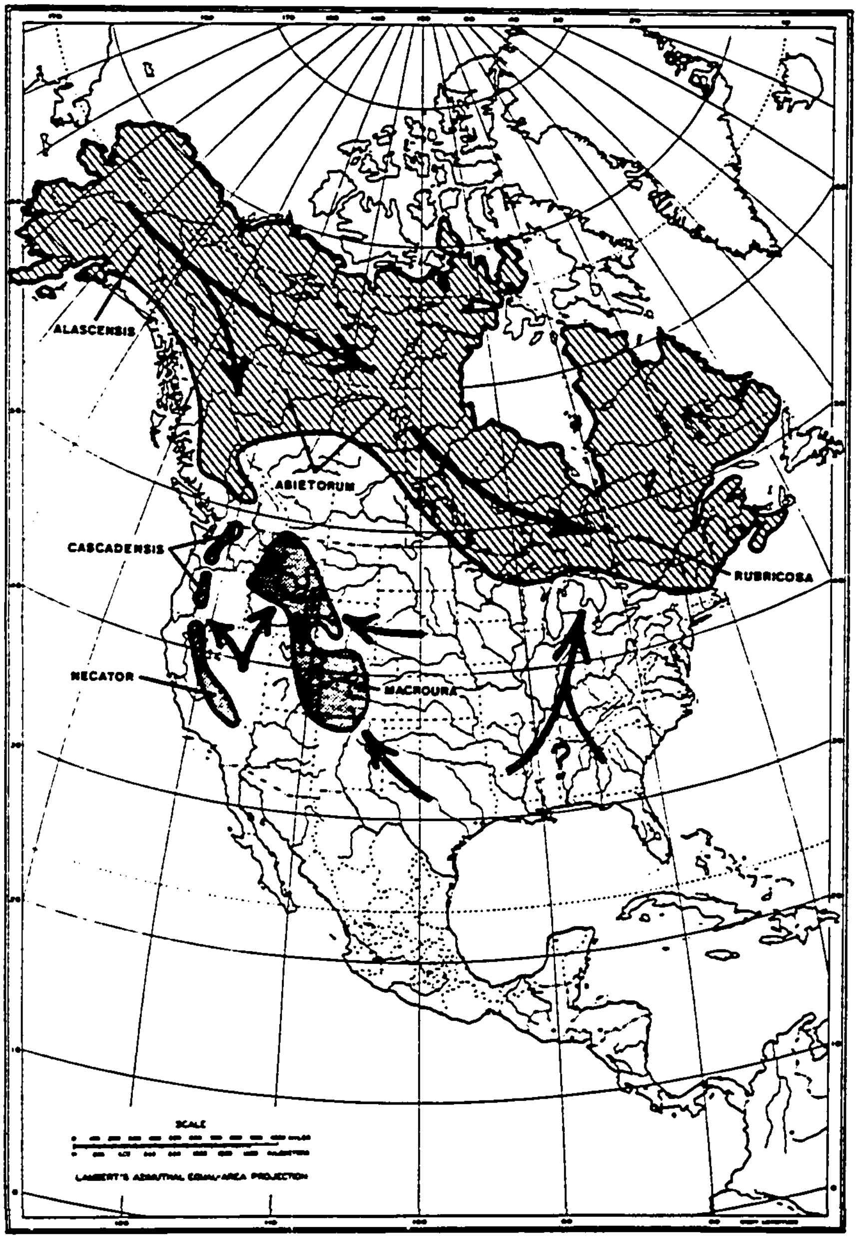

Figure 10. Hypothetical distribution of the red fox in North America during the Holocene, with postulated sources of origin and post-glacial patterns of colonization. Stippled areas represent populations believed to have been derived from the southern refugial population, and the cross-hatched area indicates populations believed to have been derived, at least in part, from the northern refugial population.

and Anderson (1968). The indigenous red fox of North America can therefore be considered to have been primarily a tundra, boreal forest or montane species.

ZOOGEOGRAPHICAL HYPOTHESIS

Red foxes occupied much of the continental United States during the Wisconsin Period, including broad areas from which they disappeared in the Holocene (Figures 9 and 10). At the height of Wisconsin glaciation, the distribution of major vegetation types was markedly different from present conditions. Many authors (e.g., Dillon, 1956; Martin, 1958 and Dorf, 1959) have postulated that during Wisconsin time, these vegetation zones existed much further south and were restricted in extent. In the East, there was apparently a continuous, narrow belt of tundra bordering the southern margin of glacial ice. South of this vegetation zone were wider bands of boreal forest and deciduous forest. A similar pattern occurred in the West, although climatic modifications resulting from the presence of high mountain ranges there greatly complicate a reconstruction of Wisconsin vegetation zones.

The presence of extensive regions of tundra and boreal forest south of the ice presumably enabled red foxes to maintain a broad distribution in the United States during

Wisconsin time. As the glaciers retreated and continental climates warmed, these vegetation zones were reestablished in the north and expanded their distribution.

With the disappearance of subarctic and cool-temperate conditions in the eastern United States, and the prey species which were dependent upon them, red foxes there either followed the retreating glaciers northward into Canada or became extinct. In the West, however, subalpine meadows at the upper elevations of the major mountain ranges provided a southern refugium of favorable habitat which was colonized by red foxes and other species with similar climatic affinities, such as the pika, *Ochotona princeps* (Hibbard, et al., 1965).

As the continental ice sheets retreated and sea level rose, the Bering Strait was reestablished. Alaska was then separated once more from Siberia and the northern refugial red foxes became a component of the North American fauna. When Canada was revegetated by boreal forests and tundra, this northern population expanded its range south-eastward and colonized most of Canada except the Rocky Mountain and Great Plains in the southwest.

While indigenous populations of the red fox in eastern Canada may reflect a mixture of the southern and northern refugial populations, it seems likely that the montane red foxes in the western United States represent a pure remnant of the southern refugial population; and that Alaskan, and north-western and central Canadian red foxes are derived from the northern refugial population.

MORPHOLOGICAL EVIDENCE

Variation in the North American red fox was originally investigated by Merriam (1900), who recognized ten species and two subspecies, all of which were later given subspecific status by Bailey (1936b). Churcher (1959) conducted an extensive re-evaluation of cranial and dental variation in North American and Eurasian red foxes. As a result of this work, all red foxes were combined within a single species, *Vulpes vulpes*.

Churcher (1957) also revised the North American subspecies, eliminating three previously recognized forms and redrawing the distributional boundaries of others; in particular, the placement of central Canadian red foxes into the subspecies *abietorum* instead of *regalis*. His results, which represent the most complete and reliable analysis to date, are as follows: *harrimani* is found on Kodiak Island in southwest Alaska; *alascensis* occupies Alaska, the Yukon and the western Northwest Territories; *abietorum*, the northern regions of British Columbia, Alberta, Saskatchewan, Manitoba and the south-eastern Northwest Territories;

rubricosa, the James Bay region of Ontario, northern Quebec, Newfoundland, Nova Scotia, Prince Edward Island and New Brunswick; *fulva*, the eastern United States east of the Mississippi River; *regalis*, the eastern United States west of the Great Lakes and the Mississippi River; and *necator*, *cascadensis* and *macroura* are restricted to high-elevation habitats in the Sierra Nevada, Cascade and Rocky Mountains, respectively.

The south-eastern subspecies, *fulva* and *regalis*, occupy regions that have only recently been colonized by red foxes. These forms are at least partly derived from introduced animals, and are not considered further here. Neither is *harrimani*, because it is a restricted, insular subspecies that may also contain introduced elements (Roest, pers. comm.). Thus, prior to European immigration, North American red foxes comprised six major forms: *alascensis* in the Northwest, *abietorum* in western and central Canada, *rubricosa* in eastern Canada and *necator*, *cascadensis* and *macroura* in the mountains of the western United States (Fig. 10).

Examining the size of red foxes from Alaska south-eastward through central Canada to eastern Canada, a continuous cline can be seen. Individuals of *alascensis* and British Columbian *abietorum* are large, central Canadian *abietorum* are somewhat smaller, and *rubricosa* are the smallest. The subspecies necator, cascadensis and macroura, however, are not part of this cline. These populations are restricted to the high elevation meadows and open forests of the western mountains and do not intergrade geographically with Canadian red foxes (Fig. 10). Furthermore, these mountain foxes are all small forms, even smaller than rubricosa (Merriam, 1900; Churcher, 1957; Roest, 1977; pers. comm.; Aubry, unpubl. data).

Most Pleistocene fossils of the red fox are fragmentary and provide little basis for assessing the relative sizes of Wisconsinian red foxes. However, a few sources do provide skull measurements for selected specimens. A late Pleistocene cranium from the Old Crow River in the Yukon Territory was described by Harington (1977). This specimen had a condylobasal length of 150.0 mm, which proved to be larger than most modern specimens from that region with which it was compared. Anderson (1968) listed average measurements for a large series of Wisconsinian fossils of the red fox from south-eastern Wyoming. Three crania were complete enough to enable measurements of total length, resulting in an average length of 132.1 mm. Using a conversion factor of 0.96 to arrive at condylobasal length (Roest, pers. comm.), gives an average of 126.8 mm. These crania averaged about 5 mm smaller than modern specimens from Colorado, whose measurements were also provided.

DISCUSSION

There are at least two possible interpretations of the observed patterns. The first, and most likely one, is that red foxes did not become extinct in eastern North America following the retreat of Wisconsin glaciers. Rather, they moved into eastern Canada as favorable habitat shifted northward with climatic warming. Populations of red foxes in the western United States maintained a southern distribution in the meadows and forests at high elevations of montane regions. The southern refugial red foxes were small in size, and gave rise to the uniformly small red foxes in the western mountains. As Canada was revegetated, the large red foxes in the northern refugium spread south-eastward while the small red foxes of eastern Canada extended their range northward. These two previously disjunct populations established sympatry in central Canada, and produced an intergrading cline in size across Canada and Alaska.

A second interpretation assumes that red foxes in the eastern United States became extinct in early Holocene time. All Alaskan and Canadian populations were therefore derived solely from the northern refugial population when it extended its range south-eastward as favorable habitat expanded in the Holocene. The observed cline in size is explained as an example of Bergmann's Rule, in which more moderate climatic conditions in the southern latitudes have favored the evolution of smaller foxes. Given the long-range dispersal abilities of red foxes and their general adaptability, it seems unlikely that Eastern red foxes would have been unable to colonize eastern Canada following glacial retreat. Furthermore, there is little validity to Bergmann's Rule (McNab, 1971) and such latitudinal gradients in size are better explained by alternative hypotheses, especially when the time available for the evolution of such a gradient has been so short.

In either case, there is compelling zoogeographical and morphological evidence that the western mountain foxes were derived solely from the southern refugial population. In southern British Columbia, the ranges of the Canadian and montane red foxes come into close contact (Fig. 10), yet sympatry does not occur. The mountain foxes are restricted to high-elevation habitats in the Cascade and Rocky Mountains, while abietorum occupies the boreal forests and aspen parklands of northern and south-central British Columbia. Red foxes from British Columbia are among the largest in North America, whereas the mountain foxes are the smallest. In light of the distribution of refugial populations during Wisconsin time, the sharp discontinuity in size between these two nearly parapatric groups strongly supports the view that they were derived from different ancestral populations that had been isolated from each other throughout the last glaciation.

CHAPTER 4

ECOLOGICAL RELATIONSHIPS IN WASHINGTON

Red foxes in the western mountains of the United States are unique among North American populations. Earlier chapters have shown that they are restricted to subalpine habitat at high elevations and do not intergrade geographically with indigenous or introduced populations from habitat at low elevations. Furthermore, as a group they are morphologically distinct being smaller, on average, than all other indigenous populations in North America. Their unique ecological and morphological attributes are best explained in light of their zoogeographical history. All three recognized subspecies of montane red foxes (*cascadensis*, *necator* and *macroura*) are derived solely from a population of small red foxes that was isolated in the southern ice-free refugium during the last glaciation. As the ice retreated, alpine habitat in the western mountains provided a southern refugium of cold climatic conditions within which red foxes persisted. All other indigenous populations in North America are derived, at least in part, from a northern population of large red foxes that was isolated in Beringia during the last glaciation.

The remoteness of their habitat and their historically low population numbers (Dalquest, 1948), have contributed to a virtual lack of information on the ecological relationships of the mountain foxes. No long-term field studies have ever been conducted. Only one source, Taylor and Shaw's (1927) work on the mammals and birds of Mt. Rainier National Park, provided first-hand information on the ecology of the Cascade red fox in Washington. They described the Cascade fox as occurring most abundantly in the subalpine zone above 1,500 m elevation, especially along ridgelines at or a little above treeline. They believed the Cascade fox to be more common at high elevations than was generally supposed, and reported a den known to have been active in 1919 near Paradise on the southern slope of the mountain. Some scats were examined, however neither the quantity nor the date of collection was given. These scats contained mainly insects, fruits, leaves and other plant parts. No vertebrate remains were found.

The objective of my research was to gather basic ecological information on the Cascade red fox in Washington. Parameters of particular interest were home range, seasonal movement patterns, reproductive ecology and food habits. This study will establish a data base on the ecology of Cascade red foxes, and help to provide a means by which informed management decisions regarding these animals may be made. It is also hoped that this study will encourage further research on these unique and little-known carnivores, and by doing so help to insure that this species remains a constituent of the indigenous Washington fauna.

THE STUDY AREA

The study area was located in the north-eastern corner of Mt. Rainier National Park and that portion of the Mt. Baker-Snoqualmie National Forest that lies between the north-eastern boundary of the Park and the Cascade Crest (Fig. 11). This area is located at approximately 46° 54' to 47° 00' N latitude and 121° 26' to 121° 40' W longitude, and encompasses an elevational range of over 1,200 m: from 850 m near the town of Silver Springs to 2,100 m on the Sourdough Ridge near Sunrise in Mt. Rainier National Park.

This area was chosen for several reasons: sighting reports of the Cascade red fox in the subalpine meadows of Mt. Rainier are more numerous than in any other area in the State (see Fig. 3); elevations were high enough to insure that only Cascade and not introduced red foxes would occur there; and the presence of numerous residents in the area (both Park Service personnel and private individuals) increased the likelihood of receiving reports of fox-sightings during the course of the study.

Both of the areas in which field work was conducted (Fig. 11) contain extensive subalpine meadows, within which research efforts were concentrated. The Yakima Park study

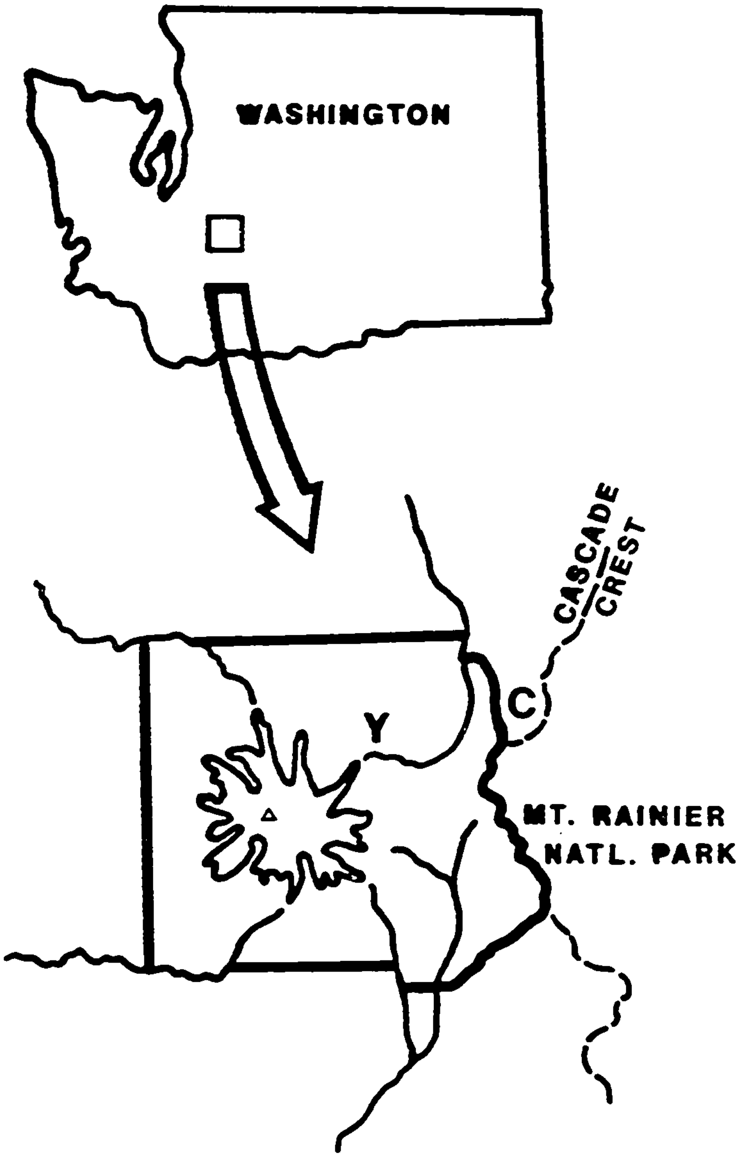

Figure 11. Location of study areas. The large 'Y' indicates the Yakima Park study area and the large 'C' indicates the Crystal Mountain study area.

area is located at approximately 1,800 to 2,100 m elevation, while the Crystal Mountain study area ranges from 1,200 to 2,000 m elevation.

Mt. Rainier lies in the Pacific Coast zone, and has a temperate, maritime climate producing generally warm, humid conditions. Mean minimum temperature for January is -7.0° C, while mean maximum temperature for July is 22.5° C (Franklin and Dyrness, 1973). Annual precipitation ranges from 25.5 to 30.5 cm, but occurs primarily from November to April resulting in a well-defined summer drought. The northeast section of the Park lies in the rain shadow of Mt. Rainier and is therefore generally drier and warmer than other sides (Taylor, 1922). In the high elevations of the subalpine zone, much of the annual precipitation falls as snow, which may remain on the ground from November through June.

Vegetationally, these subalpine meadows belong to the parkland sub-zone of the *Tsuga mertensiana* zone defined by Franklin and Dyrness (1973), which is a mosaic of forest patches and subalpine meadows. Major tree species are mountain hemlock, *Tsuga mertensiana*; subalpine fir, *Abies lasiocarpa*; Pacific silver fir, *Abiess amabilis*; and Alaska yellow cedar, *Chamaecyparis nootkatensis*. At the upper elevations of Yakima Park, particularly on exposed ridges, whitebark pine, *Pinus albicaulis*, is an important associate.

The subalpine meadow communities of Mt. Rainier have been extensively studied by Henderson (1974), who classified the Yakima Park meadows as a Dry-Grass vegetation zone. Such meadows are characterized by the dominance of mountain bunchgrass, *Festuca viridula*, and generally occur on well to excessively well-drained glacial soils or on residual soils on steep slopes. Soils in the Yakima Park area are derived primarily from the Evans Creek glacial drift which was deposited by alpine glaciers between 15,000 and 20,000 yrs. B.P. This drift occurs throughout the Park, but mostly above 1,370 m elevation and predominantly in the northeast section of the Park. The soil is usually stony, loose and well-drained with a deep profile (Henderson, 1974).

The most common plant community in Yakima Park is the *Festuca/Lupinus* type. This community is dominated by mountain bunchgrass and broadleaf lupine, *Lupinus latifolius*, with lesser occurences of Gray's lovage, *Ligusticum grayi*; American bistort, *Polygonum bistortoides*; western pasqueflower, *Anemone occidentalis*; western paintbrush, *Castilleja parviflora*; and Cascade aster, *Aster ledophyllus*.

Some of these bunchgrass-dominated meadows have resulted from the effects of fire, but Henderson (1974) does not consider fire to have been a major ecologic factor in their creation and maintenance. Northern pocket gophers, Thomomys talpoides, are the most conspicuous small mammals in these meadows and their burrowings keep the soils in a constant state of disturbance.

METHODS AND MATERIALS

Field work was initiated from July to October of 1979 in the Yakima Park area of Mt. Rainier National Park. The road to Yakima Park is closed during the winter, and extreme weather conditions during the winter of 1979/1980 hindered attempts to work during the first year. Numerous reports of Cascade red foxes occurring in the Crystal Mountain area of the Mt. Baker-Snoqualmie National Forest, and its accessibility in the winter, convinced me to establish an additional study area there from July to October of 1980. Red foxes were successfully trapped and equipped with radio-transmitters only in the Crystal Mountain area during this second field season. Consequently, the third field season from January to November of 1981, was conducted primarily in the Crystal Mountain study area. The ease of access to this area permitted me to monitor study animals throughout an entire year, and enabled the collection of a series of scats during all months of the year.

Trapping was conducted in the Yakima Park area during the summer of 1979, and in both study areas during the summer of 1980. Red foxes were trapped with No. 2 Victor coil spring steel traps. These traps were modified in an effort to reduce the risk of injury to captured animals. Welds 5 mm thick were placed on the inner surface of one jaw to prevent it from closing completely. In addition, the traps were padded by gluing strips of rubber cut from bicycle inner tubes around each jaw. These efforts were successful; only minor injuries were sustained by a few captured animals, while the majority of trapped foxes were completely unharmed. Traps were placed in dirt-hole bait sets using various malodorous materials and commercial fox urine as lures. Traps were secured by wiring them to wooden stakes which were then driven into the ground underneath the trap. Traps were checked twice each day, once in the morning and again in the evening, to minimize the amount of time captured animals were held. Captured foxes were subdued with a Ketch-all pole equipped with a noose on the end and injected intramuscularly with ketamine hydrochloride. Dosages used were 100 mg for adult red foxes and 50 mg for juveniles, with some variation depending upon the condition of the animal. This dosage will immobilize a red fox for 30 to 45 minutes, which was usually enough time to work the animal. In a few instances, additional injections were necessary, but in no cases were any problems encountered from the use of this drug. Immobilized foxes were first weighed and measured. A list of weights and measurements for captured Cascade red foxes is included as Appendix B. A sample of about 10 cc of blood was then taken from the femoral artery. Samples of anti-coagulated whole blood, serum and blood smears were sent to the Pathologists Central Laboratory in Seattle, Washington for analysis. A complete set of photographs was taken, and a small, numbered Roto-tag was attached to one ear. Radio-transmitters were then attached around the neck of each study animal. Transmitters used during the first field season were manufactured by Telemetry Systems, Inc., while hermetically sealed transmitters manufactured by Telonics, Inc., were used during the second field season. The latter collars performed exceptionally well, lasting even longer than their 12 to 14 month battery-life expectancy. When work on each fox was completed, it was placed in a secluded spot in the shade and left alone for one to two hours, at which time I returned to check on its progress. In every case, the animal had left the area.

Radio-collared foxes were located once during the middle of each day when they were presumably resting, to increase the likelihood that the animal would remain stationary between radio-fixes. All radio-tracking was done on foot because the road system was not adequate for tracking with vehicles. As a result, each set of radio-fixes required two to three hours of hiking each day. The locations of collared foxes were determined by taking three or, in few instances due to adverse conditions, only two compass bearings on the source of the signal. The locations from which bearings were taken were permanently established and plotted onto base maps. Compass bearings of radio-fixes were then drawn on the base map. Triangulations, or the point where the three bearing lines intersected, identified the location of the animal. In many cases, small triangles or so-called error polygons were formed when the bearing lines failed to intersect precisely. If the triangle formed was small and clearly indicated the general locality of the animal, the center of the triangle was used as a location. If the triangle formed was larger than approximately one hectare, or if the bearing lines failed to intersect at all, the triangulation was discarded.

Home range size was determined by the minimum convex polygon method, in which the area contained within the smallest convex polygon that encompasses all of the locations is used as an estimate of home range (Mohr, 1947). This method does have a sample size bias, i.e. estimates of home range tend to increase with sample size, and also makes a priori assumptions about the shape of home ranges

(Anderson, 1982). Unfortunately, however, no home range estimation technique is free of problems. After reviewing various techniques, Anderson (1982) concluded, "the minimum convex polygon method seems the most appropriate for a quick approximate estimate of home range size".

During field work, efforts were made to search for active and inactive dens. One active den was located and was monitored with the use of a remote camera because its location in a dense stand of trees prevented visual observations without disturbing the occupants. The cameras used were Minolta XL-401 movie cameras with an automatic aperture, single-frame shutter capability and an intervalometer that could be set from 0 to 60 sec. These cameras were mounted into weather-proof wooden boxes with a window on one end, and pointed at a den opening. The intervalometers were set at 60 sec. and the cameras were left for three days, at which time a 50 ft. roll of movie film would be completely exposed. Strobe lights could not be used without disturbing the inhabitants; consequently, only daylight frames were properly exposed. By running the cameras continuously, however, the time of day each frame was exposed could be calculated.

Scats were collected by hiking or skiing along trails in each study area on a regular basis, usually every day in the summer and three days per week in the winter. Only by collecting scats on trails that have been previously cleared, can accurate estimates of the date of deposition be made. All canid scats were collected and placed in paper bags to facilitate drying. Information on locality and the estimated age of the scat were written on the outside of the bag.

Scats were identified to species on the basis of diameter and volume. Scats found near tracks or collected from study animals or carcasses provided insight into scat morphology. Red fox scats were about 1.5 cm in diameter and usually found in only one piece 7.5 to 10 cm long. Coyote scats were larger, averaging about 2 cm in diameter with a much greater volume. More than one piece was usually deposited, often resulting in a total length of 15 to 20 cm.

Scats were thoroughly dried and broken apart to identify contents. A reference collection of mammal skeletons and hair samples was established from the collections of the Burke Memorial Washington State Museum in Seattle, Washington. Small mammal remains found in scats were identified on the basis of teeth only, because post-cranial skeletal remains were not clearly identifiable to species.

The teeth of larger mammals such as elk, deer, snowshoe hare or marmot do not generally appear in scats. Therefore, whenever ungulate, lagomorph or long rodent hairs were found, they were identified to species on the basis of their medullary and cuticular morphology. Medullary patterns were studied by mounting whole hairs with clear Karo syrup on microscope slides and examining them under a compound microscope. Cuticular scale patterns were studied by laying the hair on a strip of acetate and then placing acetone along the length of the hair with an eye dropper. A chemical reaction between the two materials solidified the acetone around the hair. After 10 min. the hair was peeled away leaving a clear impression of the cuticular scales. The strip of acetate was then mounted on a microscope slide and examined under a compound microscope.

A few feathers were found in scats, and were recorded simply as indicating the presence of birds in the diet. No attempt was made to identify the remains of feathers to species. Insect remains were identified to order. Seeds were identified to genus by comparison with a collection of fruits and seeds established during the course of the study.

RESULTS AND DISCUSSION

Seasonal Home Range Use

Yakima Park Study Area

On July 28, 1979, an adult female Cascade red fox was trapped and radio-collared in the Yakima Park study area in Mt. Rainier National Park, and named 'Eve'. She possessed fully adult dentition that showed little evidence of wear, and weighed 3.5 kg. Her pelage was clearly not juvenal, as some long, worn hairs from her winter pelage were still evident. She was therefore not a juvenile fox, but was probably not more than one or two years old, based on tooth wear. She showed no signs of having lactated, indicating that she had not given birth that year.

In accordance with earlier descriptions of pelage coloration in Cascade red foxes (Merriam, 1900; Bailey, 1936b), the fur was distinctly yellowish to grayish-brown, in contrast to the well-known cherry-red color of red foxes from the eastern United States. Her lower back and haunches were dark-gray and strikingly grizzled in appearance, and her head, upper back and sides were reddish-brown. She had a large white throat patch, and a gray underside, with dark-brown to black fur distally on all four legs and on the ears. The tail had a mottled appearance and was dark gray and buffy in color and tipped with white.

On September 16, 1979, Eve was recaptured. At 3.4 kg, she weighed a bit less than before, but appeared to be much larger because she was now in winter pelage. By mid-September, therefore, all traces of her previous winter's pelage had disappeared.

A total of 19 telemetry locations were obtained from July 28 to October 27, 1979, resulting in an estimated home range size for this period of 183.9 ha (Fig. 12, Table 8).

On September 12, 1979, a male red fox weighing 4.0 kg was trapped and radio-collared in the same general areaa, and named 'Bill'. He also possessed adult dentition that showed little wear, but his pelage showed no signs of a previous winter's coat. At this time of year, juveniles and yearlings are difficult to distinguish (Sheldon, 1949). On the basis of his size (Appendix B) and his general appearance, however, he was most likely an adult fox.

His pelage coloration did not at all resemble Eve's, but rather was very similar to that of Eastern red foxes. The entire back, haunches, sides and tail were a pure orange-red, with some white grizzling on the lower back and haunches. The belly was gray anteriorly and white posteriorly, with some white also on the chin and muzzle. The legs were black distally, but mostly on the anterior surfaces, and the tail was reddish-brown and tipped with white.

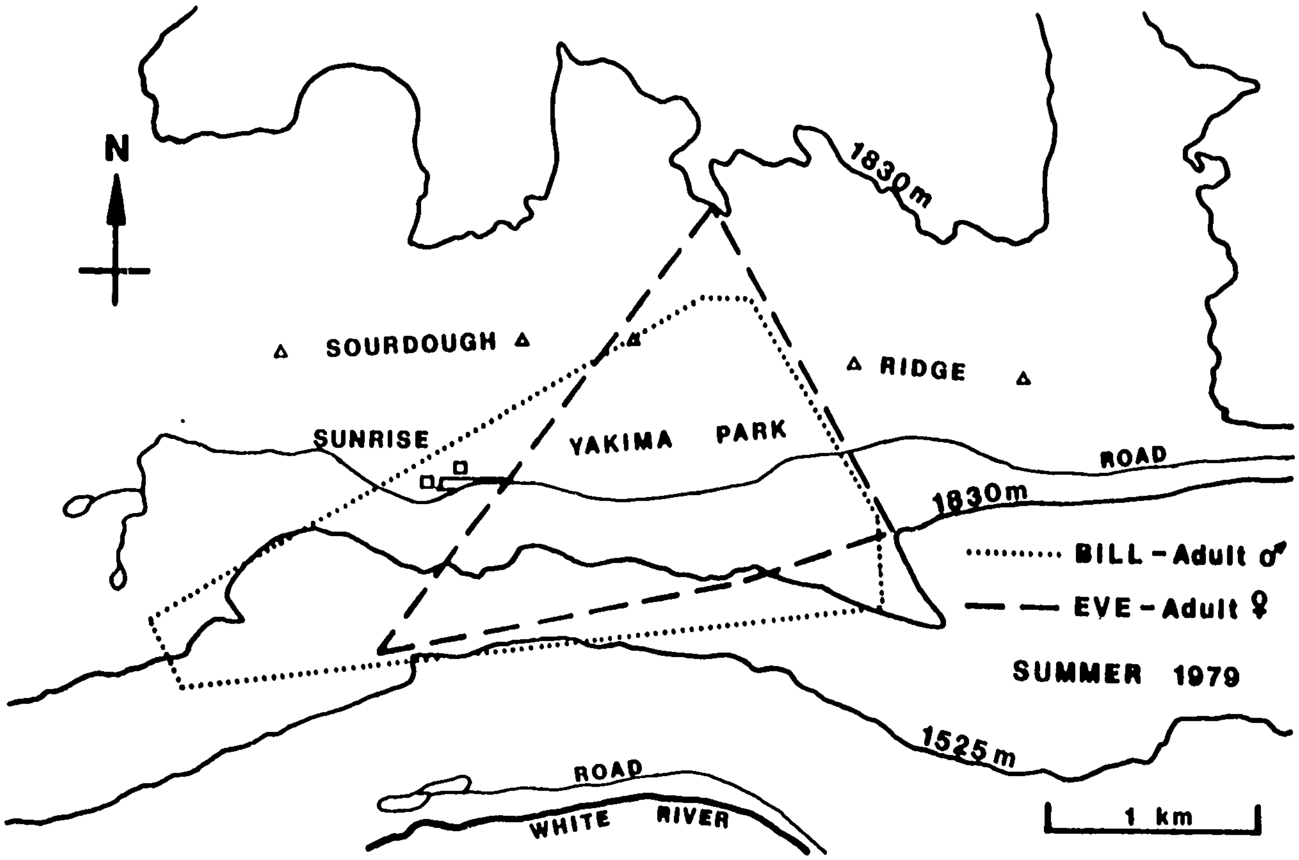

Figure 12. Home ranges of Cascade red foxes in the Yakima Park study area in the summer of 1979.

Table 8. Seasonal home range sizes of radio-collared Cascade red foxes. Home ranges are in hectares and the number of telemetry locations used in given in parentheses.

STUDY AREA AND ANIMAL	SUMMER 1979	SUMMER 1980	WINTER 1981	SUMMER 1981
YAKIMA PARK				
BILL	282.3 (n=11)			
EVE	183.9 (n=19)			
CRYSTAL MOUNTAIN				
ROCKY		132.1 (n=25)	178.7 (n=25)	170.9 (n=28)
MAGGIE		64.8 (n=21)	308.2 (n=34)	222.7 (n=27)
JEZEBEL		49.2 (n=29)	90.7 (n=31)	51.8 (n=11)
KIT		25.9 (n=11)	-	-
OKANOGAN				
FANNY				1,165.5 (n=14)

A total of 11 telemetry locations were obtained from September 12 to October 26, 1979, resulting in an estimated home range size for this period of 282.3 ha. (Fig. 12, Table 8).

Although there was extensive overlap in home range use between these two animals, there was no indication that they were associating closely. When Bill moved east into Eve's home range, Eve apparently moved west or north over the Sourdough Ridge in response. In no cases were the two signals located in the same immediate vicinity.

A few trips were made on skis and snowshoes to the Yakima Park area in the winter of 1980. On January 4, 1980, Eve was located north of the Sourdough Ridge in the same area she frequented during the summer. Bill's signal could not be located. This was the first evidence that Cascade foxes remain in the same general vicinity of their summer home ranges during the winter, and do not move down elevationally in response to extreme temperatures or a presumably declining food supply. On February 22, the area was visited again, but neither animal could be found. From July 1 to July 20, 1980, the Yakima Park area was visited daily, but neither animal could be found. On July 21, an aerial survey of the entire region was made to determine whether they had moved out of the area or if the transmitters had stopped functioning. Neither individual was found, indicating that the collars had failed during the winter.

Crystal Mountain Study Area

On the morning of July 23, 1980, a juvenile female red fox was trapped in the Crystal Mountain study area, and named 'Kit'. She weighed 2.7 kg and her lacteal dentition was in the process of being replaced. Her fur was soft and fluffy; she was clearly in juvenal pelage. She was a cross phase red fox with black, grizzled fur on her back, head, haunches and tail. Her feet and lower legs were black, while the remainder of her pelage was light tan.

In the evening of the same day and in the same trapsite, an adult male cross fox was captured. He was named 'Rocky', and weighed 4.5 kg. Long, worn hairs from last winter's pelage were evident, and his teeth showed signs of wear. His legs, shoulders and haunches were black and grizzled with silver. His back and the top of his head were black, and his tail was mottled with brown and black. On his sides and behind his ears, the fur was light brown, and his underside had a line of dark brown fur extending down the middle.

Two weeks later, on August 7, another juvenile female cross fox was captured in the same trapsite, and named 'Jezebel'. She weighed 3.2 kg and some of her lacteal teeth were still present. Her pelage was somewhat darker than Kit's, with grizzled black fur on her haunches extending forward up her back to her muzzle. Her sides and belly were a light reddish-brown, while her throat, tail and feet were black. Her underside was mottled brown in color.

On the next day, August 8, a 3.7 kg, adult female red fox was also trapped in this trapsite, and named 'Maggie'. She was clearly an adult, as her teeth were quite worn, her lower right first incisor was missing, and hairs from her winter pelage were still evident. In addition, four mammae were swollen, and three of the nipples were blackened and somewhat crusty, indicating that she had given birth this year and suckled young. She was a red phase fox, and was very different in color from the other Crystal Mountain study animals. A line of dark brown fur extended down her back onto her tail. Her hindquarters were light brown, and her sides were light red. Her head was reddish-brown and her feet and ears were a very dark brown. Her throat was white and her underside was grayish-white in color.

All four animals were recaptured once during the summer of 1980, and none showed any ill-effects from being trapped or radio-collared. Rocky was recaptured on August 12, and had gained 0.1 kg. Maggie was recaptured on August 31, and had gained 0.5 kg. Jezebel was recaptured on September 1, and had gained 0.3 kg. By this time, her adult dentition had come in completely. Kit was recaptured the next day, on September 2, and weighed 3.2 kg, a gain of 1.1 kg since she was first captured ten weeks previously. Her lacteal teeth had also been completely replaced by her adult dentition.

Trapping was conducted concurrently throughout the summer in the Yakima Park study area, but no red foxes were captured there during the 1980 field season.

From early August to early November, the movements of these four foxes were monitored with radio-telemetry. Twenty-five locations were obtained for Rocky resulting in an estimated home range size for this period of 132.1 ha; 21 locations for Maggie gave an estimate of 64.8 ha, 29 locations for Jezebel gave an estimate of 49.2 ha and 11 locations for Kit gave an estimate of 25.9 ha (Fig. 13, Table 8).

All four summer home ranges overlapped, and Rocky's home range encompassed virtually the entire home ranges of the other three foxes (Fig. 13). This, plus the fact that all four animals were trapped in the same trapsite, is strong evidence that these four foxes were a family group. In addition, in March of 1981, I located an inactive den within the area used in common by all four foxes that probably represented the natal den used by this family (Fig. 13). Sheldon (1950) found that, in New York, pups usually ranged within 800 m of the natal den, after the den was

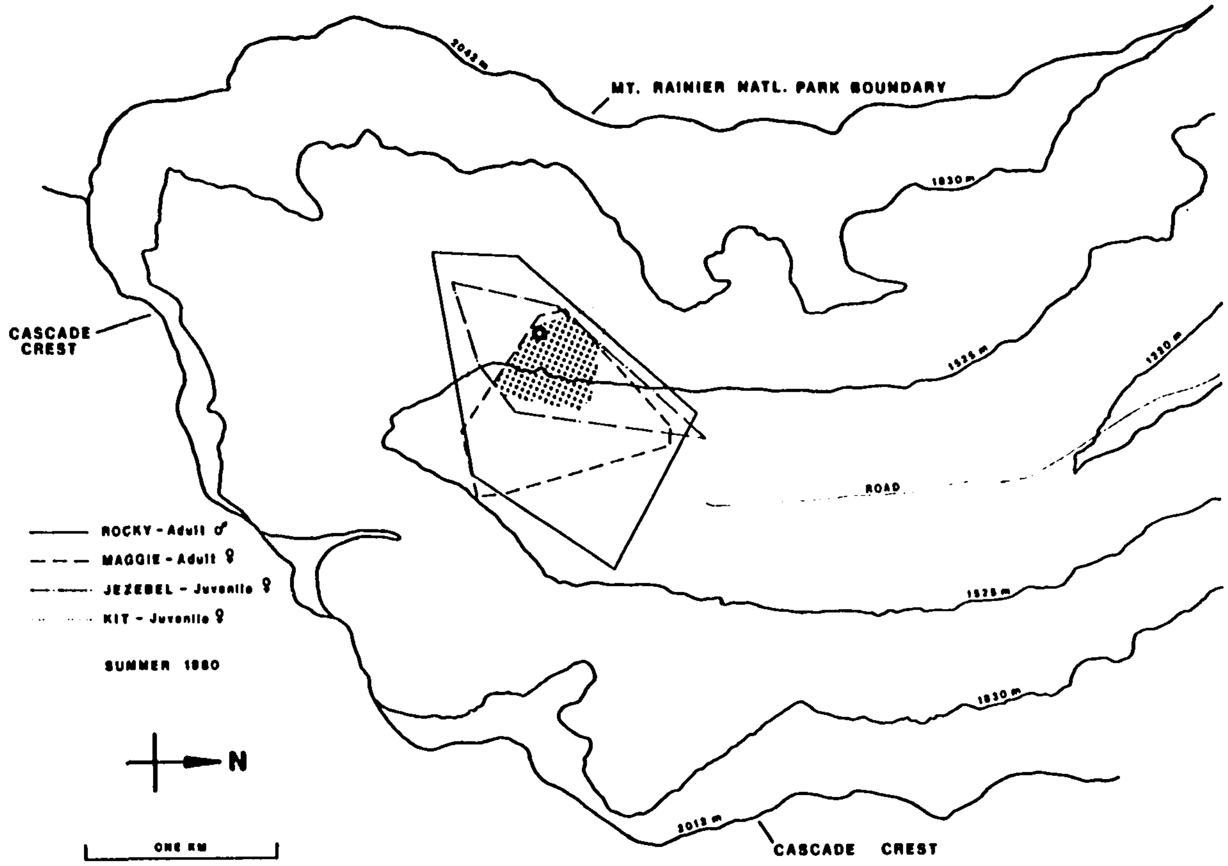

Figure 13. Home ranges of Cascade red foxes in the Crystal Mountain study area in the summer of 1980. The stippled area indicates the area used in common by all four foxes, and the circled star indicates the location of an abandoned den believed to be the natal den of these foxes.

abandoned, before dispersing in the fall. Both juvenile foxes used a much smaller area than either adult fox, which is to be expected when the young foxes are still being fed by their parents, and only beginning to hunt on their own. Because Maggie's home range was less than half the area of Rocky's, this may mean that she was spending most of the daylight hours (when all of the telemetry locations were taken) near her pups and the den, and that Rocky was patrolling a larger area, and possibly doing more of the hunting.

I continued to monitor the movements of these foxes through the winter and summer of 1981. Because the winter of 1980/1981 was mild, snow did not fall until late January in 1981. The 'winter' roughly corresponded to the period when snow covered the ground from January through May, whereas the 'summer' corresponded to the snow-free period from June through November. No telemetry data were obtained during December.

During the winter of 1981, I obtained 25 locations for Rocky, which resulted in an estimated home range for this period of 178.7 ha. Maggie was located 34 times, giving an estimated home range of 308.2 ha, and Jezebel was found 31 times, resulting in a home range estimate of 90.7 ha (Fig. 14, Table 8). These data demonstrated conclusively that Cascade red foxes do not undergo marked elevational shifts

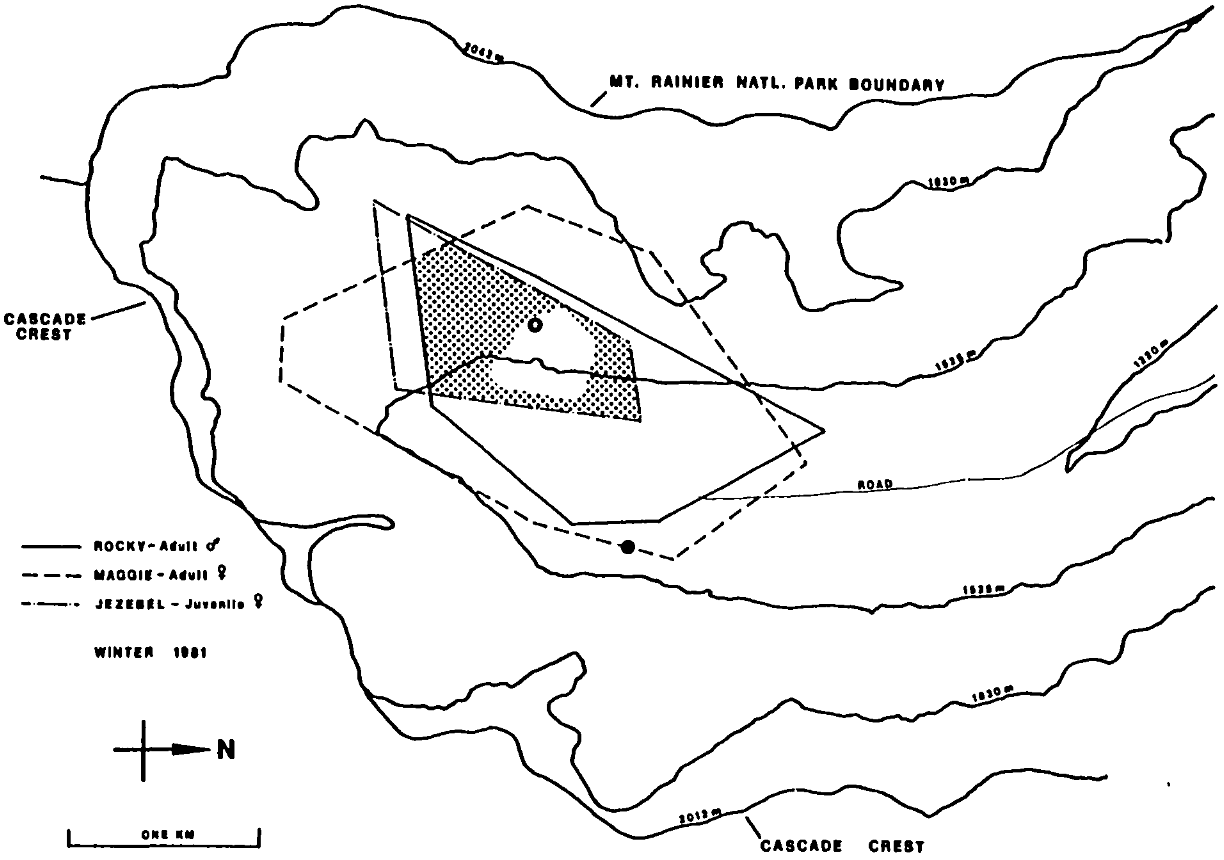

Figure 14. Home ranges of Cascade red foxes in the Crystal Mountain study area in the winter of 1981. The stippled area represents the area used in common by all three foxes, and the open area within represents the area used in common during the previous summer (Fig. 13). The black circle indicates the active den found in early May.

in habitat use between the summer and winter.

Kit was not found in this area during the winter. I learned on April 15 that she had dispersed to an area near the town of Silver Springs about 8 km to the north of her natal home range. Because she was frequenting residences there and obtaining handouts, however, I did not collect any further home range data from her.

All three foxes increased their home range use in the winter (Table 8), and all three home ranges were again overlapping (Fig. 14). An increase in home range size in the winter is not unexpected, because large areas of hunting territory are then covered with snow and small mammals are primarily using the sub-nivean environment. In addition, this increase in home range size may reflect a shift to a more widely-distributed prey base during the winter months. Sheldon (1950) also reported an increase in home range size during the winter months among red foxes in New York State.

The area of overlap during the winter was much larger than during the summer, and completely encompassed the summer area of overlap (Fig. 14). This is additional evidence indicating the use of a larger geographic area when snow is on the ground. Maggie's strikingly larger winter home range, larger even than Rocky's, may in part reflect a greater number of telemetry locations (Table 8), and the sample size bias associated with the minimum convex polygon method (Anderson, 1982). Nevertheless, a trend toward larger home ranges in the winter in Cascade foxes is clearly evident.

In early May of 1981, I located an active den on the east slope of the Crystal Basin (Fig. 14). Observations of denning foxes made visually and by remote cameras, however, indicated that none of my study animals were associated with this den. Telemetry data further supported this because none of the three collared animals frequented this area during the winter or the following summer.

During the summer of 1981, I continued to monitor the movements of these radio-collared foxes to collect further home range data and, if possible, to locate an active den. However, none of the animals established themselves in a particular locality, which indicated that none were raising litters. In addition, on June 25, I found Jezebel dead about 75 m from her presumed natal den. She had stepped through her radio-collar, and probably died from an infection that had resulted from the chafing of her collar in her axilar region. She showed no signs of lactation, indicating that she had not bred that year. She had been dead for less than three days, because I had made a visual observation of her on June 22.

During the summer of 1981, I located Rocky 28 times, and estimated his home range for this period to be 170.9 ha. Maggie was found 27 times, resulting in a home range estimate of 222.7 ha. Jezebel was located 11 times, but only from June 3 to June 25, and ranged over an area of 51.8 ha (Fig. 15, Table 8). All three foxes contracted their home ranges during the summer, further supporting a relationship between season and home range size in Cascade red foxes.

Maggie's home range data are particularly interesting. During the summer of 1980, when she was raising a litter, her home range was very restricted in extent and centered around the den. In the winter of 1981, her home range expanded considerably after the pups became independent. Her home range then contracted again in the summer of 1981, but much less so than in 1980, presumably because she did not raise another litter in 1981. Her home range also showed less overlap with Rocky's during the summer of 1981, whereas in 1980 her summer home range was located almost completely within the limits of his. Rocky, on the other hand, exhibited far less variation in home range size during the course of the study.

On April 6, 1981, an opportunity arose to compare home range use between Cascade foxes in subalpine meadow habitat with those occupying the open forests on the east slope of

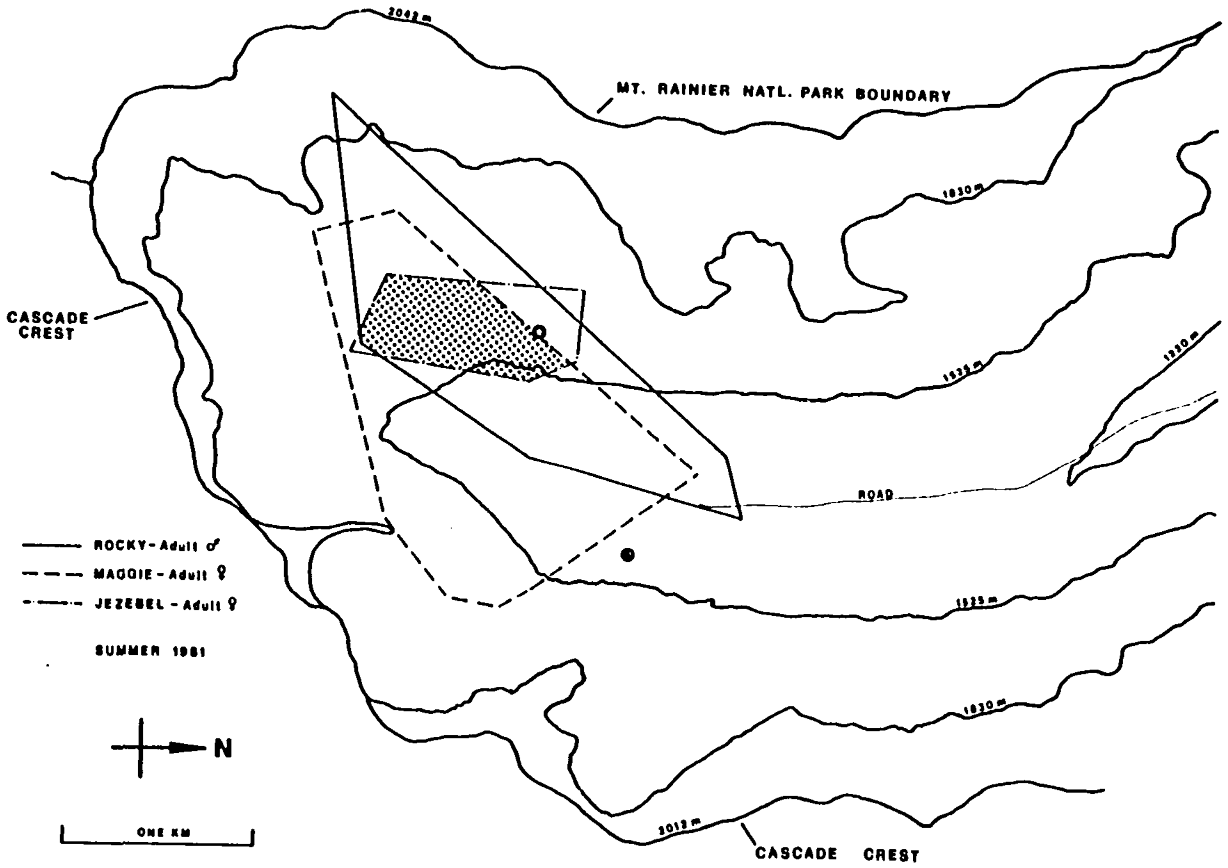

Figure 15. Home ranges of Cascade red foxes in the Crystal Mountain study area in the summer of 1981. The stippled area represents the area used in common by all three foxes. See Fig. 13 and 14 for an explanation of symbols.

the Cascades. J. David Brittell of the Washington State Department of Game captured an adult female red fox in a lynx live-trap set about 19 km west-northwest of the town of Conconully in Okanogan Co., at an elevation of 1,525 m. She was clearly an old fox; her upper right premolar was worn almost to the gumline and her upper right incisor was missing. No signs of pregnancy or recent whelping were evident.

Vegetationally, this area belongs to the _Abies grandis_ zone (Franklin and Dyrness, 1973). This is a climatically moderate forested zone distinguished from the subalpine zone by its higher temperatures and lesser accumulation of snow. The understory is generally rich in herbs, but open meadows are not an important constituent of this forest type.

The animal was named 'Fanny' and affixed with a radio-transmitter. Her pelage coloration was very similar to Bill's, being an orange-red, red phase fox with some white grizzling on her lower back and haunches. She had a reddish-brown mottled tail and a white underside. She did not have the black stockings normally found in red foxes; her feet were mostly red with small amounts of black on the anterior surfaces.

From April 6 to November 6 (at which time the transmitter apparently failed), 14 telemetry locations were obtained by Mr. Brittell and his co-workers, resulting in a home range estimate of 1,165.5 ha (Table 8). In January of 1982, she was trapped by a local trapper 1.6 km mile north of Conconully, 18.5 km from her original point of capture.

Home ranges in the Yakima Park and Crystal Mountain study areas were found to be generally less than, or in a few cases, slightly greater than 250 ha in extent. In the Okanogan area, however, a home range estimate of 1,165.5 ha was obtained even though the number of telemetry locations used was relatively small. Although the sample sizes are far too low to draw any conclusions, these data suggest that the subalpine meadows may be able to support denser populations of Cascade foxes than do the open forests of the eastern Cascade slope. Because small mammals, particularly pocket gophers and microtines, tend to be concentrated and relatively abundant in the lush subalpine meadows (Dalquest, 1948), this apparent difference may be related to variation in the abundance of prey between the two habitats.

Ables (1969) found that home ranges of red foxes in an arboretum of "great ecological diversity" in Wisconsin varied from 77.7 to 207.2 ha, whereas the home range of an adult male in a farmland habitat was 932.4 ha. His suggestion that these differences may be attributable to variation in habitat richness, reflect a situation similar to that which I found between subalpine meadow and open forest habitats in the Cascade Mountains.

Other studies reported home range sizes within this general range. Storm, et al. (1965) found the average home range of adult male red foxes in Illinois to be 388.5 ha; Murie (1936) observed red foxes in Michigan and found they occupied an area of 466.2 ha; Sargeant (1972) reported home range sizes in Minnesota between 259 and 777 ha; Schofield (1960) reported the nightly hunting area of red foxes in northern Michigan to be 725.2 ha; and Scott (1943) reported that red fox movements in Iowa were generally contained within an area of about 800 ha. According to Ables (1975), the size of red fox home ranges varies with terrain, complexity of the habitat and food supply.

Reproductive Ecology

Reliable, detailed information on the reproductive ecology of the Cascade red fox does not exist. Taylor and Shaw (1927) reported a den on Mt. Ararat near Indian Henry's on the southern slope of Mt. Rainier where pups were raised in the winter of 1919. This area is at an elevation of roughly 1,700 m. No description of the den was given, however. Animal sighting reports in the archives of Mt. Rainier National Park include several references to dens and pups in the Paradise Valley, which is also located at about 1,700 m elevation, from 1928 to 1942 but no further details were listed.

It has been speculated that Cascade red foxes in Oregon den under rocks or in holes dug under or near a rocky cover (Bailey, 1936b), although no dens were actually examined. The reason given for this presumed preference was to provide refuge from coyotes. Livezey and Evenden (1943) described a den near Corvallis in the Willamette Valley which they attributed to the Cascade red fox. As I discussed in Chapter 2, however, the inhabitants of this den were introduced lowland red foxes, not indigenous Cascade foxes. No additional information on reproduction in Cascade red foxes could be found.

On March 5, 1981, while searching for scats on skis in the Crystal Mountain study area, I found a hole in the snow at the base of a small conifer. Fox tracks were present near the hole, but whether the hole was actually being used by foxes or had simply been investigated by a wandering fox could not be determined. For the next three months, I periodically checked the area near the hole for signs that red foxes were using it as a den, but found none.

On June 3, the melting snow revealed a large den opening about 2 m from where I had found the hole in the snow. This hole was located directly underneath a 30 cm diameter fallen log that had become imbedded in the ground. The opening was 30.5 cm wide and 25.5 cm high, and a fan of packed earth extended outward from the hole. Further searching in the area revealed a network of den openings, although this hole was the largest and most obviously used. A total of six holes were found, ranging in size from this largest one to one 18 cm wide and 15 cm high. The holes were positioned roughly in a straight line and covered a ground distance of 15 m. The den was located in an area of dense coniferous trees on the edge of an abandoned dirt road. There were no rocks or talus slopes anywhere in the vicinity. The den was situated on a 12° slope that faced due east, at an elevation of 1,585 m, and a small creek ran about 10 m north of the largest opening.

Although no direct evidence of red foxes using this den was found, its general characteristics and the fact that it was located within the area used in common by all four study animals during the summer of 1980 (Fig. 13), indicated that this was the abandoned natal den of my radio-collared red foxes.

On May 6, 1981 at 1610 hrs., I saw a red phase fox, without a radio-collar, crossing a snow-covered slope in the Crystal Mountain study area with a snowshoe hare, <u>Lepus americanus</u>, in winter pelage in its mouth. It disappeared into a dense stand of conifers. A fresh covering of snow deposited the previous day provided excellent substrate for tracking. I followed the tracks through the trees, across a narrow clearcut and into another stand of conifers, and found a den entrance about 5 m into the trees with more fox tracks around the opening. The tracks continued past this hole and led to a second and more obviously used opening 15 m further into the trees in a small clearing. This hole had numerous tracks around it, and a blood stain on the snow in front of it. The general locality of this den is shown in Fig. 14.

I began observing the area from a blind, but could not find a suitable location from which to view the den-openings without disturbing the occupants. I saw this same fox leaving the vicinity of the den on several occasions, usually just before dark. This fox was easily recognizable by a patch of very light fur on its lower back. No other individuals were seen.

Intensive searching in the area revealed an extensive network of additional den entrances. A total of seven holes were found. The den was located on a 20° slope facing north-northwest, at an elevation of 1,435 m, and the holes were aligned along the contour of the slope. In addition to the first two holes found in the trees, two other holes were discovered near the small clearing within 6 m of where the second hole was found. Two additional holes were located within the clearcut between the two forest stands and a final hole was located 45 m from the clearcut within the first stand of trees I had traversed while following the tracks (Fig. 16). Although this hole was a considerable distance from the other openings, a draft of cold air could be felt coming from the hole, suggesting that it was part of this den system. The total ground distance covered by the den was roughly 90 m. The dimensions of the smallest hole was 13 cm wide and 18 cm high, but most of the entrances averaged 25 by 25 cm, and all had a fan of hard-packed dirt extending outward from them for a distance of 1 to 1.5 m.

The characteristics of these two dens were not markedly different from those found in other localities. Storm, et al. (1976) reported that dens in Illinois averaged 2.4 openings per den with a range of 1 to 6, while dens in Iowa averaged 3.0 openings with a range of 1 to 9. The average dimensions of measured den entrances were 28 by 23 cm in Illinois, and 25 by 23 cm in Iowa. Pils and Martin (1978) found that in Wisconsin, the average number of den openings varied between successive years from 2.1 to 4.0, with a range of 1 to 7. The average den opening was 28 by 23 cm in size. Ables (1975) reported having examined dens in Wyoming with 12 or more openings, and Murie (1944) described fox dens in Alaska with up to 19 entrances.

Because I could collect no further information by direct observation, I set up remote cameras on the opening in the small clearing where the most conspicuously used hole was, and on the opening located deep within the first stand

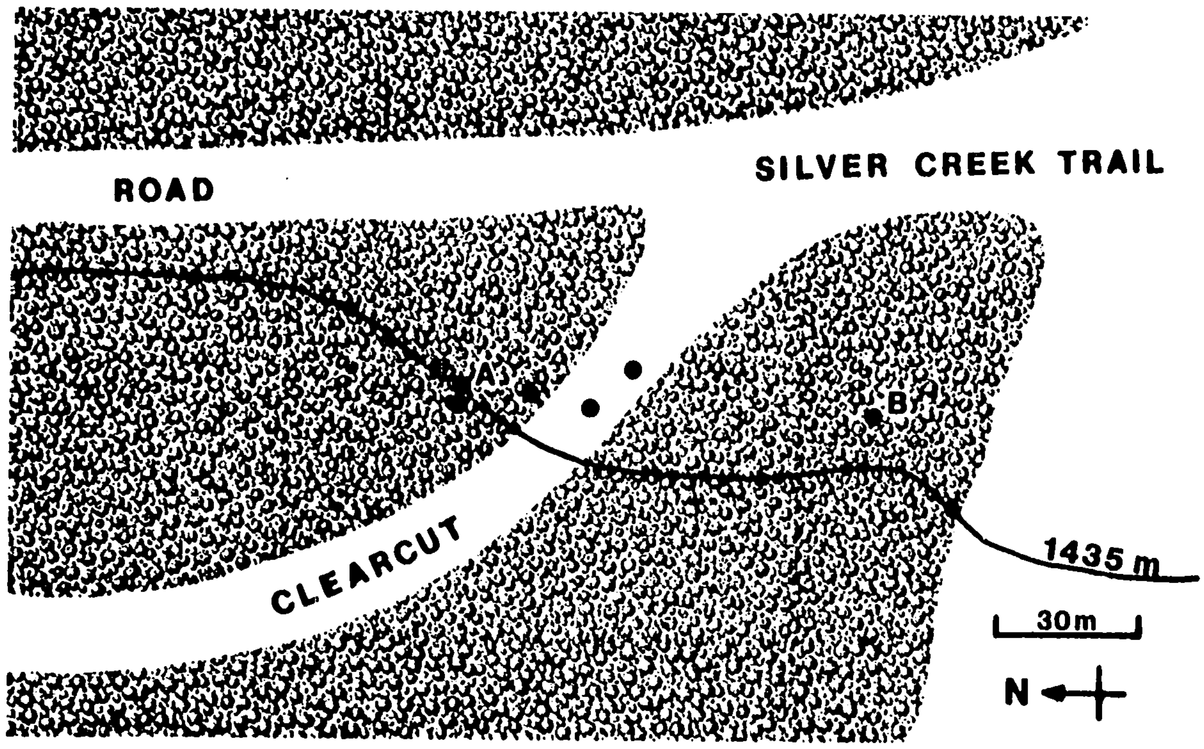

Figure 16. Active den located in Crystal Mountain study area in 1981. Solid circles represent den entrances, and 'A' and 'B' indicate the openings monitored with remote cameras.

of trees, 45 m from the clearcut (holes A and B respectively in Fig. 16). I operated the cameras from June 23 to July 22.

At hole A, I obtained eight pictures of red foxes from June 24 to July 10. From July 10 to July 22, no foxes were recorded. At hole B, I obtained three pictures of red foxes from June 29 to July 12, and none after that. All eleven pictures were of a light-colored red phase adult fox that appeared to be the same animal I had been observing visually. No pictures of pups were obtained. Seven of the pictures were taken in the early morning, two in the afternoon and two in the late evening.

While these pictures did not provide any data on the pups, they did clearly indicate that all of the holes found belonged to the same den. Furthermore, in accordance with visual observations, the pictures showed that while Cascade foxes may be active throughout the day, a preference for the early morning and late evening is indicated. They also suggest that by the middle of July, the den had been abandoned. Sheldon (1950) observed red fox dens in New York State and found that dens were not occupied after July 10.

Conclusive evidence that Cascade red foxes may breed before the age of one year was provided when Kit, one of the female pups captured during the summer of 1980, was seen with a litter of pups in the spring of 1981. On June 15, I saw Kit with three pups in the vicinity of some cabins near Silver Springs, which is about 8 km north of the Crystal Mountain study area. They were apparently using the space underneath one of the vacant cabins as a makeshift den. There was a red phase individual and two pure black pups. These were the only truly black phase red foxes seen during the course of the study. All three color phases were therefore represented in this one family. By June 25, only one of the black pups and the red one were seen, indicating that the other black pup had died. I observed the pups periodically until July 9, after which time they could not be found. As stated previously, Jezebel, the other female pup collared in the summer of 1980, did not breed in her first year and remained in the vicinity of her natal den. Sheldon (1949) reported the breeding of a juvenile red fox in New York, and Pils and Martin (1978) found that 59% of vixen pups bred in their first year in Wisconsin. According to Storm, et al. (1976), female red foxes may breed in their first winter, but the percentage of successfully breeding juveniles varies by region.

Although the date of parturition for Kit's pups could not be estimated, information on the eruption of Kit's permanent dentition when she was captured in June of 1980 provided a means of estimating her date of birth. On June 23, when she was first captured, she possessed her permanent incisors, but her canines were in the process of being replaced, i.e. both lacteal and permanent canines were present. Linhart (1968), showed that replacement of the lacteal dentition begins with the incisors at 15 to 18 weeks of age, and proceeds progressively backward until the premolars are replaced at about 20 weeks of age. Canines are replaced at 18 to 19 weeks. Assuming that she was 19 weeks old (the permanent canines were already well below the gumline) gives an estimated date of birth in the second week of March. Backdating this by a gestation period of 52 to 53 days (Smith, 1939; Asdell, 1946) results in an estimated date of conception in the first or second week of February. This agrees well with published reviews (Ables, 1975: Storm, et al., 1976) which state that red foxes breed from December to April with most matings occurring during January and early February. I found no evidence therefore that Cascade foxes exhibit any significant variation in the timing of reproduction despite the fact that they occupy a habitat with extreme winter climate, where the peak of spring reproduction among prey species would be expected to be somewhat delayed.

Food Habits

From July, 1979 to November, 1981, 413 Cascade red fox scats containing 760 food items were collected in the Yakima Park and Crystal Mountain study areas. Scats were collected in every month except December, although samples from November, January and February were relatively small. A total of 59 scats containing 85 food items were collected during the winter months, and 354 scats with 675 food items were collected in the summer months (Table 9).

Mammals were the most important item in the yearly diet, comprising 57.2% of all items found. Plant remains represented 19.9% of the diet; insects, 16.6%; birds, 4.5% and garbage, 1.8%. The low representation of garbage in the diet shows that these foxes were not commonly frequenting garbage cans or dumpsters, indicating that the diet was not biased by frequent use of artificial food sources.

During the winter, the diet consisted of 89.4% mammals, 5.9% birds and 4.7% garbage. Snowshoe hares were the most commonly represented mammal species at 22.4%; followed by southern red-backed voles, _Clethrionomys_ _gapperi_, at 16.5%; northern pocket gophers at 8.2% and heather voles, _Phenacomys_ _intermedius_, at 7.1%. Neither insects nor plant remains were found in winter scats.

Table 9. Cascade red fox scat analysis, 1979-1981.

	Winter					Summer								
	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Winter	Summer	Total
Number of Scats	6	2	12	20	19	25	64	139	98	23	5	59	354	413
Number of Occurrences	9	2	14	33	27	39	115	276	192	45	8	85	674	760
Food Items						Frequency of		Occurrence						
Mammals	88.9	100	85.7	90.9	88.9	76.9	60.0	47.5	53.2	55.7	75.0	89.4	53.1	57.2
Thomomys talpoides				9.1	14.8	28.2	23.5	12.0	12.5	6.7	25.0	8.2	14.8	14.1
Clethrionomys gapperi	11.1	50.0	7.1	21.2	14.8	5.1	6.1	8.3	5.7	20.0		16.5	7.7	8.7
Phenacomys intermedius	11.1			6.1	11.1	7.7	4.3	3.3	9.4	8.9	12.5	7.1	5.9	6.1
Lepus americanus	44.4		42.9	15.2	14.8	2.6	0.9	1.1		6.7		22.4	1.2	3.6
Zapus trinotatus	11.1			6.1		10.3	5.2	2.2	3.1			3.5	3.3	3.3
Microtus oregoni			7.1	3.0	7.4	5.1	1.7	1.1	5.2			4.7	2.5	2.8
Microtus richardsoni		50.0	14.3	3.0		2.6	1.7	2.2	1.6			4.7	1.8	2.1
Marmota caligata				6.1	3.7		0.9	1.1	1.0			3.5	0.9	1.2
Cervus elaphus						5.1	4.3		1.0				1.3	1.2
Odocoileus hemionus				9.1	3.7	5.1	2.6	0.4			12.5	4.7	1.0	1.1
Scapanus sp.							0.9	1.1	1.6				1.0	0.9
Sorex sp.								0.4	1.6				0.6	0.5
Spermophilus saturatus				3.0		2.6	0.9					1.2	0.3	0.4
Tamias townsendii				3.0	3.7		0.9					2.4	0.1	0.4
Peromyscus maniculatus								0.7	0.5				0.4	0.4
Oreamnos americanus							0.9	0.4					0.3	0.3
Ochotona princeps									1.0				0.3	0.3
Glaucomys sabrinus					3.7		0.9					1.2	0.1	0.3
Neotoma cinerea								0.4					0.1	0.1
Mustela frenata								0.4					0.1	0.1
Unidentified mammals	11.1		14.3	6.1	11.1	2.6	4.3	10.9	8.9	13.3	25.0	9.4	9.0	9.1
Birds				9.1	7.4	7.7	7.0	3.6	3.1	4.4		5.9	4.3	4.5
Insects						7.7	25.2	19.2	16.1	24.4			18.8	16.6
Orthoptera						5.1	20.0	14.9	10.9	20.0			14.2	12.5
Coleoptera						2.6	5.2	4.3	5.2	4.4			4.6	4.1
Plants						2.6	6.1	30.1	27.1	15.5	12.5		22.3	19.9
Fragaria sp.						2.6	3.5	26.1	13.0	4.4			15.4	13.7
Vaccinium sp.								3.3	11.5	2.2			4.7	4.2
Grass							2.6	0.7	2.6	8.9	12.5		2.2	2.0
Garbage	11.1		14.3		3.7	5.1	1.7	1.4	0.5		12.5	4.7	1.5	1.8

In the summer months, mammals declined in frequency because insects and plants, particularly fruits, became important food items. Mammals represented 53.1% of food items, plants 22.3%, insects 18.8%, birds, 4.3% and garbage only 1.5%. Pocket gophers were the most important mammal species at 14.8%, next were red-backed voles at 7.7%, and then heather voles at 5.9%. Snowshoe hares dropped from 22.4% occurance in the winter to 1.2% in the summer.

During the summer, when insect populations were high, Cascade foxes fed heavily on grasshoppers (Orthoptera), at 14.2% of the diet, but less so on beetles (Coleoptera), at 4.6%. Fruits were also heavily used in the summer, particularly during August and September. Strawberries, *Frageria* sp., and blueberries, *Vaccinium* sp., were the only fruits eaten, representing 15.4% and 4.7% of the diet, respectively. Grass was found to represent 2.2% of the summer diet, although some percentage cf this figure may reflect grass eaten incidentally while catching grasshoppers or eating strawberries.

The diet of Cascade foxes varied throughout the year (Fig. 17). From January through March, they depended heavily on mammals but also scavenged somewhat on garbage, which is to be expected when food is scarce. In April and May, birds appeared in low numbers, and continued at that level until November. In June and July, as insect

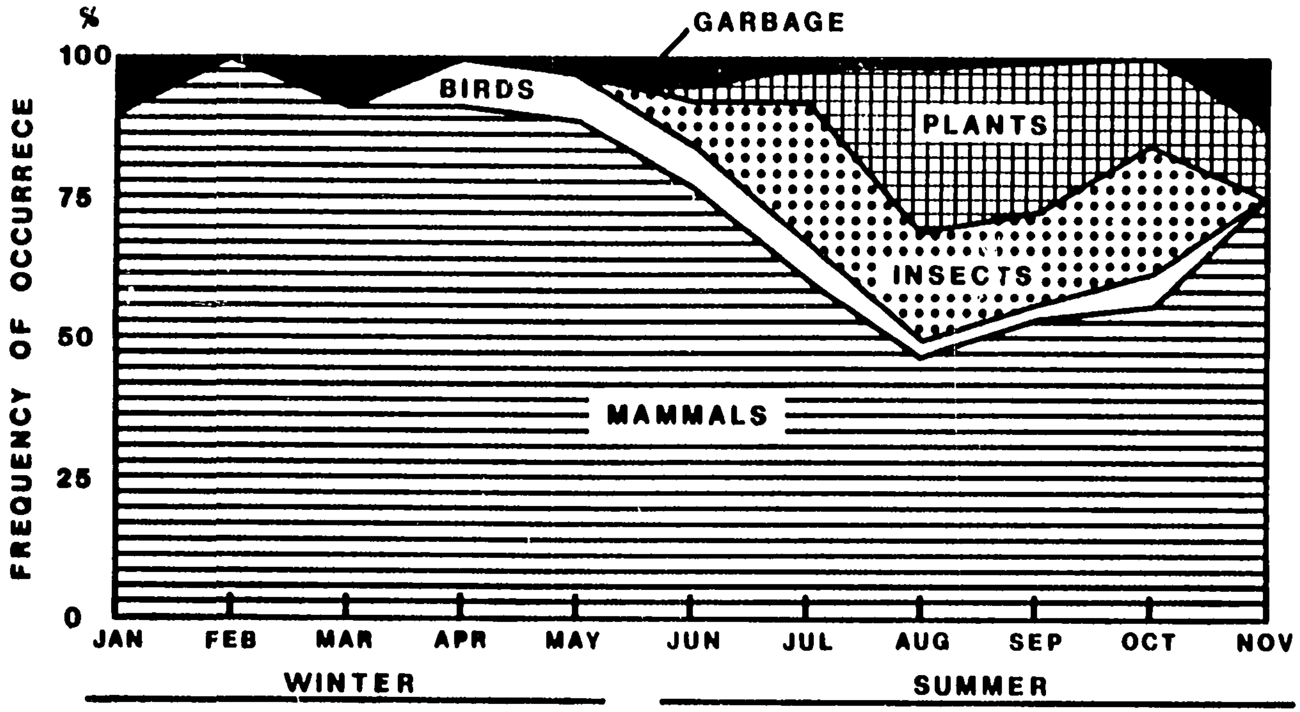

Figure 17. Monthly food habits of Cascade red foxes, 1979-1981.

populations increased, they were frequently preyed upon, whereas mammals began declining in importance. By August, fruits became abundant and were important dietary items. Mammals reached their lowest frequency level at this time. Food was plentiful at this time of year, and scavenging on garbage was rarely found. By September and October, fruits and insects began to decline in availability and became less important in the diet. Mammals began to increase in importance again. In November, insects and birds were not found in scats, and fruits continued to decline in frequency. Assuming that these trends continued in December, January levels would be about equal to those found in scats the previous year. This suggests a yearly dietary cycle that is based on the seasonal availability of potential food items.

These findings are consistant with virtually all studies on the food habits of red foxes. Small and medium-sized mammals are the most important food item, especially during the winter. Birds are often taken, but are rarely an important component of the diet. In the summer and early fall when insects and fruits are abundannt, they are heavily utilized (Errington, 1935; Scott, 1943; Cook and Hamilton, 1944; Johnson, 1970; and others). Red foxes can be characterized as opportunistic omnivores with a preference for mammalian prey.

My home range studies in the same areas where the scats were collected showed that Cascade foxes increase their home range size during the months when snow is on the ground. This may be explained by the importance of snowshoe hares in the diet at this time of year. It seems likely that snowshoe hares are less commmon and less densely distributed than either pocket gophers or microtines. A greater dependence on such a food item would be expected to require a larger hunting area. In addition, mule deer, Odocoileus hemionus, increase in importance from 1.0% in the summer to 4.7% in the winter. This indicates a heavier use of deer carcasses during the winter, which are also probably somewhat scarce and widely distributed. Since deer remains were found in winter scats only during April and May, these figures probably represent scavenging on fawn carcasses.

The most striking finding of this analysis is the importance of pocket gophers in the diet. Pocket gophers were the single most important food item (Table 9). They were found in scats from April to November, indicating that adults, and not only dispersing juveniles, were preyed upon. Although no attempt was made to quantify population levels of prey species, evidence of pocket gopher activity was rarely seen. This suggests that Cascade foxes may have been selectively preying on pocket gophers.

How Cascade foxes hunt pocket gophers is not known. No evidence of extensive digging was ever observed, so it is unlikely that foxes hunt gophers by excavating their burrows. More likely, the fox probably listens for the sounds of gopher activity while hunting in the meadows, then pounces when a gopher comes to the surface to push out dirt or clip green plants.

Pocket gophers of the genus Thomomys are found only in the western United States, whereas pocket gophers of the genus Geomys occupy the Great Plains region (Hall, 1981). Although numerous studies on the food habits of red foxes have been published, none could be found from any geographic area west of Iowa. Of the food habits work conducted within the range of Geomys, none showed pocket gophers to be important in the diet. Percent occurrences in Iowa were: 1.8% (Errington, 1935), 2.8% (Errington, 1937), <1.0% (Scott, 1950), 0.0% (Scott, 1943); and in Missouri, 0.1% (Korschgen, 1959).

Although the varied diet of Cascade foxes does not indicate a dependence on pocket gophers, it is tempting to speculate that the habitat specificity shown by Cascade foxes toward subalpine meadows is related to the distribution and abundance of pocket gophers, and that these foxes may have become specialized predators of pocket gophers. Pocket gophers do not exist west of the Cascade

Crest in Washington except in the Olympic Mountains and in the prairies south of Puget Sound on the glacial outwash aprons (Dalquest, 1948). East of the Crest, gophers are widely distributed. Although Cascade foxes occupy the forests on the east slope of the mountains, they do not occur in the Columbia Basin. Competition from dense populations of coyotes in that region may explain why Cascade foxes are unable to expand their distribution eastward.

Comparisons with the Lowland Red Fox

To investigate potential physiological, ecological and taxonomic differences between Cascade and lowland red foxes, comparisons were made whenever material for study was available. Blood characteristics, electrophoretic mobilities of blood serum proteins, karyology and internal parasite load were studied.

Hematology and Blood Chemistries

Blood samples were collected and analyzed from four adult and four juvenile Cascade red foxes (Tables 10 and 11). Carl Dugger of the Washington State Dept. of Game obtained blood samples from five adult lowland red foxes from Kitsap Co. (Table 12, Fig. 1). Seven hematological values and 21 serum chemistries were measured. Because

Table 10. Hematological values for adult Cascade red foxes from the Crystal Mountain and Okanogan study areas.

	MALES			FEMALES	
BLOOD VALUE	7/23/80 ROCKY	7/23/80 NO NAME	8/8/80 MAGGIE	8/31/80 MAGGIE	4/6/81 FANNY
HEMATOLOGY					
WBC	5.5	8.3	5.7	16.3	14.4
RBC	10.9	8.1	10.3	9.4	9.9
Hgb	17.5	13.7	16.9	15.9	16.8
Hct	55.7	41.5	32.9	54.7	48.4
MCV	51	51	50	58	49
MCH	16.1	16.8	16.3	16.9	17.0
MCHC	31.4	33.0	32.9	29.1	34.7
CHEMISTRY					
Glucose	117	124	277	182	105
BUN	35	36	34	48	40
Creatinine	0.8	1.0	1.2	0.7	0.6
Sodium	151	156	151	145	158
Potassium	4.3	3.8	3.9	4.2	4.6
Chlorine	121	122	120	113	120
Carbon Dioxide	17	11	11	22	17
T. Bilirubin	0.8	2.1	1.3	0.5	0.6
D. Bilirubin	0.1	0.4	0.2	0.1	0.2
Electr. Bal.	3.0	13.0	10.0	0.0	11.0
Ionized Ca	4.4	4.7	4.3	4.6	4.4
Calcium	8.6	9.3	8.8	9.3	9.3
Phosphorus	2.9	4.8	1.9	3.1	5.4
Alk. Phosph.	72	69	52	72	70
SGOT	322	526	374	239	99
SGPT	127	195	213	142	112
Cholesterol	100	138	116	129	162
T. Protein	5.3	5.9	5.9	5.6	6.3
Albumin	2.7	3.5	3.0	2.7	3.1
Globulin	2.6	2.4	2.9	2.9	3.2
A/G Ratio	1.0	1.5	1.0	0.9	1.0

Table 11. Hematological values for juvenile Cascade red foxes from the Crystal Mountain study area.

	FEMALES			
BLOOD VALUE	8/7/80 JEZEBEL	9/1/80 JEZEBEL	9/2/80 KIT	9/16/81 NO NAME
HEMATOLOGY				
WBC	6.0	11.1	9.4	6.2
RBC	9.4	9.6	8.8	10.9
Hgb	14.9	16.3	13.1	17.1
Hct	46.0	44.5	40.7	55.3
MCV	49	46	46	51
MCH	15.9	17.0	15.0	-
MCHC	32.4	36.6	32.2	-
CHEMISTRY				
Glucose	134	128	163	154
BUN	27	32	33	30
Creatinine	0.5	0.7	0.5	1.2
Sodium	148	149	148	155
Potassium	4.3	3.9	3.4	4.0
Chlorine	117	118	115	122
Carbon Dioxide	18	16	20	7
T. Bilirubin	1.5	1.1	0.8	0.7
D. Bilirubin	0.2	0.2	0.1	0.2
Electr. Bal.	5.0	3.0	3.0	16.0
Ionized Cal.	5.1	5.1	5.4	5.2
Calcium	9.8	9.8	10.0	9.5
Phosphorus	6.2	5.5	6.7	5.1
Alk. Phosph.	182	152	169	75
SGOT	530	531	196	64
SGPT	101	91	68	75
Cholesterol	140	148	143	194
T. Protein	5.1	5.1	4.9	4.7
Albumin	3.1	3.1	2.9	3.0
Globulin	2.0	2.0	2.0	1.7
A/G Ratio	1.6	1.6	1.5	1.8

Table 12. Hematological values for adult lowland red foxes from Kitsap Co., Washington.

BLOOD VALUE	6/6/80 MALE	5/4/81 MALE	6/23/81 FEMALE	8/11/81 FEMALE	8/19/81 FEMALE
HEMATOLOGY					
WBC	11.7	14.9	14.1	9.2	19.8
RBC	6.7	9.4	8.8	8.6	8.9
Hgb	11.4	16.3	15.6	14.5	14.3
Hct	32.4	46.1	45.6	47.2	43.4
MCV	48	49	52	55	50
MCH	16.9	17.3	17.7	-	-
MCHC	35.2	35.4	34.2	-	-
CHEMISTRY					
Glucose	165	123	113	108	98
BUN	17	27	48	13	17
Creatinine	0.6	0.8	1.3	0.8	1.1
Sodium	148	159	154	148	156
Potassium	4.0	3.5	3.0	4.0	5.4
Chlorine	112	124	123	112	109
Carbon Dioxide	25	16	12	16	11
T. Bilirubin	0.9	1.4	1.4	0.6	0.6
D. Bilirubin	0.2	0.2	0.2	0.2	0.2
Electr. Bal.	1.0	9.0	9.0	10.0	26.0
Ionized Ca	4.4	4.7	4.1	5.3	5.1
Calcium	8.9	9.7	8.7	10.8	10.1
Phosphorus	5.0	5.0	6.3	6.4	13.2
Alk. Phosph.	68	49	28	83	113
SGOT	420	181	695	55	127
SGPT	684	105	285	91	78
Cholesterol	235	179	150	181	174
T. Protein	5.6	5.9	6.2	5.9	5.6
Albumin	2.1	3.3	3.0	3.1	3.2
Globulin	3.5	1.3	0.9	2.8	2.4
A/G Ratio	0.6	1.3	0.9	1.1	1.3

sample sizes were small and blood specimens were taken from April through September, potentially introducing a seasonal bias, comparative statistical analyses between the two groups were not conducted.

Blood values have been reported for some mammalian carnivores, such as the raccoon, *Procyon lotor*, (Jacobs, 1957); the spotted skunk, *Spilogale putorius*, (Heidt and Hargraves, 1973); the black bear, *Ursus americanus*, (Svihla, et al., 1955; Youatt and Erickson, 1958; Erickson and Youatt, 1961); and other ursids (Seal, et al., 1967); yet no similar studies were found for the red fox.

These results are included here as a contribution to existing blood data for mammalian carnivores, and to provide a source of comparative data for future studies. More comprehensive research on the blood parameters of these red foxes could provide insights into the physiological differences that may distinguish Cascade from lowland populations.

Serum Protein Electrophoresis

The use of serum protein electrophoresis as a means of investigating mammalian taxonomic relationships was first described by Johnson and Wicks (1959), and has been applied in a number of subsequent studies (Johnson, et al., 1959; Nadler and Hughes, 1966; VanTets and Cowan, 1966; and others). A comparative electrophoretic analysis was performed on serum samples from seven Cascade and five lowland red foxes by Dr. Fred Utter of the Northwest and Alaska Fisheries Center, Seattle. Although sample sizes were much too small to provide conclusive results, no obvious electrophoretic differences were found for a wide array of proteins tested.

While these results are inconclusive, they sugggest that blood serum is not a useful tissue for investigating taxonomic differences between Cascade and lowland red foxes. Other tissues, such as liver, kidney and skeletal muscle may prove more useful in future studies, and should be used in preference to blood serum, if possible.

Karyology

On June 25, 1981 in the Crystal Mountain study area, a sternum bone marrow sample was collected from a female Cascade red fox (Jezebel) that had been dead for 1-3 days. Virginia R. Rausch of the Burke Memorial Washington State Museum used this material to prepare a karyogram (Fig. 18). In order to produce differential banding patterns on the chromosomes, the material was fixed in Carnoy's solution, treated with trypsin and stained with Giemsa blood stain. The karyogram follows the arrangement of Lin, et al. (1972) in which the metacentric chromosomes are shown in the first

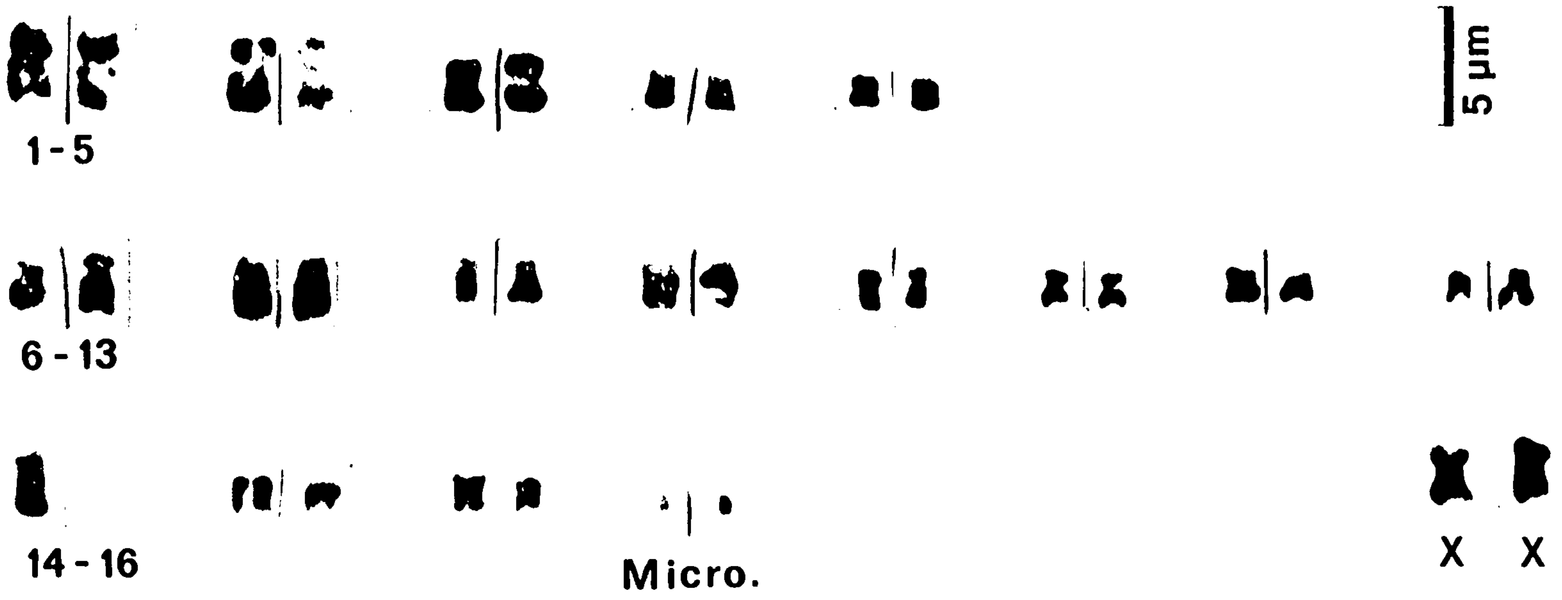

Figure 18. Karyogram of female Cascade red fox.

row, the submetacentric chromosomes in the second row and the subteleocentric and sex chromosomes in the third row. This is the first karyogram obtained from a mountain fox.

Because the animal from which the cellular material was taken had been dead for some time, the cell membranes were very fragile and, in processing, many of the cells were broken. The karyogram shown lacks one element of pair no. 14 (the largest among the subteleocentric group). This incomplete karyogram was used because it was most suitable for photographic reproduction. The validity of the karyogram as shown (2n = 34 macrochromosomes + 2 microchromosomes) was confirmed from counts of 13 complete cells. The diploid number of macrochromosomes found was in agreement with studies of the red fox from other geographic regions (e.g. Rausch and Rausch, 1979). Only two microchromosomes were present, although up to six have been reported previously from other regions (Ellenton and Basrur, 1981).

The morphological characteristics of the macrochromosomes, e.g. shape, banding and arm-ratios, were not markedly different from those found in Alaskan red foxes. In contrast to those in Alaskan foxes and in other reported karyograms, however, the microchromosomes showed evidence of banding. Microchromosomes from Alaskan foxes are uniformly dark, whereas those from the Cascade fox appear to consist of separate light and dark Giemsa bands (V. Rausch, pers. comm.).

Although it has been suggested that microchromosome number in red foxes may bear a relationship to size and weight of the individual (Ward, et al., 1972; Ellenton and Basrur, 1981), their significance is not known. This is the first evidence that microchromosomes may vary morphologically, as well as numerically. Further work on the karyology of Cascade red foxes might illuminate the evolutionary role of the microchromosomes.

Internal Parasites

Carcasses of 13 Cascade and 14 lowland red foxes were obtained from trappers or collected during the study as the result of road-kills and of the death of one study animal. Visceral organs and gastrointestinal tracts were examined by Dr. Robert L. Rausch of the University of Washington for the presence of helminth parasites. Trematodes and nematodes were found in both populations; cestodes were found only in Cascade foxes. Trichinella sp., which is a common parasite of red foxes in Alaska (R. Rausch, pers. comm.), was not found in foxes from either population (Table 13).

The Cascade foxes have a helminth-fauna typical for red foxes, whereas that of the lowland foxes is clearly depauperate (R. Rausch, pers. comm.). Three nematodes

Table 13. Helminth parasites of Cascade and lowland red foxes from Washington, total infected in parentheses.

Species of Helminth	Intermed. Host	Cascade (n=13)	Lowland (n=14)
Trematoda			
Cryptocotyle lingua	Fish	---	(8)
Nanophyetus salmincola	Fish	---	(3)
Alaria marcianae	Frogs, rodents	(3)	---
Cestoda			
Mesocestoides sp.	Small mammals	(10)	---
Dipylidium caninum	Fleas, lice	(2)	---
Taenia sp. *	Rodents, hares	(4)	---
Nematoda			
Ascarids	Direct cycle	(10)	(3)
Uncinaria stenocephala	Direct cycle	(11)	(5)
Physaloptera sp.	Insects	(2)	(1)
Trichinella sp.	Autohexeroxenous	---	---

* Two individuals were identified as belonging to the species *Taenia pisiformis*, for which leporids (probably snowshoe hares) serve as intermediate hosts.

(Ascarids, *Uncinaria stenocephala* and *Physaloptera* sp.) were found in both populations, and either have direct life cycles or insects as intermediate hosts. Fish-transmitted trematodes (*Cryptocotyle lingua* and *Nanophyetus salmincola*) were found only in lowland red foxes. Because most lowland foxes examined were obtained from areas near Puget Sound, this suggests that red foxes there commonly scavenge on fish carrion along the shore. Neither of these two trematode species was found in Cascade foxes. One species of trematode (*Alaria marcianae*) and three species of cestodes (*Mesocestoides* sp., *Dypylidium caninum* and *Taenia* sp.) were found in Cascade foxes, but did not occur in lowland foxes. These species either have small mammals or fleas and lice as intermediate hosts.

Reasons for the presence of fish-transmitted trematodes only in lowland red foxes are clearly ecologically based; the fish that carry these parasites do not occur within the range of Cascade foxes. The absence of *Alaria marcianae*, *Mesocestoides* sp. and *Taenia* sp. from lowland red foxes, however, was unexpected. These helminths are all transmitted by small mammals, and are common parasites of the red fox elsewhere (R. Rausch, pers. comm.). This indicates either that these helminth species are not present within the range of lowland foxes or that lowland foxes do not commonly utilize mammalian prey. The latter possibility is unlikely, given the importance of small mammals in the diet of red foxes, as reported widely in the literature (see previous section on Food Habits).

Reasons for the absence of these helminths from the range of lowland foxes probably relate to the fact that lowland foxes were introduced. Before ca. 1900, red foxes did not occur in western Washington (Aubry, 1983) and evidence indicates that coyotes, Canis latrans, were also absent (Dalquest, 1948). Without their canid hosts, these helminths could not have existed in the lowlands of western Washington. A similar situation was reported by Hoberg and McGee (1982) in Saskatchewan, in which raccoons occurring at the edge of their range, in areas previously unoccupied by the species, also contained a depauperate helminth-fauna compared to that of raccoons from the mid-western United States.

The striking differences found between the helminth-faunas of these populations of red foxes strongly support the conclusions of Chapter 1 that Cascade and lowland populations are restricted to habitat at high and low elevations, respectively, and are discrete biological entities.

SUMMARY AND CONCLUSIONS

The distributional range of the Cascade red fox in Washington was found to be somewhat different from previous reports. Cascade foxes do not occupy the Mt. Baker area, nor do they occur in forested habitat on the western slope of the Cascade Mountains. Cascade foxes were found to be restricted to the subalpine meadows and parklands near the Cascade Crest and the open forests on the eastern Cascade slope. Analysis of modern and historical distribution records revealed no significant changes in distribution since 1970, i.e. there was no indication that Cascade foxes had been extirpated from regions previously occupied.

An historical investigation of the circumstances surrounding the introduction of red foxes into Washington showed that red foxes from the eastern U.S. had been intentionally introduced into north-western Washington, in the early 1900's, by settlers who wished to hunt them. The escape or release of red foxes from fur-farms in the 1930's and 1940's was also an important source of introductions. Fox-farms operated throughout the Puget Sound region and in the north-eastern Olympic Peninsula, as well as in the western Columbia Basin and the Okanogan Highlands, east of the Cascades. Red foxes are occasionally reported throughout the Columbia Basin, although these records apparently do not represent established populations.

The present distribution of introduced, lowland red foxes in Washington is also related to habitat. Lowland foxes occur throughout western Washington, except in the forests on the western slope of the Cascades, the Willapa Hills, the outer coast zone and the Olympic Mountains. East of the Cascades, introduced populations occur in areas where fox-farms had operated previously: the western Columbia Basin, and the eastern Okanogan Highlands. Lowland populations clearly favor disturbed habitat, especially farmlands and suburban areas, and do not find suitable habitat in densely forested areas.

In western Washington, lowland and Cascade foxes are separated by a wide zone of dense forest on the west slope of the Cascades, uninhabited by either population. Because lowland foxes have not colonized the subalpine meadows of the Olympics, even in the absence of Cascade foxes, it is likely that they have also not colonized the subalpine meadows of the Cascades and interbred with indigenous foxes. Thus, Cascade and lowland foxes are restricted to high and low elevation habitats, respectively, and their ranges do not intergrade. A survey of parasites infecting each population provided strong evidence in favor of this conclusion. Helminth-faunas of each population were strikingly different. Cascade foxes contained parasites typical of red foxes, whereas lowland foxes harbored a depauperate fauna. The differences found clearly show that lowland foxes do not frequent high mountain habitat; otherwise, they would be infected with the parasites endemic to that region.

A distributional analysis of museum specimen localities and trapping reports in British Columbia and Oregon was conducted. In British Columbia, populations of red foxes occur in the central and northern boreal regions (subspecies *abietorum*) and near Vancouver at the mouth of the Fraser River. Specimens from the Vancouver area have previously been assigned to the Cascade red fox (subspecies *cascadensis*), yet their distribution is continuous with that of introduced populations in western Washington. In addition, the habitat occupied by this population is typical of lowland foxes, not Cascade foxes. A morphometric analysis of cranial measurements separated out Cascade and lowland populations in Washington. Specimens from the Vancouver area were morphologically very similar to specimens from the lowlands of western Washington. Thus, lowland populations in south-western British Columbia represent the northernmost extension of the range of the introduced red foxes found throughout western Washington.

Red foxes did not occur in the Willamette Valley of Oregon before 1940. They are currently found throughout the Valley, however, in habitat characteristic of introduced, lowland foxes in Washington and British Columbia. Morphometric analysis showed a statistically significant separation between Willamette Valley and Cascade foxes, from Oregon, supporting the conclusion that Willamette Valley foxes are not indigenous. Trapping records indicated that red foxes have become established in the Malheur River Valley of eastern Oregon within the last ten years, although no museum specimens are available from that area.

No museum specimen from the Cascades of Oregon post-dates 1939, yet trapping records showed that red foxes have been harvested from the east-side forests in recent years. Distribution records of Oregon Cascade foxes were located in the subalpine meadows near the Crest or in the dry, open forests on the eastern Cascade slope, in accordance with distributional patterns found in Washington. Museum specimens of red foxes from the Wallowa Mountains (subspecies macroura), have not been collected since 1930, nor have red foxes been harvested from that area by trappers in recent years. These findings suggest that indigenous red foxes may no longer occur in eastern Oregon.

The Columbia River must prevent the exchange of genes between Cascade foxes in Washington and Oregon. Nevertheless, morphometric analysis showed that these two populations were virtually identical, in terms of skull morphology. These populations were derived from the same ancestral genetic stock, and occupy ecologically analogous habitat. Their similarity probably reflects comparable environmental influences acting upon a common genotype.

Morphometric analysis between abietorum and cascadensis, showed that these populations were very different morphologically, as well as ecologically. These differences were found only between male specimens; females could not be confidently differentiated. Significantly, abietorum males are larger in relation to females than are cascadensis. This suggests that sexual selection is operating more strongly on abietorum males. Although red foxes are commonly described as a strictly monogamous species, polygyny has been reported. A higher prevalence of polygyny in abietorum could account for these results, although it has not been reported from British Columbia.

A review of available fossil records of the red fox in North America enabled a reconstruction of Quaternary zoogeography. Red foxes colonized North America from Asia during the Illinoian (penultimate) glaciation and expanded their distribution southward, at least as far as southern Canada, during the following Sangamon interglacial. At the height of Wisconsin glaciation, North American red foxes were separated into two refugial populations: a very large variety in Beringia and another, of much smaller size, south of the continental glaciers.

The southern refugial red foxes were widely distributed during Wisconsin time, but as the glaciers retreated, favorable cold climatic conditions no longer existed throughout most of this region. Red foxes in the eastern U.S. either followed the retreating glaciers northward into Canada, or became extinct. Those in the western U.S. disappeared from much of their former range, but remnants of this population retreated into climatically comparable habitat at high elevations of the western mountains.

At the same time that favorable habitat was shrinking for the southern refugial red foxes, the northern refugial foxes in Alaska were separated from Asian populations as the Bering Strait was reestablished in Holocene time. Regions to the south, which had previously been covered by glaciers, now provided suitable habitat, and this population expanded its distribution southward into Canada. Modern populations in western Canada and Alaska were derived from the northern refugial red foxes.

Although abietorum in British Columbia and cascadensis in Washington are nearly parapatric, morphological data show that they are very different in size. Abietorum are large foxes; cascadensis are small. The most likely explanation for this difference in size is that each were derived from different ancestral populations that had evolved into distinct large and small forms while isolated from each other during the Wisconsin glaciation.

This may also provide an explanation for why Cascade foxes are restricted geographically, and why they have been unable to expand their distribution under the influence of human alteration of natural habitats, unlike other populations. By virtue of their ancestry, these foxes are adapted to a climatically cold habitat. Within the geographic region occupied by this subspecies, such conditions only occur at high elevations of the Cascade Mountains.

Field work was conducted on a population of Cascade foxes in the south-central Cascade Mountains of Washington to describe their ecological relationships and investigate attributes that may be unique to these mountain foxes. Home ranges were found to be small in subalpine meadows, but larger in presumably poorer habitat on the east slope of the Cascades. A similar situation has been described in Wisconsin, and home range sizes were not markedly different from those in other regions. Cascade foxes do not migrate to lower elevations in the winter, although home ranges were larger in the winter than in the summer, in accordance with previous reports, elsewhere. This is not unexpected because large areas of hunting territory are covered with snow in the winter. In addition, food habits studies indicated a switch, in mammalian prey, from small rodents in the summer to snowshoe hares and deer carrion in the winter. The latter food items would be expected to be less densely distributed.

One active and one inactive den were located and described. Both were situated in stands of trees. No evidence was found to support earlier assertions that Cascade foxes den in and around talus slopes to escape predation by coyotes. The dens of Cascade foxes, in terms of their placement, the number of entrances and the size of entrances were not different from those of other populations in North America. Given that Cascade foxes occupy a climatically extreme habitat, it might be expected that reproduction would be delayed to compensate for the presumably delayed reproduction of mammalian prey species. However, the aging of one pup, on the basis of tooth eruption patterns, indicated that Cascade foxes breed in early February, which is a typical breeding date for red foxes in other regions. Two female pups were monitored through their first year. One raised a litter and one did not, demonstrating that Cascade foxes may breed in their first winter. Similar findings have been widely reported in the literature.

The seasonal diet of Cascade foxes closely approximated the findings of studies conducted in other localities. In the winter, mammals were the principal food items. In the spring, birds became a minor component of the diet and continued as such through the summer and fall. In the early summer, fruits and insects were abundant and became important food items, although mammals were still the most important item. In the fall, insects and fruits declined in importance in the diet, with their availability, and mammals again represented virtually the entire diet.

One striking difference was found between the diet of Cascade foxes and that of foxes from the mid-western U.S. The single most important food item was pocket gophers. In the midwest, where gophers also occur, they are only a minor component of red fox diets. Sign of extensive pocket gopher activity in the area was not seen, suggesting that gophers were not more abundant than other rodents. Thus, Cascade foxes may have been selectively preying on them, which would suggest that they might be specialized predators of pocket gophers.

Although Cascade foxes may vary karyotypically from other populations, there is little, except their small size and ecologically restricted distribution, to distinguish them from other populations. The importance of pocket gophers in the diet was the only unique ecological attribute found. The restricted range of Cascade foxes may be related to the distribution and abundance of pocket gophers, but their broadly-based diet does not indicate a dependence on gophers. More likely, the small Cascade and other mountain foxes evolved during the Wisconsin glaciation in the southern ice-free refugium and became adapted to a cold climate. Cascade foxes are a remnant of this refugial population and exhibit a similar habitat specificity.

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APPENDIX A

MUSEUM SPECIMENS OF THE RED FOX FROM THE PACIFIC NORTHWEST

The number contained in each museum is given in parentheses.

BRITISH COLUMBIA

British Columbia Provincial Museum, Victoria (32); Vertebrate Museum, University of British Columbia, Vancouver (31); National Museum of Natural History, Washington, D.C. (27); Museum of Vertebrate Zoology, University of California, Berkeley (17); Museum of Zoology, University of Michigan, Ann Arbor (12); National Museum of Natural Sciences, Ottawa, Ontario (6); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (3); American Museum of Natural History, New York (2); Museum of Natural History, University of Kansas, Lawrence (2); and the Royal Ontario Museum, Toronto (2).

WASHINGTON

Thomas Burke Memorial Washington State Museum, University of Washington, Seattle (46); National Museum of Natural History, Washington D.C. (25); Museum of Natural History, University of Puget Sound, Tacoma, Washington (21); Charles R. Conner Musuem, Washington State University, Pullman (5); National Museum of Natural Sciences, Ottawa, Ontario (2);

Denver Collection of the Bird and Mammal Laboratories, U.S. Fish and Wildlife Service (1); Batelle Pacific Northwest Laboratories, Richland, Washington (1); and the private collection of Arthur Peck Jr., Ellensburg, Washington (1).

OREGON

Museum of Natural History, Oregon State University, Corvallis (10); National Museum of Natural History, Washington, D.C. (8); San Diego Natural History Museum, Balboa Park, California (5); Museum of Natural History, University of Puget Sound, Tacoma, Washington (3); Thomas Burke Memorial Washington State Museum, University of Washington, Seattle (2); Museum of Vertebrate Zoology, University of California, Berkeley (2); and the Charles R. Conner Museum, Washington State University, Pullman (1).

APPENDIX B

WEIGHTS AND MEASUREMENTS OF CAPTURED CASCADE RED FOXES

ADULT CASCADE FOXES

	MALES			FEMALES		
MEASUREMENT	BILL 9/12/79	ROCKY 7/23/80	NO NAME 7/23/80	EVE 7/28/79	MAGGIE 7/8/80	FANNY 4/6/81
Weight (kg)	4.0	4.5	4.5	3.5	3.7	3.1*
Total l. (cm)	103.0	101.0	103.0	95.0	95.0	99.5
Tail length	39.8	39.0	32.0	37.0	39.0	35.0
Hindfoot l.	16.0	17.0	16.5	15.0	16.5	15.3
Ear notch	8.7	9.5	9.0	8.8	9.0	8.8
Ear crown	9.5	10.5	10.0	9.8	9.0	9.0
Chest girth	31.5	33.0	34.0	30.2	31.0	33.0
Neck girth	18.8	19.0	20.0	15.6	17.0	16.0
Head girth	23.5	23.0	24.0	21.0	22.0	22.0
Head width	7.5	8.5	9.0	7.1	7.0	7.2
Head length	14.9	15.0	16.5	15.0	15.0	15.5
Ht. @ shoulder	43.3	39.0	44.0	38.5	40.0	38.0

* This animal had been held in a live-trap for 3-6 days before weighing, and this figure probably reflects weight loss resulting from this period of fasting.

JUVENILE CASCADE FOXES

FEMALES

MEASUREMENT	KIT 7/23/80	KIT 9/2/80	JEZEBEL 8/7/80	JEZEBEL 9/1/80	NONAME 9/16/81
Weight (kg)	2.7	3.2	3.2	3.4	4.0
Total length (cm)	89.0	93.0	94.0	96.0	99.0
Tail length	34.0	35.0	34.5	37.0	37.0
Hindfoot length	14.5	14.5	14.5	15.0	15.0
Ear notch	8.5	8.5	7.5	8.5	9.0
Ear crown	10.0	9.0	9.0	9.0	10.0
Chest girth	27.0	28.0	29.0	30.0	32.0
Neck girth	16.0	15.0	16.5	16.0	17.0
Head girth	21.0	22.0	22.5	22.0	21.0
Head width	7.0	6.8	-	7.0	7.0
Head length	14.0	15.0	16.5	14.0	16.0
Height at shoulder	36.0	40.0	37.0	39.0	40.0

VITA

Name:

Keith Baker Aubry

Date of Birth:

October 29, 1952

Place of Birth:

Redwood City, California

Parents:

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