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

by

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Abstract

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The Cascade red fox, *Vulpes vulpes cascadensis*, was found to occur in the subalpine meadows and parklands near the Crest of the Cascade Mountains and on the eastern slope of the Cascades in open forest habitat; they do not occupy the more densely forested habitats on the western slope.

Red foxes from the eastern U.S. were intentionally introduced into low elevation areas of the Pacific Northwest by early settlers. The escape or release of farm-foxes has also been an important mechanism of introduction, and red foxes now occupy disturbed habitats at low elevations throughout this region. The dense forests of the western Cascades separate lowland and Cascade populations, however, and their ranges do not intergrade. Studies of the helminth-faunas of each population supported this conclusion.

Comparative analyses of the cranial morphology of indigenous and introduced populations of red foxes in Washington, Oregon and British Columbia were conducted. Lowland and Cascade red foxes in Washington were distinguishable, and specimens from south-western British

Columbia, although classified as _cascadensis_, were morphologically more similar to introduced foxes. Indigenous red foxes from British Columbia (subspecies _abietorum_) were very different, morphologically, from _cascadensis_, but only when male specimens were compared. Stronger sexual selection on _abietorum_ males may account for this.

A review of Pleistocene fossil records of the red fox in North America showed that red foxes colonized North America during the Illinoian glaciation. By Wisconsin time, they had become separated into two refugial populations: a large variety in the north, and another, of much smaller size, in the south. A theory proposing that Alaskan and Canadian red foxes are descended from the northern refugial population, and that the 'mountain' foxes of the western U.S. are a remnant of the southern refugial population is presented.

Study of a representative population of the Cascade red fox in south-central Washington, using radio-telemetry, revealed no important differences in home range size, seasonal habitat use patterns, reproduction or den ecology between Cascade foxes and other populations in North America. Differences in food habits were found, however. Pocket gophers have not previously been reported as important components in the diet of red foxes, yet scat analysis showed pocket gophers, _Thomomys talpoides_, to be the most important food item in the diet of Cascade foxes.

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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,

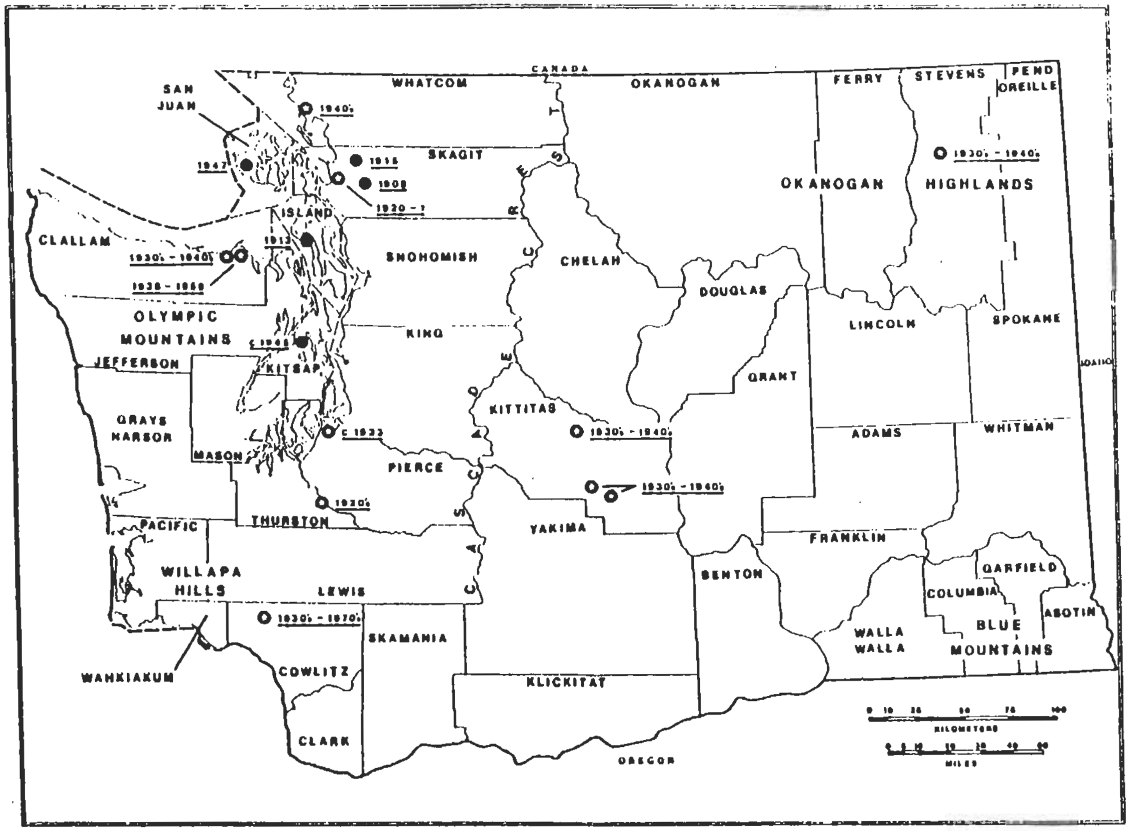

Figure 1. Dates and locations of fox-farms (circled stars) and points of introduction of red foxes (solid circles) in Washington.

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

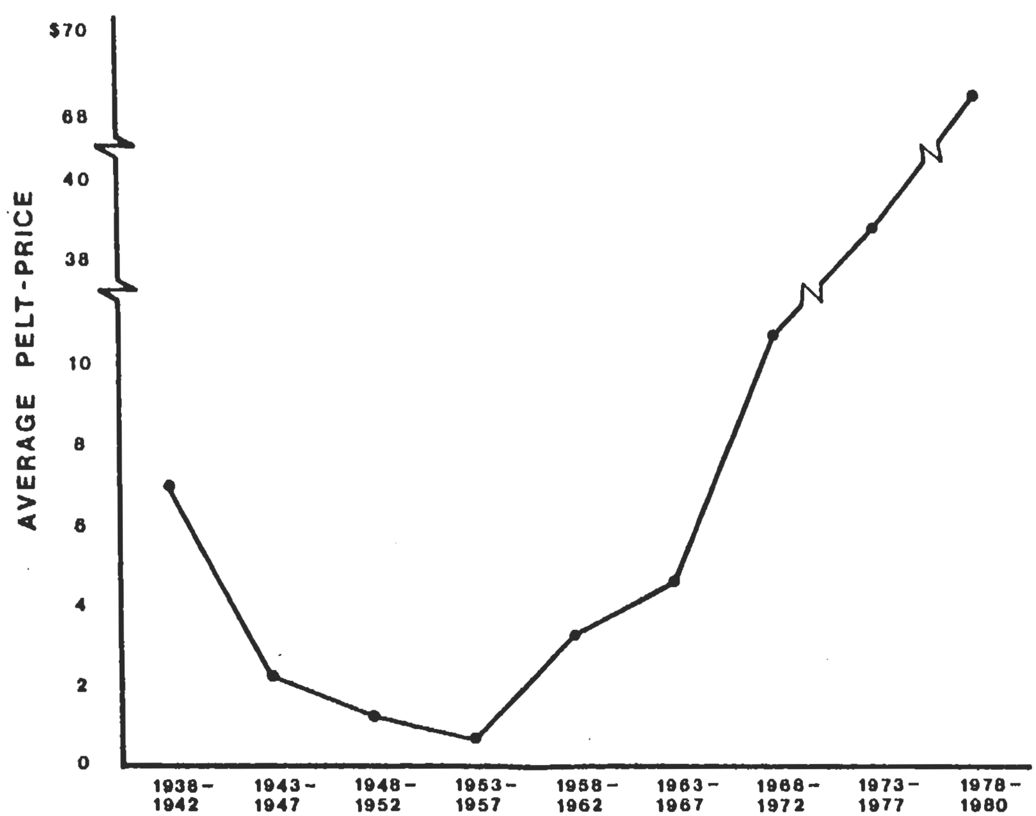

Figure 2. Average pelt-price for red fox in Washington between 1938 and 1980. No data available for 1942, 1943 1945 or 1950. Data from Washington State Dept. of Game.

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.

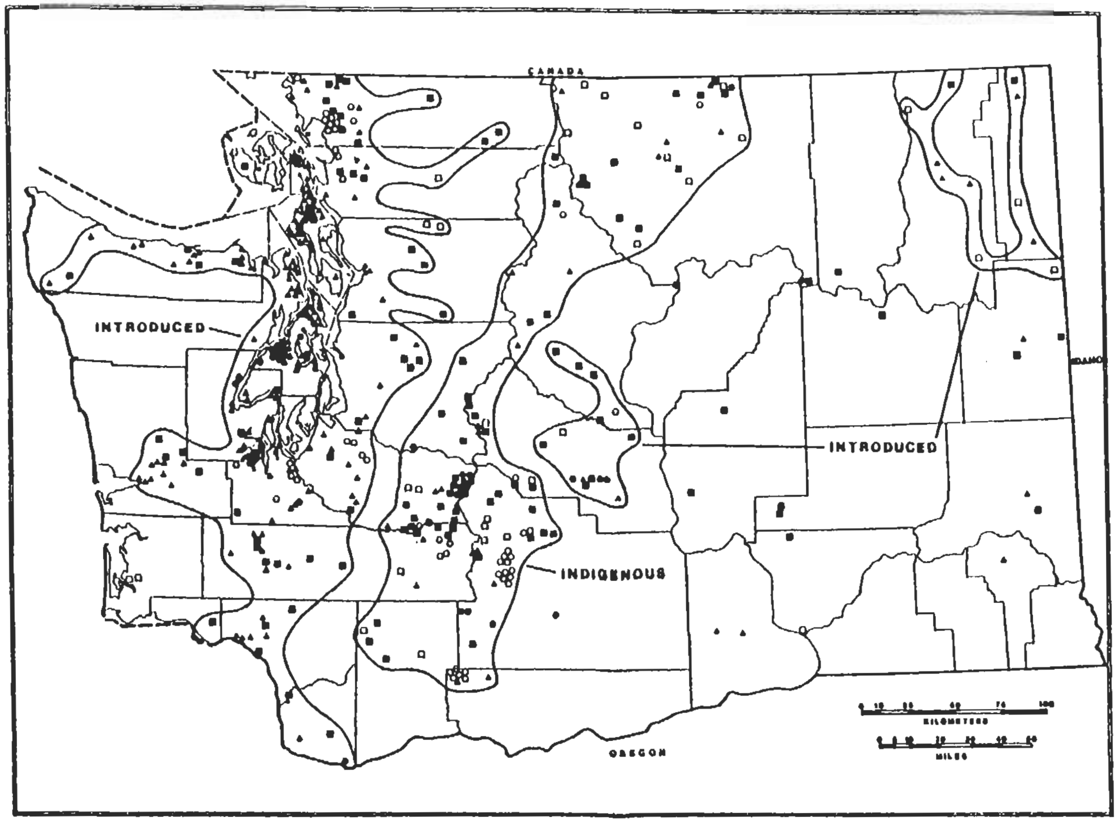

Figure 3. Distribution records and geographic ranges for indigenous and introduced populations of red foxes in Washington. Squares represent sight-reports; triangles, trapping reports; and circles, locality-records of museum specimens. Hollow symbols indicate records dated prior to 1970.

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) Total length: From anteriormost point on premaxilla to posteriormost point on occipital crest.

2) Condylobasal length: 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

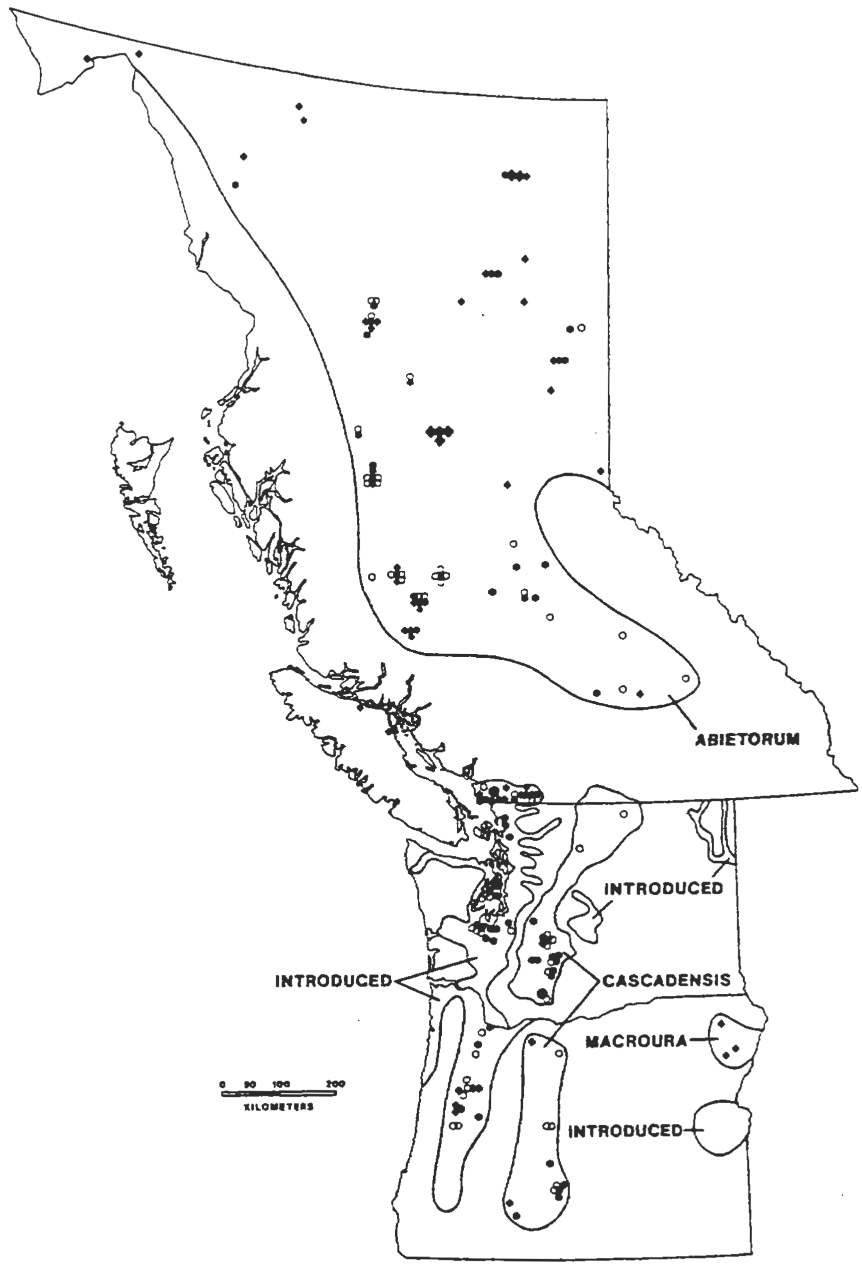

Figure 4. Museum specimen localities and distributional ranges of indigenous and introduced populations of red foxes in the Pacific Northwest. Solid circles represent adult male specimens, and open circles represent adult female specimens used in the morphometric analyses. Diamonds represent specimens 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

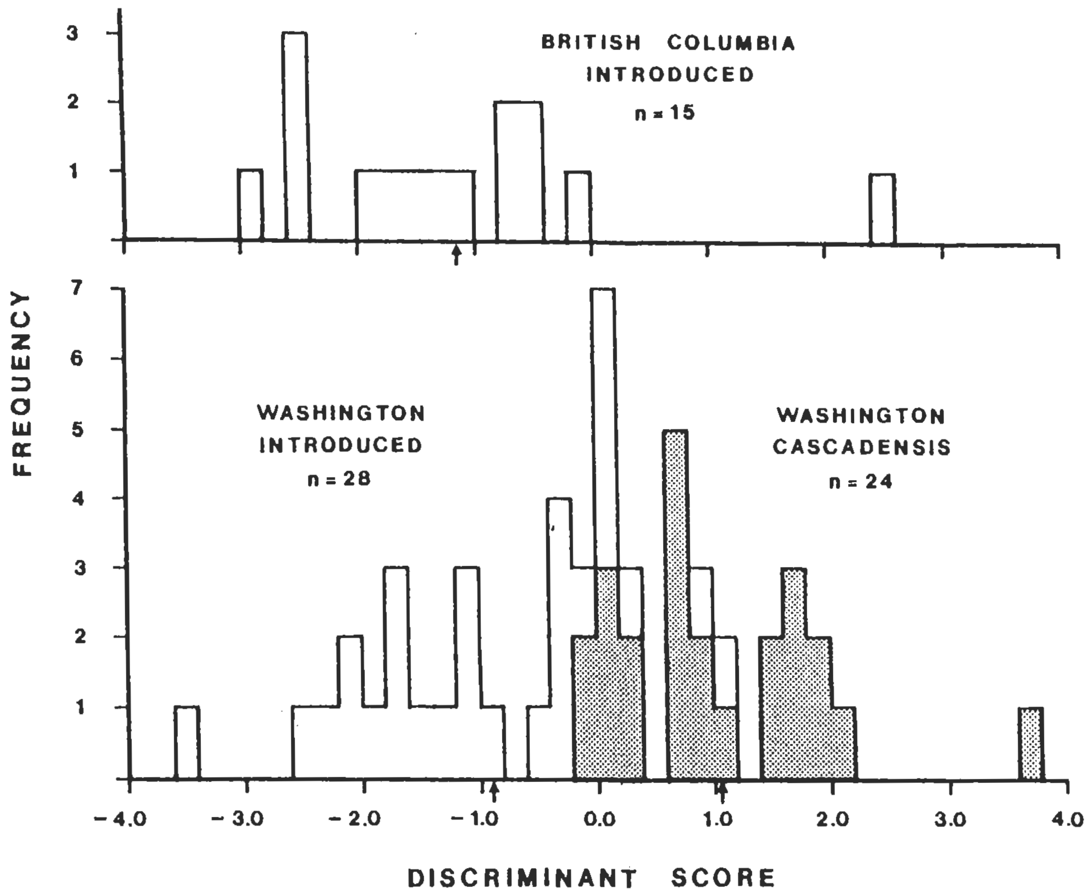

Figure 5. Lower graph: histogram of discriminant scores for introduced specimens from Washington (open bars) and *cascadensis* from Washington (stippled bars). Upper graph: histogram of discriminant scores for introduced specimens from British Columbia when included in the analysis as unknowns. Both 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; $P < .001$

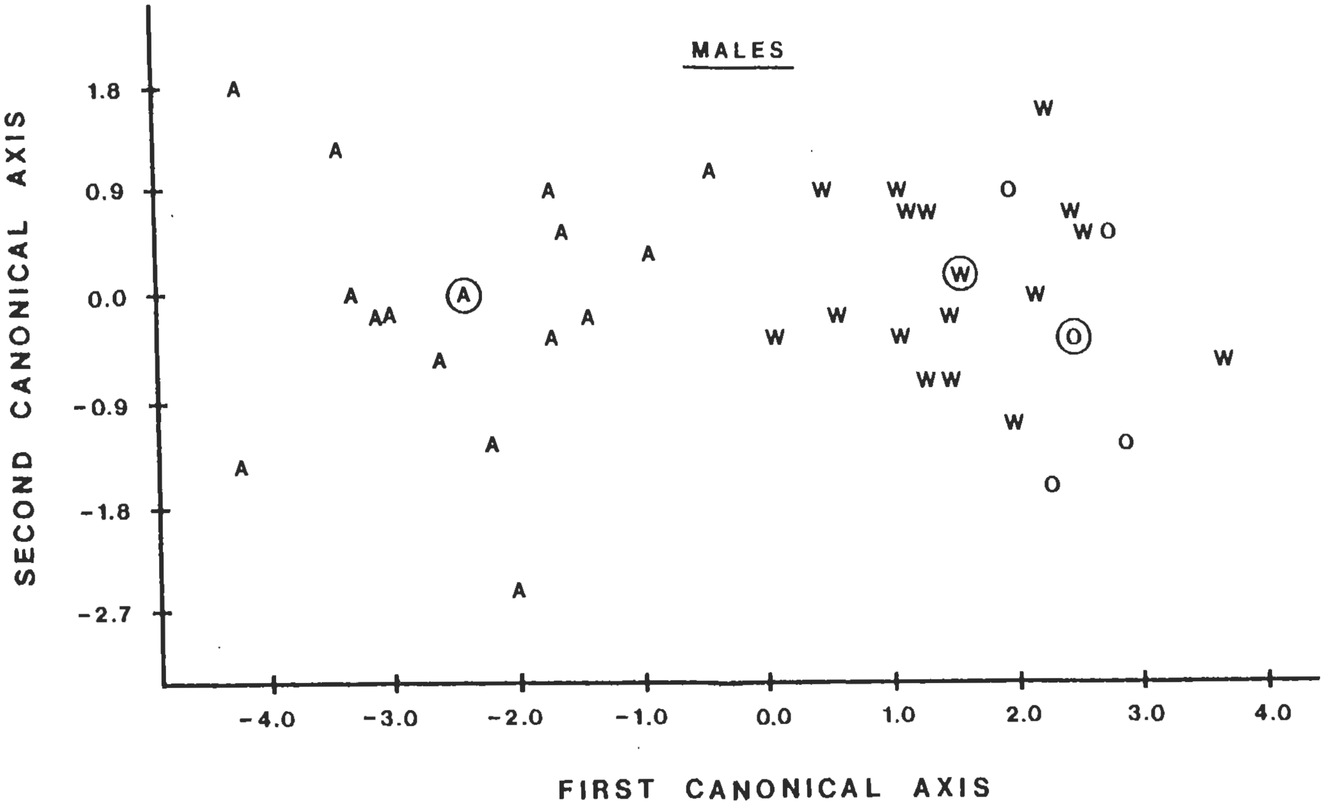

Figure 8. Graph of discriminant scores for abietorum (A's), cascadensis from Washington (W's) and cascadensis from Oregon (O's). Males only were used, and circled symbols indicate group means.

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	Character Coefficients (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

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

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 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

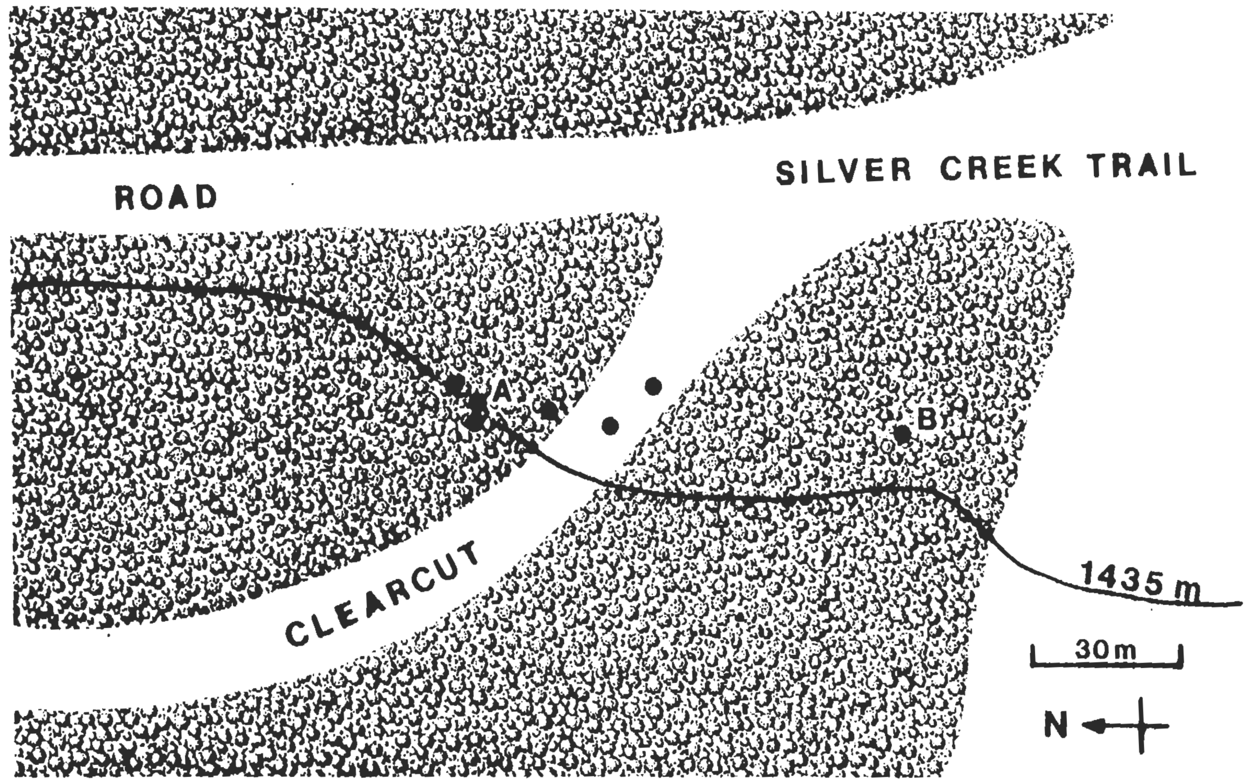

Figure 16. Active den located in Crystal Mountain study area in 1981. Solid circles represent den entrances, and 'A' and 'B' indicate the openings monitored with remote cameras.

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 58 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, <u>Frageria</u> sp., and blueberries, <u>Vaccinium</u> 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 of 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

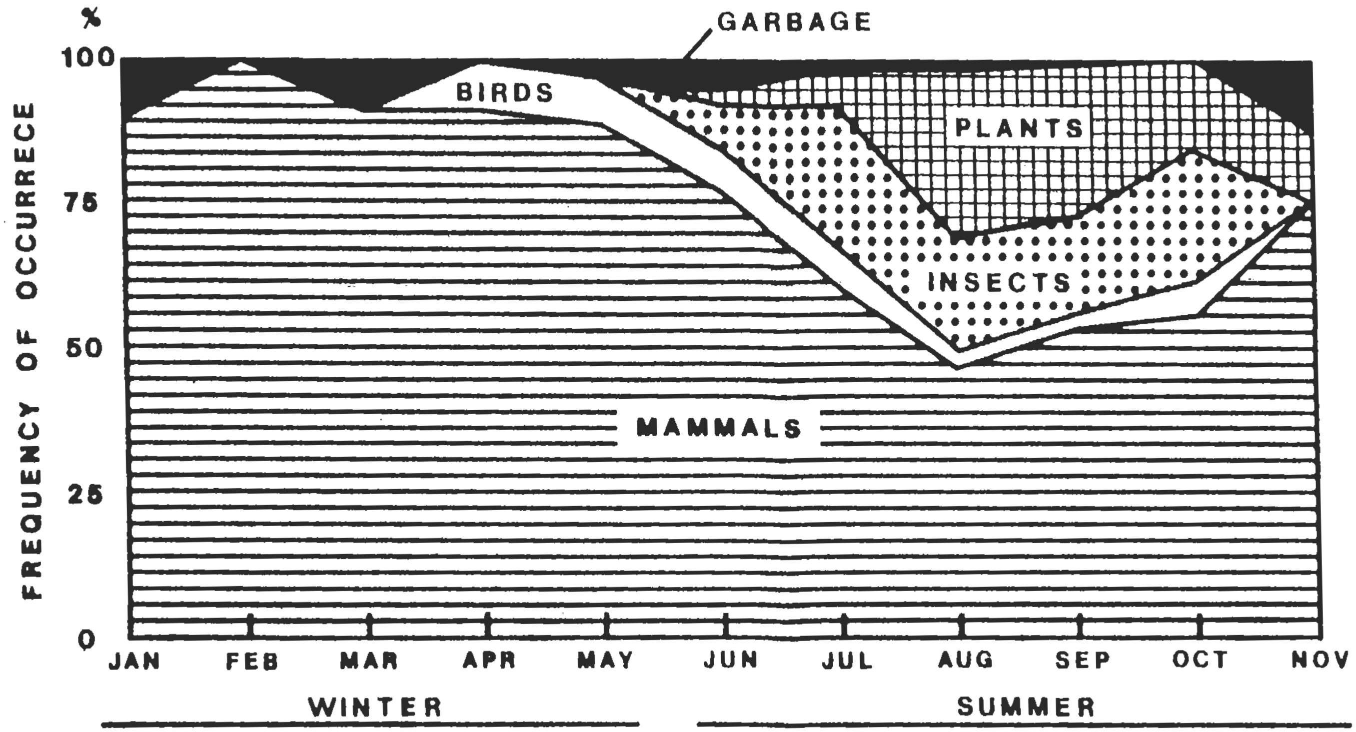

Figure 17. Monthly food habits of Cascade red foxes, 1979-1981.

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.

BLOOD VALUE	MALES 7/23/80 ROCKY	7/23/80 NO NAME	FEMALES 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.

BLOOD VALUE	FEMALES 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

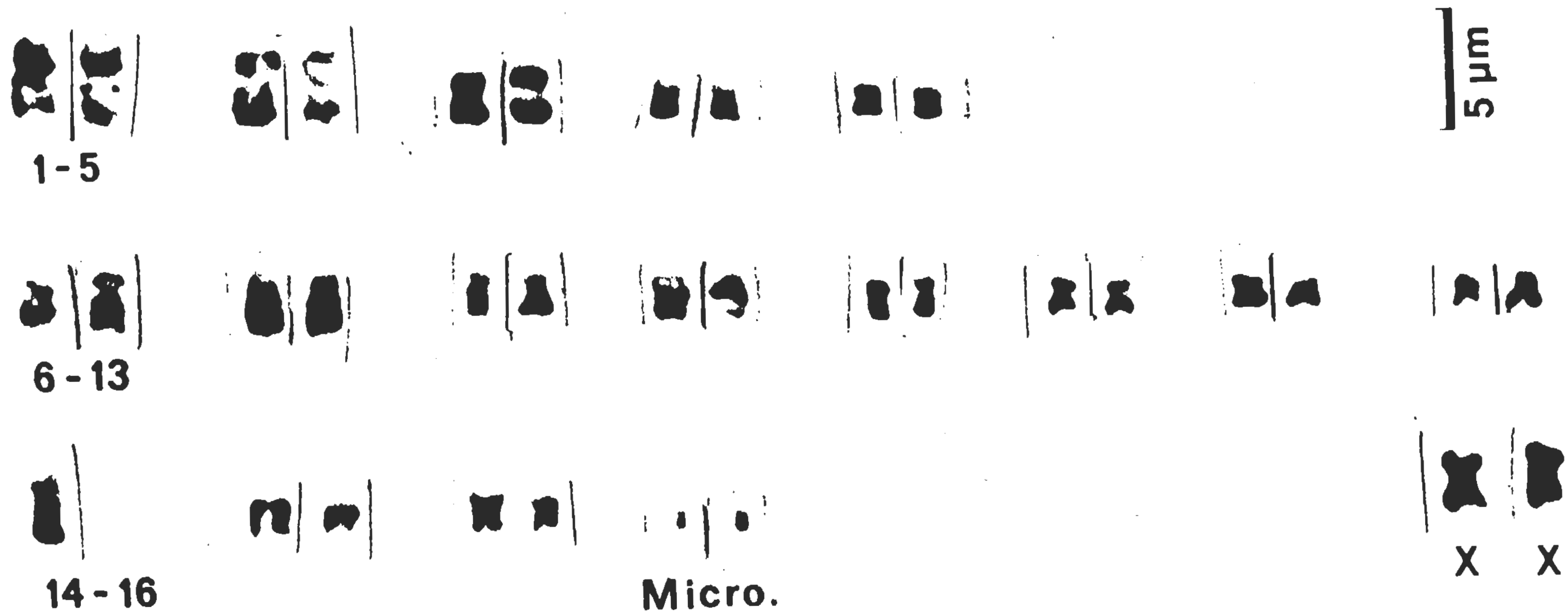

Figure 18. Karyogram of female Cascade red fox.

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

MEASUREMENT	MALES			FEMALES		
	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

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Place of Birth:

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