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TAXONOMIC STATUS OF THE RED FOX IN CALIFORNIA[1]

by

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ABSTRACT

A multivariate analysis of measurements from 129 red fox skulls revealed that
the Sacramento Valley red fox is most closely related to the red fox of the
Northern Great Plains, _Vulpes vulpes regalis_. It differs slightly from the
native Sierra Nevada red fox, but from a practical point of view it is very
difficult to separate the two forms, unless a properly programmed computer is
used. Some distinguishing features to assist in identifying, or distinguishing
between, the Sacramento Valley fox and the Sierra Nevada fox (_V. v. necator_)
are presented.

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INTRODUCTION

This report presents the results of an investigation into the taxonomic status and relationships of two separate red fox populations which are found in California, as authorized by the California Department of Fish and Game (Contract Number W54R9-11).

One fox population is native to the state, and is found in the Sierra Nevada Mountains from southern Tulare County to Siskiyou County, usually at elevations above 5000 feet (Fig. 1) (Gray, 1975). It was originally named Vulpes necator by Merriam (1900), but since then has been considered a sub-species of the North American red fox, with the name Vulpes fulva necator (Grinnell, Dixon and Linsdale, 1930). Churcher (1959) combined V. fulva with V. vulpes, so the proper name is now Vulpes vulpes necator. It has been commonly referred to as Sierra Nevada red fox. It has been reported to be a large fox with rich coloration, and the cross, silver, and black color phases are not uncommon in the population.

The other fox population is found only in the Sacramento Valley and a few adjoining regions, usually below 3000 feet elevation. These foxes were not mentioned by early explorers or settlers, and are thought to have been introduced into the Sacramento region sometime prior to the 1890s (Grinnell, Dixon and Linsdale, 1937). They are relatively large foxes with very pale coloration; their taxonomic status has not been determined, and is the subject of this report. The ranges of these two fox populations apparently do not overlap (Fig. 1).

METHODS

Specimens of foxes from both the Sierra Nevada and the Sacramento Valley populations were to be compared in order to clarify the taxonomic status of the Valley foxes. Data obtained were to be analyzed with a multivariate approach, as has been successfully done with other fox species (Waithman and Roest, 1977). Sierra Nevada red fox specimens (hereafter referred to as necator, or in abbreviated form as NEC) were examined and measured at the National Museum of Natural History, Washington, D. C., and at the Museum of Vertebrate Zoology, Berkeley, Calif. Sacramento Valley red fox specimens (hereafter referred to as Sacramento foxes, or SAC) were examined at the Museum of Vertebrate Zoology, Berkeley, at Sacramento State University, Sacramento, at the University of California, Davis, and at Chico State University, Chico, all in California. Very few were available, so 12 additional
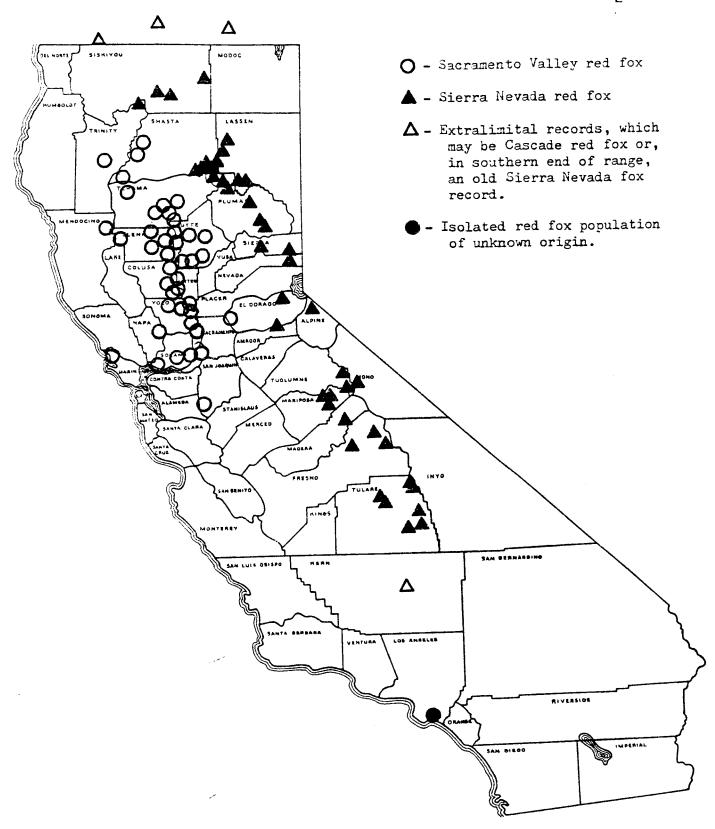
Figure 1. -- Locality records for red foxes in California (modified after Grinnell, Linsdale and Dixon, 1937, and Gray, 1975, and others).

specimens were specially collected for this study by the Department of Fish
and Game during late 1976 and early 1977. These specimens are now at the
California Polytechnic State University, San Luis Obispo, Calif.

To compare specimens from only the Sacramento and necator populations
would not, by itself, clarify the taxonomic relationships of the Sacramento
population. Most multivariate computer-assisted methods of analysis now
available for comparing differences between populations of animals would
undoubtedly reveal a difference between them. The question was not just
whether Sacramento and necator foxes were different, but rather how different
should they be to warrant taxonomic recognition. To develop a concept of
the differences between recognized fox subspecies, it was decided to include
comparable data from several other subspecies of red foxes in the analyses.

Subspecies were selected for analysis for several reasons. Some were
selected because they occurred in geographically nearby regions, such as
V. v. cascadensis and V. v. macroura (see range map, Fig. 2). Some were
selected because they were relatively large forms (like both Sacramento and
necator), such as V. v. alascensis and V. v. regalis. Some were selected
because examination of skins revealed specimens with the same pale colora-
tion characteristic of the Sacramento foxes (Table 1). V. v. abietorum was
included because it is found geographically between alascensis and cascad-
ensis. Foxes from eastern Canada were not included because they were all
much redder in color, and were smaller forms. The foxes of the eastern
United States were not included because they are probably derived from stock
introduced from Europe, rather than being native (Churcher, 1959).

Table 1. -- Origin and subspecies of pale-colored fox skins in the National
Museum of Natural History, Washington, D. C. These skins very
closely match those of Sacramento Valley foxes, and were picked
from 185 skins which were examined.

Number of skins	Origin	Subspecies
6	Oregon and Washington	V. v. cascadensis
6	Idaho, Utah, and Wyoming	V. v. macroura
4	Minnesota and Manitoba, Can.	V. v. regalis

Final comparisons in this study thus involved seven red fox populations,
listed here with the abbreviations used subsequently in this report:
Sacramento Valley red fox (SAC), Sierra Nevada red fox, V. v. necator (NEC),
Cascade Mountains red fox, V. v. cascadensis (CAS), Rocky Mountain red fox,
V. v. macroura (MAC), Northern Great Plains red fox, V. v. regalis (REG),
British Columbia red fox, V. v. abietorum (ABI), and Alaskan red fox, V. v.
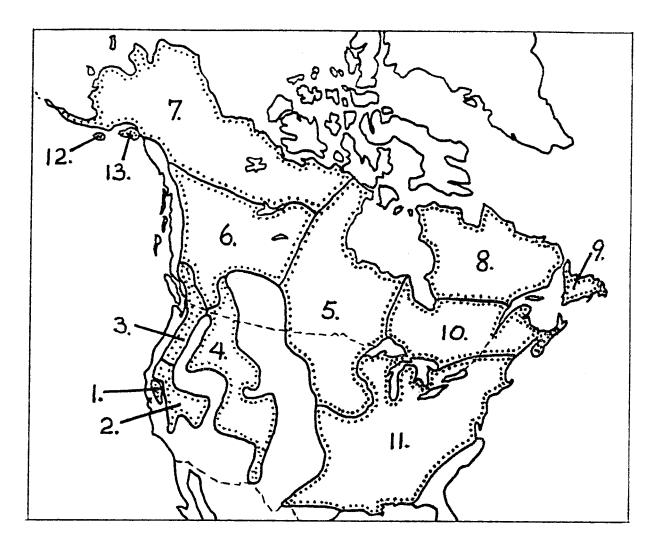alascensis (ALA).

Figure 2. -- Distribution of red fox in North America, showing approximate range for each recognized subspecies (modified after Hall and Kelson, 1959).of _Vulpes_ _vulpes_.

1. Sacramento Valley population
2. _V._ _v._ _necator_
3. _V._ _v._ _cascadensis_
4. _V._ _v._ _macroura_
5. _V._ _v._ _regalis_
6. _V._ _v._ _abietorum_
7. _V._ _v._ _alascensis_

8. _V._ _v._ _bangsi_
9. _V._ _v._ _deletrix_
10. _V._ _v._ _rubricosa_
11. _V._ _v._ _fulva_
12. _V._ _v._ _harrimani_
13. _V._ _v._ _kenaiensis_

(The first seven numbers refer to the seven populations analyzed in this study)

Measurements from the skulls of adult foxes provided the basis for the multivariate analysis used in this study. Skulls were judged to be adult if both the basioccipital-basisphenoid and basisphenoid-presphenoid sutures at the base of the skull were closed (Churcher, 1960). On each skull 15 measurements were taken, with dial calipers, to the nearest 0.1 mm. The 15 measurements are each briefly described in Appendix I, at the end of this report. A total of 155 skulls were actually measured, but some had to be deleted from the final analysis. Some were deleted because their collection site could not be located on any map, and thus they could not be assigned to a particular subspecies. This was particularly true for localities in British Columbia, where the range map indicates three different subspecies occur. Some were deleted because a complete set of measurements could not be obtained, due to slightly broken or damaged skulls. The final analysis was made on data from 129 adult skulls, from each of seven different populations, as indicated in Table 2.

Table 2. -- Sample sizes and sources of each of the seven fox populations analyzed in this study.

Group	Abbreviation	Geographic source	Sample
Sacramento	SAC	Sacramento Valley	19
V. v. necator	NEC	Sierra Nevada Mountains	13
V. v. cascadensis	CAS	Cascade Mountains, Ore. & Wash.	19
V. v. macroura	MAC	Rocky Mountains, several states	20
V. v. regalis	REG	Northern Great Plains, U.S. & Can.	22
V. v. alascensis	ALA	Alaska, Northwest Territories	29
V. v. abietorum	ABI	British Columbia, Alberta	7
		Total:	129

The small sample for V. v. abietorum is due to the difficulty of locating collection sites, as explained above. V. v. necator is also a small sample (13), but this represents the total number of necator skulls (of adults) present in the collections examined. No other adult specimens could be located. A distinct effort should be made to preserve additional necator skulls.

Skull data was analyzed with DISANAL, a computer program for multigroup discriminant analysis which emphasizes morphometrics. It is based on Blackith and Reyment (1971), Cooley and Lohnes (1971), and Hope (1968), and developed by Pimentel (1976) into its present form (last revised in April 1977). The program provides outputs which include the basic statistics of the input data, multivariate analysis of variance, principal component analysis, Geisser classification probabilities, canonical analysis of discriminance, plots of canonical variates, and other information.

Most skulls examined did not have accompanying skins, and thus provided no information on body measurements or fur color. Such skulls were obtained as pickups from around trappers cabins. When available, standard body measurements were recorded and used to supplement the analysis of skull measurements.

RESULTS

The means and standard deviations of each measurement for each of the seven groups of fox skulls measured are presented in Table 3. One of the most striking aspects of this body of skull data is the very small difference in the means from different groups, for any measurement. Condylobasal length ranges from a mean of 133.7 mm (MAC) to 142.7 mm (ABI); zygomatic width from 72.5 (CAS) to 77.7 (ALA). These differences of 9 mm and 5.2 mm constitute only 6% or less of the dimension involved. The other 13 skull measurements follow a similar pattern. When the standard deviations are considered, this small difference is reduced by distinct overlaps in the measurements for each group. In short, the differences between various skull measurements among these foxes are very small. This is illustrated graphically for two measurements (condylobasal length and lyre width) in Figure 3. Other measurements have not been graphed in order to save space, but study of Table 3 shows that all the measurements and standard deviations for any group overlap those of the other groups.

Figure 3 also illustrates a pattern which is supported by the other measurements as well, although they are not graphed. In Figure 3 the condylobasal length of SAC is clearly very much like that of REG, ALA, and ABI. The lyre width of SAC is also like that of REG, ALA, and ABI. Contrastingly, the measurements for NEC, CAS, and MAC are grouped together also. This pattern strongly suggests that SAC, REG, ALA, and ABI are related to each other, and similarly NEC, CAS, and MAC form another relationship group.

Table 4 (page 9) is the classification table developed by the DISANAL program. Each specimen, originally identified as coming from a particular group, is assigned to a group which its specific set of measurements predict it should belong to. In the case of Sacramento Valley foxes, for example, 15 of them were assigned to the SAC group, but 2 were considered more like REG, 1 like ALA, and 1 like ABI. This type of classification suggests which groups are most like the SAC group, and vice versa.

As would be expected, most specimens classify into their proper groups. NEC is apparently quite variable, since it classifies to some extent into nearly all the other groups. SAC appears most closely related to REG, ALA, and ABI, as was also suggested by the data in Table 3 and Figure 3, and NEC has a similarity to CAS and MAC.
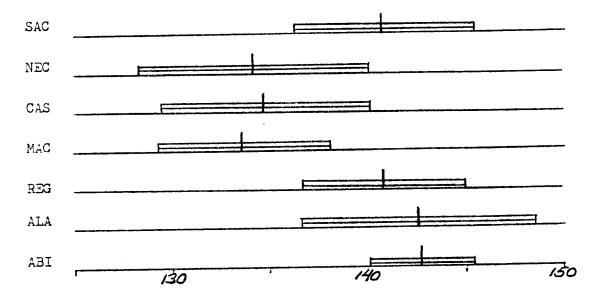
Figure 4 (page 10) plots the group centroids of the first and second canonical variates developed by DISANAL. Here again the relationship of SAC to REG, ALA, and ABI is emphasized, as is the relationship between NEC, CAS, and MAC.

Table 3. --- Means and standard deviations for 15 skull measurements (in mm.) from the 7 groups of foxes analyzed in this study.

Group:	SAC.	NEC.	CAS.	MAC.	REG.	ALA.	ABI.
No. specimens:	19	13	19	20	22	29	7
Measurement:							
Condylobasal L.	140.9 (4.6)	134.2 (5.9)	134.8 (5.3)	133.7 (4.4)	140.9 (4.1)	142.6 (5.9)	142.7 (2.6)
Zygomatic W.	74.4 (2.8)	72.7 (4.0)	72.5 (3.6)	73.1 (2.8)	75.3 (2.3)	77.7 (3.6)	77.4 (1.5)
Palatilar L.	69.7 (2.1)	67.0 (3.4)	66.0 (2.4)	66.5 (2.7)	70.1 (2.4)	71.4 (3.5)	70.3 (1.5)
Max. tooth row	65.0 (2.2)	62.5 (3.1)	62.1 (2.6)	62.1 (3.0)	64.4 (2.6)	66.2 (2.6)	64.3 (1.4)
Postpalatal L.	62.6 (2.0)	58.8 (3.0)	59.7 (3.0)	58.9 (2.3)	62.4 (2.0)	62.0 (2.6)	62.3 (2.4)
Nasal suture L.	51.9 (3.0)	50.7 (3.2)	50.7 (3.7)	48.6 (2.4)	52.2 (2.5)	54.6 (3.2)	52.9 (2.7)
Braincase Br.	47.1 (1.3)	48.2 (1.2)	48.2 (1.2)	48.7 (1.7)	48.1 (1.1)	49.0 (1.1)	48.4 (0.6)
Auditory bullae	39.8 (4.6)	39.2 (2.1)	38.4 (1.4)	39.6 (3.5)	40.6 (1.3)	41.8 (1.9)	41.3 (1.1)
Rostral Br.	21.0 (1.1)	20.4 (1.3)	20.8 (1.1)	20.8 (1.0)	21.8 (0.9)	23.3 (1.4)	23.1 (1.3)
Palatal W.	19.5 (0.9)	18.8 (1.3)	18.4 (1.1)	18.4 (0.9)	19.1 (1.1)	19.8 (2.0)	20.1 (1.3)
Interorbital Br.	26.2 (1.8)	26.2 (1.6)	26.0 (1.7)	26.2 (1.4)	27.3 (1.5)	28.3 (2.9)	27.8 (0.8)
Postorbital Br.	22.2 (1.3)	24.2 (1.4)	23.3 (1.2)	23.5 (1.3)	22.7 (1.2)	23.2 (1.4)	22.7 (1.3)
Nasal W.	11.9 (0.5)	11.0 (1.1)	11.0 (0.8)	11.1 (0.6)	11.8 (0.8)	11.7 (1.1)	12.2 (1.0)
Lyre W.	5.2 (1.7)	9.9 (4.4)	10.4 (2.2)	11.0 (2.5)	6.2 (2.2)	6.7 (2.6)	7.7 (2.0)
Diastema L.	3.5 (0.9)	3.5 (1.2)	3.4 (0.9)	4.2 (0.9)	3.8 (0.8)	2.8 (0.7)	3.3 (0.8)

Figure 3. — Graphic representation of means and standard deviations of
condylobasal length and lyre width from seven groups of foxes
analyzed. Other measurements taken present similar patterns
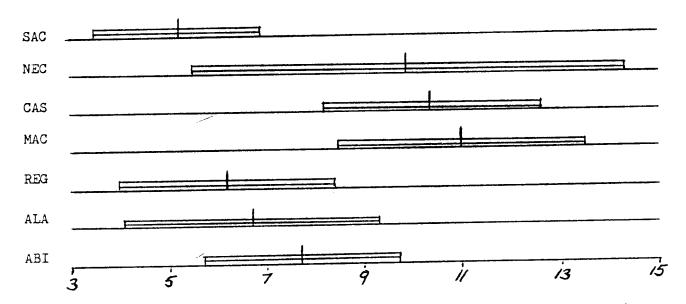when graphed. See also Table 1.

Condylobasal Length:

Lyre Width:

Table 4. -- Classification of actual specimens into predicted groups. The figures in parentheses are percentages.
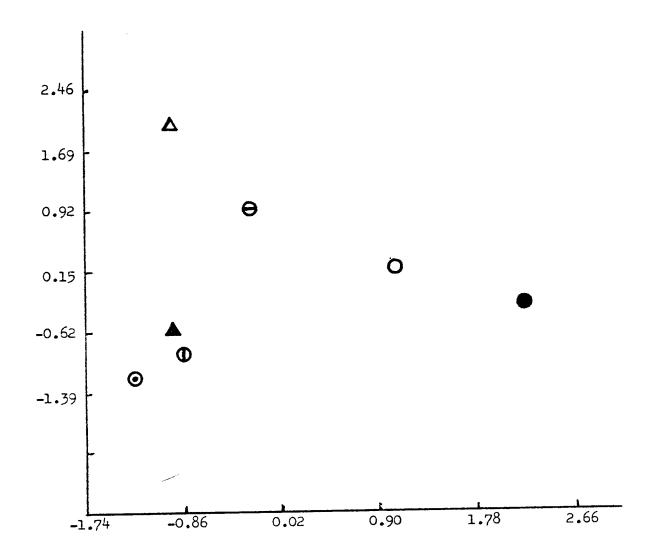
Specimen from group:	Assigned to: SAC	NEC	CAS	MAC	REG	ALA	ABI
SAC	15 (79)	0	0	0	2 (11)	1 (5)	1 (5)
NEC	2 (15)	5 (38)	2 (15)	1 (8)	2 (15)	1 (8)	0
CAS	0	2 (11)	11 (58)	3 (16)	1 (5)	0	2 (11)
MAC	1 (5)	2 (10)	2 (10)	12 (60)	2 (10)	0	1 (5)
REG	4 (18)	1 (5)	0	2 (9)	12 (55)	2 (9)	1 (5)
ALA	0	1 (3)	0	0	0	25 (86)	3 (10)
ABI	0	0	0	0	2 (29)	0	5 (71)

As mentioned above, information on body measurements and weights were not available in detail. Examination of published information in the literature produced additional approximate data. Table 5 presents a summary of the available information.

Table 5. -- Information on total length, tail length, hind foot length, ear length, and weight for various red fox populations. Measurements are in millimeters, weights in kilograms. Extremes are given in parentheses. Remarks are from the literature, primarily from Anthony (1928).

Group	N	Total	Tail	Hind Foot	Ear	Weight
SAC	16	1056 (960-1200)	386 (320-430)	166 (150-182)	97 (90-110)	4.64 (N = 10) (4.1 - 5.5)
NEC	5	975 (900-1000)	356 (305-400)	158 (132-170)	98 (85-107)	3.46 (N = 3) (3.2 - 3.6)(max to 4.1)
MAC		(1015-1041)	(461-470)	(172-178)	(longer tail and hind foot)	
CAS		(1070-1113)	(412-441)	(178-180)	112	4.1 (short-tailed)
REG		1143	432	178	(largest; long-tailed)	
ALA					(large; long tail; small ears)	
ABI					(large; similar to ALA)	

Figure 4. -- Plot of Group Centroids of the first and second canonical
variates, showing relationships of the seven groups of foxes
analyzed. Symbols: open triangle = Sacramento; black tri-
angle = necator; vertical bar circle = cascadensis; dotted
circle = macroura; horizontal bar circle = regalis; black
circle = alascensis; open circle = abietorum.

DISCUSSION AND CONCLUSIONS

The primary objective of this study was to determine whether the Sacramento Valley red fox population was different from the native Sierra Nevada red fox, Vulpes vulpes necator. The DISMAL analysis used in this study indicates that these two populations are indeed different.

Table 3 and Figure 3 show that the Sacramento foxes are most like foxes from the Northern Great Plains (ssp. regalis), Alaska (ssp. alascensis), and the Rocky Mountains of British Columbia and Alberta (ssp. abietorum). Like these other forms, the Sacramento foxes are somewhat larger than the Sierra Nevada foxes in most skull dimensions, although smaller in braincase breadth, interorbital breadth, postorbital breadth, and lyre width. The canonical graph of the group centroids (Fig. 4) shows the relationships of all seven groups of foxes, with the Sacramento group closest to regalis. The graph suggests a cline running from the Sacramento fox type through regalis to abietorum and alascensis.

The degree of difference between the seven groups is also indicated in Fig. 4, where the distances between the various centroids are proportional to the differences between each group. The greater the distance, the greater the difference. The difference between the Sacramento centroid and the necator centroid is greater than that between Sacramento and regalis, or between the three closely related forms -- necator, cascadensis, and macroura. The multivariate system used can clearly distinguish different populations in the data analyzed.

In terms of actual measurements however, the differences between foxes from the different groups are very small. The means of condylobasal lengths from the seven groups vary through a range of only 9 mm, zygomatic widths means only 5.2 mm, values amounting to only about 6% of the roughly 140 mm and 75 mm values involved. The other measurements have means which are even closer together. When standard deviation from the means are considered, it becomes clear that the measurements for the various groups are not only very similar, but overlap each other as well. If extremes from each group were included, the overlap would be even greater.

This means that if an attempt is made to classify a single skull into a particular group on the basis of its measurements, no certain classification could be made. Even with the aid of a computer, programmed properly to accept such information, a skull from the Sacramento population would be properly assigned with only 79% accuracy; if it were from the Sierra Nevada population it could be assigned properly with only 38% accuracy (Table 4), and similarly for the other groups. Even the computer has difficulty in identifying the proper group for individual skulls. Without a computer, an individual skull cannot be accurately identified at all, although some rough guesses could be made.

The Sacramento foxes are recognized by the computer as representing a different population than the Sierra Nevada foxes. Sacramento foxes are most similar to foxes from the Northern Great Plains, V. v. regalis, on the basis of their skull measurements. In addition, Sacramento foxes have the same pale coloration seen in at least some specimens of regalis (Table 1), and are also fairly large animals (Table 5), as is regalis. They approach regalis in

tail length and hind foot length. The color description given by Anthony (1928) for regalis (largest fox subspecies, with long tail; color golden yellow, becoming almost buffy white on face) comes very close to being a description of the Sacramento foxes.

There is a strong probability that the Sacramento foxes were introduced into California, as discussed in some detail by Grinnell, Dixon and Linsdale, 1937). They were sufficiently abundant during the 1890s to be trapped for their fur. This suggests they must have been introduced at least 10 years or more previously, in order that a presumably small transplant population could reproduce to the point where they could be considered common, or occurring in "great numbers" on the plains near the Marysville Buttes (op. cit., p. 381).

Considering the similarities shown by the skull analysis presented previously, the Sacramento foxes are most likely descendants of regalis stock, were probably brought to California after 1869, and probably came from Iowa or Minnesota. The transcontinental railroad was completed in 1869, and it is unlikely that captive foxes would have been brought across the country by wagon train; they could easily have been shipped by rail. Iowa and Minnesota were settled at the time, but after the Civil War many families packed up and moved west, especially when rail transport made such moves easier, gold was still an attractant, and free or inexpensive land was available. A number of settlers in the midwest were of English descent, some even born in England, and might have wished to continue the sport of fox-hunting in their new home, California. Their predecessors probably brought English foxes to the eastern United States over 100 years before (Churcher, 1959), and other animals have also been moved for the sake of providing sport, before a wide variety of regulations began to make such transplants difficult.

Whether the Sacramento fox should be considered sufficiently different to warrant a scientific name presents another question. Although the relationship with V. v. regalis is clear, Fig. 4 shows Sacramento foxes to be as different from regalis as regalis is from abietorum, or abietorum from alascensis. The differences recognized by the computer are similar to the differences between recognized subspecies. However, actual measurements, without computer assistance, cannot be used to identify a skull as that of a Sacramento fox. The differences which exist between regalis and the Sacramento population are possibly the result of relatively uniform genetic stock in the original transplant (perhaps from a single farm?) combined with 100 years of slightly different selection pressures (Sacramento versus Iowa or Minnesota). In my opinion they are not sufficient to warrant formal taxonomic treatment. Since they are different from the Sierra Nevada foxes, they can be referred to as Sacramento Valley red foxes, or more simply, Valley foxes.

The Valley fox is slightly larger than the native Sierra Nevada fox, V. v. necator, and has paler coloration, and a different habitat. Although no single measurement or group of measurements is sufficiently unique to permit certain identification, a number of features can be used to assist in making an identification. A particular specimen which meets all the specifications for one of the two types is probably of the type indicated. Problems in identification will arise when incomplete information is available, or with specimens which are intermediate in measurements or color. A list of potential identifying features is presented below.

Valley Red Fox	Sierra Nevada Red Fox
	Vulpes vulpes necator
Size larger, usually over 1050 mm total length; tail usually over 375 mm; hind foot usually over 160 mm; weight usually over 4 kg.	Size smaller, usually less than 1050 mm total length; tail usually less than 360 mm; hind foot usually less than 160 mm; weight usually less than 4 kg.
Color pale, yellowish; facial area very pale, whitish; brownish area with white-tipped hairs over rump. No color phases known.	Color distinctly reddish, especially along dorsal region, when in red phase. Cross, silver, and black color phases occur regularly.
Condylobasal length of skull usually more than 137 mm.	Condylobasal length of skull usually less than 139 mm.
Lyre width usually less than 7 mm.	Lyre width usually more than 7 mm.
Collected below 3000 ft. elevation, in the Sacramento Valley south to the San Francisco Bay region.	Collected above 4000 ft. elevation, in the Sierra Nevada region or the Siskiyou and Marble Mountains of northern California.

Additional skull measurements should be checked by referring to Table 3. It is not possible to identify a particular specimen with 100% accuracy.

SUMMARY

1. Red foxes from the Sacramento Valley population are most like V. v. regalis of the Northern Great Plains, and are probably descended from stock introduced from Iowa or Minnesota during the 1870s.

2. Although differing slightly from V. v. regalis, they are not sufficiently different to give them a formal scientific name. They could be referred to as regalis, but are probably best termed Sacramento Valley fox, or more simply -- Valley fox, or Valley red fox.

3. Sacramento Valley foxes differ from the native Sierra Nevada red fox, but the variation which exists in each population makes it very difficult to identify a particular specimen, even with sophisticated multivariate analysis. General differences in size, color, skull measurements, and collecting sites can assist in making tentative identifications.

LITERATURE CITED

Anthony, H. E. 1928. Field Book of North American Mammals. Putnam, New York.

Blackith, R. E. and R. A. Reyment. 1971. Multivariate Morphometrics. Academic Press, New York.

Churcher, C. S. 1959. The specific status of the New World red fox. J. Mamm., 40 (4): 513-520.

_____ 1960. Cranial variation in the North American red fox. J. Mamm., 41 (3): 349-360.

Cooley, W. W. and P. R. Lohnes. 1971. Multivariate Data Analysis. Wiley, New York.

Gray, R. L. 1975. Sacramento Valley red fox survey. Calif. Dept. Fish and Game, Nongame Wildlife Investigations, Job II-1.2, Progress Report.

Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. Cal. Publ. Zool., 35: 1-594.

_____ 1937. Fur-bearing Mammals of California. Univ. Calif. Press, Berkeley.

Hall, E. R. and K. R. Kelson. 1959. The Mammals of North America. Ronald Press, New York.

Merriam, C. H. 1900. Preliminary revision of the North American red foxes. Proc. Wash. Acad. Sci., 2: 661-676.

Pimentel, R. A. 1976. Morphometrics. Privately published; available from El Corral Bookstore, Calif. Poly. St. Univ., San Luis Obispo.

Waithman, J. and A. Roest. 1977. A taxonomic study of the kit fox, _Vulpes macrotis_. J. Mamm., 58 (2): 157-164.

APPENDIX I

Brief descriptions of the 15 measurements taken on each skull:

Condylobasal length -- from anteriormost point on premaxillae to a line across the posteriormost margins of the occipital condyles.

Zygomatic width -- greatest width across the zygomatic arches.

Palatilar length -- from posterior edge of first incisive alveoli to anteriormost point on the posterior edge of the palatine bone, usually taken on the left side.

Maxillary tooth row length -- from anterior edge of canine alveolus to the posterior edge of alveolus of last molar, usually taken on the left side.

Postpalatal length -- from anteriormost point on the posterior edge of the palatine bone to the anteriormost edge of the ventral margin of the foramen magnum.

Nasal suture length -- length of the suture between the two nasal bones.

Braincase breadth -- maximum breadth across the braincase, usually taken just above the zygomatic processes of the temporal bone.

Auditory bullae breadth -- maximum distance between the two lateral surfaces of the auditory bullae.

Rostral breadth at premolar 1/premolar 2 -- narrowest width of the rostrum, which is usually somewhere between the level of these two teeth.

Palatal width at molar 1 -- width between the inner edges of the alveoli of the first molars.

Interorbital breadth -- minimal distance between the uppermost margins of the orbits.

Postorbital constriction breadth -- minimal distance between the sides of the braincase, just posterior to the postorbital processes.

Nasal width at their tips -- width across the anterior lateral points of the nasal bones, across the upper portion of the anterior nares.

Lyre width at frontal/parietal suture -- width of the lyre-shaped ridge which extends from the postorbital processes to the occipital crest, taken where it crosses the frontal-parietal suture.

Diastema between canine and premolar 1 -- distance from the posterior edge of the canine alveolus to the anterior edge of the first premolar alveolus; this is a difficult measurement to obtain accurately if teeth are present in the alveoli.