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The history of arid-land fox discoveries in North America

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ABSTRACT: Meriwether Lewis and William Clark in 1805 wrote the first substantial details of an arid-land fox. It was not until 1823, however, that Thomas Say described this same species of fox scientifically, and gave it a Latin name. Since then several other arid-dwelling foxes have been discovered. It almost seems that each south-western state in the United States and northern Mexico had its own fox, neatly described and named. But with the advent of modern biology and genetics, and the re-thinking of the "species concept", has the rich history of arid-land fox discoveries become just a footnote? In this paper I bring the work of nineteenth- and twentieth-century explorers and naturalists to the modern reader, providing the historical accounts that can only be found in library archives. I focus only on foxes that occur in North American desert and prairie habitats, excluding those fox species that occur in woodland and forested communities.

KEY WORDS: desert – Great Plains – kit fox – swift fox – *Vulpes macrotis* – *Vulpes velox*.

INTRODUCTION

Today, there are considered to be two species of arid-land foxes occupying the western United States and the northern half of Mexico. *Vulpes velox* (Say, 1823), called the swift fox, occurs in the Great Plains from north-central Texas to southern Canada. *V. macrotis* (Merriam, 1888), the kit fox, occurs in the deserts of south-western North America, the Central Valley of California, and central to northern Mexico (Figure 1). Both species are adapted to arid conditions, weigh approximately five pounds (2.3 kg), and are typically buff-coloured with black-tipped tails.

As explorers moved westward across the United States many new animals were discovered, including these small foxes. The nineteenth and twentieth centuries witnessed a paramount effort to capture and describe these species, adding to the natural history of these territories. Herein I focus on the arid-land foxes, excluding the red fox (*Vulpes vulpes* (Linnaeus, 1758)), the gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)), and the Channel Island gray fox (*U. littoralis* (Baird 1858)). Although these foxes can occupy arid environments, they are not necessarily adapted to these habitats, and typically occur in forested or wooded communities. *U. littoralis* is restricted to the California Channel Islands which, while arid, possess woodlands and shrublands.

FIRST DESCRIPTIONS OF ARID-LAND FOXES

In their explorations from 1804 to 1806, Meriwether Lewis and William Clark encountered a small burrowing fox in the northern portion of the Great Plains. Their journal entry for

Figure 1. Distributions of subspecies: 1. *Vulpes velox hebes*; 2. *V. velox velox*; 3. *V. macrotis arsipus*; 4. *V. macrotis devia*; 5. *V. macrotis macrotis*; 6. *V. macrotis mutica*; 7. *V. macrotis neomexicana*; 8. *V. macrotis nevadensis*; 9. *V. macrotis tenuirostris*; 10. *V. macrotis zinseri*. Circles indicate the type localities. The boundaries of the ranges of the separate subspecies are based on Hall and Kelson (1959: figure 448), while the dashed line denotes the hybrid zone.

The range of *Vulpes macrotis arizonensis* was not delineated; the square indicates the type locality.

The hexagon indicates where the kit fox from Fort Mojave, Arizona, was collected by Private Ruby.

14 April 1805 mentioned that the Assiniboin Indians traded skins of a small fox with the English (Thwaites 1904: **1**: 306). This fox was probably *Vulpes velox*. On 6 July 1805, Lewis wrote (Thwaites 1904: **2**: 213):

> There is a remarkable small fox which ascociate in large communities and burrow in the praries something like the small wolf but we have not as yet been able to obtain one of them; they are extreemly watchfull and take reffuge in their burrows which are very deep; we have seen them no where except near these falls.

On 8 July 1805, in his description of the small fox, he noted that "Their tallons appear longer than any species of fox I ever saw and seem therefore prepared more amply by nature for the purpose of burrowing" (Thwaites 1904: **2**: 216). The fox Lewis was describing was a female killed by Clark, and Lewis referred to it as a "kit fox" delicate in form and exceedingly fleet. On 26 July 1806, Lewis wrote, "we saw a few Antelopes some wolves and 2 of the smallest speceis of fox of a redish brown colour with the extremity of the tail black. It is about the size of the common domestic cat and burrows in the plains" (Thwaites 1905: **5**: 219). It is assumed again that this small fox was *V. velox*. In the early literature, the English names "kit fox" and "swift fox" were often interchanged but today "kit fox" refers to *V. macrotis* and "swift fox" to *V. velox* (Wilson and Cole 2000).

It was not until 1823 that the fox observed by Lewis and Clark was described and named *Canis velox* by Thomas Say (James 1823: **1**: 486), who was the zoologist on a government-sponsored expedition to the western United States. The expedition travelled by steamboat down the Ohio River, then up the Mississippi and Missouri rivers, intending to explore the Yellowstone area. The expedition's botanist and geologist, Edwin James, compiled an account from the journals of its commander Major Stephen Harriman Long, Thomas Say, and other members of the party. The expedition produced the first scientific data on the flora and fauna of the Santa Fe Trail. Say's description was based on an animal caught on 20 June 1820 at the "camp on the river Platte, at the fording place of the Pawnee Indians, twenty-seven miles below the confluence of the North and South, or Paduca Forks", at 40° 59′ 15″ N, in Colorado (James 1823: **1**: 486).

Harlan (1825) kept this fox in the genus *Canis*, and noted that Lewis and Clark called the animal the "burrowing fox" in the second volume of their journals on page 351. Godman (1831) followed Say (James 1823) and Harlan (1825) and also noted that Lewis and Clark referred to it as the "burrowing fox" in their journals. These citations refer to the original manuscript journals.

Audubon and Bachman (1851) transferred the "burrowing" fox to *Vulpes* but gave no reason for their decision. In a list of synonyms Audubon and Bachman (1851: 13) noted that Lewis and Clark had referred to the fox as the "Kit fox, or small burrowing fox of the plains. Lewis and Clark, vol. i., p. 400. Vol. iii., pp. 28. 29."

Clinton Hart Merriam (1888) was next to describe a new species of arid-land fox. The type specimen was an adult male killed by Frank Stephens on 1 November 1885 at Riverside, San Bernardino County, California. It was later discovered that this type specimen was not from San Bernardino County at all, but from the western margin of the San Jacinto Plain in the vicinity of Box Springs, about ten miles south-east of Riverside in Riverside County (Grinnell 1913). Merriam (1888) reported that the specimen was so different from other North American foxes that a detailed comparison was not needed. The most striking detail was the size of the ears, which was enough to distinguish the long-eared fox.

It was surprising to Merriam (1888) that such a large animal remained undiscovered until 1885, given that California was a relatively well-explored state by then. Curiously, he suggested that the new fox was actually a Mexican species, and its northernmost limit was southern California; the type locality was only 100 miles from the Mexican border. This statement is odd because no arid-land fox was described from Mexico before 1888, so how Merriam concluded this is unknown. But, he was probably correct, and, unbeknownst to him, provided the first hint of a future scientific field known as "corridor theory" (see McEuen 1993).

Merriam (1902) described three more arid-land foxes. The collections of the United States Geological Survey contained specimens of swift foxes from Alberta to Colorado, and long-eared foxes from New Mexico and California. Merriam concluded, based on four male and two female swift foxes collected by W. G. Mackay and G. F. Dippie in 1900 from Calgary, Alberta, Canada (Poole and Schantz 1942), that these foxes should be considered a northern subspecies of *Vulpes velox*: he named it *V. velox hebes*.[1]

Describing a specimen taken in New Mexico by C. Barber on 4 April 1899, Merriam (1902) wrote that the skull resembled that of foxes from the Central Valley of California (see below) more than it did *Vulpes macrotis*, but he placed it as a subspecies of *V. macrotis* anyway: *V. macrotis neomexicana* (as "*neomexicanus*"). The type locality was stated as "San Andreas Range, New Mexico (about 50 miles north of El Paso)" (Merriam 1902). However, comments from other authors contributed to the confusion. Poole and Schantz (1942: 51) stated the type locality as "Band's ranch, San Andreas Range, Doña Ana County, N. Mex. (about 50 miles north of El Paso, Tex.)." Bailey (1931) provided the measurements of a New Mexico desert fox "collected near the type locality at Parker Lake on the east slope of the San Andres Mountains". These statements led Halloran (1945) to interview local ranchers and others regarding this locality. He could not find any reference to a "Band's Ranch" on maps, but did find an old ranch in Doña Ana County, belonging to Walter Baird, which had lands on the eastern side of the San Andres Mountains. Halloran provided these details to H. H. T. Jackson, of the Fish and Wildlife Office in Washington DC. Halloran (1945) citing Jackson:

> It would, however, be very easy to mistake as 'Band's' a poorly written 'Baird's' on the temporary label and thus transcribe the error to the catalog. This I assume is what was done, and I have accordingly had changed the catalog, labels, and other records to Baird Ranch, which is undoubtedly the correct locality.

Halloran (1945) also noted that the spelling of "San Andres" (spelled "Andreas" by Merriam (1902: 74)) had caused confusion. He discovered that the 1916 edition of the Point of Sands Quadrangle, New Mexico, of the U. S. Geological Survey, included part of the San Andres Mountains, as well as part of Baird's Ranch, settling the question of the type locality.

Merriam (1902) also named *Vulpes mutica* (as "*muticus*"), a fox collected by George Leonard on 5 November 1895, near the town of Tracy, in San Joaquin County, California. *V. mutica* was similar to *V. macrotis* but was much larger; the tail and the hind foot were longer and the skull larger.

No sooner had Merriam described three new foxes that *Vulpes arsipus* (Elliot 1903) was discovered in the Mojave Desert by Edmund Heller on 28 March 1903 at Daggett, San Bernardino County, California. Elliot (1903) noted that *V. arsipus* was similar to *V. macrotis*, but was paler and smaller. Heller collected several foxes from Daggett north to Wild Rose Spring at the base of the Panamint Mountains. According to Elliot (1903)

V. arsipus lacked the reddish summer pelage characteristic of *V. macrotis* and *V. velox* and retained its pale grayish pelage throughout the year.

A small fox was collected in October 1887 by Private Charles Ruby, Company A, of the 9th U. S. Infantry, at Fort Mojave, Arizona. Ruby was assisting Spencer F. Baird in collecting material for the Smithsonian Institution. The specimen was a nearly complete skeleton of an adult male and was sent to Dr Robert Wilson Shufeldt while he was stationed at Fort Wingate, New Mexico, as post surgeon. The skeleton, which lacked one tooth, the clavicles, part of the hyoidean arch, and the os penis, was labelled *Vulpes velox*. When Ruby had collected the skeleton, only one arid-land fox was known, the swift fox, *V. velox*. It therefore makes sense that it was labelled as such.

Shufeldt had the specimen examined in 1900 by Gerrit Smith Miller, Jr., of the Department of Mammals of the United States National Museum, Washington DC, who identified the skeleton as belonging to *Vulpes macrotis*, not *V. velox*. This detail is intriguing, because, if Baird had been more interested in identifying the specimen, he would have surely discovered that it was not *V. velox* at all, and instead of using the name *V. macrotis*, or at least in addition to it, we would be employing a different Latin name. Miller as well could have described this fox from Fort Mojave as a new species (or subspecies), as no other desert foxes were described from continental North America east of California by 1900. Miller compared the skull with swift fox skulls in the Museum's collections but apparently did not have a *V. macrotis* skull. How Miller figured the Fort Mojave fox was *V. macrotis* is not known, but it was a good guess, taking into consideration the limited knowledge of arid-land foxes at the time. It is highly likely that the Fort Mojave specimen would have been identified as *V. arsipus* if it had been examined in 1904 rather than 1900.[2]

Further review of the arid-land foxes was provided by Joseph Grinnell, who was curator of the Museum of Vertebrate Zoology, Berkeley, from the Museum's inception in 1908 until his death in 1939. He was one of the first to think in terms of habitat loss and species conservation (Grinnell and Storer 1916). He was prolific in publishing about the fauna of California, and had a role in revising the classification of California's arid-land foxes.

Grinnell (1913) provided an account of all mammals known in California at the time, including three arid-land foxes. He relegated these foxes to subspecies of *Vulpes macrotis*: *V. macrotis macrotis*, *V. macrotis mutica*, *V. macrotis arsipus*. He also provided common names for two of them: "San Joaquin kit fox" for *V. macrotis mutica*[3], and "Mojave Desert kit fox" for *V. macrotis arsipus* (he retained "long-eared fox" for *V. macrotis macrotis* but added "kit" – "long-eared kit fox").

Ten years later, Grinnell (1923) published a systematic list of the mammals of California to motivate others to study the fauna of California. He also wanted to make known the many additions and discoveries that had occurred since the previous list (Grinnell 1913).

In 1933, Grinnell published a more detailed account of the mammals of California, making one change to the names of California's arid-land foxes; he dropped "Mohave" from the English name for *Vulpes macrotis arsipus* and left it as "desert kit fox." In this work, Grinnell provided additional details on the distribution of California's mammals, and wrote that the long-eared kit fox, *V. macrotis macrotis*, was believed to be extinct because the last time this subspecies had been captured was in 1903. He cited Frank Stephens as providing more information on the type locality of the long-eared kit fox, that is, "More exactly, on western margin of the San Jacinto Plain in vicinity of Box Springs, within 10 miles south-east of Riverside (*fide* F. Stephens)" (Grinnell 1933).

Eleven new mammals were described from Baja California ("Lower California"), Mexico, by Nelson and Goldman (1909), including one new kit fox subspecies, *Vulpes macrotis devia* (as "*devius*"), the peninsula desert fox. This adult male fox was collected on 13 December 1905 from Llano de Yrais, opposite Isla Magdalena. Nelson and Goldman (1909) wrote that this new fox was similar to *V. macrotis macrotis* but that the sides of the nose were much darker and blackish, the tail was smaller and more slender, and the pelage was shorter. The skull was equal in size but the rostrum was broader and heavier, the nasals were broader, and were also tapered more abruptly posteriorly.

Nelson and Goldman (1931) described another new kit fox subspecies from Mexico, the Trinidad Valley desert fox, *Vulpes macrotis tenuirostris*. The subspecies was only known from the open desert in Trinidad Valley, on the Pacific slope of the mountains. Nelson and Goldman (1931) stated that this new subspecies was allied closely with *V. macrotis macrotis*, but the skull differed with a more depressed frontal outline and in other details. They argued that it was similar to *V. macrotis arsipus*, but somewhat darker in colour and the outside of the limbs were ochre-tawny. It differed from *V. macrotis devia* in being larger in size with a larger skull. The type locality of this subspecies was less then 50 miles from the international border, and it is plausible that kit foxes regularly moved between the United States and Mexico in the past. These movements fit the view Merriam (1888) had when he mentioned that *V. macrotis* was likely a Mexican species.

On 9 December 1913 Edward A. Goldman collected a desert fox two miles south of Tule Tanks, Yuma County, Arizona (near the Mexico-United States boundary; Goldman 1931). Goldman described the fox as a small, light buffy subspecies with short pelage lacking much of the silver white found in the kit fox group. He named it the Arizona long-eared desert fox, *Vulpes macrotis arizonensis*. Goldman (1931) wrote that this new subspecies was allied with *V. macrotis arsipus* but was smaller with shorter winter pelage. In addition, *V. macrotis arizonensis* was similar to *V. macrotis neomexicana*, but smaller. Goldman also mentioned that the Colorado River separated *V. macrotis arizonensis* from *V. macrotis arsipus* – the first mention of an actual barrier that might explain the differences between subspecies.[4] Goldman examined six specimens of this subspecies to complete his descriptions: one from Tacna, two from Tule Tanks, two from Yuma, and one from Vicksburg.

Goldman (1931) also described a new desert fox subspecies from Nevada: the Nevada long-eared desert fox, *Vulpes macrotis nevadensis*. Mike Gill collected the type specimen from Willow Creek Ranch, near Jungo, Humboldt County, Nevada, on 14 December 1915. Goldman wrote that this new subspecies was closely allied with *V. macrotis arsipus*, but less silvery white, with the hair tips more black over the dorsal portions of the fox. Goldman (1931) noted that this specimen marked the northernmost fox collected to date. Fourteen specimens were used to describe this new subspecies, with one from Idaho, two from Utah, and the rest from Nevada.

Benson (1938) realized that little was known about the desert foxes of Mexico, and set out to study them in 1937. He visited Sonora and Coahuila and found that the area was occupied by a population of desert foxes, extending the range further south. Benson also studied 68 desert fox specimens housed in the Museum of Vertebrate Zoology from California, Nevada, Arizona, New Mexico, Sonora, and Coahuila. He realized that a comprehensive systematic review of the desert foxes was needed, but he did not have access to enough museum specimens to write such a review. However, there was enough material to make systematic comparisons of foxes occurring in south-western Arizona and north-western Sonora.

Three kit foxes were collected by Margarito Delgadillo and Seth Benson between 13 and 15 January 1937 near the fishing village of Punta Peñasca on the Gulf of California in north-western Sonora. Benson reasoned that these three foxes should belong to the subspecies *Vulpes macrotis arizonensis* because the capture site fell within the range that Goldman (1931) delineated in his description of the subspecies. However, upon careful review, Benson could not attribute the newly caught foxes to *arizonensis* – none of the characteristics matched! This discovery led Benson to study other desert foxes within the range of *arizonensis*. He found that kit foxes occurring in the range of *arizonensis* did not match the characteristics of *arizonensis* either. Benson then compared foxes from California, Nevada, and Utah in an attempt to figure out the mysterious *arizonensis*. After much study, Benson determined that all the foxes attributed to *arizonensis* were indistinguishable from *V. macrotis arsipus*. Benson was able to make three conclusions from his research: *V. macrotis arizonensis* was a synonym of *V. macrotis arsipus*; the Colorado River was not an effective barrier between kit foxes; and the north-western Sonoran foxes were *V. macrotis arsipus*.

On 15 June 1937 three kit foxes were captured by Guillermo Rodriguez near San Antonio de Jaral. From these specimens, Benson (1938) determined that they represented a new subspecies of desert fox: *Vulpes macrotis zinseri*. Benson wrote that this new subspecies was as large as *V. macrotis mutica* or *V. macrotis neomexicana*, and darker and heavier. The new fox was named after Señor Juan Zinser, from the Department of Forestry in Mexico.

Benson (1938) concluded that there was a great need for more studies on kit foxes. Because so little was known about them, more information was needed on their distribution and geographic variation, and every effort should be made to preserve specimens that had been killed. He stated that because there was so much variation in the physical appearance of foxes and the shapes of skulls, even foxes occurring in the same geographic area, it was likely that using these physical characteristics was not a good way of describing subspecies. A new revision of definitions and diagnoses was needed to determine if a newly discovered fox was a new subspecies or not. Benson did not have specimens of *Vulpes velox* to examine, so he was unable to determine if *V. velox* and *V. macrotis* were different species, and he was not able to shed further light on *V. macrotis macrotis*, as it was probably extinct, or *V. macrotis tenuirostris* and *V. macrotis devia*. However, he was able to determine that *V. macrotis mutica* was distinct from *V. macrotis arsipus*. Benson was able to examine some foxes falling within the range of *V. macrotis nevadensis* and identified them as *V. macrotis arsipus*, and guessed that the differences between *nevadensis* and *arsipus* would probably not be well marked if further studied. *V. macrotis neomexicana*, however, appeared to be distinct enough to remain a valid subspecies.

INTERBREEDING IN THE ARID-LAND FOXES

Vulpes velox and *V. macrotis* have overlapping ranges in eastern New Mexico and possibly south-central Texas (Figure 1). The taxonomic status of the various kit fox subspecies had been called into question by Benson (1938), so should the specific status between kit and swift foxes be questioned as well? Rohwer and Kilgore (1973) analysed 60 kit fox and 44 swift fox skulls, and 78 geographic intermediates using discriminant analysis and a modified principal component analysis on 14 skull measurements. The kit fox and swift fox reference skulls fell into two distinct groups, and most of the geographic intermediates fell

into one group or the other, with only a few falling in between. These analyses suggested that there seemed to be occasional sporadic interbreeding with some backcrossing. However, Rohwer and Kilgore (1973) surmised that natural selection would oppose hybrids and favor separate swift and kit fox forms. In this example, the "species concept"[5] held true in that isolating mechanisms were working. Swift foxes tend to occur primarily in high plains grassland whereas kit foxes occur primarily in desert habitats. The regions in New Mexico and Texas where these two species overlap have both of these habitats and occasional interactions are bound to happen, and if these interactions occur during the breeding season, hybridization may result.

THE TAXONOMIC STATUS OF ARID-LAND FOXES

Thornton *et al.* (1971) concluded that major differences in cranial characteristics clearly separate the three *Vulpes* species: *V. vulpes*, *V. macrotis* and *V. velox*. Comparatively, the skull of the red fox is distinctly larger and more massive than either the kit fox or swift fox. The skull of *V. macrotis* can be distinguished from *V. velox* by using several diagnostic characteristics.

Thornton and Creel (1975) analysed the external measurements of eight swift foxes and five kit foxes; compared electrophoregrams of serum proteins and hemoglobins; and presented cytogenetic differences between the species. They stated that kit foxes and swift foxes can be distinguished on the basis of ear size and position, shape of the head, and tail length. Thornton and Creel (1975) mentioned that some critics suggest that the kit fox and swift fox are actually two extremes of one species, a geographic cline, or two uniform groups of the same species separated geographically. However, Thornton and Creel (1975) concluded that the kit fox and swift fox were two separate species. They based this conclusion on the distinguishing characteristics mentioned above, and when comparing serum proteins between species, the electrophoregrams were recognizably different in albumen and alpha globulin fractions. Pelage coloration was of little use in distinguishing between species. The chromosome count for both species was $2n = 50$ and had not been reported before.

Waithman and Roest (1977) analysed five subspecies of kit fox by stepwise discriminant analysis of nine cranial measurements from 104 specimens. Although they began their analysis using 22 measurements, only nine had F values[6] greater than 4.0 (with an alpha of 0.05) that had value in discriminating between different groups of kit foxes. The subspecies examined were: *Vulpes macrotis arsipus*, *V. macrotis devia*, *V. macrotis macrotis*, *V. macrotis mutica* and *V. macrotis tenuirostris*.

The results of their analyses showed that *Vulpes macrotis mutica* was a distinct subspecies. *V. macrotis mutica* had a significantly larger skull and therefore fell into its own grouping. Their results also showed that Benson (1938) was correct in synonymizing *V. macrotis arizonensis* with *V. macrotis arsipus*. The other foxes, *V. macrotis arsipus*, *V. macrotis devia*, *V. macrotis macrotis*, and *V. macrotis tenuirostris* were all very similar to each other, but some variation was noted. Waithman and Roest (1977) suggested that this variation was clinal in nature, but not distinct enough to be subspecific. Therefore, all of these foxes were synonymized as *V. macrotis macrotis*, as this name has priority according to nomenclatural rules. As a result of their research, only two kit fox subspecies should be recognized: *V. macrotis macrotis* and *V. macrotis mutica*. This conclusion was supported

geographically as well. *V. macrotis mutica* was isolated in the Central Valley of California due to a mountain range barrier, whereas the other foxes did not have such a substantial barrier as a mountain range. The Colorado River had previously been recognized as a barrier, but the similarities between *V. macrotis arizonensis* with *V. macrotis arsipus* suggested that the river was not an effective barrier to genetic exchange.

The three other recognized subspecies, *Vulpes macrotis neomexicana*, *V. macrotis nevadensis* and *V. macrotis zinseri*, were not analysed in this study and were not lumped into *V. macrotis macrotis*. However, Waithman and Roest (1977) suggested that *V. macrotis nevadensis* was not recognizably different from kit fox populations further south (that is, *V. macrotis arsipus*) and should be included with *V. macrotis macrotis*, but did not take that final step in this publication; they were only able to make conclusions with kit foxes in the western portion of the range.

The swift fox was rather abundant throughout its range in the 1800s, but by the 1950s, it became very rare and appeared to be extirpated in Canada. Canadian wildlife groups, and others, in co-operation with the United States began a swift fox reintroduction program with foxes originating from Colorado. Stromberg and Boyce (1986) voiced concern regarding this program, stating that bringing foxes from Colorado to Canada might lead to loss of genetic diversity if the Colorado foxes interbred with any remaining Canadian swift foxes, or with swift foxes occurring in the northern United States.

Also pressing was the subspecific status of the swift fox; were *Vulpes velox velox* and *V. velox hebes* recognized subspecies? Stromberg and Boyce (1986) analysed 250 specimens using 18 cranial and dental measurements. They found no significant differences between males and females, and therefore sexes were pooled. The results of their analyses suggest that subspecific status was not warranted. There was no geographic barrier between the northern and southern populations and therefore differences in cranial morphology were likely to be due to geographic variation and a clinal function.

FURTHER RESEARCH IN THE 1980s AND 1990s

Although no additional arid-land foxes were being discovered by the late twentieth century, researchers switched their focus to the various taxonomic questions that have been troubling biologists for several decades. In the late 1980s Dragoo and colleagues felt that the taxonomic status of the kit fox and swift fox was uncertain and variation within populations was poorly known, which hindered attempts to evaluate the differences found in specimens from widely separated locations (Dragoo *et al.* 1987). The authors analysed the skulls of the San Joaquin kit fox (*Vulpes macrotis mutica*) and the swift fox (*V. velox*). The taxonomic controversy was renewed by Hall (1981) who used Rohwer and Kilgore (1973) to justify synonymizing all kit foxes with the swift fox. It is not known why Hall (1981) lumped all of these foxes together into one species, as Rohwer and Kilgore (1973) distinctly concluded that swift foxes and kit foxes were separate species. Dragoo *et al.* (1987) concluded that the kit fox and swift fox showed marked inter-species differences; corroborating what Merriam (1888) concluded more than a century earlier.

In the 1990s genetic analyses was becoming a common tool in determining the taxonomic relationships between species. Dragoo *et al.* (1990) were the first to use genetic analysis to evaluate the genetic histories within and among kit foxes and swift foxes. Not all subspecies could be analysed, however; tissue samples were only available for *Vulpes velox*

velox, *V. macrotis arsipus*, *V. macrotis mutica*, *V. macrotis neomexicana* and *V. macrotis nevadensis*. No tissue samples were available from *V. velox hebes*, *V. macrotis devia*, *V. macrotis macrotis*, *V. macrotis tenuirostris* or *V. macrotis zinseri*.

Dragoo *et al.* (1990) concluded that *Vulpes velox* and *V. macrotis* could be sibling species or simply subspecies of one species. Morphometrically, the two fox species did not have dramatic differences – rather – the differences were consistent as would be expected from either closely related species or well-differentiated subspecies of one species. The main differences between swift foxes and kit foxes are size – kit foxes have longer ears, a narrower rostrum, and larger bullae than the swift fox. These differences may be a result of environmental influences over a vast desert range, rather than evolutionary divergence. Dragoo *et al.* (1990) suggested that the clinal pattern of genetic variation is a result of the foxes differentiating morphologically, but the process of speciation was not complete, and therefore, *Vulpes velox* and *V. macrotis* should be considered subspecies of one species.

As a result of this study, all arid-land foxes were collapsed into one species, *Vulpes velox*, as this name has priority according to nomenclatural rules. All foxes previously considered subspecies of *V. macrotis* were consolidated into *V. velox macrotis* and the two swift fox subspecies were consolidated into *V. velox velox*.

Mercure *et al.* (1993) tested the relatedness between swift, kit, and arctic foxes by analysing mitochondrial DNA restriction-site data and 800 base pairs of the cytochrome *b* sequence. The restriction site and cytochrome *b* sequence analyses supported older studies (that is, Thornton and Creel 1975) that claimed the swift fox and kit fox groups are distinct. The degree of divergence between the kit fox and the swift fox are as great as the kit and swift foxes are from the arctic fox, *Alopex lagopus* (= *Vulpes lagopus*; Geffen *et al.* 1992). The analyses also show that the San Joaquin kit fox, *V. macrotis mutica*, should be considered a distinct subspecies, as it is isolated from other kit foxes by the Sierra Nevada and Tehachapi mountain ranges. The other kit fox subspecies were not distinct enough to warrant subspecific status. The final conclusion of the analyses is that the kit fox and swift fox should be considered separate species, *V. macrotis* and *V. velox*, respectively.

In the two previous genetic studies of arid-land foxes (Dragoo *et al.* 1990; Mercure *et al.* 1993), kit foxes from Mexico were not addressed. Maldonado *et al.* (1997) analysed the Mexican kit fox, *Vulpes macrotis zinseri*. Mexican kit foxes were found to be related closer to kit foxes in the United States rather than to the swift fox. Maldonado *et al.* (1997) concluded that the Mexican kit foxes have only recently been isolated from the United States kit foxes, with a shared ancestor approximately 10,000 to 25,000 years ago.

CONCLUSION

The term “species concept” was coined by Mayr (1942) who defined biological species as “groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr 1942). Researchers of kit and swift foxes found that interbreeding not only occurred between kit and swift fox subspecies, but between kit and swift foxes as well. However, inter-species breeding, creating hybrids, only occurred along limited contact zones, and hybrids did not persevere within populations. Mayr (1942) did not consider geographic isolation a “reproductive isolating mechanism” – reproductive isolation must be a property of individuals. Because kit-swift fox hybrids do not do well within established populations of kit and swift foxes, it certainly seems that a reproductive isolating mechanism

is at work – although initial reproduction is possible on a limited scale, further reproduction by hybrids is not carried on resulting in significant mixing and diluting of genetic material. Mayr realized that reproductive isolation mechanisms were not perfect, and this induced him to revise the definition of isolating mechanisms to "biological properties of individuals which prevent the interbreeding [fusion] of populations" (Mayr 1970: 56). Mayr concluded that "isolating mechanisms do not always prevent the occasional interbreeding of non-conspecific individuals, but they nevertheless prevent the complete fusion of such species populations" (Mayr 1996: 265).Therefore applying Mayr's species concept to the arid-land foxes supports the current conclusion that there are two unique species of arid-land foxes, *Vulpes macrotis* and *V. velox*.

The history of arid-land fox discoveries is rich and fascinating. The rapid exploration of western North America in the nineteenth and twentieth centuries led to multiple discoveries of mammalian species, including small desert-adapted foxes. Descriptions of new species were typically based on morphology and physical appearance, such as skull dimensions and pelage colour. However, as new classification tools became available, such as genetic analysis, and a general re-thinking of the concept of species, these early morphologically-based classifications were collapsed into fewer and fewer species. Indeed, the most current taxonomic authority (Wilson and Reeder 2005) recognizes two arid-land fox forms, the swift fox (*Vulpes velox*) and the kit fox (*V. macrotis*) with all subspecies, including the San Joaquin kit fox (*V macrotis mutica*) synonymized under the nominal species.[7] The story behind arid-land fox discoveries has biological value as an example in the exploration of the "species concept".

NOTES

[1] By following nomenclatural rules, when a species is split into subspecies, the originally described species is converted to a subspecies by repeating the specific epithet, known as a "nominate subspecies"; see Gardner and Hayssen 2004. Therefore, the swift fox described by Thomas Say becomes *Vulpes velox velox*.

[2] Shufeldt's description of the *Vulpes macrotis* skeleton was unfavourably reviewed by "P." (1900). The work was dismissed based on the reviewer's dislike of Shufeldt's statement, that, although the clavicles were missing in the specimen, "there is every reason to suppose that they agreed in their general character with the vulpine carnivora generally; that is, in some respects they were rudimentary and did not reach either the acromion or the sternum." Statements of this kind add nothing of importance to skeletal descriptions, and tend to discredit what was otherwise a commendable collection of anatomical details (P. 1900).

[3] Elliot (1905: 385) provided a common name for *Vulpes mutica*, the curtailed fox. Elliot was the first to match the specific epithet gender with the generic gender: *V. mutica* rather than *V. muticus*. Grinnell (1913) did not reflect Elliot's changes.

[4] Goldman (1937) mentioned this barrier idea but stated that *Vulpes macrotis macrotis* on the western or northern side of the river, and *V. macrotis arizonensis* on the eastern or southern side as the separated subspecies, rather than *V. macrotis arsipus* and *V. macrotis arizonensis*.

[5] Under Mayr's (1996) "species concept" a species is defined as: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" (Mayr 1996).

[6] An F value is a result of an F-test, which is any statistical test in which the test statistic has an F-distribution under the null hypothesis. The name was coined by George W. Snedecor, in honour of Sir Ronald Fisher who initially developed the statistic as the variance ratio in the 1920s (see Lomax 2007: 10).

[7] The synonymization of the San Joaquin kit fox was probably not warranted. Wilson and Reeder (2005) cited Mercure *et al.* (1993) to justify the synonymization, however, Mercure *et al.* (1993) clearly indicated that the San Joaquin kit fox should remain a distinct subspecies based on their mitochondrial DNA restriction-site data analyses.

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