influencing prey selection; communication; adaptations in urban and rural environments; and interactions with threatened species.

Core literature

Andelt 1985, 1987; Bekoff and Gese 2003; Bekoff and Wells 1986; Gese *et al*. 1996a, b, c; Gier 1968; Knowlton *et al*. 1999; Young and Jackson 1951.

Reviewers: William Andelt, Lu Carbyn, Frederick Knowlton. **Editors:** Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.2 Red wolf
Canis rufus Audubon and Bachman, 1851
Critically Endangered – CR: D (2004)

B.T. Kelly, A. Beyer and M.K. Phillips

Other names

None.

Taxonomy

Canis rufus Audubon and Bachman, 1851. Viviparous quadrupeds of North America, 2:240. Type locality: not given. Restricted by Goldman (1937) to "15 miles of Austin, Texas" [USA].

In recent history the taxonomic status of the red wolf has been widely debated. Mech (1970) suggested red wolves may be fertile hybrid offspring from grey wolf (*Canis lupus*) and coyote (*C. latrans*) interbreeding. Wayne and Jenks (1991) and Roy *et al*. (1994b, 1996) supported this suggestion with genetic analysis. Phillips and Henry (1992) present logic supporting the contention that the red wolf is a subspecies of grey wolf. However, recent genetic and morphological evidence suggests the red wolf is a unique taxon. Wilson *et al*. (2000) report that grey wolves (*Canis lupus lycaon*) in southern Ontario appear genetically very similar to the red wolf and that these two canids may be subspecies of one another and not a subspecies of grey wolf. Wilson *et al*. (2000) propose that red wolves and *C. lupus lycaon* should be a separate species, *C. lycaon*, and their minor differences acknowledged via subspecies designation. A recent meeting of North American wolf biologists and geneticists also concluded that *C. rufus* and *C. lupus lycaon* were genetically more similar to each other than either was to *C. lupus* or *C. latrans* (B.T. Kelly unpubl.). Recent morphometric analyses of skulls also indicate that the red wolf is likely not to be a grey wolf × coyote hybrid (Nowak 2002). Therefore, while the red wolf's taxonomic status remains unclear, there is mounting evidence to support *C. rufus* as a unique canid taxon.

Chromosome number: 2n=78 (Wayne 1993).

Description

The red wolf generally appears long-legged and rangy with proportionately large ears. The species is intermediate in size between the coyote and grey wolf. The red wolf's almond-shaped eyes, broad muzzle, and wide nose pad contribute to its wolf-like appearance. The muzzle tends to be very light with an area of white around the lips extending up the sides of the muzzle. Coloration is typically brownish or cinnamon with grey and black shading on the back and tail. A black phase occurred historically but is

Art Beyer

Male red wolf, age unknown.

Table 4.2.1 Body measurements for the red wolf from Alligator River National Wildlife Refuge, North Carolina, USA (USFWS unpubl.).

HB male	1,118mm (1,040–1,250) n = 58
HB female	1,073mm (990–1,201) n = 51
HF male	234mm (213–270) n = 55
HF female	222mm (205–250) n = 42
E male	116mm (107–129) n = 54
E female	109mm (99–125) n = 49
SH male	699mm (640–772) n = 60
SH female	662mm (590–729) n = 45
T male	388mm (330–460) n = 52
T female	363mm (295–440) n = 47
WT male	28.5kg (22.0–34.1) n = 70
WT female	24.3kg (20.1–29.7) n = 61

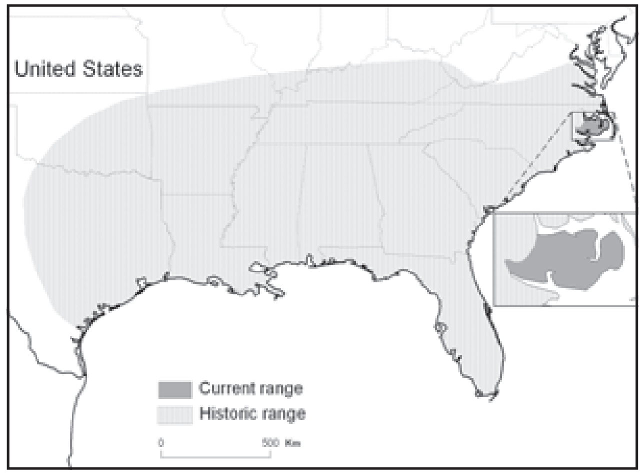

Figure 4.2.1. Current distribution of the red wolf.

probably extinct. The dental formula is 3/3-1/1-4/4-2/3=42.

Subspecies *C. rufus gregoryi, C. rufus floridanus, and C. rufus rufus* were initially recognised by Goldman (1937) and subsequently by Paradiso and Nowak (1972). *Canis rufus gregoryi* is thought to be the only surviving subspecies and is the subspecies believed to have been used for the current reintroduction and conservation effort of red wolves in the eastern United States. Genetic methodologies have not been applied to subspecific designation. Current disagreement about the relatedness of wolves in eastern North America (see Taxonomy section above), if resolved, may alter currently accepted subspecific classification of *C. rufus*.

Similar species The red wolf, as a canid intermediate in size between most grey wolves and coyotes, is often noted as being similar to both of these species in terms of general conformation. However, the coyote is smaller overall with a more shallow profile and narrower head. Grey wolves typically have a more prominent ruff than the red wolf and, depending on subspecies of grey wolf, typically are larger overall. Also, most grey wolf subspecies have white and/or black colour phases. Although red wolves historically had a black phase, no evidence of this melanism has expressed itself in the captive or reintroduced population.

Distribution

Historical distribution As recently as 1979, the red wolf was believed to have a historical distribution limited to the south-eastern United States (Nowak 1979). However, Nowak (1995) later described the red wolf's historic range as extending northward into central Pennsylvania and more recently has redefined the red wolf's range as extending even further north into the north-eastern USA and extreme eastern Canada (Nowak 2002). Recent genetic evidence (see Taxonomy section above) supports a similar but even greater extension of historic range into Algonquin Provincial Park in southern Ontario, Canada.

Current distribution Red wolves exist only in a reintroduced population in eastern North Carolina, USA (Figure 4.2.1). The current extant population of red wolves occupies the peninsula in eastern North Carolina between the Albermarle and Pamilico Sounds.

Range countries Historically, red wolves occurred in the United States of America and possibly Canada (Wilson *et al.* 2000; Nowak 2002). Currently, red wolves only reside in eastern North America as a reintroduced population (Phillips *et al.* 2003) and possibly Canada (Wilson *et al.* 2000).

Relative abundance

Extinct in the Wild by 1980, the red wolf was reintroduced by the United States Fish and Wildlife Service (USFWS) in 1987 into eastern North Carolina. The red wolf is now common within the reintroduction area of roughly 6,000km^2 (Table 4.2.2). However, the species' abundance outside the reintroduction area is unknown.

Estimated populations/relative abundance and population trends

Table 4.2.2 The status of red wolves in USA (Trend: S=stable, EX=extinct).

	Population size	Trend
Reintroduced population	<150	S
Former range (south-eastern USA)	–	EX

Habitat

Very little is known about red wolf habitat because the species' range was severely reduced by the time scientific investigations began. Given their wide historical distribution, red wolves probably utilised a large suite of habitat types at one time. The last naturally occurring population utilised the coastal prairie marshes of south-west Louisiana and south-east Texas (Carley 1975; Shaw 1975). However, many agree that this environment probably does not typify preferred red wolf habitat. There is evidence that the species was found in highest numbers in the once extensive bottomland river forests and swamps of the south-east (Paradiso and Nowak 1971, 1972; Riley and McBride 1972). Red wolves reintroduced into north-eastern North Carolina and their descendants have made extensive use of habitat types ranging from agricultural lands to pocosins. Pocosins are forest/wetland mosaics characterised by an overstory of loblolly and pond pine (*Pinus taeda* and *Pinus serotina*, respectively) and an understory of evergreen shrubs (Christensen *et al.* 1981). This suggests that red wolves are habitat generalists and can thrive in most settings where prey populations are adequate and persecution by humans is slight. The findings of Hahn (2002) seem to support this generalisation in that low human density, wetland soil type, and distance from roads were the most important predictor of potential wolf habitat in eastern North Carolina.

Food and foraging behaviour

Food Mammals such as nutria (*Myocastor coypus*), rabbits (*Sylvilagus* spp.), and rodents (*Sigmodon hispidus*, *Oryzomys palustris*, *Ondatra zibethicus*) are common in south-east Texas and appear to have been the primary prey of red wolves historically (Riley and McBride 1972; Shaw 1975). In north-eastern North Carolina, white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), and rabbits are the primary prey species for the reintroduced population, comprising 86% (Phillips *et al.* 2003) of the red wolves' diets.

Foraging behaviour Red wolves are mostly nocturnal with crepuscular peaks of activity. Hunting usually occurs at night or at dawn and dusk (USFWS unpubl.). While it is not uncommon for red wolves to forage individually, there is also evidence of group hunting between pack members (USFWS unpubl.). Also, resource partitioning between members of a pack sometimes occurs. In one study, pack rodents were consumed more by juveniles than adults, although use of rodents diminished as the young wolves matured (Phillips *et al.* 2003).

Damage to livestock or game Historically, the red wolf was believed to be a killer of livestock and a threat to local game populations, despite lack of data to support such a belief. As of September 2002, the reintroduced population in north-eastern North Carolina has been responsible for only three depredations since 1987 (USFWS unpubl.).

Adaptations

Red wolves are well adapted to the hot, humid climate of the south-eastern United States. Their relatively large ears allow for efficient dissipation of body heat, and they moult once a year, which results in them replacing their relatively thick, heat-retaining, cold-season pelage with a thin and coarse warm-season pelage. Such a moult pattern ensures that red wolves are not only able to tolerate the warm humid conditions that predominate in the south-eastern United States, but also the wide range of annual climatic conditions that characterise the region in general. A potential specific adaptation appears to be the ability of the red wolf to survive heartworm infestation. All the adult wild red wolves tested for heartworm in the restored population in North Carolina test positive for heartworm; yet, unlike in domestic dogs and other canids, it is not known to be a significant cause of mortality. More general adaptations include the tolerance of the red wolf's metabolic system to the feast/famine lifestyle that results from the species' predatory habits.

Social behaviour

Like grey wolves, red wolves normally live in extended family units or packs (Phillips and Henry 1992; Phillips *et al.* 2003). Packs typically include a dominant, breeding pair and offspring from previous years. Dispersal of offspring typically occurs before individuals reach two years of age (Phillips *et al.* 2003). Group size in the reintroduced population typically ranges from a single breeding pair to 12 individuals (Phillips *et al.* 2003; USFWS unpubl.). Red wolves are territorial and, like other canids, appear to scent mark boundaries to exclude non-group members from a given territory (Phillips *et al.* 2003; USFWS unpubl.). Home range size varies from 46–226km^2, with variation due to habitat type (Phillips *et al.* 2003).

Reproduction and denning behaviour

Red wolves typically reach sexual maturity by 22 months of age, though breeding at 10 months of age may occur (Phillips *et al.* 2003). Mating usually occurs between February and March, with gestation lasting 61–63 days (Phillips *et al.* 2003). Peak whelping dates occur from mid-April to mid-May producing litters of 1–10 pups (USFWS unpubl.). In a given year, there is typically one litter per pack produced by the dominant pair. Two females breeding within a pack is suspected but has not yet been proven. During the denning season, pregnant females may establish several dens. Some dens are shallow surface depressions located in dense vegetation for shelter at locations where the water table is high, while other dens are deep burrows often in wind rows between agricultural fields or in canal banks; dens have also been found in the hollowed out bases of large trees (Phillips *et al.* 2003; USFWS unpubl.). Pups are often moved from one den to another before abandoning the den altogether, and den attendance by male and female yearlings and adult pack members is common (USFWS unpubl.).

Competition

The degree of competition for prey and habitat between red wolves, coyotes and red wolf × coyote hybrids, is uncertain. Studies to determine this are currently underway (see Current or planned research projects below). In contrast, competition for mates between red wolves and coyotes or red wolf x coyote hybrids appears to be significant (Kelly *et al*. 1999) (see Conservation status: Threats below). Red wolves may also compete, to a lesser degree, with black bears (*Ursus americanus*). The destruction of red wolf dens by black bears has been observed, although it is unknown if these dens had already been abandoned (USFWS unpubl.). Conversely, wolves have also been observed killing young bears (USFWS unpubl.).

Mortality and pathogens

Natural sources of mortality Natural mortality accounts for approximately 21% of known mortality. There are no known major predators of red wolves, although intraspecific aggression accounts for approximately 6% of known red wolf mortalities (USFWS unpubl.).

Persecution Human-induced mortality in red wolves is significant in the reintroduced population and more substantial than natural causes of mortality. It accounts for approximately 17% of known red wolf deaths (primarily from gunshot, traps, and poison) (USFWS unpubl.). Direct persecution by humans was a key factor in the eradication of red wolves from much of the south-eastern United States.

Hunting and trapping for fur There are currently no legal hunting or trapping for fur programmes for red wolves in the United States. Wolves purported to be red wolf-like wolves *Canis lupus lycaon* (see Taxonomy section above) are trapped for fur in Canada when they migrate out of Algonquin Provincial Park.

Road kills In the reintroduced population, road kills are the most common mortality factor accounting for 18% of known red wolf deaths (USFWS unpubl.). However, a proportionately higher number of deaths from vehicle strikes occurred earlier in the reintroduction efforts when captive wolves were released, suggesting that a tolerance in those wolves to human activities predisposed them to spend more time on or near roads (Phillips *et al*. 2003; USFWS unpubl.).

Pathogens and parasites Heartworms (*Dirofilaria immitis*), hookworms (*Ancylostoma caninum*), and sarcoptic mange (*Sarcoptes scabiei*) have been considered important sources of mortality in red wolves (USFWS 1990). In the reintroduced population in North Carolina, both heartworms and hookworms occur, but, neither appear to be a significant source of mortality (Phillips and Scheck 1991; USFWS unpubl.). Mortalities related to demodectic mange and moderate to heavy tick infestations from American dog ticks (*Dermacentor variabilis*), lone star ticks (*Amblyomma americanum*), and black-legged ticks (*Ixodes scapularis*) have also occurred in the reintroduced population but, likewise, do not appear to be significant mortality factors (USFWS unpubl.). Tick paralysis of a red wolf has been documented in North Carolina (Beyer and Grossman 1997).

Longevity Appears to be similar to other wild canids in North America. In the absence of human-induced mortality, red wolves have been documented to have lived in the wild as long as 13 years (USFWS unpubl.).

Historical perspective

Although red wolves ranged throughout the south-eastern United States before European settlement, by 1980 they were considered Extinct in the Wild (McCarley and Carley 1979; USFWS 1990). There are no known traditional uses of red wolves by Native Americans or early settlers. Rather, it is likely that red wolves were viewed by early settlers as an impediment to progress and as pests that were best destroyed. Demise of the species has largely been attributed to human persecution and destruction of habitat that led to reduced densities and increased interbreeding with coyotes (USFWS 1990). These factors were largely responsible for the eradication of the species, with the exception of those individuals found occupying marginal habitats in Louisiana and Texas in the 1970s. In these habitats, red wolves frequently suffered heavy parasite infestation (Goldman 1944; Nowak 1972, 1979; Carley 1975).

The plight of the species was recognised in the early 1960s (McCarley 1962), and the red wolf was listed as endangered in 1967 under United States legislation that preceded the Endangered Species Act (ESA) of 1973. A recovery programme was initiated after passage of the ESA in 1973. It was during the early 1970s that the USFWS determined recovery of the species could only be achieved through captive breeding and reintroductions (see Conservation measures taken below) (USFWS 1990).

Conservation status

Threats Hybridisation with coyotes or red wolf x coyote hybrids is the primary threat to the species' persistence in the wild (Kelly *et al*. 1999). While hybridisation with coyotes was a factor in the red wolf's initial demise in the wild, it was not detected as a problem in north-eastern North Carolina until approximately 1992 (Phillips *et al*. 1995). Indeed, north-eastern North Carolina was determined to be ideal for red wolf reintroductions because of a purported absence of coyotes (Parker 1986). However, during the 1990s, the coyote population apparently became well established in the area (P. Sumner pers. comm.; USFWS unpubl.).

It has been estimated that the red wolf population in North Carolina can sustain only one hybrid litter out of every 59 litters (1.7%) to maintain 90% of its genetic diversity for the next 100 years (Kelly *et al.* 1999). However, prior to learning of this acceptable introgression rate, the introgression rate noted in the reintroduced population was minimally 15% (Kelly *et al.* 1999) or approximately 900% more than the population can sustain to maintain 90% of its genetic diversity for 100 years. If such levels of hybridisation continued beyond 1999, non-hybridised red wolves could disappear within 12–24 years (3–6 generations). An adaptive management plan designed to test whether hybridisation can be reduced to acceptable levels was initiated in 1999 (Kelly 2000) (see Current or planned research projects below). Initial results from this plan suggest that the intensive management specified in the plan may be effective in reducing introgression rates to acceptable levels (B. Fazio pers. comm.).

In the absence of hybridisation, recovery of the red wolf and subsequent removal of the species from the U.S. Endangered Species List is deemed possible. It is noteworthy that similar hybridisation has been observed in the population of suspected red wolf-type wolves in Algonquin Provincial Park, Ontario, Canada (see Taxonomy above). If these wolves are ultimately shown to be red wolf-type wolves, this will enhance the conservation status of the species and nearly triple the known number of red wolf-type wolves surviving in the wild.

As noted above (see Mortality), human-induced mortality (vehicles and gunshot) can be significant. However, the threat this mortality represents to the population is unclear. Most vehicle deaths occurred early in the reintroduction and were likely due to naive animals. Nonetheless, the overall impact of these mortality factors will depend on the proportion of the losses attributable to the breeding segment of the population (effective population (N_e) and what proportion of the overall population is lost due to these human factors (both N and N_e).

Commercial use None.

Occurrence in protected areas The only free-ranging population of red wolves exists in north-eastern North Carolina in an area comprised of 60% private land and 40% public land. This area contains three national wildlife refuges (Alligator River NWR, Pocosin Lakes NWR, and Mattamuskeet NWR) which provide important protection to the wolves. Red wolves or a very closely related taxon may also occupy Algonquin Provincial Park, Ontario, Canada (see Taxonomy above).

Protection status CITES – not listed.

Current legal protection The red wolf is listed as 'endangered' under the U.S. Endangered Species Act (ESA) (United States Public Law No. 93-205; United States Code Title 16 Section 1531 *et seq.*). The reintroduced animals and their progeny in north-eastern North Carolina are considered members of an experimental non-essential population. This designation was promulgated under Section 10(j) of the ESA and permits the USFWS to manage the population and promote recovery in a manner that is respectful of the needs and concerns of local citizens (Parker and Phillips 1991). Hunting of red wolves is prohibited by the ESA. To date, federal protection of the red wolf has been adequate to successfully reintroduce and promote recovery of the species in North Carolina.

Conservation measures taken A very active recovery programme for the red wolf has been in existence since the mid-1970s (Phillips *et al.* 2003; USFWS 1990), with some measures from as early as the mid-1960s (USFWS unpubl.). By 1976, a captive breeding programme was established using 17 red wolves captured in Texas and Louisiana (Carley 1975; USFWS 1990). Of these, 14 became the founders of the current captive breeding programme. In 1977, the first pups were born in the captive programme, and by 1985, the captive population had grown to 65 individuals in six zoological facilities (Parker 1986).

With the species reasonably secure in captivity, the USFWS began reintroducing red wolves at the Alligator River National Wildlife Refuge in north-eastern North Carolina in 1987. As of September 2002, 102 red wolves have been released with a minimum of 281 descendants produced in the wild since 1987. As of September 2002, there is a minimum population of 66 wild red wolves in north-eastern North Carolina, with a total wild population believed to be at least 100 individuals. Likewise, at this same time, there is a minimum population of 17 hybrid canids present in north-eastern North Carolina. The 17 known hybrids are sterilised and radio-collared (USFWS unpubl.).

During 1991 a second reintroduction project was initiated at the Great Smoky Mountains National Park, Tennessee (Lucash *et al.* 1999). Thirty-seven red wolves were released from 1992 to 1998. Of these, 26 either died or were recaptured after straying onto private lands outside the Park (Henry 1998). Moreover, only five of the 32 pups known to have been born in the wild survived but were removed from the wild during their first year (USFWS unpubl.). Biologists suspect that disease, predation, malnutrition, and parasites contributed to the high rate of pup mortality (USFWS unpubl.). Primarily because of the poor survival of wild-born offspring, the USFWS terminated the Tennessee restoration effort in 1998 (Henry 1998).

Occurrence in captivity
As of September 2002, there are approximately 175 red wolves in captivity at 33 facilities throughout the United States and Canada (USFWS unpubl.). The purpose of the captive population is to safeguard the genetic integrity of the species and to provide animals for reintroduction. In addition, there are propagation projects on two small islands off the South Atlantic and Gulf Coasts of the U.S. which, through reintroduction of known breeding individuals and capture of their offspring, provide wild-born pups for release into mainland reintroduction projects (USFWS 1990).

Current or planned research projects
In an effort to understand and manage red wolf hybridisation with coyotes and red wolf x coyote hybrids, the USFWS is implementing a Red Wolf Adaptive Management Plan (RWAMP) (Kelly 2000). The plan, which employs an aggressive science-based approach to determine if hybridisation can be managed, was developed after consultation with numerous wolf biologists and geneticists and first implemented in 1999 (Kelly *et al.* 1999; Kelly 2000). The goal of the plan is to assess whether hybridisation can be managed such that it is reduced to an acceptably low level (see Conservation status: Threats above). As of September 2002, the initial results from the RWAMP indicate that this seems to be the case. If these initial results hold, the next questions that need to be addressed for the conservation of the red wolf in the wild will be: (1) what is the long-term feasibility of sustaining the intensive management of the RWAMP?; and (2) will introgression rates remain at an acceptable level in the absence of the current intensive management? As part of the RWAMP, several research projects are underway:

L. Waits and J. Adams (University of Idaho, USA) are using non-invasive genetic techniques to monitor presence and distribution of canids in the reintroduction area, and are working to improve genetic identification techniques.

The USFWS is examining whether red wolves and coyotes compete with each other for space or share space and partition resources, and is testing the use of captive-reared pups fostered into the wild red wolf population to enhance genetic diversity.

P. Hedrick and R. Frederickson (Arizona State University, USA) are conducting sensitivity analyses of a deterministic genetic introgression model.

D. Murray (Trent University, Canada) is developing a survival-based spatial model of wolf-coyote interactions.

M. Stoskopf and K. Beck (North Carolina State University, USA) are studying the use of GPS collars to monitor wolf movements, the social behaviour of red wolves and coyotes, and the epidemiology of coyote introgression into the wild red wolf population.

K. Goodrowe (Point Defiance Zoo and Aquarium, Washington, USA) is conducting extensive research regarding various aspects of the red wolf reproductive cycle.

D. Rabon (University of Guelph, Canada) is studying the roles of olfactory cues and behaviour in red wolf reproduction.

Core literature
Kelly 2000; Kelly *et al*. 1999; Nowak 1979, 2002; Paradiso and Nowak 1972; Phillips. *et al*. 1995, 2003; Riley and McBride 1972; USFWS 1990.

Reviewers: David Mech, Richard Reading, Buddy Fazio.
Editors: Claudio Sillero-Zubiri, Deborah Randall, Michael Hoffmann.

4.3 Gray fox
Urocyon cinereoargenteus
(Schreber, 1775)
Least Concern (2004)

T.K. Fuller and B.L. Cypher

Other names
English: tree fox; **Spanish:** zorro, zorro gris, zorra gris (Mexico), zorro plateado, gato de monte (southern Mexico), gato cervan (Honduras).

Taxonomy
Canis cinereoargenteus Schreber, 1775. Die Säugethiere, 2(13):pl. 92[1775]; text: 3(21):361[1776]. Type locality: "eastern North America" ("Sein Vaterland ist Carolina und die Wärmeren Gegenden von Nordamerica, vielleicht auch Surinam").

Gray foxes traditionally were considered to be distinct from other foxes. Clutton-Brock *et al*. (1976) and Van Gelder (1978) proposed reclassifying gray foxes as *Vulpes*. However, Geffen *et al*. (1992e) determined that gray foxes represent an evolutionary lineage that is sufficiently distinct from vulpine foxes to warrant recognition as a separate genus.

A molecular phylogenetic analysis of the Canidae showed that there are four monophyletic clades (*Canis* group, *Vulpes* group, South American foxes and the bush dog/maned wolf clade) and three distantly related basal taxa, one of which is the gray fox (*U. cinereoargenteus*; Wayne *et al*. 1997). The gray fox often clusters with two other ancient lineages, the raccoon dog (*Nyctereutes procyonoides*) and the bat-eared fox (*Otocyon megalotis*) but the exact relationship among these taxa is unclear. The early origination of these lineages has resulted in significant sequence divergence that may have masked unique sequence similarities (i.e., synapomorphies) that would have resulted