

Behavioral and Physiological Adaptations of Foxes to Hot Arid Environments: Comparing Saharo-Arabian and North American Species

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Abstract: The principal adaptations to the hot desert environment demonstrated by foxes are behavioral and morphological. Desert foxes are not physiologically well adapted to tolerate heat load and so avoid heat stress behaviorally. All species spend the hot hours of the day in deep burrows and delay activity to the cooler hours of the night. Their small body size increases dissipation of metabolic heat by passive conductance, but limits heat storage potential as utilized by larger animals. Foxes rely on non-evaporative heat loss for dissipating heat, and can increase conductance by behavioral or morphological mechanisms. When ambient temperatures rise above the thermal neutral zone, small canids employ evaporative cooling by panting. Small desert canids can be independent of drinking water if evaporative water loss can be restricted. Low basal metabolic rate, a wide thermal neutral zone, seasonal change in fur density and body fat, and active heat dissipation by a change in skin vasoconstriction are additional mechanisms to avoid heat load without the need to evaporate water.

Diet selection is a critical component of the survival strategy of desert-adapted fox species. Foxes are capable of maintaining water balance for an indefinite time with water input from the diet alone. All 5 fox species in the Saharo-Arabian region include fruit and vegetative material, a water-rich food component in their diet. However, kit and swift foxes feed almost exclusively on rodents. Foxes are able to produce concentrated urine, although not at the levels known in rodents. Reduced urine volume, reduced evaporative water loss, and selection of succulent food items in the diet combine to allow small canids to survive in the desert without drinking.

Five fox species inhabit the Saharo-Arabian deserts. The red fox is the largest species (2–4 kg), the pale fox and Ruppell's sand fox are intermediate in size (1.5–3.6 kg), and the fennec and Blanford's fox are the smallest (0.8–1.5 kg). The red fox is a Palearctic species that has extended its range to the Arabian Peninsula and northern Africa (Fig 1a). This species is the most opportunistic and occupies a wide range of habitat types, including human habitation, but it avoids the extreme arid deserts. The pale fox is the only species restricted to Africa, and it inhabits sandy or stony plains in the deserts and semi-deserts of the southern Sahara (Fig. 1b). Ruppell's sand fox is found in similar habitats throughout central and northern Sahara, the Arabian Peninsula, and eastwards to Afghanistan (Fig. 1b). The 2 smallest species are the most specialized in habitat type. The fennec fox occupies the extreme sandy deserts, and the Blanford's fox is restricted to rocky mountains and canyons (Fig. 1c; Harrison and Bates 1991, Kingdon 1997).

The North American congeners are the swift and kit foxes. The kit fox (1.4–3.0 kg) inhabits exclusively arid and semiarid deserts, and shrub-steppe habitats of southwestern US and northwestern Mexico. The swift fox (1.8–3.0 kg) is found in short-, mid-, and mixed grass prairies of the Great Plains in central North America (O'Farrell 1987, Scott-Brown et al. 1987).

The fox species in the Saharo-Arabian region can be divided into 2 phylogenetic lineages (Geffen et al. 1992d). The fennec and Blanford's fox lineage is about 4 million years (my), and coincides with the appearance of the deserts in this region (Fig. 2). The second lineage (red fox and Ruppell's sand foxes) suggests that Ruppell's sand fox may have entered the deserts more recently (1–2 my; Fig. 2). Both lineages are relatively old, permitting extensive time periods for all these fox species to adapt to their arid environments. In comparison, the North American kit and swift foxes are both a much more recent divergence than the red fox lineage (0.2–0.5 my; Fig. 2; Geffen et al. 1992d). These 2 species are sister taxa (0.34% divergence; Geffen et al. 1992d, Mercure et al. 1993), and are closely related to the Arctic fox.

The Physical Environment

The Saharo-Arabian region, roughly 10,000,000 km², consists of a series of deserts and semi-deserts. The deserts of the Arabian Peninsula, southern Iran, and Afghanistan are a continuation of the Sahara desert. These areas were disconnected from Africa about 30 million years ago with the formation of the Red Sea (Braithwaite 1987). Terrestrial faunal interchange resumed during the Miocene (5–20 my) and the peak glaciation of the Holocene (17 ky), when the shallow straits of Bab el Mandeb (130 m) were above sea level (Braithwaite 1987, Sheppard et al. 1992). A second route for faunal interchange remained open (until the construction of the Suez Canal in 1869) through the Sinai land bridge.

The Arabian deserts encompass a variety of habitats: sand dunes, flats, pebble plains, rocky plateaus, mountainous escarpments, and deep canyons. This region is characterized by extreme aridity, high temperature, and violent winds. Rainfall is notoriously unpredictable, and tends to come as sudden storms at irregular intervals. The northern fringe of the region receives rain in winter and the southern border during summer. Annual rainfall ranges between 20–150 mm. Relative mid-day humidity during the warmest months is usually below 20%. The Saharo-Arabian zone is the most extensive desert region of the world with an average of 10 hours of sunshine per day, and an average global radiation exceeding 550 Langleys per day; these high values are a consequence of the absence of

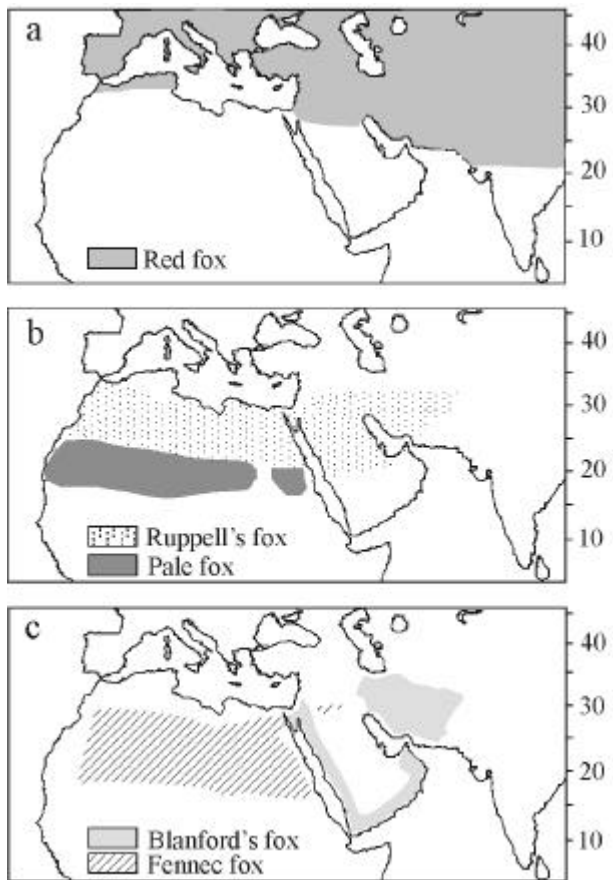


Figure 1. Distribution maps for the five Saharo-Arabian fox species. Latitude is indicated on the right side of each map.

clouds (Smith 1984). Until 2.5–5 my ago, the Saharo-Arabian region was much wetter. The current Sahara desert was then a Savannah land with lakes and rivers. Changes in the atmospheric circulation due to several major geological events created a jet stream of dry air over the region and an increase in wind velocity. These climatic changes caused evaporation of the lakes and obliteration of the rivers by wind-blown sands (Wickens 1984, Williams 1984).

The present distribution of flora largely reflects the recolonization of the deserts following the dry late Pleistocene (20–15 ky). Mediterranean elements are still able to survive in wet and isolated pockets, but following the gradual decrease in precipitation over the past 6,000 years much of the flora has been replaced by southern species (e.g., *Acacia*). Although more than 1,000 plant species are recognized for this region, remarkably no single truly endemic family is known. At least 4 latitudinal centers of floral endemism have been defined across the Sahara and Arabia (Wickens 1984).

In North America, the decrease in rainfall had already

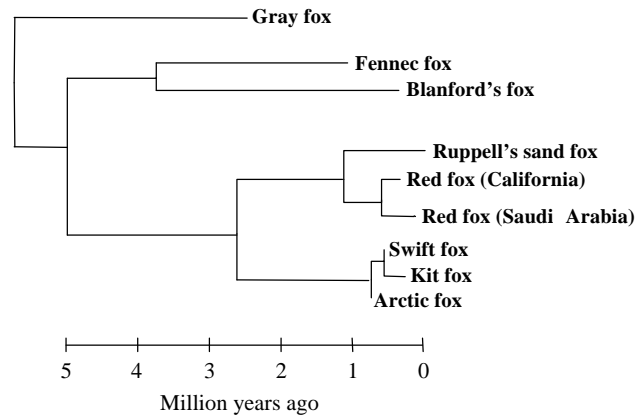


Figure 2. A phylogenetic tree (modified from Geffen et al. 1992d) for the fox species mentioned above. Phylogenetic data for the pale fox is currently not available. The gray fox (*Urocyon cinereoargenteus*) was used as the outgroup.

begun during the Eocene (38–55 my), but the development of current deserts and dry prairies began in the Pliocene (5 my) with the formation of basins by a series of uplifts. These events developed isolated local rainshadows and more extended deserts in northern Mexico (Macmahon, 1979). This long period of dryness allowed the evolution of desert fauna and flora or the migration of xerophilic elements from South America. During the glaciation periods of the Pleistocene (2 my) the desert fauna and flora were driven south into desert refugia such as in central Mexico, Baja California, and the Sonoran-Sinai coast. The Mexican highlands and peninsular Florida provided refugia for arid grassland species. Geomorphologically, the current North American deserts are very young (8,000–10,000 years old). During the last ice age maximal (around 50,000 years ago) many of the basins were filled with water and the current desert regions were much more moist. Only after the last glaciers retreated were the deserts and prairies of the Midwest reformed (Macmahon, 1979).

The deserts in North America are divided into 2 types: northern and southern. The Great Basin desert is characterized by its northern location, high elevation, and predominantly winter moisture input in the form of snow. The southern deserts have rain in winter (Mohave desert), summer (Chihuahuan desert) or in both (Sonoran desert). Annual precipitation ranges 60–410 mm, and varies by location. Average number of days of precipitation ranges 15–91. Mean summer temperature is around 30°C, excluding the Great Basin where the temperature is 5–8°C lower. Extremely high temperatures of 57°C have been recorded only at Death Valley.

The North American deserts are characterized by the distribution of creosote bush (*Larrea tridentata*). Other typical plants are the sagebrush (*Artemisia tridentata*) and shade scale (*Atriplex confertifolia*). The Sonoran desert is especially rich in cacti species, and the Mohave Desert in

Joshua trees (*Yucca brevifolia*). The North American deserts extend contiguously from southeast Oregon to central Mexico; therefore it is not surprising that the distribution of many species form a continuum. There is a great similarity in floral species composition between the southern North American desert and the “Monte” desert in Argentina (Macmahon 1979).

Interspecific Variations in Adaptation for Arid Environments

Animals living in warm and arid or semiarid environments have to cope with relatively high heat loads and accelerated water losses. Different species cope with heat and water stress by employing specialized morphological structures, modification of behavior, and a variety of physiological capabilities. Below, we review the main known adaptive mechanisms that permit these fox species to survive in the vast hot and arid lands of the Saharo-Arabian and North American deserts. The ecology and behavior of kit (*Vulpes macrotis*) and swift (*V. velox*) foxes have been intensively studied at several localities in the wild. On the other hand, pale fox (*V. pallida*) and the fennec fox (*Fennecus zerda*) have never been systematically studied in the wild, and the information about the ecology of these species is anecdotal. The ecology of Ruppell’s sand fox (*V. rueppelli*) has been studied only in Oman and that of the Blanford’s fox (*V. cana*) only in Israel. The ecology and behavior of red fox (*V. vulpes*) has been thoroughly investigated in Europe and North America, but within the Saharo-Arabian region it has been studied only in Israel and Saudi Arabia. The fennec and the kit foxes are the only species whose physiology have been comprehensively studied under laboratory conditions, and Blanford’s, kit and swift foxes are the only species whose eco-physiology has been studied in free-ranging individuals.

BODY SIZE AND MORPHOLOGY: Fox species in the North American and the Saharo-Arabian arid regions range from 1–4 kg in weight. Small canids have substantially less heat storage potential due both to the small absolute mass and to the non-linear relationship of body volume to relative surface area (Phillips et al. 1981). In all desert fox species, heat storage by body temperature elevation is a minute fraction of the heat budget, and provides little benefit under conditions of heat stress. Consequently, in all desert fox species the small body mass hinders storage of activity heat. However, small body size facilitates a relatively high passive thermal conductance that is highly effective for dissipating exercise heat. Because heat is lost from surfaces and a small animal has a larger surface to volume ratio, conductance is relatively higher in smaller animals. For example, heat transfer across the surface of a 1 kg fox is 3 times faster than in a 5 kg fox (Bradley and Deavers 1979). In fact, arid land foxes may increase minimum summer thermal conductance from that predicted for small

body mass. In the fennec, minimal thermal conductance was 77–122% of that expected by the body mass (0.023–0.0365 ml/g hr °C; Noll-Banholzer 1979a, Maloiy et al. 1982), and the kit fox (1.82 kg) had a minimum summer thermal conductance 120–145% of that expected by the body mass (Golightly and Ohmart 1983).

Body fur of Blanford’s fox and swift fox during winter is much denser than in summer, thus improving body insulation (Scott-Brown et al. 1987, Geffen 1994). Seasonal changes in fur density also occur in red and Ruppell’s sand foxes (personal observation). A thin coat during summer is adaptive to a sprinter, such as a fox, to enhance passive dissipation of exercise heat load. In addition, areas of the body that are permanently covered with very short hair serve as “thermal windows.” These areas represent 38.16% of the total surface area in kit fox, 32.85% in red fox, and only 21.61% in the Arctic fox (*Alopex lagopus*; Klir and Heath 1992). Using infrared thermography, Klir and Heath (1992) have shown that kit fox responded to increase in ambient temperature by increasing heat dissipation, mainly through the surface regions covered by short fur. A change in circulation of blood through these areas occurred at temperatures of 20–23°C, and maximum vasodilation was reached at 33°C (Klir and Heath 1992). Vasocontrol of surface circulation and the increase in proportion of “thermal windows” in the arid land foxes appear to be adaptations to the warmer climates.

Cooling passively by conductance can also be improved by maximizing surface area. At high ambient temperature, kit fox stands in a sprawling manner with legs apart (Golightly and Ohmart 1983). This posture maximizes heat loss but elevates the metabolic expenditure. Maloiy et al. (1982) suggested that the large ears of the fennec (surface area of 228 cm²; 16–20% of total body surface) may play a considerable role in heat dissipation. They observed that at high ambient temperature, ear temperature was lower than ambient or body temperatures, thus suggesting evaporation from the ear surface. These observations suggest that the characteristically large ears of the arid land foxes are also an adaptation to increase heat dissipation.

At low ambient temperatures, as occurs at night and in winter, the high thermal conductance of small foxes can result in substantial heat loss during cold stress. Compensatory seasonal changes in body fat content and/or in fur density can reduce conductance to conserve heat. Body weight in Blanford’s fox showed significant seasonal change, with both sexes being heaviest in winter and lightest in summer; seasonal changes in activity or diet were not observed (Geffen et al. 1992a, 1992b; Geffen and Macdonald 1993). Total body water volume as a percentage of body mass in Blanford’s fox was significantly higher in summer than in winter (Geffen et al. 1992c), suggesting an increase in body fat during winter. In contrast, the North American kit fox did not have extensive fat stores

and their body weight did not fluctuate significantly between summer and winter (Golightly and Ohmart 1984, Girard 1998). The constant body mass and fat content of the kit fox relative to the Blanford's fox may be related to differences in body size and diet composition.

ACTIVITY: All fox species in the Saharo-Arabian and North American arid regions are nocturnal or crepuscular. Red foxes at the southern Rift Valley in Israel were active at night for 10–13 hours, and became active immediately after sunset (Assa 1990). Often, these red foxes extend their activity to the early morning hours during summer. Ruppell's sand foxes in Oman and Blanford's foxes in Israel were active only at night (Lindsay and Macdonald 1986, Geffen and Macdonald 1993). Activity duration of the Blanford's fox ranged from 8–11 hours, with onset of activity at sunset throughout the year (Geffen and Macdonald 1993). The North American kit fox is also nocturnal, with onset of activity around sunset and activity duration of 7–10 hours per night (Morrell 1972, O'Farrell 1987, Girard 1998). Girard (1998) showed that in the kit fox, emergence for activity 2 hours earlier in summer resulted in a 25% increase in daily water intake. Avoiding the heat of the day by burrowing and delaying activity to the coolest hours minimizes water intake. However, this physiological reasoning can not explain why most desert species are nocturnal year round. During winter, daytime temperatures are within the thermal neutral zone (TNZ) or lower and water intake is not expected to rise with earlier onset of activity. Geffen and Macdonald (1993) suggested that the nocturnal activity of foxes is also an adaptive behavior against raptor predation. Indeed, fox mortality can be substantial where foxes are active by day (Island gray fox; *Urocyon littoralis*) and large raptors are present (G. Roemer, University of California, Los Angeles, personal communication).

METABOLISM: Small desert-adapted fox species exhibit a relatively wide TNZ (Noll-Banholzer 1979a, Golightly and Ohmart 1983). At the TNZ range of ambient temperatures, oxygen consumption and body temperature are at the minimum. For fennec foxes, the TNZ ranged from 23–32°C. Above 32°C, body temperature rises quickly to a critical value (Noll-Banholzer 1979a). In the kit fox, the TNZ ranged from about 20–34°C (Golightly and Ohmart 1983). The temperature ranges of the TNZ indicate that both the kit fox and the fennec are intolerant of the high diurnal temperatures characteristic of the desert environment (Noll-Banholzer 1979a, Golightly and Ohmart 1983). All Saharo-Arabian and North American desert fox species make use of burrows during the day when temperatures are extreme. In the desert regions where mean ambient temperatures can reach 43°C, burrows provide an escape into an environment where metabolic rate is reduced and water loss is minimal. Excluding the Blanford's fox, which exploits the natural cavities under boulders and rock piles, all other fox species considered

here actively construct their own burrows (Egoscue 1962, Lindsay and Macdonald 1986, Assa 1990, Geffen and Macdonald 1993, Kingdon 1997). The temperature range inside a fennec's burrow during summer is usually within the TNZ range, and never exceeds 34°C (Noll-Banholzer 1979a). In comparison, annual temperature in burrows of kit fox ranges 13–22°C, and mean summer burrow temperature is well within the TNZ range (Girard 1998).

The basal metabolic rate (BMR) is greatly reduced, relative to the expected, in many desert mammals (McNab 1966). A BMR lower than expected is considered an adaptation to the desert environment because it minimizes the endogenous heat load. Further, low BMR saves water needed for body cooling, and reduces the amount of energy required for body maintenance. Therefore, a reduced BMR may be advantageous during periods when food is scarce. The BMR of the fennec fox is only 61% of the level predicted on the basis of body mass (Noll-Banholzer 1979a). However, BMR in the kit fox ranges between 97–117% in summer and winter, respectively (Golightly and Ohmart 1983), whereas in the red fox BMR is unmodified by season and reaches 122% of the expected (Irving et al. 1955). Although there is some evidence that canids are capable of facultatively adjusting their BMR to different environments (Shield 1972), reducing BMR does not appear to be a widespread strategy employed by desert foxes.

Although some evidence indicates reduced field metabolic rates (FMR) among desert mammals compared with mesic mammals, the most recent review of the allometry of FMR in mammals challenges this view (Nagy 1994, Nagy et al. 1999). In a traditional analysis of FMR in 25 species of desert and 48 species of terrestrial mesic mammals, desert mammals demonstrated a steeper allometric slope; small (<1 kg) desert mammals tend to have lower FMR than similarly sized non-desert mammals, while large (>10 kg) desert mammals have relatively higher FMR. No differences in the scaling existed between desert and non-desert mammals in a comparative analysis of FMR where phylogeny was considered. Of the 5 canids for which FMR data are available (*Vulpes cana*, *V. macrotis*, *V. velox*, *Lyacon pictus*, and *Canis lupus*), 4 have FMR above that predicted for eutherian mammals (*V. cana* is the exception). This trend of elevated FMR among canids may be related to the relatively long daily movement distances typical of canids and other carnivores (Garland 1983, Goszczynski 1986), and may lead to increased energy stress in desert foxes during food shortages. Seasonal changes in FMR were observed in kit and swift foxes, but not in Blanford's foxes. FMR in Blanford's fox was similar in summer and winter (0.652–0.689 and 0.630–0.668 kJ/g day, respectively; Geffen et al. 1992c). In contrast, FMR in kit fox was significantly higher in summer than in winter (0.841–0.953 and 0.676–0.710 kJ/g day, respectively; Girard 1998). A similar trend in FMR was

observed in the swift fox (0.990 in summer and 0.709 kJ/g day in winter, Covell et al. 1996). On average, FMR in the kit fox was 37% higher in summer and 6% higher in winter than FMR in Blanford's fox. The increased FMR in the kit fox is presumably related to the high summer movement distances and supported by higher prey intake rates. The reduced FMR in the Blanford's fox required a lower total energy intake and thus a reduced water input from food (Girard 1998).

WATER ECONOMY AND DIET: Water is thought to be a limiting factor and a major selective force in desert carnivores. While the high surface to volume ratio of small canids facilitates non-evaporative heat loss, the principal method for large canids to dissipate heat load is to cool evaporatively by panting. Although small canids demonstrate a reduced dependence on evaporative water loss (EWL) for temperature regulation (Golightly and Ohmart 1984), heat load and consequent EWL may be extreme during pursuit of prey or with exposure to very high ambient temperatures. The water loss in the fennec fox is rather constant under laboratory conditions (0.65–0.91 mg/g hr) below 30°C, but it increases to 3.5 times the basal rate when the ambient temperature is 38°C (Noll-Banholzer 1979a). At such high temperatures, a maximum of 75% (mean 56%) of the metabolic heat can be lost by evaporation. The fennec fox loses an increasingly greater percentage of its metabolic heat by evaporation as ambient temperature increases (Noll-Banholzer 1979a). In contrast, EWL in kit fox was shown to rise with increasing ambient temperature up to the upper limit of the TNZ, and then decreased (Golightly and Ohmart 1983). Additionally, at temperatures above the TNZ, fennec fox dissipates a greater proportion of its metabolic heat by evaporation than kit fox (at 32°C, 23% for kit fox and 36% for fennec fox; Golightly and Ohmart 1983). A unique surface area in canids is the nose, which is hairless and wet. Heat is dissipated through the nose area by evaporation, especially at high ambient temperatures (Klir and Heath 1992), and it has been suggested that the nose in foxes is part of a brain-cooling mechanism (Baker et al. 1974).

Reduction of urinary water loss is also an important adaptation to the water limitation typical of arid environments. The ability to physiologically conserve water by reducing urinary water loss is dependent on an efficient kidney. Desert rodents minimize water loss by producing highly concentrated urine (e.g., *Dipodomys* sp. 4090–5540 mOsm/l; Schmidt-Nielsen 1964), although foxes do not have the high mass-specific metabolic rates thought to be essential for producing such concentrations (MacMillen 1972). Carnivorous and insectivorous desert foxes also face substantial nitrogen loads from the high protein content of their diets, requiring urinary excretion of excess nitrogen. Fennec foxes fed on mice had a urine osmotic concentration of 1480–3828 mOsm/l (max. 4022 mOsm/l; Noll-Banholzer 1979b). Under these conditions, they were

able to maintain or gain body weight without access to water or a water-rich diet (e.g., fresh fruit). Daily urine water loss in the fennec fox was reduced to only 59% of that expected based on body size (Noll-Banholzer 1979b). During dehydration, there is little change in EWL but a profound reduction in urine volume (water loss via urine is 45–48% in normal condition versus 27% in dehydrated animals; Noll-Banholzer 1979b). Fennec foxes produce a higher urine concentration than reported for other carnivores, and their kidneys have a distinct papilla (relative medullary thickness = 5.35; Noll-Banholzer 1979b). The relative medullary thickness in the red fox is shorter (4.1), and probably reflects a reduced kidney performance. In comparison, a maximum field concentration of 3,600 mOsm/l was measured in the kit fox (Girard 1998). During summer, urinary water loss is predicted to account for 39–43% of the total water loss in non-drinking kit foxes (Girard 1998). Reduction in urine volume is an adaptive mechanism when food is relatively dry and drinking water is unavailable.

Water turnover rate is largely related to availability of drinking water and type of diet. Although succulent plants and animal prey provide similar amounts of pre-formed water per gram (70–80%; Degen 1997), succulent plants contain much less energy per gram. To meet energy requirements, herbivores must consume a large mass of plant material, and consequently have high water input with food. In contrast, carnivores consume energy-dense foods, and may meet energy requirements with relatively low water input from prey. Foxes under water stress should consume large quantities of succulent but energy-poor foods, to meet water requirements without exceeding energy requirements (which would result in fat deposition, a thermally disadvantageous situation). Because passive heat dissipation is maximized in arid foxes, they may face water stress rarely or not at all. All 5 fox species in the Saharo-Arabian region are omnivorous and opportunistic feeders. The red fox is the most opportunistic, feeding on earthworms, insects, and any other live prey up to the size of a hare or turkey. It will also consume carrion, human garbage, fruit, and vegetables (Gasperetti et al. 1985, Voight 1987). In the southern Rift Valley in Israel, red foxes feed mostly on rodents, insects, and fruit (e.g., watermelons; Assa 1990). Ruppell's sand foxes in Oman feed mostly on rodents, reptiles, and grasses (Lindsay and Macdonald 1986). Diet of the pale fox consists of rodents, lizards, invertebrates, and berries (Haltenorth and Diller 1980, Kingdon 1997). The fennec fox feeds on rodents, lizards, invertebrates and plant material (Schmidt-Nielsen 1964), whereas Blanford's fox consumes mostly invertebrates and fruit (Geffen et al. 1992b). Further, Blanford's fox consumed more fruit during summer than in winter (Geffen et al. 1992c). These data show that all the fox species inhabiting the Saharo-Arabian region include fruit and succulents in their diet. In contrast, the kit fox feeds

mostly on lagomorphs and rodents (O'Farrell 1987, White et al. 1996, Girard 1998). Because foxes use evaporative cooling, consuming fruit and succulents helps them maintain water balance even under extremely arid and hot conditions. However, fennec and kit foxes (and probably the other desert-adapted species as well) are capable of sustaining their water balance for an indefinite period from the body liquids of their prey, providing EWL is reduced to a fraction of total water input from food. Considering diet composition, it has been suggested that Blanford's fox forage more for water than for energy, whereas kit fox forage more for energy during winter and spring and more for water during summer (Geffen et al. 1992c, Girard 1998).

Mean water turnover rate (WTR) of free-ranging individuals of Blanford's fox was 0.11–0.13 ml/g day during summer and 0.08–0.10 ml/g day during winter (Geffen et al. 1992c). Kit foxes monitored under natural and semi-natural conditions showed similar water influxes (0.06–0.130 ml/g day; Golightly and Ohmart 1984, Girard 1998). Captive fennec foxes, kept at 25°C and fed different diets, had a WTR range of 0.05–0.06 ml/g day. Both Blanford's fox and kit fox showed a significant increase (20–27%) in WTR in summer as compared to winter (Geffen et al. 1992c, Girard 1998). This small seasonal change in WTR demonstrates a limited dependence on EWL for cooling during the hot summer.

Conclusions

1. The principal adaptations to the desert environment demonstrated by small canids are behavioral and morphological. Desert foxes are not well adapted to tolerate heat load and avoid heat stress behaviorally. All species spend the hot hours of the day in deep burrows and delay activity to the cooler hours of the night. The small body size increases dissipation of metabolic heat by passive conductance, but limits heat storage potential as utilized by larger animals. Above ambient temperatures of 32–34°C, body temperature rises quickly to a critical level. Small canids rely on non-evaporative heat loss for dissipating heat, and can increase conductance through assuming a sprawling position of the legs, by having large ears, and through use of "thermal windows" where fur is thin and short. When ambient temperatures rise above the TNZ, small canids employ evaporative cooling by panting; at ambient temperatures higher than 37°C, a maximum of 75% of the metabolic heat can be lost by evaporation, when cooling by conductance is inefficient.

2. Small desert canids can be independent of drinking water if EWL can be restricted. Evaporation is the limiting factor in the water balance of desert-adapted fox species, and the primary mechanisms for reducing EWL are the avoidance of high temperature and a large surface area to volume ratio for increased passive heat dissipation. Low BMR, a wide TNZ, seasonal change in fur density and

body fat, and active heat dissipation by a change in skin vasoconstriction are additional mechanisms to avoid heat load without the need to evaporate water.

3. Diet selection is a critical component of the survival strategy of desert-adapted fox species. Only on rare occasions is drinking water available in the wild during the hot summer in the deserts, but foxes are capable of maintaining water balance for an indefinite time with water input from the diet. All 5 fox species in the Saharo-Arabian region include fruit and vegetative material, a water-rich food component in their diet. In severe water deprivation conditions (e.g., dried food in laboratory experiments), foxes would have to drink water to maintain body water balance (Noll-Banholzer 1979b, Girard 1998), but can be independent of drinking water even in the hot seasons if food contains at least 70% water, as is typical for vertebrate and invertebrate prey. Foxes are able to produce concentrated urine, although not at the levels known in rodents. In the fennec, the kidney has relatively thicker medulla and specific structure. In response to water deprivation, foxes decrease their urine output and food intake (Noll-Banholzer 1979b, Girard 1988). In normal conditions, water loss via urinary output is 30–50% of total water loss. Thus, reduced urine volume, reduced EWL, and selection of succulent food items in the diet combine to allow small canids to survive in the desert without drinking.

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