

Energy Expenditure and Water Flux of Rüppell's Foxes in Saudi Arabia

Joseph B. Williams^{1,*}

Danny Lenain^{2,3}

Stephane Ostrowski²

B. I. Tieleman⁴

Philip J. Seddon^{2,†}

¹Department of Evolution, Ecology, and Organismal Biology, 1735 Neil Avenue, Columbus, Ohio 43210; ²National Wildlife Research Center, P.O. Box 1086, Taif, Saudi Arabia; ³c/o VSO Thailand, 301 Hydon Compound, 223 Sukumvit Soi 4, Bangkok 10110, Thailand; ⁴Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

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ABSTRACT

Scattered populations of Rüppell's foxes (*Vulpes rueppelli*) occur across the deserts of northern Africa and Arabia. Little is known about the biology of these canids, especially the physiological mechanisms that contribute to their ability to live in such harsh environments. For individuals from Saudi Arabia, we tested the hypotheses that Rüppell's foxes have a reduced basal metabolic rate and total evaporative water loss (TEWL), parameters measured in the laboratory, and a reduced field metabolic rate (FMR) and water flux when free-living. Under basal conditions in the laboratory, males, which averaged 1,858 g in body mass, had an oxygen consumption of 914.9 mL O₂/h, whereas females, which weighed on average 1,233 g, consumed 682.9 mL O₂/h; rates of oxygen consumption translated to 441.4 kJ/d and 329.4 kJ/d, respectively. TEWL averaged 52.6 g H₂O/d for males and 47.5 g H₂O/d for females. We found no evidence that basal metabolism is reduced in Rüppell's foxes, but their TEWL was remarkably low: 50.9% of allometric prediction for males and 64.5% for females. In the wild during winter, males expended energy at a rate of 1,306.5 kJ/d, whereas females had an expenditure of 722.8 kJ/d. Analysis of covariance with FMR as the dependent variable, sex as a fixed factor, and body mass as a covariate showed no statistical difference in FMR between

sexes. Water flux did not differ significantly between sexes and averaged 123 mL H₂O/d, a value 30% lower than the kit fox from the deserts of southwestern North America. FMR was positively related to nocturnal activity levels as FMR (kJ/d) = -2,900.1 + 55.5 (% of time moving). The water content of prey items varied between 1.9 and 4.1 g H₂O/g dry matter consumed. Based on these values and knowledge of their diet, we calculated that foxes captured about one rodent and a variety of arthropods per night of foraging.

Introduction

The environments of hot deserts can include periods of high ambient air temperature (T_a), sometimes in excess of 50°C, intense solar radiation, desiccating winds, lack of surface water for drinking, and low primary productivity, conditions that in combination pose a serious challenge to the survival and reproduction of inhabitants (Meigs 1953; Louw and Seely 1982; Williams and Tieleman 2000a, 2000b). Studies of small mammals, such as rodents, that live in these habitats have often implicated both physiological and behavioral specializations that function in concert to maintain a positive energy and water balance (Bartholomew 1964; Dawson and Bartholomew 1968; Louw and Seely 1982; Walsberg 1999). Studies of the physiology of species of Canidae that occupy desert environments are few; some have suggested a reduction in basal metabolism among desert-dwelling canids (Noll-Banzoler 1979) while others have found little adjustment in metabolism or evaporative water loss (Afik and Pinshow 1993).

Scattered populations of Rüppell's fox (*Vulpes rueppelli*) occur in deserts from Morocco eastward across northern Africa and throughout the arid Arabian Peninsula (Linn 1990; Olferman 1996). These foxes can be found in the interior of the Rub' al-Khali, or "Empty Quarter," of Arabia, the largest sand sea in existence and one of the driest regions of the world, contra Geffen et al. (1992a, 1992b), who believed that *V. rueppelli* did not persist in poor-quality habitats.

Basal metabolic rate (BMR), the minimum rate of oxygen consumption of postabsorptive animals in their rest phase experiencing thermal neutral temperatures, is a standard physiological measurement used for comparison of species and as a baseline to evaluate the level of activity metabolism within a species (King 1974; McNab 1986; Hammond and Diamond 1997). An integrated measure of all catabolic processes within

* Corresponding author; e-mail: williams.1020@osu.edu.

† Present address: Zoology Department, University of Otago, P.O. Box 56, Dunedin, New Zealand.

an animal, BMR is presumably under the influence of natural selection. Among species that inhabit deserts, advantages attributable to a reduction of BMR include a lower overall energy demand, lower total evaporative water loss (TEWL; the sum of respiratory and cutaneous water losses), and lower endogenous heat production, which would have to be dissipated in a warm environment, often by evaporative means (Dawson 1984; Williams 1999; Williams and Tieleman 2000a, 2000b). The idea that mammals inhabiting desert environments have a reduced BMR is firmly entrenched in the literature (Shield 1972; Noll-Banholzer 1979; Maloiy et al. 1982; Bennet 1988; Asa and Wallace 1990; Geffen et al. 1992b; Afik and Pinshow 1993; Degen 1994; Garland and Carter 1994), but some have suggested that climate has had little influence on the level of metabolism in endotherms (Scholander et al. 1950). McNab (1986, 1989) thought that a reduction in BMR among mammals was related primarily to diet rather than climate, but Elgar and Harvey (1987) and Harvey et al. (1991) failed to find an association between BMR and diet when they controlled for phylogeny. Factors influencing BMR remain obscure, and as the debate continues (Derrickson 1989; McNab 1992; Anderson et al. 1997), more data will be necessary to resolve these issues.

A diminution in BMR gains ecological significance if a reduced BMR translates into a reduced field metabolic rate (FMR) as estimated by the doubly labeled water method (DLW; Speakman 1997); the coupling between BMR and FMR has become a central issue to understanding organismal design and function (Ricklefs et al. 1996). Among 33 species of mammals, Ricklefs et al. (1996) found a significant positive association between BMR and FMR. To date, only a few studies have measured FMR of members of the Carnivora or attempted to relate their activity patterns to energy expenditure (Chevalier 1989; Geffen et al. 1992b; Nagy 1994; Covell et al. 1996; Williams et al. 1997; Girard 2001). As a carnivore that lives in an environment of low productivity, Rüppell's foxes might be expected to travel long distances while foraging, which would have a significant impact on their energy expenditure (Gittleman and Harvey 1982; Covell et al. 1996; Girard 2001).

Animals that live in deserts should employ a frugal water economy in order to survive, but the carnivorous grasshopper mouse (*Onychomys torridus*) living in an arid environment had a TEWL within 2% of allometric expectation (Whitford and Conley 1971). Whitford and Conley speculated that a reduced pulmocutaneous water loss in desert-dwelling carnivorous species was unnecessary because their prey contained ample water. In contrast, fennec foxes had a TEWL only 36.4% of allometric prediction (Maloiy et al. 1982). Geffen et al. (1992b) suggested that although prey items were rich in water for desert carnivores, their foods also were rich in proteins, necessitating water loss via excretion of urea. Hence, economy of water loss was important for desert carnivores.

In this article, we report on BMR and TEWL, measured in the laboratory, and field metabolism and water flux of free-

living Rüppell's foxes, a desert canid whose biology is poorly known (Lindsay and MacDonald 1986). We explore the hypotheses that rates of metabolism and water loss, in the laboratory and field, are reduced in Rüppell's foxes compared to species that live in more mesic environments. Using information on their diet, the water content of their prey, and their water intake, we estimate the metabolizable energy intake of Rüppell's foxes and compare these estimates to those obtained by DLW.

Study Area and Methods

Mahazat as-Sayd

Our study site, a 2,244-km² protected area known as Mahazat as-Sayd, lay in the west-central region of Saudi Arabia (22°15' N, 41°50' E). Characterized as arid landscape (Meigs 1953), Mahazat as-Sayd is covered with open gravel and sandy plains on the eastern half and a mixture of undulating basalt and chert plains on the remainder. No permanent sources of drinking water are available in the reserve. Mean monthly maximum temperatures range from 19° to 42°C during winter and summer, respectively, and mean minimum temperatures from 6° to 25°C. Rainfall is patchily distributed and unpredictable, with an interannual variation of 50 to 250 mm. During October–December 1998, when foxes were labeled with isotopes, nighttime mean air temperature averaged 15°, 11°, and 10°C, respectively, and no rain fell (NWRC annual report, 1998).

Measurement of TEWL and Oxygen Consumption

From steel plate we welded a 113-L metabolic chamber with a flat black interior (Porter 1969) that was surrounded by an insulated water jacket, the temperature of which was controlled by a Neslab RTE-140 ($\pm 0.1^\circ\text{C}$). A rubber gasket rendered the lid of the chamber airtight. During experiments, foxes were placed in the chamber on wire mesh above mineral oil that trapped urine and feces, eliminating them as sources of water.

During August 1999, we determined rates of TEWL and oxygen consumption ($\dot{V}\text{O}_2$) for six foxes that had been without food 8 h before measurement. An air compressor pushed air through two drying columns filled with Drierite, through a mass flow controller (Brooks model 5851E) that had been previously calibrated against a 5-L bubble meter (Levy 1964), and then into the metabolism chamber. Flow rates were regulated at 5 L/min. Subsamples of excurrent air passed through a dewpoint hygrometer (General Eastern model Hygro M4) and through columns of silica gel, ascarite, and silica gel before passing through an O₂ analyzer (Applied Electrochemistry model S-3AII), the latter calibrated with dry CO₂-free outside air (Gessaman 1987). We monitored dewpoint and O₂ concentration of the excurrent air stream continuously with a Campbell CR10 data logger and PC208 software. Visual inspection of the data in real time showed that foxes were calm in the

chamber for the entire 3-h measurement period. In practice we used the data collected the last 20 min of the period for analyses. Values of TEWL were calculated using the equation $TEWL (g/d) = [(V_e \rho_{out} - V_i \rho_{in})] \times 1.44 \times 10^{-3}$, where ρ_{in} and ρ_{out} are the absolute humidities ($g H_2O/m^3$) of inlet and outlet air, V_i is the flow rate (mL/min) of air entering the chamber, and V_e is the flow rate of exiting air. Absolute humidity (STP) was determined with the equation $\rho (g/m^3) = 216.7e_s / (T_{dp} + 273.15)[P_0(T_{dp} + 273.15)] / [P_a(T_0 + 273.15)]$, where e_s is the saturation vapor pressure (mbar) at a given dewpoint, T_{dp} is the temperature ($^{\circ}C$) of the air in the dewpoint hygrometer, P_0 is standard pressure (1,013 mbar), P_a is barometric pressure (mbar), and T_0 is standard temperature ($0^{\circ}C$). We calculated $\dot{V}O_2$ with equation 4 of Hill (1972). Metabolic trials were performed during the day, the normal rest phase of Rüppell's foxes, at a T_a of $35^{\circ}C$, a temperature previously determined to be within their thermal neutral zone (S. Ostrowski, unpublished data). Body mass was determined before and after metabolic trials using a 2-kg Pesola scale (± 10 g).

Activity Patterns of Foxes in the Field

Trapping and radio-tracking procedures that we used are detailed in Lenain (2000). In short, foxes were captured with collapsible live traps (Tomahawk Live Trap Co., Tomahawk, Wis.), sexed, weighed, and fitted with a radio collar (84 g, Biotrack, Dorset; Kenward 1987); radios were equipped with a motion switch that increased pulse rate with movement. Before experiments with DLW, we identified the location of all dens within the territory of foxes that we used in experiments (Lenain 2000). Radio fixes were obtained using a hand-held two-element antenna and radio receiver (LA12, AVM Instrument Co., Colfax, Calif.). We followed each individual labeled with isotopes from a distance of 300–1,000 m for 24 h beginning 2 h before sunset, when foxes were in their dens. Every 10 min, we recorded whether foxes were moving, stationary, or in their den as judged visually or from radio pulse rate. Because foxes followed a circuitous path while foraging, it was not possible to measure the total distance they moved at night. As a proxy for distance moved, we used the proportion of the total number of point observations of activity that foxes were moving. We recorded the activity schedule for only five of six individuals because of a transmitter malfunction.

Measurement of Energy Expenditure and Water Flux

Measurements of FMR and water flux were obtained by means of the DLW technique, in which the rate of decline of an isotope of hydrogen in the body-water pool provides a measure of water flux (Nagy and Costa 1980) and the loss rates of both a hydrogen isotope and ^{18}O yield an estimate of CO_2 production (Lifson and McClintock 1966; Nagy 1980; Speakman 1997). Our procedures for using the DLW method have been detailed

elsewhere (Williams 1987, 2000; Williams et al. 1997). In brief, foxes were trapped, an initial blood sample was taken from them for background concentrations of isotopes, and they were then injected intraperitoneally with 4.25 mL/kg of a mixture of deuterated water and 95 atom percent ^{18}O . After a 3-h period for equilibration of isotopes, we removed a 2-mL blood sample from the jugular vein. Foxes were then weighed, ear tagged, and released. We retrapped foxes 4.8 to 5.8 d later, took a second blood sample, and weighed and released them. We enclosed the bait that we used in the traps in a wire mesh so as not to influence food intake or water flux of foxes.

Blood samples were analyzed in duplicate for isotope concentrations at the Center for Isotope Research, University of Groningen, under the direction of H. Visser (Visser and Schekerman 1999). We calculated water influx using the equation of Nagy and Costa (1980) and rates of CO_2 production using equation 7.17 of Speakman (1997). Background levels of isotopes obtained from each animal were subtracted from values before calculations.

Estimates of water flux using isotopes of hydrogen are typically within $\pm 10\%$ of values obtained by standard laboratory methods (Nagy and Costa 1980), and estimates of CO_2 production as given by DLW are within 8%–10% (Williams and Nagy 1984; Speakman 1997). To calculate energy expenditure for foxes, we used a conversion factor of 25.7 J/mL CO_2 (Nagy 1983).

For calculation of CO_2 production, total body water must be evaluated, a parameter usually estimated indirectly from isotope dilution (Speakman 1997). We measured total body water of Rüppell's foxes directly. We killed one male (1,845.8 g) and one female (1,377.8 g), cut the body into small pieces, and placed the components into an oven at $65^{\circ}C$ until they reached constant mass. We found that total body water was 64.9% and 67.7%, respectively. For DLW calculations we used the average of these two values, 66.3%.

For animals that live in burrows, rebreathing of labeled CO_2 can cause errors in estimates of FMR (Nagy 1983). However, because dens of Rüppell's foxes were shallow, only extending <0.8 m below ground (Olferman 1996), we assumed there was significant exchange of air in the burrow with the atmosphere to obviate any potential for rebreathing of isotopes (Williams et al. 1997).

Diet during Winter

In order to calculate dry-matter food intake of foxes, we needed information on their diet. In a 2-yr study, Olferman (1996) found significant seasonal variation in the foods eaten by Rüppell's foxes in Mahazat as-Sayd. Based on an analysis of 149 scats collected during October–December over a 2-yr period, he showed that their diet by volume consisted of 70% small mammals and 15% arthropods when rodent densities were high, but about 35% small mammals and 55% arthropods when

rodent densities were reduced. Small birds, reptiles, leaves, and seeds consistently represented a small proportion of food intake, although it was unclear whether foxes directly selected vegetable material as food or whether it was in the stomachs of prey. The most common small mammals eaten were *Gerbillus cheesmani*, *Gerbillus nanus*, and *Meriones crassus*, whereas ants, termites, and beetles were the invertebrates most often consumed.

Water Content of Prey

We measured the percentage of water in the important dietary items of Rüppell's foxes (Olferman 1996). Small mammals, scorpions, and beetles were individually dried to constant mass at 70°C. Ants and termites were dried in groups of 15–25 individuals.

Statistics

Computations were performed using SPSS 10.0 for Windows (SPSS, Chicago). Values are presented ± 1 SD. Means were compared using *t*-test or by analysis of covariance with sex as a fixed factor and body mass as a covariate with statistical significance set at $P = 0.05$. Percentages were arcsine transformed before running parametric statistics (Zar 1996).

Results

Basal Metabolism and Evaporative Water Loss

For laboratory metabolism trials, male Rüppell's foxes averaged $1,858 \pm 150$ g, whereas females had a mean body mass of $1,233 \pm 236$ g, values that differed significantly ($t = 3.9$, $P < 0.02$; Table 1). Oxygen consumption of males was 914.9 mL O₂/h and of females was 682.9 mL O₂/h, values that translate to 441.4 kJ/d and 329.4 kJ/d, respectively ($t = 3.1$, $P < 0.04$).

When we divided BMR by mass^{0.712}, where the exponent 0.712 is the slope of the line for the relationship between log BMR and log body mass (g) for carnivores (McNab 1989), we found no significant differences between male and female metabolism ($t = 0.23$, $P > 0.1$). Analysis of covariance with BMR as the dependent variable, sex as a fixed factor, and body mass as a covariate also showed no statistical differences between sexes ($F = 0.2$, $P > 0.6$).

TEWL averaged 52.5 g H₂O/d for males and 47.5 g H₂O/d for females, values that were not significantly different ($t = 0.6$, $P > 0.5$). With data combined, TEWL averaged 50.1 g H₂O/d.

Activity Patterns

Foxes emerged from their dens around sunset and reentered their dens on average 1.5 h before sunrise; about one-half of each 24 h period was spent within the den (Table 2). Though they did not reenter their dens at night, they rested above ground periodically for periods up to 1 h during foraging. While foraging, males tended to be more active than females (Table 2).

DLW Measurements

During winter, males with a mean body mass of 1,918 g had a FMR of 1,306.5 kJ/d, whereas females that averaged 1,583 g had a FMR of 722.8 kJ/d (Table 3). The change in body mass for foxes during measurement intervals averaged -3.7% . Although body masses did not differ significantly between the sexes ($t = 2.6$, $P = 0.06$), FMR was significantly different ($t = 4.5$, $P < 0.02$). Analysis of covariance with FMR as the dependent variable, sex as a fixed factor, and body mass as a

Table 1: Basal metabolic rate (BMR) and total evaporative water loss (TEWL), determined at 35°C, of Rüppell's foxes from Mahazat as-Sayd, Saudi Arabia

Animal	Mass (g)	Oxygen Consumption (mL O ₂ /h)	BMR (kJ/d)	TEWL (g H ₂ O/d)
Males:				
138	2,000	940.5	453.7	49.3
03	1,700	839.5	405.0	62.9
134	1,875	964.7	465.5	45.5
Mean (SD)	1,858 (150.7)	914.9 (154.2)	441.4 (32.1)	52.6 (9.1)
Females:				
02	1,500	811.3	391.4	60.8
04	1,150	610.7	294.6	40.5
05	1,050	626.7	302.3	41.3
Mean (SD)	1,233 (236.3)	682.9 (111.4)	329.4 (53.8)	47.5 (11.5)
Mean (male and female)	1,546	798.9	385.4	50.1

Table 2: Percentage of 24-h day that foxes were in their dens and percentage of nocturnal active period that they were moving or stationary but outside of dens

Animal	Date	% Time in Den ^a	% Time Moving ^b	% Time Stationary	Number of Records/Total Possible (%) ^a
Females:					
174	February 15–16	54.8	61.5	28.5	144/144 (100)
177	December 1–2	51.4	67.6	32.4	144/144 (100)
107	October 26–27	50.0	68.7	31.3	131/144 (90.9)
Males:					
08	December 8–9	52.1 ^c	76.3	23.7	103/144 (71.5)
84	October 28–29	52.8	74.5	25.5	129/144 (89.6)

^a Based on 24-h day.

^b Based on time out of den during night.

^c Time of reentry into den was not observed but was estimated.

covariate showed that males had a FMR indistinguishable from females ($F = 4.3$, $P = 0.13$).

Although water influx was higher in males than females, 152.2 versus 93.7 mL H₂O/d, these differences did not achieve statistical significance ($t = 2.1$, $P > 0.09$; Table 3). For males and females combined, water flux averaged 123.0 mL H₂O/d.

Activity versus FMR

Fox activity, evaluated as the percentage time that they were moving (Table 2), was correlated with FMR: $FMR (kJ/d) = -2,900.1 + 55.5 (\% \text{ time moving})$; Fig. 1; $r^2 = 0.87$, $F = 20.3$, $P < 0.02$). These data suggest that males, which accounted for the two highest data points, are more active than females and as a result of this increased activity have higher FMRs.

Water Content of Prey

Small mammals (*Meriones crassus* and *Gerbillus cheesmani*), ants, scorpions (*Compsobuthus* spp.), and birds contained around 65%–70% water and provided 1.9–2.4 g H₂O/g dry-matter intake, whereas large beetles (Tenebrionidae and Carabidae) were only 53.3% water (Table 4). Termites (*Psammodermes hybostoma*) contained 80.5% H₂O and provided 4.13 g H₂O/g dry matter.

Discussion

Body mass is generally acknowledged to be the primary factor influencing the level of BMR in mammals (Kleiber 1961; McNab 1980; Hayssen and Lacy 1985). However, there remains considerable residual variation around these regressions. Converting the mass-specific equation of McNab (1989), who compiled BMR for 43 species of carnivores ranging in size from 77 g to 138.2 kg, yields the relationship $BMR (kJ/d) = 1.952 \text{ mass (g)}^{0.712}$. For a 1,858-g male and a 1,233-g female Rüppell's fox, this equation gives a BMR of 415.0 and 310.0 kJ/d, re-

spectively. Values of BMR that we measured were about 6% higher for both sexes than predictions for carnivores primarily from mesic habitats.

Averaging values for males and females, we found a BMR of 385.4 kJ/d for a Rüppell's fox of 1,546 g, or a normalized value of 2.07 kJ/mass^{0.712}, where 0.712 is the exponent of McNab's equation for carnivores. For other species of foxes, values for BMR were 1.79 kJ/mass^{0.712} (fennec fox; Maloiy et al. 1982), 2.38 kJ/mass^{0.712} (arctic fox; Fuglei and Oritsland 1999), 2.53 kJ/mass^{0.712} (kit fox; Golightly and Ohmart 1983), and 2.73 kJ/mass^{0.712} (red fox; Irving et al. 1955). Adjusted BMR of the Rüppell's fox is only 13% lower than the arctic fox. We find no support for the hypothesis that Rüppell's foxes possess a reduced BMR compared to more mesic species.

As emphasized by some authors, phylogeny is a potentially confounding factor in an analysis wherein one searches for relationships between physiological phenotype and environment because species may not be biologically or statistically independent (Felsenstein 1985; Harvey et al. 1991; Garland et al. 1992). However, studies have suggested that application of methods that purportedly eliminate historical bias in which the evolutionary model, branch lengths, or topology of the phylogeny are inaccurate may lead to erroneous conclusions (Westoby et al. 1995; Ricklefs and Stark 1996; Björklund 1997; Price 1997; Díaz-Uriate and Garland 1998). We fabricated a "best guess" phylogeny for five species of foxes based on sequences for the cytochrome b gene (Geffen et al. 1992a) and on sequences of allozymes (Wayne et al. 1989; Fig. 2). Branch lengths are based on Wayne and O'Brien (1987). Next we tested the assumption that BMR or body mass was significantly related to phylogenetic history using the test for serial independence, a procedure that does not depend on a particular model of evolutionary change nor on an accurate assessment of branch lengths (Abouheif 1999). We calculated a randomized C-statistic by rotating nodes within our topology 1,000 times and compared this with our observed C-statistic using the computer program Phylogenetic Independence (Reeve and Abouheif

1999). Because neither body mass ($P > 0.3$) nor BMR ($P > 0.3$) was significantly correlated with phylogeny, traditional statistical analyses are justified (Abouheif 1999). The allometric equation describing BMR in relation to body mass in foxes is $\log \text{BMR (kJ/d)} = -0.478 + 0.955 \log \text{body mass (g)}$. BMR in Rüppell's foxes is within 4.2% of prediction, further supporting the view that these desert animals do not have a reduced BMR.

For mammals experiencing temperatures between 18°C and 29°C, TEWL was related to body mass by the equation $\text{TEWL (g h}^{-1}\text{)} = 2.58 \text{ mass (kg)}^{0.826}$ (Chew 1965). Even though measured at 35°C, TEWL rates for Rüppell's foxes were only 50.9% of prediction for males and 64.5% for females. Hence, despite having a BMR similar to expectation, these comparisons suggest the hypothesis that Rüppell's foxes have a depressed TEWL compared to other mammals.

For FMR of seven species of carnivores including three species of foxes (Blanford's, kit, and swift), Nagy et al. (1999) produced the allometric equation $\text{kJ/d} = 1.67 \text{ mass (g)}^{0.869}$. Female Rüppell's foxes, with a mean body mass of 1,583 g, had a FMR 27.7% less than prediction, but males, with an average body mass of 1,918 g, had a FMR 9.8% higher. Comparing the average FMR of Rüppell's foxes, males and females combined, with other species by dividing their FMR by $\text{mass}^{0.869}$, we found that during winter, swift fox had the highest value at 2.31 kJ/mass^{0.869} (Covell et al. 1996), followed by kit fox at 2.07 kJ/mass^{0.869} (Girard 1998) and Blanford's fox at 1.61 kJ/mass^{0.869} (Geffen et al. 1992b). Also during the winter, the Rüppell's fox had the lowest mass-adjusted FMR thus far reported for foxes.

As a carnivore living in an environment of low rainfall and attendant low resource density, foxes might be expected to move relatively large distances in search of prey (Gittleman and Harvey 1982; Girard 2001). Rüppell's foxes that were active a

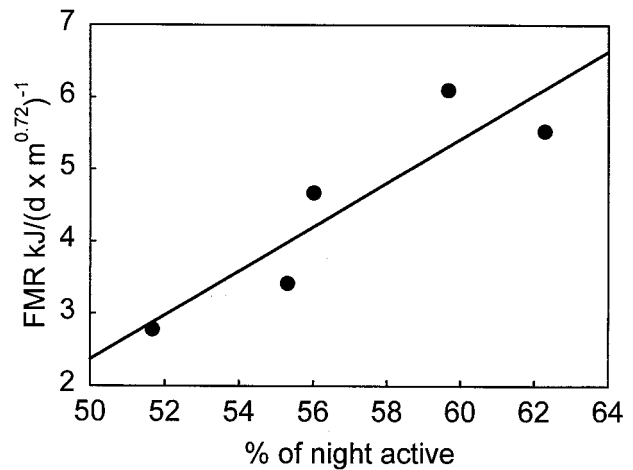


Figure 1. Normalized field metabolic rate (FMR) of Rüppell's foxes in relation to percentage of time they spent active during the night.

larger percentage of nighttime, a proxy for distance moved, had a higher normalized FMR. This relationship is driven in part by the fact that males travel over larger distances during winter, a result attributable to their heightened territorial defense with the onset of mating activities beginning in November (Olferman 1996).

Geffen et al. (1992b) hypothesized that owing to costlier movements in mountainous habitats, FMR of Blanford's foxes was significantly higher than that of other similar-sized canids occupying more level terrain. To support their idea they pointed out that Blanford's foxes had a FMR 30% higher than that of

Table 3: Field metabolic rate and water flux of free-living Rüppell's foxes in Saudi Arabia during October–December 1998

Animal	Mean Body Mass (g)	mL H ₂ O/d	L CO ₂ /d	kJ/d	kJ/mass ^{0.869a}	Measurement Interval (d)
Females:						
174	1,645	67.6	22.4	575.4	.92	5.8
177	1,638	107.7	27.4	704.4	1.13	6.0
107	1,465	105.8	34.6	888.7	1.57	5.7
Mean (SD)	1,583 (102)	93.7 (22.6)	28.1 (6.1)	722.8 (157.5)	1.20 (.33)	5.8 (.15)
Males:						
111	1,700	104.9	43.8	1,126.6	1.75	5.8
08	2,079	183.5	52.6	1,352.9	1.77	5.3
84	1,975	168.2	56.0	1,439.9	1.97	4.8
Mean (SD)	1,918 (195)	152.2 (41.7)	50.8 (6.3)	1,306.5 (161.7)	1.83 (.12)	5.3 (.5)
Mean (male and female)	1,750	123.0	39.5	1,014.7	1.52	5.6

^a Exponent from Nagy et al. (1999).

Table 4: Percentage water in dietary items of Rüppell's foxes

Category	% H ₂ O (SD)	g H ₂ O/g Dry Matter	N ^a
Vertebrates:			
Rodents	70.2 (.01)	2.36	6 ^b
Birds	66.6 (.02)	1.99	2 ^c
Arthropods:			
Coleoptera	53.3 (.09)	1.14	5
Ants	67.6 (.02)	2.09	5
Termites	80.5 (.01)	4.13	5
Scorpions	65.4	1.89	1
Plant material	69.8 ^d		

Note. Diet of foxes based on Olferman (1996).

^a Number of samples dried for determination of water content.

^b Five individuals of *Meriones crassus* and one *Gerbillus cheesemani*.

^c *Passer domesticus* and *Alaemon alaudipes*.

^d Seeds and leaves of *Indigofera* spp., *Acacia* spp., and *Fagonia* spp.

kit foxes, a result based on the study of Golightly and Ohmart, who estimated daily energy expenditure of kit foxes from laboratory measurements (Golightly and Ohmart 1983) and determined that the putative "cost of activity" in Blanford's foxes, calculated as (FMR - BMR)/BMR, was unusually high, 7.7-9.3. Because they assumed that BMR of Blanford's foxes was equivalent to that of the fennec fox (Noll-Banholzer 1979), a species with one of the lowest BMRs for any carnivore, firm conclusions about the "cost of activity" cannot be drawn. Moreover, values for FMR include all energy costs summed over the measurement interval, including those of thermoregulation and the heat increment of feeding, not just those of activity. The ratio of FMR/BMR in this study was 2.63, suggesting that BMR is a much larger component of FMR than for Blanford's foxes. However, during winter Blanford's foxes had a mass-adjusted FMR of 1.61 kJ/mass^{0.869}, only 4.6% higher than we measured for the Rüppell's fox, a species of flat terrain. In addition, more recent data, obtained using DLW, on FMR of kit foxes (Girard 1998), a species of the arid flats of the Sonoran, Mojave, and Great Basin deserts of North America, showed that they have a FMR 28.6% higher than Blanford's foxes, contrary to the hypothesis of Geffen et al. (1992b). Taken together these comparisons do not lend support to their hypothesis that living in mountainous areas mandates an unusually high FMR.

Small desert eutherians of less than 2 kg body mass are thought to have lower water fluxes than nondesert species of the same body mass, an expectation founded on the idea that desert mammals have evolved mechanisms that reduce their water requirements below that of relatives living in more mesic environs (Nagy and Peterson 1988). The allometric equation of Nagy and Peterson (1988) predicts for a desert eutherian of

1,750 g a water flux of 180.2 mL H₂O/d, a higher value than predictions for a carnivore of mesic habitats (94.0 mL H₂O/d) or for a eutherian mammal (146.5 mL H₂O/d), contrary to conventional wisdom. These predictions support the counter-intuitive alternative view that desert carnivores have higher rates of water flux than do more mesic species, perhaps because their environment extracts from them more evaporative water. Compared to other carnivores, Rüppell's foxes had a water flux of 123.0 mL H₂O/d, 30.9% higher than expectation but 31.7% less than the prediction for a desert mammal. Swift foxes (*Vulpes velox*), which averaged 1,990 g and were living in a short-grass prairie in Colorado in winter, had a water flux of 205 mL H₂O/d (Covell et al. 1996). Comparing mass-adjusted values, Rüppell's foxes had a water flux 33.5% lower than swift foxes. With drinking water continuously available, kit foxes (*Vulpes macrotis*), a species of the southwestern deserts of North America, had a water flux of 155.3 mL H₂O/d (1,500 g body mass) during winter, or a mass-adjusted value of 0.464 mL H₂O/(d × mass^{0.795}) (Girard 1998). Rüppell's foxes had a mass-adjusted water flux of 0.325 mL H₂O/(d × mass^{0.795}), a value 30% less.

In this study, total water influx, the sum of preformed water intake and metabolic water production, averaged 123.0 mL H₂O/d. Because Rüppell's foxes did not drink, all of their preformed water came from their food. On average foxes produced 39.5 L CO₂/d, which results in 26.1 mL of metabolic water production, assuming 0.66 μL H₂O/mL CO₂ (Nagy 1983), leaving a remainder of 96.9 mL preformed water intake. Olferman (1996) showed that the diet of Rüppell's foxes in Mahazat as-Sayd varied depending on the densities of rodents. Because rodent densities were low in 1998 (Wells 1999), we assumed

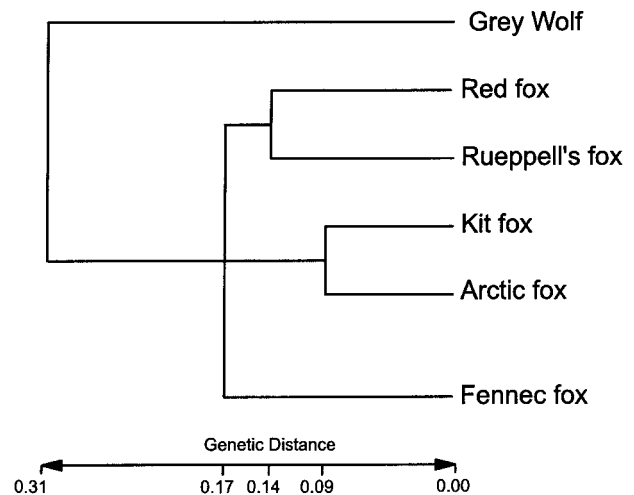


Figure 2. Phylogeny of foxes based on sequences of cytochrome b gene and sequences of allozymes. Genetic distances from Wayne and O'Brien (1987).

that the food intake of Rüppell's foxes during winter was 35% rodents, 55% arthropods, and 5% seeds and leaves (Olferman 1996). Based on this diet, we calculated that foxes obtained 1.97 g H₂O/g dry matter consumed. To obtain 96.9 mL water, foxes would need to eat 49.2 g dry matter. Given that for carnivores 20.3 kJ of metabolizable energy is typically obtained for each gram dry matter eaten (Vogtsberger and Barret 1973; Nagy 1983) and that for herbivores 6.4 kJ/g dry matter is obtained (Nagy and Milton 1979), we calculated a weighted average of 18.9 kJ metabolizable energy per gram dry matter for a fox diet (90% meat and 10% plants). Hence foxes obtain 930 kJ metabolizable energy when they have a preformed water intake of 96.9 mL H₂O, an intake 9.2% less than that which we have measured using DLW. For the six rodents that we dried from Mahazat as-Sayd, the average dry mass was 21.9 ± 10.8 g. This suggests that Rüppell's foxes captured about one rodent per night during their foraging along with a variety of arthropods.

In conclusion, we have measured the rates of metabolism and water loss, in the laboratory and field, of Rüppell's foxes. We found no evidence that their basal metabolism is reduced compared to other carnivores or other foxes, but their mass-corrected FMR during winter is the lowest thus far reported for foxes. Laboratory measurements of TEWL were only 50%–65% of allometric predictions, suggesting an evolutionary specialization in either respiratory or cutaneous water loss. Comparisons of water influx in the field were ambiguous; Rüppell's foxes had a water influx rate about 30% higher than predicted for carnivores but about 30% lower than other desert mammals. Our calculations of metabolizable energy intake based on water influx were within 9.2% of our DLW estimates of energy expenditure.

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