J Comp Physiol B (2004) 174: 29–39
DOI 10.1007/s00360-003-0386-0

ORIGINAL PAPER

J. B. Williams · A. Muñoz-Garcia
S. Ostrowski · B. I. Tieleman

A phylogenetic analysis of basal metabolism, total evaporative water loss, and life-history among foxes from desert and mesic regions

Accepted: 27 August 2003 /

Abstract We measured basal metabolic rate (BMR) and total evaporative water loss (TEWL) of species of foxes that exist on the Arabian Peninsula, Blanford's fox (*Vulpes cana*) and two subspecies of Red fox (*Vulpes vulpes*). Combining these data with that on other canids from the literature, we searched for specialization of physiological traits among desert foxes using both conventional least squares regression and regressions based on phylogenetic independent contrasts. Further, we explored the consequences of reduced body size of foxes on life history parameters such as litter size and neonate mass. For Blanford's foxes, Red foxes from the central desert of Arabia, and Red foxes from the more mesic Asir mountains, body mass averaged 1,285 ± 52 g, 1,967 ± 289 g, and 3,060 ± 482 g, respectively, whereas mean BMR, during summer, was 304.5 ± 32.3 kJ/day, 418.0 ± 32.4 kJ/day, and 724.1 ± 120.2 kJ/day (± SD). An analysis of covariance with body mass as a covariate showed no statistical differences in BMR among foxes. Analysis of covariance indicated that Red fox from the Asir mountains had a higher TEWL than Red foxes from central Arabia or than Blanford's foxes also from the mountains. Comparisons of all species of desert and mesic foxes showed no significant differences in BMR, nor did desert foxes have a significantly lower BMR than other carnivores. TEWL of desert foxes was lower than other more mesic carnivores; deviations in TEWL ranged from −17.7% for the Fennec fox (*Fennecus zerda*) to −57.4% for the Kit fox (*Vulpes velox*). Although desert foxes have a BMR comparable to other more mesic species, it appears that desert foxes do have a smaller body mass, lowering overall energy requirements. We attribute this reduction in body size to the "resource limitation hypothesis" whereby natural selection favors smaller individuals in a resource-limited environment, especially during periods of severe food shortage. However, until common garden experiments are performed, developmental plasticity and acclimation cannot be ruled out as contributors to this pattern.

Keywords Foxes · Desert · Basal metabolism · Total evaporative water loss · Phylogenetic independent contrasts

Abbreviations *BMR* basal metabolic rate · *CLSR* conventional least squares regression · *MYA* million years ago · *PIC* phylogenetic independent contrasts · T_a ambient temperature · *TEWL* total evaporative water loss · *TNZ* thermoneutral zone · VO_2 oxygen consumption

Introduction

Environments of hot deserts include periods of high ambient air temperature (T_a), intense solar radiation, desiccating winds, unpredictable rainfall, lack of surface water, and low primary productivity, conditions that pose a challenge to the survival and reproduction of inhabitants (Meigs 1953; Louw and Seely 1982; Williams and Tieleman 2000). Studies on small mammals, such as rodents, that live in these habitats have often implicated both physiological and behavioral specializations that function to maintain energy and water balance (Bartholomew 1964; Schmidt-Nielsen 1964; Dawson and Bartholomew 1968; Louw and Seely 1982; Walsberg 2000; Lovegrove 2003). Studies on the physiology of species of Canidae that occupy desert environments are few with some suggesting a reduction in basal metabolism among desert dwelling canids (Noll-Banholzer

Communicated by G. Heldmaier

J. B. Williams (✉) · A. Muñoz-Garcia
Department of Evolution, Ecology and Organismal Biology,
318 W 12th Avenue, Columbus, OH 43210, USA
E-mail: Williams.1020@osu.edu

S. Ostrowski
National Wildlife Research Center,
P.O. Box 1086, Taif, Saudi Arabia

B. I. Tieleman
Zoological Laboratory, University of Groningen,
P.O. Box 14, 9750 AA Haren, The Netherlands

1979) whereas others have found little adjustment compared to mesic relatives (Afik and Pinshow 1993; Williams et al. 2002). Despite this equivocal evidence, the idea that carnivores inhabiting deserts have lower rates of basal energy expenditure and water flux compared with non-desert species is firmly entrenched in the literature (Evenari 1985; Bennett 1988; Chevalier 1991; Geffen et al. 1992b).

Basal metabolic rate (BMR), the minimal rate of oxygen consumption of post-absorptive animals in their rest phase at thermal neutral temperatures, is a standard measurement used for comparison among species (King 1974; McNab 1986). For species that inhabit deserts, selective advantages attributable to a diminution of BMR would include lower energy demand, reduced total evaporative water loss (TEWL), and lower endogenous heat production which would have to be dissipated in a warm environment, often by evaporative means (Dawson 1984; Bennett 1988; Williams 1999). The idea that mammals inhabiting desert environments have a reduced BMR has support, especially among studies on rodents (Bartholomew 1964; Dawson and Bartholomew 1968; Shield 1972; Noll-Banholzer 1979; Louw and Seely 1982; Bennett 1988; Chevalier 1991; Lovegrove 2000; Walsberg 2000). McNab (1986, 1989) thought that a reduction in BMR among mammals was related to diet rather than climate, an idea challenged by Elgar and Harvey (1987) and by Harvey et al. (1991) who failed to find an association between BMR and diet when they controlled for phylogenetic history. If species of mammals have a reduced BMR in response to the desert environment, one might expect associated changes in attributes of their life-history, such as smaller litter size or neonate mass (Ricklefs and Wikelski 2002).

Animals that live in deserts are thought to possess mechanisms that minimize water loss, but data for TEWL for carnivores from deserts are few and results ambiguous. The insectivorous Grasshopper mouse (*Onychomys torridus*) living in an arid environment had a TEWL within 2% of allometric expectation (Whitford and Conley 1971), whereas Fennec foxes had a TEWL only 36.4% of allometric prediction (Maloiy et al. 1982), the latter result suggesting selection for reduced TEWL. Although Afik and Pinshow (1993) argued that wolves from the deserts of Israel did not show a reduction in TEWL, especially during the summer, it is unclear what comparisons they used to arrive at such a conclusion. Geffen et al. (1992b) suggested that, because prey items were rich in proteins, carnivores necessarily lose relatively large amounts of water via excretion of urea. Hence economy of water loss was thought to be important for desert carnivores even though prey items contained large amounts of water.

Rüppell's foxes (*Vulpes rueppelli*) from the desert of central Arabia had a BMR equivalent to other carnivores from more mesic environments, but TEWL was only 50–65% of allometric expectation (Williams et al. 2002). In this report we test, for six species of foxes, the general hypotheses that species in deserts possess reduced BMR and/or TEWL relative to body mass. Because of the paucity of data on the physiology of desert foxes, we measured BMR and TEWL of Blanford's fox and two subspecies of Red fox on the Arabian Peninsula. After combining these data with that of Rüppell's fox (Williams et al. 2002) and other canids from the literature, we searched for specialization of physiological traits among desert foxes using both conventional least squares regression and regressions based on phylogenetic independent contrasts. Finally, we examine the connection between reduced body mass and life history parameters, such as litter size and neonate mass, among canids.

Materials and methods

Capture of foxes

We captured Blanford's foxes and Red foxes [hereafter called Red fox (Asir)] around Al-Lith (20°49′N, 40°45′E; altitude 2,200 m) and Biljurshi (19°45′N, 41°42′E; altitude 2,100 m) on the edge of the escarpment in the western Arabian highlands using Tomahawk collapsible traps baited with tuna, sardines, and bread. Both sites were covered with *Juniper procera*. Mean monthly maximum and minimum temperatures along the escarpment are 36 °C and 3 °C during summer and winter, respectively, and rainfall occurs during the spring and summer, 200–300 mm (Fisher and Membery 1998).

We trapped desert-dwelling Red foxes [hereafter called Red fox (Mahazat)] in Mahazat as-Sayd, a 2,244-km^2 protected area in the west-central region of Saudi Arabia (22°15′N, 41°50′E). Characterized as arid landscape (Meigs 1953), Mahazat as-Sayd contains flat gravel and sandy plains in its eastern half and a mixture of undulating basalt and chert plains in the remainder (Mandaville 1990). No permanent sources of drinking water are available in the reserve. Mean monthly maximum and minimum temperatures are 42 °C and 6 °C during summer and winter, respectively. Rainfall is patchily distributed and unpredictable with an inter-annual variation from 35 mm to 200 mm (NWRC Annual Report).

Measurement of TEWL and oxygen consumption

To measure oxygen consumption ($\dot{V}O_2$) and TEWL, we welded a 113-l metabolic chamber from steel plate 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 (±0.1 °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 feces. Metabolic trials were performed during daytime, the normal rest phase for foxes, and in summer.

Rates of TEWL and $\dot{V}O_2$ were determined for foxes that had been without food for 8–12 h prior to measurements. An air compressor pushed air through two drying columns filled with Drierite, through a mass flow controller set at 5 l/min (Brooks model 5851E), calibrated against a 5-l bubblemeter (Levy 1964), and then into the metabolism chamber. Sub-samples of excurrent air passed through Teflon tubing to a dewpoint hygrometer (General Eastern model Hygro M4; calibrated against an NIST standard), and through columns of silica gel, ascarite, and silica gel, before passing through an O_2 analyzer (Applied Electrochemistry model S-3AII), the latter calibrated with dry CO_2-free outside air. We monitored dewpoint and O_2 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 remarkably 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. We calculated $\dot{V}O_2$ with Eqn. 4 of Hill (1972). Values of oxygen consumption were converted to energy expenditure using 20.08 J/ml O_2 consumed (Schmidt-Nielsen 1997). Metabolic trials were performed at a T_a of 34–35 °C, a temperature previously determined to be within the thermal neutral zone for Rüppell's foxes (Williams et al. 2002). Body mass was determined using a 5-kg Pesola scale (± 100 g).

To calculate absolute humidity (ρ) of downstream air from measurements of dewpoint, we used an equation derived from the ideal gas law (List 1951): g H_2O/ m^3 air $= (216.7 \times e_s)/T_{dph} + 273.15$ K, where e_s is saturation vapor pressure of water and T_{dph} is the temperature of the dewpoint hygrometer as indicated by a 38-gauge thermocouple placed close to the mirror. Saturation vapor pressure was calculated from an empirically derived equation (List 1951): $e_s\ (dp) = (1.0007 + 0.00000346 \times P_{atm})\ 6.1121\ \exp(17.502 \times dp/240.97 + dp)$, where dp is the dewpoint (°C) and P_{atm} is atmospheric pressure in millibars. Because absolute humidity as given by this equation is at atmospheric temperature and pressure, we corrected values to STP by multiplying them by a factor $(P_{std} \times T_1)/(P_{atm} \times T_o)$, where P_{std} is standard pressure (1013 mbar), P_{atm} is atmospheric pressure as measured by an analog barometer (Vaisala PTB 101; repeatability ±0.05 mbar), T_o is standard temperature (273.15 °K) and T_1 is the temperature of the dewpoint hygrometer (°K; Tieleman and Williams et al. 2002). TEWL was evaluated as $\text{TEWL} = [(\dot{V}_E \rho_{out} - \dot{V}_I \rho_{in})] \times 1.44 \times 10^{-3}$ (Tieleman et al. 2002). Airflow after the chamber, $\dot{V}_E$, was calculated as $\dot{V}_E$ (ml/min) $= \dot{V}_I + \dot{V}_{H2O} + \dot{V}_{CO2} - \dot{V}_{O2}$. In this equation, $\dot{V}_I$ is the incoming air flow as given by the mass flow controller (ml/min), $\dot{V}_{O2}$ the volume of oxygen consumed (ml/min), $\dot{V}_{CO2}$ the volume of CO_2 produced, evaluated as $\dot{V}_{CO2} = RQ \times \dot{V}_{O2}$, and $\dot{V}_{H2O}$ is the volume of water vapor produced (ml/min). This latter value can be calculated from the water added to the air stream by the animal: $V\ (ml/m^3) = [(g\ H_2O/m^3 \times (18.01\ g/mole) \times (83144.7\ ml \times mbar/mole \times K) \times 273.15\ °K]/1{,}013$ mbar. $\dot{V}_{H2O} = (V/10^6) \times V_I$. We assumed an RQ of 0.71.

Body temperature was taken immediately after each trial with an ALP K2 electronic rectal thermometer (model FT-70 M) calibrated against a thermometer traceable to National Institute of Standards and Technology.

Williams et al. (2002) reported that 35 °C was within the thermoneutral zone (TNZ) of Rüppell's fox, but the TNZ of Blanford's foxes may differ. To estimate the TNZ of Blanford's fox, we quantified $\dot{V}O_2$ at T_as of 5–35 °C in 5-°C increments for two individuals (mean body mass = 1,267.6 g). Following Kendeigh et al. (1977), we determined that the lower critical temperature was around 20 °C. A repeated measures ANCOVA with $\dot{V}O_2$ as the dependent variable, T_a as a fixed effect, and body mass as a covariate for T_as between 20 °C and 35 °C confirmed no differences in metabolic rate for these temperatures ($F = 0.1$, $P > 0.9$). At 25 °C, BMR was 290.4 kJ/day, whereas at 35 °C, it was 299.1 kJ/day. However, for TEWL, between 20 °C and 35 °C, TEWL significantly increased ($F = 10.6$, $P < 0.03$). At 20, 25, 30, and 35 °C, TEWL was 22.3, 30.0, 32.9, and 47.5 g H_2O/day, respectively. Despite this elevation in TEWL, we did not observe any of the species of foxes that we measured panting in the chamber.

Construction of a phylogeny

Based on molecular and fossil evidence from the literature, we constructed a phylogeny of ten species of canids for which we had physiological data, including subspecies of coyotes, red-foxes, and wolves with branch lengths given in millions of years ago (MYA) (Fig. 1). Most agree that extant canids radiated during the late Miocene, around 12 MYA, the time period that we chose for the separation between the wolf-like canids (Wolf, Coyote, Cape-hunting dog, and South American species) and fox-like canids (Martin 1989; Wayne et al. 1989, 1991; Bininda-Edmonds et al. 1999). For divergence times among the wolf-like canids, we employed genetic information of Wayne et al. (1989, 1991) and fossil evidence from Kurtén and Anderson (1980). However, unlike Wayne et al. (1989), we assumed that the Cape-hunting dog separated from other wolf-like canids 3 MYA, consistent with Geffen et al. (1996). Because *Canis lepophagus*, the direct ancestor of coyotes and wolves, was common during the Pliocene, 3.5–2 MYA, we chose 2.5 MYA for the separation of wolves and coyotes, in disagreement with Savolainen et al (2002). With estimates for divergence times of subspecies of coyotes ranging from 1 MYA to 0.15 MYA (Kurtén and Anderson 1980; Lehman and Wayne 1991;Wilson et al. 2000), we elected to use an intermediate branch length of 0.42 MYA, in agreement with Vilà et al. (1999). We assumed that subspecies of wolf diverged 0.1 MYA.

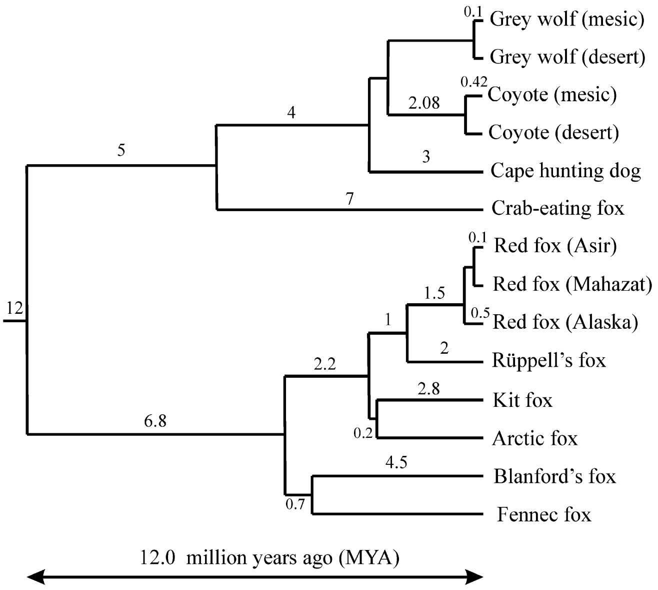

Fig. 1 A phylogeny of fox-like and wolf-like canids. *Numbers* represent branch lengths in millions of years ago (*MYA*)

Relationships within our fox-like clade were based on divergence of restriction sites of mtDNA (Geffen et al. 1992a), and the assumption that a divergence of 2% between species equaled approximately 1 MYA (Shields and Wilson 1987; Wayne et al. 1997). Under this assumption, we inferred from Geffen et al. (1992a) that Kit fox and Arctic fox diverged about 0.25 MYA, but because fossil evidence indicated an earlier divergence (Kurtén and Anderson 1980), we used 2.8 MYA (Wayne et al. 1989). The Red fox evolved in Eurasia during the Pleistocene (Frati et al. 1998); we assumed that the subspecies for which we had physiological data separated 0.5 MYA.

Calculations of phylogenetic independent contrasts were performed using PDTREE in the Phenotypic Diversity Analysis Program (PDAP) (Garland et al. 1999; Garland and Ives 2000) with branch lengths as in Fig. 1. Standardization of independent contrasts was verified by plotting absolute values of standardized independent contrast versus their standard deviation (Garland et al. 1992). Sets of independent contrasts with values for log body mass "positivized" were regressed forcing the line through the origin. Intercepts were determined following Garland et al. (1999).

In our calculations of phylogenetic Independent Contrasts (PIC), we have used two phylogenies, one with subspecies included, the other with values for subspecies averaged; the former protocol was recommended by Garland et al. (1999).

Life history correlations

To explore the association of physiology, body mass, and life-history parameters, we collected information from the literature on female body mass, litter size, neonate weight, and litter mass for the canids for which we had data on BMR and TEWL (Table 4). Given that litter size can vary for the same individual between years, and among individuals during the same year, we have used average values where possible. In our correlation analysis of BMR and life-history variables, we estimated BMR for a female of a given body mass based on mass-specific values calculated from data in Table 2.

Statistical tests

Means are presented ±1 SD. We used ANOVA to test for differences among means and a post-hoc Tukey test to search for differences between groups with $P = 0.05$ the criteria for rejection of the null hypothesis (Zar 1996). Designed to measure the degree of non-randomness in a sequence of continuous variables, the test for serial independence evaluates the assumption of phylogenetic independence in comparative data (Von Neumann et al. 1941; Abouheif 1999). The test for serial independence is a parametric test that does not depend on a model of evolutionary change, or information on branch lengths, but does assume that the phylogenetic topology reflecting the evolutionary relationships among the organisms of interest is known. We used the test for serial independence to test for phylogenetic autocorrelation among physiological trait values among canids. We compared the observed mean C statistic, generated by rotating nodes within the topology, to the estimated null hypothesis sampling distribution of randomized mean C statistics to determine the number of times that the observed mean C statistic fell within the null distribution out of 1,000 trials (see Abouheif 1999).

Results

BMR and TEWL

For Blanford's foxes, Red foxes (Mahazat), and Red foxes (Asir), body mass and BMR is presented in Table 1. In an analysis of covariance with BMR as the dependent variable, group as a factor, and body mass as a covariate, we found no statistical differences in BMR among species ($F = 1.4$, $P > 0.2$). A positive correlation existed between BMR and body mass among the foxes of the Arabian Peninsula, Blanford's fox, two subspecies of Red fox, and Rüppell's fox (Williams et al. 2002) ($F = 58.3$, $r^2 = 0.85$, $P < 0.001$). Thus, larger foxes expend more energy in basal conditions, as one might expect, but levels of metabolism were not different between species or subspecies from different environments after accounting for body mass.

Among Blanford's foxes, Red foxes (Asir), and Red foxes (Mahazat), TEWL at 35 °C differed significantly (Table 1; $F = 21.3$, $P < 0.0001$). A post-hoc Tukey test showed that Red fox from the Asir Mountains had a significantly higher TEWL than the other two groups ($P < 0.0001$). An analysis of covariance indicated that, after accounting for differences in body mass, the Red fox (Mahazat) had a lower TEWL than did the other two groups ($F = 13.6$, $P < 0.003$). We found a positive association between TEWL, measured at 35 °C, and body mass among groups of foxes ($r^2 = 0.66$, $F = 31.5$, $P < 0.001$).

Allometric equations—conventional least squares regression

To generate allometric equations, we combined data for foxes from this study with measurements of BMR and TEWL of other canids from the literature (Table 2). Because our measurements were made during the summer, we have selected values from the literature measured during the same season, except for the grey wolf (mesic) and cape-hunting dog where season was not specified. We included subspecies of coyote, wolf and red fox because each lived in a different geographic location with minimal gene flow between populations, some had different BMR despite similar body masses (wolf, coyote), and some had markedly different body masses (subspecies of red fox). Equations using conventional least squares regression (CLSR) and their associated statistics, for all species and subspecies included, for canids with values for subspecies averaged, and for foxes only, are presented in Table 3. Slopes of equations were similar and <1 for both analyses

Table 1 Basal metabolic rate and total evaporative water loss (*TEWL*) of foxes from Saudi Arabia. Measurements made at 34–35 °C. (*BMR* basal metabolic rate, T_b body temperature)

Species	Sex	Body Mass (g)	T_b	BMR (kJ/day)	TEWL (g/day)
Blanford's Fox	Male	1,320	38.4	275.3	48.2
Blanford's Fox	Male	1,355	38.4	269.0	53.5
Blanford's Fox	Male	1,262	38.4	344.4	37.7
Blanford's Fox	Female	1,203	38.9	329.2	41.6
Mean	-	1,285	38.5	304.5	45.2
(SD)	-	(52)	(0.2)	(32.3)	(5.6)
Red fox (Asir Mts.)	Male	-	-	650.1	101.2
Red fox (Asir Mts)	Male	3,645	39.1	964.5	172.8
Red fox (Asir Mts.)	Female	2,336	38.8	563.6	90.4
Red fox (Asir Mts.)	Female	3,200	39.0	718.3	144.0
Mean	-	3,060	38.9	724.1	127.3
(SD)	-	(482)	(0.1)	(120.2)	(31.5)
Red fox (Mahazat)	Male	2,159	39.0	437.8	49.2
Red fox (Mahazat)	Male	2,050	38.1	383.8	46.7
Red fox (Mahazat)	Male	2,417	38.4	454.0	57.0
Red fox (Mahazat)	Female	1,670	38.8	442.9	41.0
Red fox (Mahazat)	Female	1,541	38.8	371.2	46.0
Mean	-	1,967	38.7	418.0	48.0
(SD)	-	(289)	(0.3)	(32.4)	(4.1)

Table 2 Basal metabolic rate and TEWL of canids. Measurements on foxes were made during summer

Species	Mean Body Mass (g)	BMR (kJ/day)	TEWL (g/day)	Source
Fennec Fox (*Fennecus zerda*)	1,215	281	59.8[a]	Maloiy et al. 1982
Blanford's Fox (*Vulpes cana*)	1,285	304.5	45.3[a]	This study
Rüppell's Fox (*Vulpes rueppelli*)	1,545	385.4	50.4[a]	Williams et al. 2002
Kit Fox (*Vulpes macrotis*)	1,769	519.7	42.2[a]	Golightly and Ohmart 1983
Red fox (Mahazat) (*Vulpes vulpes arabica*)	1,967	418.0	48.0[a]	This study
Red fox (Asir Mts.)	3,060	724.0	127.3[a]	This study
Arctic Fox (*Alopex lagopus*)	3,600	892.7	?	Fuglei and Oritsland. 1999
Red fox (Alaska) (*Vulpes vulpes alascensis*)	4,440	1,176.8	?	Irving et al. 1955
Crab-eating Fox (*Cerdocyon thous*)	5,444	721.5[b]	?	Hennemann et al. 1983
Cape-hunting dog (*Lycaon pictus*)	8,750	2,108[d]	?	Taylor et al. 1971
Coyote (desert) (*Canis latrans mearnsi*)	10,000	1,296	?	Golightly and Ohmart 1983
Coyote (mesic) (*Canis latrans incolatus*)	10,300	2,165.5	?	Shield 1972
Grey Wolf (mesic) (*Canis lupus*)	18,950	3,029	?	McNab in: Hayssen and Lacy 1985
Grey Wolf (desert) (*Canis lupus pallipes*)	20,000	2,747.5	169.9[c]	Afik and Pinshow 1993

[a] Measurement made at 35 °C

[b] Measurements made on captive-born animals, $n = 2$, during February–May

[c] Values for summer at 25 °C

[d] Value of 3.0 Kcal/g·h read from graph for an 8.75-kg wild dog at 35 °C, reduced by 20% for the heat increment of feeding, converted to kJ/day using 4.184 J/cal

Table 3 Comparisons among regressions from conventional least squares (*CLSR*) and phylogenetic independent contrasts (*PIC*) methods for canids and foxes

		Regressions from CLSR						Regressions from PIC						
Condition[a]	*n*	a[b]	b[b]	r^2	*F*	*P*	Pred[c]	a[b]	b[b]	r^2	*F*	*P*	Pred[c]	% Difference[d]
A	14	−0.006	0.813	0.94	177.1	$P < 0.000$	369.93	−1.108	1.113	0.82	56.4	$P < 0.001$	260.6	29.55
B	10	−0.023	0.818	0.91	84.1	$P < 0.000$	368.93	−0.176	0.854	0.88	59.6	$P < 0.001$	337.23	8.59
C	8	−0.755	1.044	0.97	174.1	$P < 0.000$	355.23	−0.857	1.077	0.97	168.8	$P < 0.000$	357.26	−0.57
TEWL	6	0.643	0.329	0.83	19.0	$P < 0.012$	48.38	0.695	0.330	0.73	11.1	$P < 0.029$	54.93	−13.54

[a] *Condition A* = all species and subspecies; *condition B* = all values for subspecies averaged; *condition C* = values for foxes

[b] "*a*" is intercept and "b" is slope of the allometric equations: log BMR (kJ/day) = a + b × log body mass (g) and log TEWL (g/day) = a + b × log body mass (g)

[c] *Pred* = prediction of BMR (kJ/day) or TEWL (g/day) for the modal body mass of canids (1,466.2 g, $n = 10$)

[d] % Difference = [(prediction from regression from CLSR−prediction from regression from PIC) × 100]/prediction from regression from CLSR

including all carnivores, or when we used a single value for each species, but when we analyzed data for foxes only, the slope was near unity. A plot of BMR vs. body mass revealed that desert and mesic foxes fell near the line predicted for carnivores (McNab 1989), but that desert foxes tended to be smaller in body size (Fig. 2A), a statistically significant result ($t = 6.1$, $P < 0.001$).

Phylogenetic signal

We tested whether BMR, TEWL, and body mass are correlated with phylogeny among canids by using the test for serial independence (Von Neumann et al. 1941; Abouheif 1999). We found that body mass ($P < 0.001$) and BMR ($P < 0.01$) were significantly correlated with phylogeny when each species was represented by a single average value in the phylogeny, but that TEWL was not ($P > 0.2$). We also ran the test for serial independence using the topology with subspecies included as in Fig. 1, again with the result that mass ($P < 0.003$) and BMR ($P < 0.009$) were correlated with phylogeny, but that TEWL ($P > 0.18$) was not. We reran these same analyses after calculating independent contrasts (Felsenstein 1985; Garland et al. 1992); in all cases our test for serial independence using contrasts yielded insignificant results indicating that this method adequately standardized traits (Abouheif 1999). Similar tests restricted to six species of foxes showed that body mass, BMR, and TEWL were not phylogenetically autocorrelated in this clade ($P > 0.2$ all cases).

Considering that we were interested in evaluating metabolic rates and evaporative water loss apart from body mass, we also normalized BMR and TEWL, dividing by $\mathrm{Mass}^{0.852}$ and $\mathrm{Mass}^{0.826}$, respectively, and reran our tests for phylogenetic autocorrelation. Here the exponent 0.852 comes from our equation log BMR = −0.17 + 0.852 log mass, generated using phylogenetic independent contrasts, and the exponent 0.826 from an equation relating TEWL to body size for mammals ranging in size from 15.8 g to 3,630 kg ($n = 49$; Chew 1965). We found that neither mass-adjusted BMR nor TEWL was correlated with phylogeny, again when each species was represented by a single average value ($P > 0.5$ both cases), or when we used a topology with subspecies included ($P > 0.4$ in both cases). If traits are

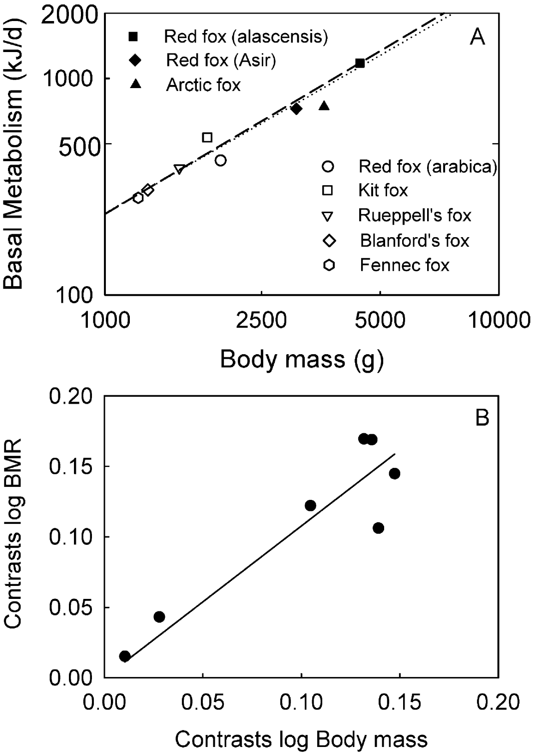

Fig. 2 **A** Plot of basal metabolic rates in relation to body mass of foxes from deserts (*unfilled symbols*) and mesic regions (*filled symbols*). The *dotted line* is from the allometric equation of McNab (1989) for basal metabolism of carnivores. The *dashed line* is the allometric curve generated for foxes using phylogenetic independent contrasts. **B** Plot of contrasts of log basal metabolic rate in relation to contrasts of log body mass with values for log body mass "positivized"

not significantly correlated with phylogeny, then traditional statistical analyses can be applied (Ackerly and Donoghue 1998).

Allometric equations—regressions using PIC

Using PIC, we calculated regressions for BMR for all species and subspecies of canids, for species with values averaged for subspecies, and for foxes only (Table 3). For TEWL, we calculated a regression based on PIC for species means only, because of a lack of data. Predictions of regressions for BMR using CLSR and PIC showed differences of as much as 30% when subspecies were included but only about 9% when average values were used (Table 3). A plot of contrasts for log BMR and log body mass with values positivized showed a linear trend with a slope of 1.1 (Fig. 2B).

Desert vs. mesic comparisons

In an analysis of covariance for desert and mesic canids, $n=7$ and $n=6$, respectively, with group as a fixed factor, log BMR as the dependent variable, and log body mass as a covariate, the interaction term was insignificant indicating no difference between slopes for desert and mesic canids ($F=1.1$, $P>0.18$). Assuming a common slope, differences between groups were insignificant ($F=1.1$, $P=0.3$). We performed the same analyses restricting the data to desert and mesic foxes with similar results; the interaction term was insignificant in the model ($F=0.1$, $P>0.9$), and with a common slope, group was insignificant ($F=2.0$, $P>0.2$).

To test for differences in BMR between desert and mesic canids, we used the topology of Fig. 1 and calculated mass-adjusted BMR by dividing by mass$^{0.949}$, where 0.949 is the exponent of PIC equation for all species and subspecies included. Next we assigned as trait 2 a value of 0 for desert species and 1 for mesic species. Our analysis indicated that contrasts were adequately standardized after using Grafen's rho (Grafen 1989) to adjust branch lengths. For all canids, we found no correlation with mass-adjusted BMR and environment ($n=14$, $F=3.4$, $r^2=0.22$, $P>0.5$). When we restricted the analysis to foxes only, we found similar results ($n=8$, $\mathrm{F}=0.07$, $r^2=0.1$, $P>0.9$).

We also tested whether desert foxes have a reduced BMR by comparing values for desert foxes with other representatives from the Carnivora. For carnivores, mostly from mesic habitats, ranging in size from 77 g to 204 kg, an equation that describes the relationship between BMR and body mass is: BMR (kJ/d) = 1.952 Mass (g)$^{0.712}$ (McNab 1989). For Red fox (Mahazat), Rüppell's fox, Fennec fox, and Kit fox, BMR was −3.4%, 5.9%, −9.1%, and 23.5%, of predictions from McNab's equation, respectively (Fig. 2A). Taken together, these comparisons do not support the hypothesis that foxes in deserts have a reduced BMR.

For 49 species of mammals experiencing temperatures between 18 °C and 20 °C, TEWL was related to body mass as TEWL (g/h) = 2.58 mass (kg)$^{0.826}$ (Chew 1965). Comparing desert foxes to this equation showed that all species had lower TEWL than predicted, −17.7% for Fennec fox, −57.4% for Kit fox, −55.7 for Red fox (Mahazat), and −43.2% for Rüppell's fox (Fig. 3). Thus we find evidence consistent with the idea that TEWL among desert foxes is lower than in mesic species. A desert fox with modal body size of 1,466.2 g would lose 48.4 g H_2O/day, whereas Chew's equation predicts a TEWL of 84.9 g H_2O/day, a reduction of 57%.

Life history correlations

Although foxes in deserts do not appear to have a reduced BMR, they are smaller in body mass, an alternative mechanism to lower energy needs. To explore the possible effects of reduced body size on life history within the fox-like canids, we collated information on litter size, neonate mass, and litter weight for canids for which we had physiological data (Table 4), and plotted them against body mass (Fig. 4). Using

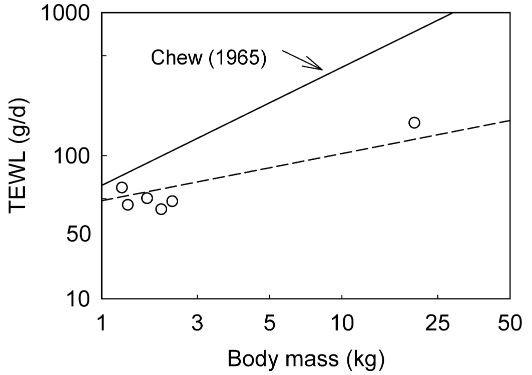

Fig. 3 Plot of total evaporative water loss in relation to body mass. The *dashed line* is the regression generated using phylogenetic independent contrasts. The *solid line* represents the regression generated by Chew (1965) for total evaporative water loss in mammals

CLSR, the relationship between body mass and these parameters was: litter size = 3.29 + 0.000128 body mass (g) ($n = 14$, $r^{2=}0.44$, $F = 8.470$, $P < 0.03$), log neonate mass = −0.991 + 0.813 log body mass (g) ($n = 9$, $r^2 = 0.96$, $F = 188.8$, $P < 0.0001$), and litter weight = 159.4 + 0.086 body mass (g) ($n = 9$, $r^2 = 0.76$, $F = 21.8$, $P < 0.002$). A logarithmic regression model of neonate mass against female body mass was a significantly better fit than a linear model ($F_{\text{ratio}=}13.6$, $P < 0.001$; Zar 1996), perhaps indicating a constraint on neonate size relative to the pelvic girdle of female foxes. Neonate mass was positively correlated with litter size ($n = 9$, $r^2 = 0.51$, $F = 7.2$, $P < 0.04$). When we compared the residuals of litter size on body mass between desert and mesic species, we found that desert canids had significantly lower residuals indicating that desert foxes tend to have smaller litters (Fig. 4C; $n = 13$, $t = 2.2$, $P < 0.05$).

We also analyzed relationships between female body mass and life-history variables using phylogenetic independent contrasts: litter size = 3.59 + 0.00013 body mass (g) ($n = 14$, $r^2 = 0.32$, $F = 5.2$, $P < 0.04$); log neonate mass (g) = −0.658 + log body mass (g) ($n = 9$, $r^{2=}0.83$, $F = 33.6$, $P < 0.001$); litter mass (g) = 445.7 + 0.055 body mass (g) ($n = 9$, $r^2 = 0.40$, $F = 4.7$, $P = 0.07$).

Using CLSR, basal metabolism was correlated with litter size and neonate mass; litter size = 3.13 + 0.000827 (BMR) ($n = 9$, $r^2 = 0.58$, $F = 14.9$, $P < 0.003$); neonate mass = 41.3 + 0.059 BMR ($n = 9$, $r^{2=}0.92$, $F = 76.0$, $P < 0.0001$). We found similar equations using PIC.

Discussion

Depressions in metabolic rate have been documented for desert representatives among species of pigeons, larks, and rodents (McNab and Morrison 1963; Dawson and Bennett 1973; MacMillen 1983; Lovegrove 2003; Tieleman et al. 2002). Some workers have argued that foxes living in deserts have a reduced BMR (Noll-Banholzer 1979). Williams et al. (2002) reported that Rüppell's foxes in Arabia have metabolic rates similar to mesic relatives in contradistinction to what one might expect, but that they had reduced TEWL. In this study we extend this finding to five species of desert foxes; we find no evidence for the hypothesis that desert foxes have reduced BMR relative to more mesic species of the same body mass. But foxes in deserts have a smaller body size than mesic foxes, a characteristic that would also lower their energy requirements. Further, in addition to small size, desert foxes had a lower TEWL than that of mesic relatives after taking into account body mass.

The "resource limitation hypothesis" states that because smaller animals require less energy, they have a selective advantage over larger phenotypes in environments of low resource abundance (Roth 1990; Williams et al. 2002). Natural selection could reduce energy needs by reducing metabolic rate per unit body mass (Tieleman et al. 2002) or by reducing body size (McNab 1990). For foxes in deserts, our data are consistent with the idea that selection has operated to reduce body size and attendant energy needs rather than mass-specific metabolism. Intraspecific comparisons further support

Table 4 Life-history variables of canids

Species	Female mass (g)	Litter size	Neonate mass (g)	Litter mass (g)	Source
Fennec Fox	1,300	3.5	28.0	98.0	Geffen et al. 1996[a]
Blanford's Fox	1,100	2.0	29.5	59.0	Geffen et al. 1996
Rueppel's Fox	1,533	3.2	-	-	Olferman 1996
Red fox (Mahazat)	2,409	3.2	-	-	Olferman 1996
Kit Fox	1,900	2.0	39.9	179.6	White and Ralls 1993; Geffen et al. 1996
Coyote (desert)	10,000	4.3	-	-	Windberg et al. 1997
Grey wolf (desert)	16,447	4.0	-	-	Mendelssohn and Yom-Tov 1999
Arctic Fox	2,900	6.3	75.0	472.5	Geffen et al. 1996
Red fox (Alaska)	4,000	6.0	104.8	413.9	Storm and Ables 1966
Crab-eating fox	6,000	3.5	140.0	490.0	Geffen et al. 1996
Cape-hunting dog	25,000	10.1	365.0	3,686.5	Geffen et al. 1996
Coyote (mesic)	11,600	5.3	274.0	1,452.2	Geffen et al. 1996
Grey wolf (mesic)	37,400	6.0	400.0	2,400.0	Geffen et al. 1996

[a] We selected litter size of two for Kit fox during year with normal rain fall in San Joaquin Valley, Calif. Values for Cape-hunting dog from zoo-raised animals

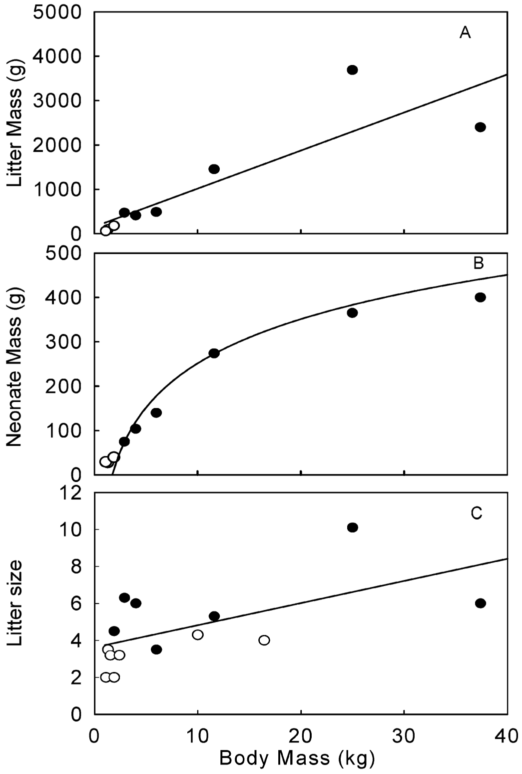

Fig. 4 A Plot of litter mass of canids in relation to body mass. *Unfilled circles* are foxes from deserts, *filled circles* are canids from more mesic regions. **B** Plot of neonate mass in relation to body mass of canids. *Symbols* as in **A**. **C** Plot of litter size in relation to body mass in canids. *Symbols* as in **A**

the resource limitation hypothesis as an explanation for small body size in desert foxes; Red foxes are smaller in the desert (Mahazat) than in the mountains of Arabia (Asir). And, in the Negev desert of Israel, Blanford's foxes averaged about 960 g (Geffen et al. 1992b), but in the more mesic Asir Mountains mean body mass was 1,215 g.

To understand physiological evolution, one needs to consider acclimation, developmental plasticity, and natural selection (Tracy and Walsberg 2001). Although one could argue that limited food during development reduces body size of foxes in deserts, we do not think this a likely explanation for their reduced body size. Foxes in Saudi Arabia breed during early spring. In some years, after rains, small mammals are abundant, whereas in other years when rains do not come, they are scarce (Olferman 1996; S. Ostrowski unpublished data). We have monitored the fox population in Mahazat since 1996 and have not observed any variation in body mass associated with small mammal abundance, and consequently, we think that stunted development is an unlikely explanation for the differences in body mass. However, we cannot completely rule out that the differences that we have identified could be attributed to phenotypic plasticity or to acclimation. Interestingly, in the wolf-like clade, subspecies in desert environments have depressed metabolic rates: coyotes in deserts had a BMR 40% less than coyotes from Alaska, even though both subspecies had similar body mass, and wolves from the desert had a lower BMR (−10%) than those individuals from mesic environments.

We think that the most likely explanation for small body size of foxes in deserts is a response to limited resources in their environment rather than in response to their need to dissipate heat, an alternative hypothesis (Brown and Lee 1969). In support of this idea, comparisons of island and mainland populations of Grey foxes, *Urocyon littoralis*, and *Urocyon cinereoargenteus*, respectively, showed that island populations were 33% smaller than mainland conspecifics, a shift in body size that occurred in less than 11,000 years (Foster 1964; Trapp and Hallberg 1975; Case 1978; Wayne et al. 1991; Smith 1992). Islands on which foxes live do not experience high T_as as one might find in an inland desert, and therefore it is difficult to argue that problems of heat dissipation (see Brown and Lee 1969; Smith et al. 1995) have driven a reduction in body size, especially given the nocturnal behavior of foxes. Typically diversity of prey species is lower on islands, which may mean foxes have few alternative prey items.

A frugal water economy is of pivotal importance for desert organisms (Williams and Tieleman 2002). With a reduction in body size, TEWL will be less, but desert foxes also have remarkably reduced TEWL, even when corrected for body mass. Although the mechanism(s) by which foxes achieve a reduction in TEWL is unknown, we think that a likely candidate is reduced cutaneous water loss (see also Tieleman and Williams 2002).

Because body mass is largely determined by genotype (Dayan et al. 1989; Roth 1990; Geffen et al. 1996), and because changes in body mass presumably affect life-history parameters (Peters 1983; Schmidt-Nielsen 1984; Gittleman 1986; Oftedal and Gittleman 1989), elucidation of factors that influence body size is important in our understanding of the ecology and evolution of a species (Western and Ssemakula 1982; Smith et al. 1995). Correlations of body size and life-history traits among birds and mammals have led some to posit that body size per se may be the key variable determining life-history variation (Calder 1984; Bennett and Owens 2002; but see Kosowski and Weiner 1997). However, after correcting for phylogeny, Geffen et al. (1996) concluded that body size explained only 26% of variation in litter size within the Canidae (see also Charnov 1991). Among fox-like canids, we argue that body mass has been reduced in desert environments, and that changes in body mass within this clade occur over relatively short evolutionary periods, as evidenced by the markedly different body masses of subspecies of Red foxes and by our comparisons between island and mainland grey foxes (Wayne et al. 1991). Our analyses indicate that a reduction in body mass of female foxes diminishes their energy needs, number of young produced, and the weight of the neonate at birth, the latter two being important life-history variables. If selection reduced the body size of female foxes from 4 kg to 2 kg, then their basal metabolism would decline by 43%, litter size by 8%, and neonate size by 23%. Moreover, when we compared the residuals of litter size on body mass between desert and mesic species, we found that desert canids had significantly lower residuals indicating that desert foxes tend to have smaller litters. During years of drought, desert foxes may forego reproduction, further reducing their lifetime reproductive success (Windberg et al. 1997; White and Ralls 1993). These attributes, low litter size, small neonates, and low reproductive output, may indicate that desert foxes have increased longevity compared with mesic relatives, a hypothesis in need of testing (Williams et al. 2002; Ricklefs and Wikelski 2002).

Conclusions

Three salient features of our data are that desert foxes do not have a reduced BMR relative to their body size, that their body size is smaller than more mesic foxes, which also reduces energy needs, and that their TEWL is less than mesic species. Our results are consistent with the hypothesis that selection has operated on foxes in desert environments to bring about a reduction in body size. However, differences in body mass could be the result of nutritional deficiencies during development, or acclimation, alternative hypotheses. A diminution in body size affects life-history traits; litter size is consistently lower in desert than in mesic foxes. We think that selection promotes adult survival instead of large reproductive investment in desert foxes.

Acknowledgements We wish to express our appreciation to the National Commission for Wildlife Conservation and Development (NCWCD), Riyadh, Saudi Arabia, for support during our research efforts. Wildlife research programs at the National Wildlife Research Center (NWRC) have been made possible through the initiative of Prince Saud Al Faisal and under the guidance of Dr. Abdulaziz H. Abuzinada. We thank A. Khoja and P. Paillat for logistical support throughout the study. For critical comments on an early version of the manuscript, we thank E. Geffen and several anonymous reviewers. Funding for this project was received from the NWRC and from the National Science Foundation (JBW). Experiments were approved by the NCWCD, Riyadh, Saudi Arabia.

References

Abouheif E (1999) A method for testing the assumption of phylogenetic independence in comparative data. Evol Ecol Res 1:895–909

Ackerly DD, Donoghue MJ (1998) Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). Am Nat 152:767–791

Afik D, Pinshow B (1993) Temperature regulation and water economy in desert wolves. J Arid Environm 24:197–209

Bartholomew GA (1964) The roles of physiology and behavior in maintenance of homeostasis in the desert environment. Symp Soc Exp Biol 18:7–29

Bennett AF (1988) Structural and functional determinates of metabolic rate. Am Zool 28:699–708

Bennett PM, Owens IPF (2002) Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford

Bininda-Emonds ORP, Gittleman JL, Purvis A (1999) Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). Biol Rev 74:143–175

Brown JH, Lee AK (1969) Bergmann's rule and climatic adaptation in woodrats (*Neotoma*). Evolution 23:329–338

Calder WA (1984) Size, function and life-history. Harvard University Press, Cambridge

Case TJ (1978) A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59:1–18

Charnov EL (1991) Evolution of life-history variation among female mammals. Proc Nat Acad Sci USA 88:1134–1137

Chevalier CD (1991) Aspects of thermoregulation and energetics in the Procyonidae (Mammalia, Carnivora). PhD dissertation, University of California, Irvine

Chew RM (1965) Water metabolism in mammals. In: Mayer WV, Van Gelder RG (eds) Physiological mammalogy. Academic Press, New York, pp 43–178

Dawson WR (1984) Physiological studies of desert birds: present and future considerations. J Arid Environ 7:133–155

Dawson WR, Bartholomew GA (1968) Temperature regulation and water economy of desert birds. In: Brown GW Jr (ed) Desert biology. Academic Press, New York, pp 357–394

Dawson WR, Bennett AF (1973) Roles of metabolic level and temperature regulation in the adjustment of western plumed pigeons (*Lophophaps ferruginea*) to desert conditions. Comp Biochem Physiol A 44:249–266

Dayan T, Tchernov E, Yom-Tov Y, Simberloff D (1989) Ecological character displacement in Saharo-Arabian *Vulpes*: outfoxing Bergmann's rule. Oikos 55:263–272

Elgar MA, Harvey PH (1987) Basal metabolic rates in mammals: allometry, phylogeny and ecology. Funct Ecol 1:25–36

Evenari M (1985) The desert environment. In: Evenari M, Noy-Meir I, Goodall DW (eds) Hot deserts and shrublands. Elsevier, Amsterdam, pp 1–22

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Fisher M, Membery DA (1998) Climate. In: Ghanzafar SA, Fisher M (eds) Vegetation of the Arabian Peninsula. Kluver Academic Press, London, pp 5–38

Foster JB (1964) Evolution of mammals on islands. Nature 202:234–235

Frati F, Hartl GB, Lovari S, Delibes M, Markov G (1998) Quaternary radiation and genetic structure of the red fox *Vulpes vulpes* in the Mediterranian Basin, as revealed by allozymes and mitochondrial DNA. J Zool 245:43–51

Fuglei E, Oritsland NA (1999) Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (*Alopex lagopus*) at Svalbard. J Comp Physiol B 169:361–369

Garland T Jr, Ives AR (2000) Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. Am Nat 155:346–364

Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst Biol 41:18–32

Garland T Jr, Midford PE, Ives AR (1999) An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. Am Zool 39:374–388

Geffen E, Mercure DW, MacDonald DW, Wayne RK (1992a) Phylogenetic relationships of the fox-like canids: mitochondrial DNA restriction fragment, site and cytochrome b sequence analysis. J Zool 228:27–39

Geffen EAA, Degen M, Kam R, Hefner R, Nagy KA (1992b) Daily energy expenditure and water flux of free-living Blanford's foxes (*Vulpes cana*), a small desert carnivore. J Anim Ecol 61:611–617

Geffen E, Gompper ME, Gittleman JL, Luh H, MacDonald DW, Wayne RK (1996) Size, life-history traits, and social organization in the Canidae: a reevaluation. Am Nat 147:140–160

Gittleman JL (1986) Carnivore life-history patterns: allometric, phylogenetic, and ecological associations. Am Nat 127:744–771

Golightly RT Jr, Ohmart RD (1983) Metabolism and body temperature of two desert canids: coyotes and kit foxes. J Mammal 64:624–635

Grafen A (1989) The phylogenetic regression. Trans R Soc Lond Biol 326:119–157

Harvey PH, Elgar MA, Rees JA (1991) Mammalian metabolism and life histories. Am Nat 137:556–566

Hayssen V, Lacy RC (1985) Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comp Biochem Physiol 81:741–754

Hennemann WWI, Thompson SD, Konecny M (1983) Metabolism of crab-eating foxes *Cerdocyon thous*: ecological influences on the energetics of Canids. Physiol Zool 56:319–324

Hill RW (1972) Determination of oxygen consumption by use of the paramagnetic analyser. J Appl Physiol 33:261–263

Irving L, Krog H, Monson M (1955) The metabolism of some Alaskan animals in winter and summer. Physiol Zool 28:173–185

Kendeigh SC, Dolnik VR, Gavrilov VM (1977) Avian energetics. In: Pinowski J, Kendeigh SC (eds) Granivorous birds in ecosystems. Cambridge University Press, Cambridge, pp 127–204

King JR (1974) Seasonal allocation of time and energy resources in birds. In: Paytner RA Jr (ed) Avian energetics. Nuttall Ornithological Club, Cambridge, pp 4–85

Kozowski J, Weiner J (1997) Interspecific allometries are the by-products of body size optimization. Am Nat 149:352–380

Kurtén B, Anderson E (1980) Pleistocene mammals of North America. Columbia University Press, New York

Lehman N, Wayne RK (1991) Analysis of coyote mitochondrial DNA genotype frequencies: estimation of the effective number of alleles. Genetics 128:405–416

Levy A (1964) The accuracy of the bubble meter for gas flow measurements. J Sci Instruments 41:449–453

List RJ (1951) Smithsonian meteorological tables. Smithson Misc Collns 114:1–385

Louw GN, Seely MK (1982) Ecology of desert organisms. Longman, London

Lovegrove BG (2000) The zoogeography of mammalian basal metabolic rate. Am Nat 156:201–219

Lovegrove BG (2003) The influence of climate on the basal metabolic rate of small mammals: a slow–fast metabolic continuum. J Comp Physiol B 173:87–112

MacMillen RE (1983) Adaptive physiology of heteromyid rodents. Great Basin Nat Mem 7:65–76

Maloiy GMO, Kamau JMZ, Shkolnik A, Meir M, Arieli R (1982) Thermoregulation and metabolism in a small desert carnivore: the fennec fox (*Fennecus zerda*, Mammalia). J Zool 198:279–291

Mandaville JP (1990) Flora of eastern Saudi Arabia. Kegan Paul International, London

Martin LD (1989) Fossil history of the terrestrial Carnivora. In: Gittleman JL (ed) Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, pp 536–568

McNab BK (1986) The influence of food habits on the energetics of eutherian mammals. Ecol Monogr 56:1–19

McNab BK (1989) Basal rate of metabolism, body size and food habits in the order Carnivora. In: Gittleman JL (ed) Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, pp 335–354

McNab BK (1990) The physiological significance of body size. In: Damuth J, MacFadden BJ (eds) Body size in mammalian paleobiology. Estimation and biological implications. Cambridge University Press, Cambridge, pp 11–23

McNab BK, Morrison P (1963) Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecol Monogr 33:63–82

Meigs P (1953) Reviews of research on arid zone hydrology. UNESCO

Mendelssohn H, Yom-Tov Y (1999) A report of birds and mammals which have increased their distribution and abundance in Israel due to human activity. Isr J Zool 45:35–47

Noll-Banholzer UG (1979) Body temperature, oxygen consumption, evaporative water loss and heart rate in the fennec. Comp Biochem Physiol A 62:585–592

Oftedal OT, Gittleman JL (1989) Patterns of energy output during reproduction in Carnivores. In: Gittleman JL (ed) Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, pp 355–378

Olferman EW (1996) Population ecology of the Rüppell's fox (*Vulpes rueppelli*, Schinz 1825) and the red fox (*Vulpes vulpes*, Linnaeus 1758) in a semi-desert environment of Saudi Arabia. PhD dissertation, University of Bielefeld, Germany

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Porter WP (1969) Thermal radiation in metabolic chambers. Science 166:115–117

Ricklefs RE, Wikelski M (2002) The physiology/life-history nexus. Trends Ecol Evol 17:462–468

Roth VL (1990) Insular dwarf elephants: a case study in body mass estimation and ecological inference. In: Damuth J, MacFadden BJ (eds) Body size in mammalian paleobiology. Estimation and biological implications. Cambridge University Press, Cambridge, pp 151–179

Savolainen P, Zhang Y, Luo J, Lundeberg J, Leitner T (2002) Genetic evidence for an East Asian origin of domestic dog. Science 298:1610–1613

Schmidt-Nielsen K (1964) Desert animals: physiological problems of heat and water. Clarendon Press, Oxford

Schmidt-Nielsen K (1984) Scaling: why is animal size so important? Cambridge University Press, Cambridge

Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge

Shield J (1972) Acclimation and energy metabolism of the dingo (*Canis dingo*) and the coyote (*Canis latrans*). J Zool 168:483–501

Shields GF, Wilson AC (1987) Calibration of mitochondrial DNA evolution in geese. J Mol Evol 24:212–217

Smith FA (1992) Evolution of body size among woodrats from Baja California, Mexico. Funct Ecol 6:265–273

Smith FA, Betancourt JL, Brown JH (1995) Evolution of body size in the woodrat over the past 25,000 years of climate change. Science 270:2012–2014

Storm GL, Ables ED (1966) Notes on the newborn and full-term wild red foxes. J Mammal 47:116–118

Taylor CR, Schmidt-Nielsen K, Dmi'el R, Fedak MA (1971) Effect of hyperthermia on heat balance during running in the African hunting dog. Am J Physiol 20:823–827

Tieleman BI, Williams JB (2002) Cutaneous and respiratory water loss in larks from arid and mesic environments. Physiol Biochem Zool 75:67–75

Tieleman BI, Williams JB, Buschur ME (2002) Physiological adjustments to arid and mesic environments in larks (*Alaudidae*). Physiol Biochem Zool 75:305–313

Tracy RL, Walsberg GE (2001) Developmental and acclimatory contributions to water loss in a desert rodent: investigating the time course of adaptive change. J Comp Physiol B 171:669–679

Trapp GR, Hallberg DL (1975) Ecology of the grey fox (*Urocyon cinereoargenteus*): a review. In: Fox MW (ed) The wild canids. Van Nostrand-Reinhold, New York, pp 164–178

Vilà C, Amorim IR, Leonard JA, Posada D, Castroviejo J, Petrucci-Fonseca F, Crandall KA, Ellegren H, Wayne RK (1999) Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. Mol Ecol 8:2089–2103

Von Neumann J, Kent RH, Bellinson HR, Hart BI (1941) The mean square successive difference. Ann Math Stat 12:153–162

Walsberg GE (2000) Small mammals in hot deserts: some generalizations revisited. Bioscience 50:109–120

Wayne RK, Benveniste RE, Janczewski DN, MacDonald DW (1989) Molecular and biochemical evolution of the carnivore. In: Gittleman JL (ed) Carnivore behavior, ecology and evolution. Cornell University Press, Ithaca, pp 465–494

Wayne RK, Van Valkenburgh B, O'Brien SJ (1991) Rates of molecular evolution in carnivores and primates. Mol Biol Evol 8:297–319

Wayne RK, Geffen E, Girman DJ, Koepfli KP, Lau LM, Marshall CR (1997) Molecular systematics of the Canidae. Syst Biol 46:622–653

Western D, Ssemakula J (1982) Life-history patterns in birds and mammals and their evolutionary interpretation. Oecologia 54:281–290

White PJ, Ralls K (1993) Reproduction and spacing patterns of kit foxes relative to changing prey availability. J Wildl Manage 57:861–867

Whitford WG, Conley MI (1971) Oxygen consumption and water metabolism in a carnivorous mouse. Comp Bioch Physiol A 40:797–803

Williams JB (1999) Heat production and evaporative water loss of Dune larks from the Namib desert. Condor 101:432–438

Williams JB, Tieleman BI (2000) Flexibility in basal metabolism and evaporative water loss among Hoopoe larks exposed to different environmental temperatures. J Exp Biol 203:153–159

Williams JB, Tieleman BI (2002) Ecological and evolutionary physiology of desert birds. Integ Comp Biol 42:68–75

Williams JB, Lenain D, Ostrowski S, Tieleman BI (2002) Energy expenditure and water flux of Rüppell's foxes in Saudi Arabia. Physiol Biochem Zool 75:33–42

Wilson PJ, Grewal S, Lawford ID, Heal JNM, Granacki AG, Pennock D, Theberge JB, Theberge MT, Voigt DR, Waddell W, Chambers RE, Paquet PC, Goulet G, Cluff D, White BN (2000) DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. Can J Zool 78:2156–2166

Windberg LA, Ebert SM, Kelly BT (1997) Population characteristics of coyotes (*Canis latrans*) in the northern Chihuahuan desert of New Mexico. Am Midl Nat 138:197–207

Zar JH (1996) Biostatistical analysis. Prentice Hall, Engelwood Cliffs