

# Physiological Adjustments of Sand Gazelles (*Gazella subgutturosa*) to a Boom-or-Bust Economy: Standard Fasting Metabolic Rate, Total Evaporative Water Loss, and Changes in the Sizes of Organs during Food and Water Restriction

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## ABSTRACT

To test the hypothesis that desert ungulates adjust their physiology in response to long-term food and water restriction, we established three groups of sand gazelles (*Gazella subgutturosa*): one that was provided food and water ( $n = 6$ ; CTRL) ad lib. for 4 mo, one that received ad lib. food and water for the same period but was deprived of food and water for the last 4.5 d ( $n = 6$ ; EXPT<sub>1</sub>), and one that was exposed to 4 mo of progressive food and water restriction, an experimental regime designed to mimic conditions in a natural desert setting ( $n = 6$ ; EXPT<sub>2</sub>). At the end of the 4-mo experiment, we measured standard fasting metabolic rate (SFMR) and total evaporative water loss (TEWL) of all sand gazelles and determined lean dry mass of organs of gazelles in CTRL and EXPT<sub>2</sub>. Gazelles in CTRL had a mean SFMR of  $2,524 \pm 194$  kJ d<sup>-1</sup>, whereas gazelles in EXPT<sub>1</sub> and EXPT<sub>2</sub> had SFMRs of  $2,101 \pm 232$  and  $1,365 \pm 182$  kJ d<sup>-1</sup>, respectively, values that differed significantly when we controlled for differences in body mass. Gazelles had TEWLs of  $151.1 \pm 18.2$ ,  $138.5 \pm 17.53$ , and  $98.4 \pm 27.2$  g H<sub>2</sub>O d<sup>-1</sup> in CTRL, EXPT<sub>1</sub>, and EXPT<sub>2</sub>, respectively. For the latter group, mass-independent TEWL was 27.1% of the value for CTRL. We found that normally hydrated sand gazelles had a low mass-adjusted TEWL compared with other arid-zone

ungulates:  $13.6$  g H<sub>2</sub>O kg<sup>-0.898</sup> d<sup>-1</sup>, only 17.1% of allometric predictions, the lowest ever measured in an arid-zone ungulate. After 4 mo of progressive food and water restriction, dry lean mass of liver, heart, and muscle of gazelles in EXPT<sub>2</sub> was significantly less than that of these same organs in CTRL, even when we controlled for body mass decrease. Decreases in the dry lean mass of liver explained 70.4% of the variance of SFMR in food- and water-restricted gazelles. As oxygen demands decreased because of reduced organ sizes, gazelles lost less evaporative water, probably because of a decreased respiratory water loss.

## Introduction

The deserts of the Arabian Peninsula are among the most austere of terrestrial environments, with low, unpredictable rainfall and high ambient temperature ( $T_a$ ), often in excess of 45°C during summer. There exist few sources of drinking water, so animals must rely on food resources for both their food and water requirements. They experience long periods of drought, sometimes 6–8 mo, punctuated by brief rainfall after which plants become green and succulent for a short period. Thereafter, vegetation dries in response to heat, making nutrients and water progressively less available until the next pulse of rain (Louw and Seely 1982). Deserts are an unlikely habitat for large and medium-sized herbivores because they cannot escape the daytime heat as do small burrowing mammals and because they need large quantities of vegetation to meet their daily energy and water requirements. Yet deserts of Saudi Arabia are home to the Arabian oryx (*Oryx leucoryx*; 80–100 kg) and to three species of medium-sized wild herbivores (10–40 kg): the Nubian ibex (*Capra ibex nubiana*), the mountain gazelle (*Gazella gazella*), and the sand gazelle (*Gazella subgutturosa*; Mallon and Kingswood 2001).

Previous studies that investigated flexibility of physiological phenotype of wild ungulates to desert conditions consisted of short-term experiments that lasted several days to a few weeks; most involved acute water stress and/or exposure to high  $T_a$  (Wilson 1989; Schmidt-Nielsen 1997). In these experiments, responses of arid-zone ungulates to water deprivation were

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evaluated by measuring water intake and avenues of water loss. Total evaporative water loss (TEWL) was estimated in these studies by subtracting water loss in urine and feces from total water intake. When deprived of water, ungulates typically lost body mass in these experiments and reduced their evaporative water loss by 25%–55% (Taylor and Lyman 1967; Maloiy 1970; Taylor 1970; Maloiy and Hopcraft 1971). Studies on domestic desert ungulates have indicated that they respond to acute water deprivation or short-term food restriction by lowering their metabolic rate by 20%–40% (Schmidt-Nielsen et al. 1967; Brosh et al. 1986; Choshniak et al. 1995).

The ability to extrapolate these findings to a natural setting where both food and water supplies progressively deteriorate over months remains uncertain. Given a pattern of long periods of increasingly poor-quality food (Spalton 1999), one might predict that wild herbivores have evolved the capability to adjust their physiology depending on resource abundance. However, whether they alter their physiology in a similar way as when exposed to acute food and water restriction—and if they do, the magnitude of these changes relative to variation in environment—is poorly known.

Many herbivorous desert mammals show a reduction of resting metabolic rate when deprived of food (Merkt and Taylor 1994; Choshniak et al. 1995). The physiological mechanisms involved in this process may include (i) reducing the size of organs such as digestive tract, liver, kidney, and heart, some of which are thought to have high mass-specific rates of oxygen consumption (Martin and Fuhrman 1955; Konarzewski and Diamond 1995; Finegan et al. 2001); and (ii) reducing the rates of tissue-specific oxygen consumption mediated by functions such as protein synthesis and metabolite and ion transport across cell membranes (Ferraris and Diamond 1989; Rolfe and Brown 1997). Evidence seems to support the existence of the latter mechanism among desert rodents. Several of these species use torpor to reduce metabolic rate when food is restricted (Degen 1997; Bae et al. 2003), a process that translates to a decrease in body temperature and presumably the slowing of biochemical reactions in tissues. The golden spiny mouse (*Acomys russatus*) “switches” resting metabolic rate to a lower level within a day when food intake is reduced to half the amount required for maintenance, without using torpor. This rapid change may indicate a reduction of the rate of energy-consuming processes rather than the size of organs (Merkt and Taylor 1994).

Fewer efforts have been dedicated to understanding the plasticity of TEWL, the sum of respiratory and cutaneous water losses, to ungulates exposed to drought conditions. For species that inhabit deserts, phenotypic advantages attributable to a diminution of metabolic rate during periods of food restriction would include reduced TEWL because ventilation frequency and/or tidal volume would be decreased, resulting in reduced respiratory water loss (Willmer et al. 2000).

The rate of food consumption in desert herbivores is thought to be mediated by water in plants (Macfarlane and Howard

1972), and among mammals, herbivores typically have high rates of water turnover (Nagy and Peterson 1988). Recently, Ostrowski et al. (2006) subjected Arabian oryx, a large desert ungulate, to progressive food and water restriction over a 5-mo period that ended in their receiving less than one-half of their normal requirements. The authors showed that oryx reduced their mass-specific standard fasting metabolic rate (SFMR) and TEWL by 16% and 26%, respectively.

In this study, we examine the relationships among SFMR, TEWL, and the sizes of organs in sand gazelles exposed to long-term food and water restriction. Sand gazelles (15–20 kg) are capable of surviving prolonged drought in central Asia and the Arabian Peninsula, including the Rub’ al-Khali, one of the driest deserts in the world (Meigs 1953). We hypothesized that a progressive restriction of food and water over a long period of time would result in a reduction in organ size of gazelles, leading to a reduction in overall resting metabolism and TEWL. In order to place earlier work on ungulates in a more realistic ecological setting, we compared the effects of short-term food and water deprivation with the effects of progressive, long-term food and water restriction as encountered in free-ranging conditions. During short-term food and water deprivation, SFMR and TEWL may be reduced because of immediate adjustment of tissue metabolism. However, when food and water intake decrease during prolonged periods, such as during summer drought, organs involved in anabolism (digestive tract, liver), oxygen transport to the tissues (heart), and activity (muscles) may shrink, resulting in a lower total oxygen consumption and a decreased evaporative water loss.

## Material and Methods

### *Animals and Experimental Design*

We conducted this study at the National Wildlife Research Center, Taif, Saudi Arabia (21°17’N, 40°40’E), between April and August 2004. After selecting 18 adult male sand gazelles, we randomly assigned them either to a control group (CTRL;  $n = 6$ ) or to one of two experimental groups (EXPT<sub>1</sub> and EXPT<sub>2</sub>;  $n = 6$  each). Gazelles in the three groups had similar initial body masses ( $F_{2,17} = 1.30$ ,  $P = 0.3$ ) and similar tarsus lengths ( $F_{2,17} = 0.08$ ,  $P > 0.7$ ). During the entire experiment, gazelles were kept individually in 10-m<sup>2</sup> outdoor pens and weighed ( $\pm 0.1$  kg) every sixth day on an electronic platform scale (model 561 SG, GIM, Beauprout, France).

For 4 mo, we provided gazelles in CTRL and EXPT<sub>1</sub> with 600 g d<sup>-1</sup> of dry alfalfa (*Medicago sativa*; min. 15% crude protein) and 1.5 L d<sup>-1</sup> of water, quantities 10%–15% above their average daily requirements (S. Ostrowski, unpublished data). At the end of the 4-mo period, we deprived gazelles in EXPT<sub>1</sub> of food and water for 4.5 d, and thereafter we measured their SFMR and TEWL. For gazelles in EXPT<sub>2</sub>, we reduced food and water intake by 15% every 3 wk during 4 mo, from CTRL levels down to 220 g d<sup>-1</sup> of dry alfalfa and 0.55 L d<sup>-1</sup> of water, a

60%–70% reduction. For this latter group, we waited 3 wk after the final level of food and water was reached before taking measurements of SFMR and TEWL.

#### Measurement of SFMR and TEWL

We measured minimum SFMR and TEWL for gazelles in all groups during the day, their resting phase, at the beginning and end of the acclimation period, using standard flow-through respirometry and hygrometry methods (Gessaman 1987; Williams et al. 2001). Because of residual microbial activity in the rumen after 2 d of fasting, measurements of true basal metabolism may be difficult to achieve in ruminants (Hudson and Christopherson 1985; Blaxter 1989). Before measuring their SFMR and TEWL, we deprived gazelles in CTRL and EXPT<sub>2</sub> of food for 50 h, an appropriate fasting interval to achieve stable values of SFMR in Arabian oryx (Williams et al. 2001). Gazelles were placed in a water-jacketed metabolic chamber constructed of welded sheets of galvanized steel (inner chamber: 90 cm × 89.5 cm × 35 cm) that had a Plexiglas door with a rubber gasket, which, when bolted shut, rendered the system airtight. Before each measurement, we checked for air leaks around the lid using a solution of soap and water. During measurements,  $T_a$  within the chamber was controlled by a Neslab circulating water bath (RTE-140) at  $30^\circ \pm 0.5^\circ\text{C}$ , a temperature within the thermoneutral zone of many tropical ungulates (Parker and Robbins 1985). Gazelles were placed on a wire-mesh platform over a layer of mineral oil that trapped feces and urine, excluding both as a source of evaporative water during measurements. During experiments, air under positive pressure from a compressor coursed through two large (100 cm × 21 cm) drying columns containing anhydrous CaSO<sub>4</sub> (Drierite, W. A. Hammond, Xenia, OH), through a mass-flow controller set at 40 L min<sup>-1</sup> (model 2925V, Tylan, San Diego, CA; calibrated against a primary standard traceable to the National Institute of Standards and Technology by Flow, Scottsdale, AZ), and then into the chamber. A sample of exiting air was routed to a dew point hygrometer (model M4-DP, General Eastern, Wilmington, MA) and then to columns of silica gel, Ascarite, and silica gel again (Thomas Scientific, Swedesboro, NJ) to remove water and CO<sub>2</sub> from the air stream before entering the O<sub>2</sub> analyzer (model S3A-II, Applied Electrochemistry, Pittsburgh). Our dew point hygrometer was calibrated using a dew point generator and was found to be accurate to within <2%. Dry inlet air was assumed to be 20.95% oxygen (Blaxter 1989). Outlet air had a relative humidity that was always below 25% (Lasiewski et al. 1966). Lying gazelles remained inside the chamber for 4–5 h before we initiated our recordings. After this time, when traces of oxygen consumption were stable, we recorded O<sub>2</sub> concentration, dew point of outlet air, temperature of the dew point hygrometer, and  $T_a$  within the chamber every minute for at least 15 min with a data logger (model 21X, Campbell Scientific, Logan, UT). We calculated rates of oxygen

consumption using equation (4) of Hill (1972). We used the value 20.08 J mL O<sub>2</sub><sup>-1</sup> to convert oxygen consumption to heat production (Schmidt-Nielsen 1997).

Evaporative water loss was calculated using TEWL =  $(V_e\rho_{\text{out}} - V_i\rho_{\text{in}}) \times 1.44 \times 10^{-3}$ , where TEWL is in g d<sup>-1</sup>,  $\rho_{\text{in}}$  and  $\rho_{\text{out}}$  are the absolute humidity (g H<sub>2</sub>O m<sup>-3</sup>) of inlet air and outlet air, respectively,  $V_i$  is the flow rate (mL min<sup>-1</sup>) of air entering the chamber, and  $V_e$  is the flow rate (mL min<sup>-1</sup>) of exiting air. To incorporate a correction of saturated vapor pressure at the dew point to standard temperature and pressure, we determined absolute humidity using the equation  $\rho = [216.7e_s/(T_{\text{dp}} + 273.15)] \times [P_0(T_{\text{dp}} + 273.15)]/[P_a(T_0 + 273.15)]$ , where  $e_s$  is the saturation vapor pressure (mbar) at a given dew point,  $T_{\text{dp}}$  is the temperature (°C) of the air in the dew point hygrometer,  $P_0$  is standard pressure (1,013 mbar),  $P_a$  is barometric pressure (mbar), and  $T_0$  is standard temperature (0°C). We calculated  $V_e = V_i - V_2(1 - \text{RQ}) + \dot{V}_{\text{H}_2\text{O}}$ , following Williams and Tieleman (2001). In this equation,  $V_i$  (mL min<sup>-1</sup>) and  $\dot{V}_{\text{O}_2}$  (mL min<sup>-1</sup>), the rate of oxygen consumption, are known, the respiratory quotient (RQ) is assumed to equal 0.71 (Robbins 1993), and the rate of water loss,  $\dot{V}_{\text{H}_2\text{O}}$  (mL min<sup>-1</sup>), is calculated as  $\dot{V}_{\text{H}_2\text{O}} = \rho(V_i + \dot{V}_{\text{CO}_2} - \dot{V}_{\text{O}_2})/(1 - \rho)$ . This equation is derived from the absolute humidity  $\rho = \dot{V}_{\text{H}_2\text{O}}/(V_i + \dot{V}_{\text{CO}_2} - \dot{V}_{\text{O}_2} + \dot{V}_{\text{H}_2\text{O}})$ , the fraction of water in air flowing through the dew point hygrometer.  $\dot{V}_{\text{CO}_2}$  is the rate of CO<sub>2</sub> production (mL min<sup>-1</sup>).

#### Measurement of Skin Surface and Organ Dry Lean Mass

After respirometry measurements, gazelles in CTRL and EXPT<sub>2</sub> were anesthetized by intramuscular injection of etorphine hydrochloride, a potent opioid agent, and killed by intravenous injection of sodium pentobarbital, a procedure recommended by the American Veterinary Medicine Association (2001). We excised the brain, heart, liver, kidneys, rumen, intestine, skin, and one muscle of the pelvic limb (fibularis tertius muscle) on the left side of the body. To estimate the surface area of the skin, we traced its outline on plastic film, cut out its replica, and weighed the resulting piece of plastic. We converted weight to surface area by weighing pieces of plastic film with known area, then multiplying by the total weight. Internal organs, muscle, and skin were weighed, cut into 2-cm<sup>2</sup> pieces, dried to constant mass for 6 d at 65°C, and weighed on an electronic balance (Sauter, model RE 1614) to  $\pm 0.1$  g. Dried tissues were then ground twice in an electric grinder, placed in a plastic container, and stored at  $-70^\circ\text{C}$  for 1–2 wk pending further analysis.

To extract lipids from tissues, we filled predried extraction thimbles with  $3 \pm 0.1$  g of homogenized dry tissue, dried thimbles and contents to constant mass at 65°C, and then extracted them in a Soxhlet fat extractor (Behr Labor-Technik, Düsseldorf). Preliminary tests showed that constant lean dry mass was achieved after 6 h of extraction using petroleum ether as a nonpolar solvent at 90°C (Dobush et al. 1985). We used

an extraction time of 9 h for all samples. After extraction of lipids, we dried the thimble plus contents to constant mass to determine lean dry mass. Percentage fat removed was calculated as fat (%) =  $100 \times [(dry\ mass\ sample - lean\ dry\ mass\ sample) / dry\ mass\ sample]$ .

### Statistical Analysis

We verified normality and homoscedasticity of variables with Kolmogorov-Smirnov goodness-of-fit and Levene's tests, respectively (Zar 1996). Proportions were arcsine square-root transformed before parametric statistics (Zar 1996) were performed. We used ANCOVA to test for differences in SFMR and TEWL between groups. When comparing three groups, we ran post hoc Newman-Keuls multiple-range tests to explore for statistical differences. To compare parameters between treatments and times, we used either repeated-measures ANOVAs or two-tailed *t*-tests after sequential Bonferroni correction in the level of significance (Rice 1989; Sokal and Rohlf 1995). Statistical significance was accepted at  $P = 0.05$ . Means are reported  $\pm 1$  SD. We also consistently tested the interaction between covariates and fixed factors, although we do not always report the results of insignificant interactions.

## Results

### Body Mass

After 4 mo of acclimation, gazelles in CTRL and EXPT<sub>1</sub> weighed  $17.1 \pm 1.2$  and  $17.0 \pm 0.6$  kg, respectively, an insignificant change from their mean masses at the beginning of the experiment ( $F_{1,5} < 4.9$ ,  $P > 0.05$ ). After 4.5 d of food and water deprivation, gazelles in EXPT<sub>1</sub> weighed on average  $15.7 \pm 0.6$  kg, a loss of  $1.4 \pm 0.6$  kg, or  $8.1\% \pm 3.1\%$  of their initial body mass. Gazelles in EXPT<sub>2</sub> weighed on average  $15.2 \pm 0.9$  kg, resulting from the gradual loss of  $2.3 \pm 0.6$  kg, or  $13.1\% \pm 2.9\%$ , over the 4-mo period of progressive food and water restriction. Repeated ANOVA with treatment and time as fixed effects and body mass as the dependent variable showed a significant effect of time  $\times$  treatment ( $F_{2,15} = 33.9$ ,  $P < 0.0001$ ). At the end of the experiment, mean body masses of gazelles in EXPT<sub>1</sub>, after 4.5 d of starvation, and in EXPT<sub>2</sub>, after 4 mo of progressive food and water restriction, were not significantly different, but both were lower than those of gazelles in CTRL (Newman-Keuls,  $P < 0.05$ ).

### Standard Fasting Metabolic Rate

Before acclimation, SFMR averaged  $110.3 \pm 10.9$  L O<sub>2</sub> d<sup>-1</sup>, or  $2,215 \pm 218$  kJ d<sup>-1</sup> ( $n = 6$ ), for gazelles in CTRL;  $120.1 \pm 12.8$  L O<sub>2</sub> d<sup>-1</sup>, or  $2,411 \pm 257$  kJ d<sup>-1</sup> ( $n = 6$ ), for those in EXPT<sub>1</sub>; and  $119.7 \pm 18.1$  L O<sub>2</sub> d<sup>-1</sup>, or  $2,403 \pm 363$  kJ d<sup>-1</sup> ( $n = 6$ ), for those in EXPT<sub>2</sub>. These values did not differ significantly ( $F_{2,15} = 0.90$ ,  $P = 0.42$ ; Fig. 1). After 4 mo, SFMR

averaged  $125.7 \pm 9.6$  L O<sub>2</sub> d<sup>-1</sup>, or  $2,524 \pm 194$  kJ d<sup>-1</sup>, for the CTRL group;  $104.6 \pm 11.6$  L O<sub>2</sub> d<sup>-1</sup>, or  $2,101 \pm 232$  kJ d<sup>-1</sup>, for the EXPT<sub>1</sub> group; and  $68.0 \pm 9.0$  L O<sub>2</sub> d<sup>-1</sup>, or  $1,365 \pm 182$  kJ d<sup>-1</sup>, for the EXPT<sub>2</sub> group. An ANCOVA indicated that after treatment, SFMR differed significantly between groups ( $F_{2,14} = 25.7$ ,  $P < 0.0001$ ; Fig. 1). Because some of the reduction in SFMR for gazelles in the EXPT<sub>1</sub> and EXPT<sub>2</sub> groups might have been attributable to loss of body mass (Kleiber 1975), we calculated the difference between pre- and posttreatment body mass as the independent variable and the difference in SFMR between initial and final as the dependent variable for each individual of the three groups and tested for an interaction. Finding none ( $F_{2,12} = 0.89$ ,  $P > 0.4$ ), we reran the analysis with the interaction term removed and found no effect of the difference in body mass ( $P > 0.05$ ) but a significant effect of the treatments ( $F_{2,14} = 7.66$ ,  $P < 0.006$ ). The mass-independent decrease in SFMR was significantly larger in EXPT<sub>2</sub> than in EXPT<sub>1</sub>, and both were significantly different from that of CTRL (Newman-Keuls,  $P < 0.05$ ). Treatments alone explained 79.6% of the difference in SFMR between groups ( $F_{2,15} = 34.2$ ,  $P < 0.0001$ ). Mass-specific SFMR of gazelles in EXPT<sub>2</sub> was 39.2% lower than that of those in CTRL.

### Total Evaporative Water Loss

Initial measurements of TEWL at 30°C did not differ between groups ( $F_{2,15} = 0.64$ ,  $P = 0.54$ ) and averaged  $165.8 \pm 16.2$  g H<sub>2</sub>O d<sup>-1</sup> ( $n = 18$ ). After 4 mo, TEWL of CTRL averaged  $151.1 \pm 18.2$  g H<sub>2</sub>O d<sup>-1</sup>, whereas TEWL of EXPT<sub>1</sub> averaged  $138.5 \pm 17.5$  g H<sub>2</sub>O d<sup>-1</sup>, and TEWL of EXPT<sub>2</sub> was  $98.4 \pm 27.2$  g H<sub>2</sub>O d<sup>-1</sup>. An ANCOVA indicated that TEWL differed significantly between treatments ( $F_{2,14} = 4.72$ ,  $P < 0.03$ ; Fig. 1). We also tested whether treatment alone explained the difference in TEWL, as we had done for SFMR. After finding no significant interaction term ( $F_{2,12} = 1.21$ ,  $P = 0.33$ ), we eliminated it and found no effect of the difference in body mass ( $F_{1,14} = 0.47$ ,  $P = 0.51$ ). Mass-independent TEWL was significantly lower for gazelles in EXPT<sub>2</sub> than for those in EXPT<sub>1</sub> and CTRL, but it was not significantly different between these latter two groups (Newman-Keuls,  $P < 0.05$ ). Treatment alone explained 61.1% of the difference in TEWL between groups ( $F_{2,15} = 14.3$ ,  $P < 0.001$ ). Corrected for body mass, TEWL of gazelles in EXPT<sub>2</sub> after acclimation was 27.1% and 26.5% lower than in CTRL and EXPT<sub>1</sub>, respectively.

### Standard Fasting Metabolic Rate and Organ Masses

The organ masses of gazelles in CTRL differed from those of gazelles in EXPT<sub>2</sub> (Table 1). The sum of the wet masses of brain, heart, intestine, kidneys, liver, fibularis tertius muscle, rumen, and skin was larger for gazelles in CTRL ( $2,277 \pm 155$  g,  $n = 6$ ) than for those in EXPT<sub>2</sub> ( $2,029 \pm 46$  g,  $n = 6$ ,  $t = 3.8$ ,  $P = 0.004$ ). This difference was maintained when we

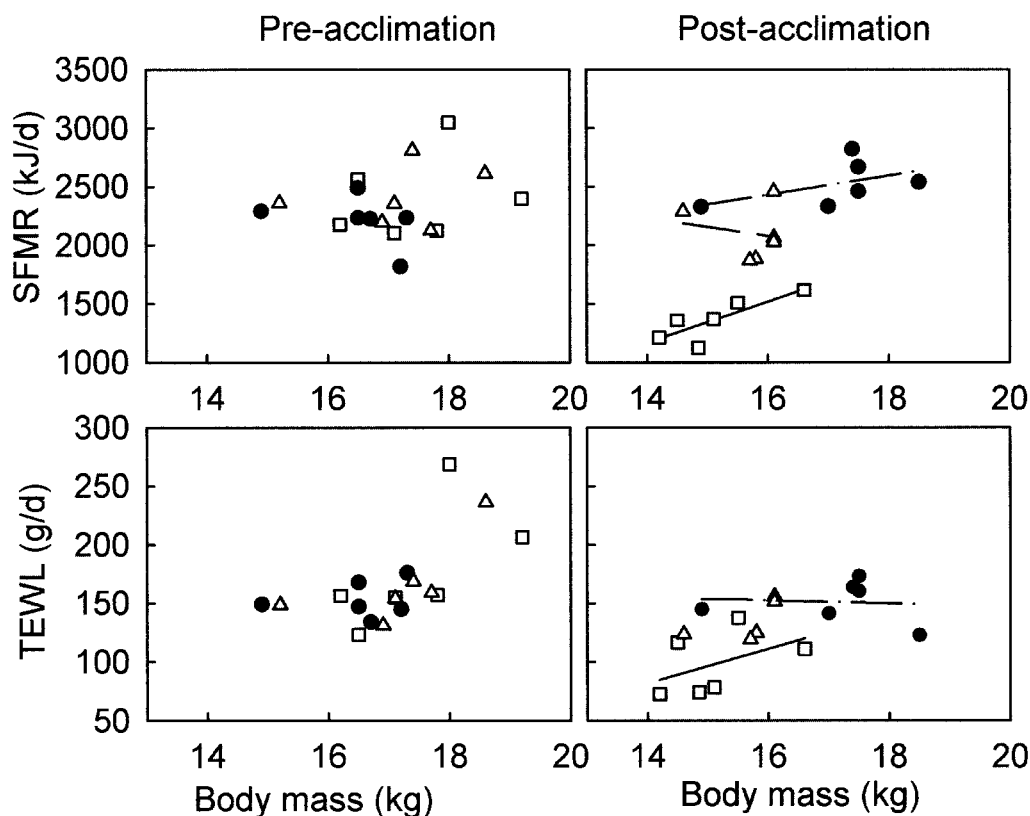


Figure 1. Standard fasting metabolic rate (SFMR) and total evaporative water loss (TEWL) as a function of body mass for *Gazella subgutturosa* assigned to (i) prolonged food and water restriction (squares), (ii) 4.5 d of fasting after being fed and watered ad lib. (triangles), or (iii) feeding and watering ad lib. (circles), before (preacclimation) and after (postacclimation) acclimation to the three different food and water regimens. Lines indicate significant differences between groups acclimated to the different regimens.

excluded skin from the comparison ( $df = 10$ ,  $t = 0.3$ ,  $P = 0.008$ ). When the size of each organ was expressed as a proportion of total body mass, the liver was significantly smaller in individuals deprived of food and water than in those fed and watered ad lib. (Table 1). We compared the dry masses of each organ between treatment and control groups and found that all of them differed except for the brain and rumen. However, after fat was extracted from these samples, the difference was no longer significant for intestine, kidneys, rumen, and skin (Table 1). Except in the brain, the proportion of lipid in organs was significantly higher for gazelles in CTRL than in EXPT<sub>2</sub> (Table 2). We also compared the lean dry masses of each organ between gazelles in CTRL and EXPT<sub>2</sub> using an ANCOVA with body mass as covariate. In this analysis, we found that the lean dry mass of the liver, heart, and muscle was significantly smaller for gazelles under long-term food and water restriction ( $F_{1,10} > 11.3$ ,  $P < 0.009$ ).

We calculated the relationship between SFMR and body mass and between the lean dry mass of each organ and body mass for the entire data set (Table 3). The association between SFMR in kilojoules per day and body mass ( $M$ ) in grams was given

by the equation  $SFMR = -3,689.92 + 0.349 \text{ mass}$  ( $r^2 = 0.61$ ,  $F_{1,11} = 17.9$ ,  $P = 0.002$ ). The lean dry masses of the brain, heart, liver, kidneys, and muscle were closely associated with body mass, but masses of the intestine, rumen, and skin were not (Table 3). To alleviate the effect of body mass in the relationship between SFMR and lean dry masses of organs, we calculated the residual SFMR of each gazelle (measured SFMR minus predicted SFMR) and the residual of each organ dry lean mass (measured organ mass minus predicted mass). We calculated the correlation of residual SFMR with residuals of each organ and found that those for the liver, heart, and muscle were significant (Table 3; Fig. 2). We therefore conclude that the reduced size of these organs contributed disproportionately to the low SFMR in gazelles that endured food and water restriction. Moreover, our data suggest that part of the reduction in organ size is accomplished by reduction in nonpolar lipid content (Table 2).

We searched for the best one-parameter model that would predict variation of residual SFMR. We designed a stepwise multiple regression with residual SFMR as dependent variable, treatment as a categorical independent effect, and rumen, in-

Table 1: Mean ( $\pm$ SD) organ masses of sand gazelles (*Gazella subgutturosa*) fed and watered ad lib. (CTRL) or restricted in food and water (EXPT<sub>2</sub>) for 4 mo

Organ	Wet Mass (% Body Mass) <sup>a</sup>			Dry Mass (g)			Dry Lean Mass (g)		
	CTRL	EXPT <sub>2</sub>	<i>P</i>	CTRL	EXPT <sub>2</sub>	<i>P</i>	CTRL	EXPT <sub>2</sub>	<i>P</i>
Brain	.40 $\pm$ .04	.39 $\pm$ .02	.46	14.65 $\pm$ 1.31	13.75 $\pm$ .71	.17	7.96 $\pm$ .65	6.97 $\pm$ .34	.009*
Heart	.99 $\pm$ .03	.88 $\pm$ .07	.008	44.03 $\pm$ 3.91	26.60 $\pm$ 3.97	<.0001*	31.79 $\pm$ .93	25.15 $\pm$ 2.99	<.001*
Intestine	1.31 $\pm$ .15	1.47 $\pm$ .34	.33	52.33 $\pm$ 6.49	36.13 $\pm$ 6.59	.0016*	35.24 $\pm$ 6.72	34.44 $\pm$ 6.42	.83
Kidneys	.35 $\pm$ .02	.37 $\pm$ .02	.14	12.9 $\pm$ 1.34	11.30 $\pm$ .33	.016*	11.55 $\pm$ 1.14	10.76 $\pm$ .32	.13
Liver	1.54 $\pm$ .11	1.12 $\pm$ .07	<.001*	77.03 $\pm$ 7.38	40.43 $\pm$ 4.10	<.0001*	70.53 $\pm$ 7.40	38.41 $\pm$ 4.10	<.0001*
Muscle <sup>b</sup>	.12 $\pm$ .01	.10 $\pm$ .01	.009	5.45 $\pm$ .32	4.00 $\pm$ .20	<.0001*	5.04 $\pm$ .30	3.87 $\pm$ .19	<.0001*
Rumen	1.67 $\pm$ .17	1.78 $\pm$ .25	.41	58.15 $\pm$ 10.47	44.03 $\pm$ 9.35	.034	47.96 $\pm$ 7.14	42.56 $\pm$ 9.13	.28
Skin	6.92 $\pm$ .28	7.25 $\pm$ .50	.15	478.90 $\pm$ 24.78	436.95 $\pm$ 18.96	.009*	439.35 $\pm$ 8.25	422.20 $\pm$ 17.46	.054

<sup>a</sup> Wet mass is expressed as percentage of total body mass and was arcsine square-root transformed before *t*-tests were performed.

<sup>b</sup> Includes only left fibularis tertius muscle.

\* Significant *P* value after sequential Bonferroni correction.

testine, and skin dry lean masses and residuals of brain, heart, kidneys, liver, and muscle masses as continuous independent effects. We found that the effect of residual liver was the most predictive one-parameter model ( $F_{1,10} = 27.2$ ,  $P < 0.001$ ), explaining 70.4% of the variability of residual SFMR.

#### Total Evaporative Water Loss and Skin

After 4 mo of progressive food and water restriction, skin surface area (SA) was  $5,271 \pm 404$  cm<sup>2</sup> for gazelles in CTRL and  $4,870 \pm 62$  cm<sup>2</sup> for those in EXPT<sub>2</sub>, results that were significantly different ( $F_{1,11} = 5.8$ ,  $P = 0.03$ ). The association between SA and body mass (*M*) in grams was given by the equation  $SA = 2,099.2 + 0.184M$  ( $r^2 = 0.55$ ,  $F_{1,11} = 14.7$ ,  $P = 0.003$ ).

Using the same procedure as for SFMR, we searched for the best one-parameter model that would predict variation in TEWL after acclimation. We designed the analysis with TEWL as dependent variable, treatment as a categorical independent effect, and body mass, skin dry lean mass, and residuals of SA as continuous independent effects. The effect of treatment was the most predictive one-parameter model ( $F_{1,10} = 15.5$ ,  $P < 0.003$ ) of TEWL variation, explaining 56.8% of the variability of TEWL.

#### Discussion

Earlier studies that investigated flexibility of physiological phenotype of ungulates to desert conditions assumed that physiological adjustments operating in free-ranging ungulates could be deduced from short-term water or food restriction (Schmidt-Nielsen et al. 1967; Wilson 1989; Grenot 1992). However, the differences we have found between physiological adjustments of gazelles fasted for 4.5 d and those observed in gazelles restricted in food and water for 4 mo prompt caution when extrapolating laboratory findings to natural situations in deserts where food and water supplies are progressively de-

pleted. Although the body mass decrease after treatment was insignificantly different between experimental groups, gazelles that had been restricted in food and water for 4 mo had a significantly larger reduction in SFMR and TEWL than those exposed to a short-term food and water deprivation.

The physiological adjustments to short-term fasting and to prolonged food and water restriction could be different. Much of the 8% body mass loss in gazelles fasted for 4.5 d may have resulted from the late consumption and excretion of digestive tract content or from water loss. The mechanism that contributes to reduction in metabolism is unclear. This rapid change probably indicates a reduction of the rate of energy-consuming processes rather than the size of organs. In domestic sheep, Webster (1980) estimated that approximately half of the heat production associated with food intake occurred in tissues other than the gastrointestinal tract; the other half included the energy costs of eating, rumination, digestive tract metabolism, and heat of fermentation. The decrease of SFMR observed in gazelles

Table 2: Mean ( $\pm$ SD) lipid content (percentage dry mass) of organs collected from sand gazelles (*Gazella subgutturosa*) fed and watered ad lib. (CTRL) or restricted in food and water (EXPT<sub>2</sub>) for 4 mo

Organ	CTRL	EXPT <sub>2</sub>	Change (%)	<i>P</i>
Brain	45.58 $\pm$ .63	49.28 $\pm$ .51	+3.7	<.0001
Heart	27.30 $\pm$ 6.84	5.10 $\pm$ 3.24	-22.2	<.0001
Intestine	32.39 $\pm$ 11.27	4.73 $\pm$ 2.27	-27.7	<.0001
Kidneys	10.30 $\pm$ 2.31	4.52 $\pm$ 1.35	-5.8	.0003
Liver	8.48 $\pm$ 1.61	4.87 $\pm$ 1.52	-3.6	.0024
Muscle <sup>a</sup>	7.31 $\pm$ .81	3.20 $\pm$ 1.13	-4.1	.0001
Rumen	17.17 $\pm$ 3.00	3.35 $\pm$ 1.41	-13.8	<.0001
Skin	8.57 $\pm$ 3.64	3.47 $\pm$ 1.32	-5.1	.0042

Note. For both groups,  $n = 6$ . All *P* values were significant after sequential Bonferroni correction.

<sup>a</sup> Includes only left fibularis tertius muscle.

Table 3: Regressions of standard fasting metabolic rate (SFMR;  $\text{kJ d}^{-1}$ ) and lean dry organ mass (g) vs. body mass (g) for 12 sand gazelles (*Gazella subgutturosa*)

Dependent Variable	Regression Equation	$r_1^2$	$P_1$	$r_2$	$P_2$
SFMR	$-3,689.92 + .349 \text{ mass}$	.61	.002	...	...
Brain	$1.71 + .00035 \text{ mass}$	.47	.008	.11	.732
Heart	$.28 + .002 \text{ mass}$	.33	.029	.74	.005
Intestine	$19.87 + .00092 \text{ mass}$	.05	.503	.11	.723
Kidneys	$4.05 + .00044 \text{ mass}$	.45	.009	.25	.424
Liver	$-96.86 + .009 \text{ mass}$	.55	.003	.85	<.001
Muscle <sup>a</sup>	$-1.12 + .00035 \text{ mass}$	.57	.002	.75	.004
Rumen	$4.47 + .003 \text{ mass}$	.11	.151	.15	.630
Skin	$369.20 + .004 \text{ mass}$	.03	.264	.28	.380

Note.  $r_1^2$  is the fraction of the variance explained by body mass,  $P_1$  is the significance level of the regression line,  $r_2$  is the coefficient of correlation between residuals of SFMR and of organ mass, and  $P_2$  is the significance level of this correlation.

<sup>a</sup> Includes only left fibularis tertius muscle.

starved for a short period could be viewed simply as a reduction of nutrient metabolism. However, white-tailed deer (*Odocoileus virginianus*; Silver et al. 1969), pronghorn antelope (*Antilocarpa americana*; Wesley et al. 1973), moose (*Alces alces*; Renecker and Hudson 1986), and domestic sheep (*Ovis aries*; Robbins 1993), all ruminant species larger than sand gazelles, seemed to achieve minimum oxygen consumption after 48 h without food, suggesting that a reduction of energy-consuming processes not related to nutrition could also be involved in the reduction of metabolism of gazelles fasted for 4.5 d. Concomitantly with a reduction of organ sizes, a mechanism of similar nature may also operate in gazelles restricted in food and water for prolonged periods.

Our measurements support the idea that sizes of organs are important determinants of SFMR in sand gazelles when restricted in food and water for a prolonged period of time. In domestic ruminants, wet and lean dry masses of liver and gastrointestinal tract appear to increase or decrease in direct proportion to dietary intake (Burrin et al. 1990; Johnson et al. 1990). Both organs have high mass-specific metabolic rates (Krebs 1950). In ruminants, oxygen consumption by the liver and gut (<6% of body mass) accounts for 45%–50% of the whole-animal heat production at rest and up to 70% of the heat increment above maintenance (Webster 1981; Johnson et al. 1990). With respect to individual organs, we confirmed that liver as well as heart and muscle lean dry masses contributed significantly to the mass-independent decrease of SFMR in food- and water-restricted gazelles. In the stepwise multiple-regression analysis, liver alone explained 70.4% of the variance in SFMR, confirming the important role of this organ in energetic adjustments in this species. However, we did not expect a lack of correlation between SFMR and rumen or intestine

lean dry mass. In ruminants, the gastrointestinal tract is responsible for a disproportionately high fraction of whole-body protein turnover, an energy-consuming process (McBride and Kelly 1990). The gut wall constitutes 6% of the protein pool of the body but accounts for 28%–46% of whole-body protein synthesis (Reeds 1988). We hypothesize that desert ruminants decrease mitochondrial density in the gastrointestinal tract

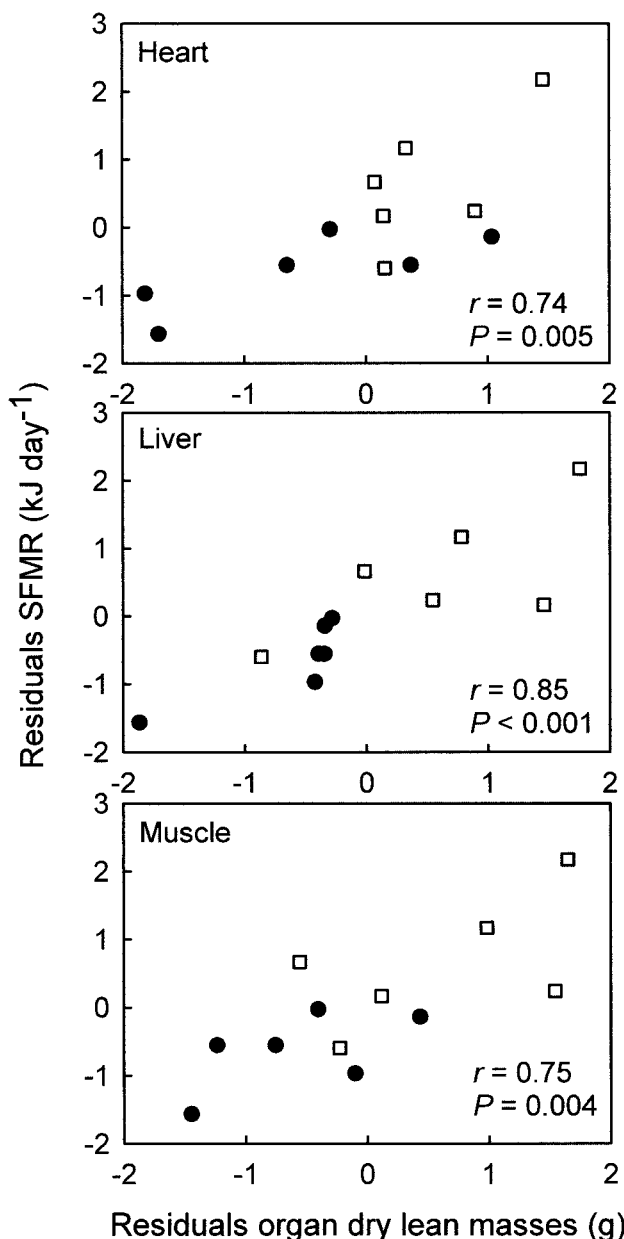


Figure 2. Relationship between residuals of organ dry lean masses to body mass and residuals of standard fasting metabolic rate to body mass in sand gazelles *Gazella subgutturosa*. Squares represent gazelles fed and watered ad lib.; circles represent gazelles acclimated to progressive food and water restriction as encountered in the wild.

when restricted in food, contributing also to the decrease in SFMR. Maintaining a relatively large gut size would then be part of a "readiness strategy" in order for the organism to optimize assimilation of food when green vegetation becomes available after rains.

Gazelles presumably used nonpolar lipids stored in organs as a source of energy during prolonged food and water restriction. Because we used petroleum ether, which is a solvent that extracts nonpolar lipids (Christie 1982), in lipid extraction, few structural phospholipids were presumably removed from dry organs. Compared with individuals in CTRL, neutral lipid content of dry organs was 5.1%–27.7% lower in food- and water-restricted animals, depending on the organ, corresponding on average to 65.2 g less organ fat per animal in this cohort. Unexpectedly, fat content of dry brain tissue was 3.7% higher in food- and water-restricted gazelles than in those in CTRL. It could be that gazelles store fats in the brain to secure brain metabolism during prolonged food deprivation.

Williams et al. (2001) produced an allometric equation that related SFMR to body mass of 15 species of artiodactyls; this equation predicts a value for SFMR of 2,907 kJ d<sup>-1</sup> for a gazelle weighing 17 kg. Our measurement of 2,343 kJ d<sup>-1</sup>, the average SFMR for the 18 gazelles before acclimation, is 19.4% below allometric predictions for artiodactyls. After prolonged food and water restriction, SFMR was 48.7% below predictions. Both results suggest that sand gazelles have evolved specializations that reduce resting metabolic rate.

The relationship between SFMR and TEWL provides some indications about the partitioning of evaporative water losses in this species. Gazelles acclimated to prolonged food and water restriction decreased their SFMR by 39.2% and their TEWL by 27.1%, compared with those fed and watered ad lib. One might predict that a decrease of SFMR would reduce TEWL. With decreased oxygen requirements, gazelles would reduce respiratory water loss. Robertshaw and Taylor (1969), working on sweat gland activity of African antelopes, predicted that a correlation existed between cutaneous water loss and size, with smaller species dissipating most of their heat through the respiratory tract rather than through cutaneous water loss. In food- and water-restricted gazelles, the amount of evaporative water lost per unit of metabolism was 0.071 ± 0.014 g H<sub>2</sub>O kJ<sup>-1</sup> after acclimation, compared with 0.073 ± 0.014 g H<sub>2</sub>O kJ<sup>-1</sup> before acclimation, values that were not significantly different ( $P = 0.79$ ). Similarly, the amount of evaporative water lost per unit of metabolism was 0.066 ± 0.008 g H<sub>2</sub>O kJ<sup>-1</sup> after 4.5 d of food and water restriction in gazelles in EXPT<sub>1</sub>, compared with 0.069 ± 0.011 g H<sub>2</sub>O kJ<sup>-1</sup> before restrictions, values that were not significantly different ( $P = 0.41$ ). These results show a positive and direct relationship between reduction of SFMR and TEWL in gazelles when restricted in food and water and suggest that respiratory water loss is an important component of TEWL.

Evaporative water loss might be expected to be a trait under

strong selection among desert-dwelling ungulates because in these species TEWL is the primary route of water expenditure (Wilson 1989). We have previously evaluated the allometric relation between TEWL and body mass in 15 species of arid-zone ungulates (Ostrowski et al. 2006). Dividing TEWL by (body mass)<sup>0.898</sup> is one way of standardizing comparisons between species, where 0.898 is the slope of allometric curve for hydrated arid-zone ungulates. We found that gazelles had a low mass-adjusted TEWL, 13.6 g H<sub>2</sub>O kg<sup>-0.898</sup> d<sup>-1</sup>, which is only 17.1% of allometric predictions and is the lowest TEWL ever measured in an arid-zone ungulate. Grant's gazelle *Gazella granti* and Thomson's gazelle *Gazella thomsonii*, two species that occupy arid savannahs in eastern Africa, had mass-adjusted TEWL values of 64.9 and 84.2 g H<sub>2</sub>O kg<sup>-0.898</sup> d<sup>-1</sup> (Taylor 1970), respectively, more than five times higher than the value for the sand gazelle. Such low TEWL suggests that the sand gazelle has evolved a remarkable capacity to reduce water expenditures, which is likely to be a component of their success in deserts of Saudi Arabia.

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#### Literature Cited

- American Veterinary Medicine Association. 2001. 2000 report of the AVMA panel on euthanasia. *J Am Vet Med Assoc* 218: 669–696.
- Bae H.H., J.E. Larkin, and I. Zucker. 2003. Juvenile Siberian hamsters display torpor and modified locomotor activity and body temperature rhythms in response to reduced food availability. *Physiol Biochem Zool* 76:858–867.
- Blaxter K.L. 1989. *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge.
- Brosh A., A. Shkolnik, and I. Choshniak. 1986. Metabolic effects

- of infrequent drinking and low-quality feed on Bedouin goats. *Ecology* 67:1086–1090.
- Burrin D.G., C.L. Ferrell, R.A. Britton, and M. Bauer. 1990. Level of nutrition and visceral organ size and metabolic activity in sheep. *Br J Nutr* 64:439–448.
- Choshniak I., N. Ben-Kohav, C.R. Taylor, D. Robertshaw, R.J. Barnes, A. Dobson, V. Belkin, and A. Shkolnik. 1995. Metabolic adaptations for desert survival in the Bedouin goat. *Am J Physiol* 268:R1101–R1110.
- Christie W.W. 1982. *Lipid Analysis: Isolation, Separation, Identification, and Structural Analysis of Lipids*. 2nd ed. Pergamon, Toronto.
- Degen A.A. 1997. *Ecophysiology of Small Desert Mammals: Adaptations of Desert Organisms*. Springer, New York.
- Dobush G.R., C.D. Ankney, and D.G. Krentz. 1985. The effect of apparatus, extraction time and solvent type on lipid extractions of snow geese. *Can J Zool* 63:1917–1920.
- Ferraris R.P. and J.M. Diamond. 1989. Specific regulation of intestinal nutrient transporters by their dietary substrates. *Annu Rev Physiol* 51:125–141.
- Finegan E.J., J.G. Buchanan-Smith, and B.W. McBride. 2001. The role of gut tissue in the energy metabolism of growing lambs fed forage or concentrate diets. *Br J Nutr* 86:257–264.
- Gessaman J.A. 1987. Energetics. Pp. 289–320 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird, eds. *Raptor Management Techniques Manual*. Yale University Press, New Haven, CT.
- Grenot C.J. 1992. Ecophysiological characteristics of large herbivorous mammals in arid Africa and the Middle East. *J Arid Environ* 23:125–155.
- Hill R.W. 1972. Determination of oxygen consumption by use of the paramagnetic analyzer. *J Appl Physiol* 33:261–263.
- Hudson R.H. and R.J. Christopherson. 1985. Maintenance metabolism. Pp. 121–142 in R.H. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC, Boca Raton, FL.
- Johnson D.E., K.A. Johnson, and R.L. Baldwin. 1990. Changes in liver and gastrointestinal tract energy demands in response to physiological workload in ruminants. *J Nutr* 120:649–655.
- Kleiber M. 1975. Metabolic turnover rate: a physiological meaning of the metabolic rate per unit body weight. *J Theor Biol* 53:199–204.
- Konarzewski M. and J. Diamond 1995. Evolution of basal metabolic rate and organ masses in laboratory mice. *Evolution* 49:1239–1248.
- Krebs H.A. 1950. Body size and tissue respiration. *Biochim Biophys Acta* 4:249–269.
- Lasiewski R.C., A.L. Acosta, and M.H. Bernstein. 1966. Evaporative water loss in birds. I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp Biochem Physiol* 19:445–457.
- Louw G.N. and M.K. Seely. 1982. *Ecology of Desert Organisms*. Longman, London.
- Macfarlane W.V. and B. Howard. 1972. Comparative water and energy economy of wild and domestic animals. Pp. 261–296 in G.M.O. Maloiy, ed. *Comparative Physiology of Desert Animals*. Proceedings of a symposium held at the Zoological Society of London on July 15–16, 1971. Vol. 31. Academic Press, London.
- Mallon D.P. and S.C. Kingswood. 2001. *Antelopes: Global Survey and Regional Action Plans*. Part 4: North Africa, the Middle East, and Asia. International Union for the Conservation of Nature and Natural Resources/Species Survival Commission Antelope Specialist Group, Gland, Switzerland.
- Maloiy G.M.O. 1970. Water economy of the Somali donkey. *Am J Physiol* 219:1522–1527.
- Maloiy G.M.O. and D. Hopcraft. 1971. Thermoregulation and water relations of two East African antelopes: the hartebeest and impala. *Comp Biochem Physiol* 38A:525–534.
- Martin A.W. and F.A. Fuhrman. 1955. The relationship between summated tissue respiration and metabolic rate in the mouse and the dog. *Physiol Zool* 28:18–34.
- McBride B.W. and J.M. Kelly. 1990. Energy cost of absorption and metabolism in the ruminant gastrointestinal tract and liver: a review. *J Anim Sci* 68:2997–3010.
- Meigs P. 1953. *Review of Research on Arid Zone Hydrology*. UNESCO, Paris.
- Merkt J.R. and C.R. Taylor. 1994. “Metabolic switch” for desert survival. *Proc Natl Acad Sci USA* 91:12313–12316.
- Nagy K.A. and C.C. Peterson. 1988. *Scaling of Water Flux Rate in Animals*. University of California Press, Berkeley.
- Ostrowski S., J.B. Williams, P. Mésochina, and H. Sauerwein. 2006. Physiological acclimation of a desert antelope, Arabian oryx (*Oryx leucoryx*), to long-term food and water restriction. *J Comp Physiol B* 176:191–201.
- Parker K.L. and C.T. Robbins. 1985. Thermoregulation in ungulates. Pp. 201–234 in R.H. Hudson and R.G. White, eds. *Bioenergetics of Wild Herbivores*. CRC, Boca Raton, FL.
- Reeds P.J. 1988. Nitrogen metabolism and protein requirements. Pp. 55–72 in K. Blaxter and I. Macdonald, eds. *Comparative Nutrition*. Libbey, London.
- Renecker L.A. and R.J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. *Can J Zool* 64:322–327.
- Rice W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Robbins C.T. 1993. *Wildlife Feeding and Nutrition*. Academic Press, New York.
- Robertshaw D. and C.R. Taylor. 1969. A comparison of sweat gland activity in eight species of east African bovines. *J Physiol* 203:135–143.
- Rolfe D. and G.C. Brown. 1997. Cellular energy utilization and molecular origin of standard metabolic rate in mammals. *Physiol Rev* 77:731–758.
- Schmidt-Nielsen K. 1997. *Animal Physiology: Adaptation and Environment*. 5th ed. Cambridge University Press, New York.

- Schmidt-Nielsen K., E.C. Crawford, A.E. Newsome, K.S. Rawson, and H.T. Hammel. 1967. Metabolic rate of camels: effect of body temperature and dehydration. *Am J Physiol* 212: 341–346.
- Silver H., N.F. Colovos, J.B. Holter, and H.H. Hayes. 1969. Fasting metabolism of white-tailed deer. *J Wildl Manag* 33: 490–498.
- Sokal R.R. and F.J. Rohlf. 1995. *Biometry: The Principles of Statistics in Biological Research*. 3rd ed. W.H. Freeman, New York.
- Spalton J.A. 1999. The food supply of Arabian oryx (*Oryx leucoryx*) in the desert of Oman. *J Zool (Lond)* 248:433–441.
- Taylor C.R. 1970. Strategies of temperature regulation: effect of evaporation in East African ungulates. *Am J Physiol* 219: 1131–1135.
- Taylor C.R. and C.P. Lyman. 1967. A comparative study of the environmental physiology of an East African antelope, the eland, and the Hereford steer. *Physiol Zool* 40:280–295.
- Webster A.J.F. 1980. Energy costs of digestion and metabolism in gut. Pp. 469–484 in Y. Ruckebush and P. Thivend, eds. *Digestive Physiology and Metabolism in Ruminants*. AVI, Westport, CT.
- . 1981. The energetic efficiency of metabolism. *Proc Nutr Soc* 40:121–128.
- Wesley D.E., K.L. Knox, and J.G. Nagy. 1973. Energy metabolism of pronghorn antelopes. *J Wildl Manag* 37:563–573.
- Williams J.B., S. Ostrowski, E. Bedin, and K. Ismail. 2001. Seasonal variation in energy expenditure, water flux and food consumption of Arabian oryx *Oryx leucoryx*. *J Exp Biol* 204: 2301–2311.
- Williams J.B. and B.I. Tieleman. 2001. Physiological ecology and behavior of desert birds. Pp. 299–353 in V.J. Nolan and C.F. Thompson, eds. *Current Ornithology*. Vol. 16. Kluwer, New York.
- Willmer P., G. Stone, and I. Johnston. 2000. *Environmental Physiology of Animals*. Blackwell Science, Malden, MA.
- Wilson R.T. 1989. *Ecophysiology of the Camelidae and Desert Ruminants*. Springer, New York.
- Zar J.H. 1996. *Biostatistical Analysis*. 3rd ed. Prentice Hall, Englewood Cliffs, NJ.