

SEASONAL VARIATION IN ENERGY EXPENDITURE, WATER FLUX AND FOOD CONSUMPTION OF ARABIAN ORYX *ORYX LEUCORYX*

JOSEPH B. WILLIAMS^{1,*}, STÉPHANE OSTROWSKI², ERIC BEDIN² AND KHAIRI ISMAIL²

¹*Department of Evolution, Ecology and Organismal Biology, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA* and ²*National Wildlife Research Center, PO Box 1086, Taif, Saudi Arabia*

*e-mail: Williams.1020@osu.edu

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Summary

We report on the energy expenditure and water flux, measured in the laboratory and in the field, of the Arabian oryx *Oryx leucoryx*, the largest desert ruminant for which measurements of the field metabolic rate of free-living individuals have been made using doubly labeled water. Prior to extirpation of this species in the wild in 1972, conservationists sequestered a number of individuals for captive breeding; in 1989, oryx were reintroduced in Saudi Arabia into Mahazat as-Sayd (2244 km²). Apart from small pools of water available after rains, oryx do not have free-standing water available for drinking and therefore rely on grasses that they eat for preformed water intake as well as their energy needs. We tested whether oryx have a reduced fasting metabolic rate and total evaporative water loss (TEWL) in the laboratory, as do some other arid-adapted mammals, and whether oryx have high field metabolic rates (FMRs) and water influx rates (WIRs), as predicted by allometric equations for large arid-zone mammals. We measured FMR and WIR during the hot summer, when plant moisture content was low and ambient temperatures were high, and after winter rains, when the water content of grasses was high.

For captive oryx that weighed 84.1 kg, fasting metabolic rate averaged 8980 kJ day⁻¹, 16.7% lower than predictions for Artiodactyla. Our own re-analysis of minimal metabolic rates among Artiodactyla yielded the equation: $\log \dot{V}_{O_2} = -0.153 + 0.758 \log M$, where \dot{V}_{O_2} is the rate

of oxygen uptake in l h⁻¹ and M is body mass in kg. Fasting metabolic rate of oryx was only 9.1% lower than predicted, suggesting that they do not have an unusually low metabolic rate. TEWL averaged 870.0 ml day⁻¹, 63.9% lower than predicted, a remarkably low value even compared with the camel, but the mechanisms that contribute to such low rates of water loss remain unresolved.

For free-living oryx, FMR was 11076 kJ day⁻¹ for animals with a mean body mass of 81.5 kg during summer, whereas it was 22081 kJ day⁻¹ for oryx in spring with a mean body mass of 89.0 kg, values that were 48.6% and 90.4% of allometric predictions, respectively. During summer, WIR averaged 1310 ml H₂O day⁻¹, whereas in spring it was 3438 ml H₂O day⁻¹. Compared with allometric predictions, WIR was 76.9% lower than expected in summer and 43.6% lower in spring. We found no evidence to support the view that the WIR of large desert ungulates is higher than that of their mesic counterparts. On the basis of the WIR of the oryx averaged over the year and the water contents of plants in their diet, we estimated that an oryx consumes 858 kg of dry matter per year.

Key words: Arabian oryx, *Oryx leucoryx*, field metabolic rate, water flux, doubly labeled water, metabolic rate, desert mammal, Artiodactyla.

Introduction

Deserts are water-controlled ecosystems characterized by high ambient temperature (T_a), intense solar radiation, desiccating winds and low annual rainfall and primary production (Noy-Meir, 1973). Understanding of the influence of rainfall on deserts is complicated by the fact that precipitation is highly stochastic, with long periods of drought punctuated by pulses of rain; in some areas, all water input to the system occurs in 1–3 storm events during the year. Because primary production closely parallels rainfall, it can be argued that rates of energy flow through desert ecosystems are

controlled by available water (Noy-Meir, 1973). If the rate of food consumption of desert herbivores is mediated by water in plants (Macfarlane and Howard, 1972), then secondary as well as primary energy flows are coupled to, and often dominated by, the availability of water in desert ecosystems.

Animals that occupy arid climes face the challenge of meeting their daily energy and water requirements in an environment that, on average, provides little of either. Desert-dwelling rodents have ostensibly evolved mechanisms that result in a diminution in basal metabolic rate (BMR), reducing

overall energy demand, which facilitates survival in a desert environment (MacMillen, 1983; Bennett, 1988; Tracy and Walsberg, 2000). These rodents achieve water balance by reducing evaporative water loss (MacMillen and Lee, 1967; Tracy and Walsberg, 2000), eliminating nitrogenous wastes with minimal water (Schmidt Nielsen and O'Dell, 1961), remaining within a subterranean burrow during the day to reduce solar heat load and foraging at night when environmental conditions are more favorable (Schmidt-Nielsen, 1990; Walsberg, 1999).

A number of species of large ruminants have also evolved the capacity to live in arid ecosystems, a counterintuitive phenomenon when one considers that their size prohibits them from burrowing, that herbivory is typically associated with high rates of water turnover (Nagy and Peterson, 1988; Berteaux and Thomas, 1999) and that, during episodes of drought, grasses provide relatively small amounts of preformed water (Spalton et al., 1999; S. Ostrowski, unpublished results). Little is known about the physiological mechanisms employed by desert ungulates that enable them to survive in such demanding environments. In general, members of the Artiodactyla have high minimum fasting metabolic rates compared with most other mammalian orders, but it is not known whether constituents of this coterie that live in deserts conform to this expectation (Hayssen and Lacy, 1985; Lovegrove, 2000). Calculations from equations for field metabolic rate (FMR) of free-living desert mammals indicate that a 100 kg ungulate would have an FMR approximately 206 % higher than estimates for similar-sized eutherians from mesic regions (Nagy et al., 1999). However, because the largest mammal in the data set for desert mammals was the springbok (*Antidorcas marsupialis*), which weighed 43.3 kg, predictions are based on extrapolation beyond available data, a practice that should be performed only with caution (Zar, 1996). For water influx rates (WIRs) of free-living mammals, the equations proffered by Nagy and Peterson (Nagy and Peterson, 1988) yield the counterintuitive prediction that large desert mammals will have a higher WIR than similar-sized non-desert mammals. Recently Ostrowski et al. (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted) tested this idea on Arabian oryx *Oryx leucoryx* during the summer and found that their water influx rate was 2222.8 ml day⁻¹, only 32 % of the predicted value for a herbivorous eutherian mammal (Nagy and Peterson, 1988).

The Arabian oryx, an 80–100 kg desert antelope that once ranged throughout most of the Arabian Peninsula, was extirpated from the wild by 1972 (Henderson, 1974; Stanley Price, 1989). Prior to this time, conservationists captured a number of animals and reared them for reintroduction to native habitats (Grimwood, 1962; Stanley Price, 1989; Gorman, 1999). Since their release in 1989 into Mahazat as-Sayd, a protected area 160 km northeast of Taif, Saudi Arabia, the oryx population has increased significantly (Ostrowski et al., 1998; Treydte et al., 2001). Once near the cusp of extinction, oryx in Mahazat provide an opportunity to explore functional adaptations possessed by this large desert herbivore that allow

it to live in such an austere environment without access to drinking water.

Recently Treydte (Treydte, 2000) developed a computer model that explored the risk of extinction of oryx in Mahazat as-Sayd when one of four management strategies was applied to 100 virtual oryx populations over 100 years. Using data-driven assumptions for birth rate and survival, their analyses indicated that the management scheme that provided a low probability of extinction and a relatively stable population size consisted of removing all oryx above 70 % of the carrying capacity in Mahazat as-Sayd each year. These authors pointed out that assessment of annual carrying capacity assumed, among other things, knowledge of the food consumption of oryx. As a first step in approximating dry matter intake of wild oryx, Ostrowski et al. (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted) used data for their water influx rate (WIR) during summer and for water contained in plants in the oryx diet to calculate that the dry matter intake (kg) of oryx ranged from 2.5 to 3.5 % body mass day⁻¹. However, food consumption of oryx may vary considerably between dry periods when plants provide less water and after rains when water levels in plants are at a maximum (Macfarlane and Howard, 1972).

In this study, we measured minimum fasting metabolic rate and total evaporative water loss (TEWL) for Arabian oryx in the laboratory, data available for only a few large desert ungulates, and compared our results with allometric predictions testing the hypothesis that oryx have reduced metabolic rates and TEWL. We then quantified FMR and WIR of free-living oryx, the largest desert ungulate for which these measurements have been made, using the doubly labeled water method, during the hot summer when plant moisture content was low and T_a values were high, the latter forcing oryx to forage mainly at night, and just after winter rains when plant moisture content was relatively high and T_a values were moderate, and oryx foraged primarily during the day. These data allowed us to test the hypothesis that FMR and WIR of desert ungulates are elevated after rains when food is abundant. We used our data to calculate the annual food consumption of oryx, an important input parameter in population models for the management of this endangered species.

Materials and methods

Study area

Mahazat as-Sayd consists of a 2244 km² tract of flat, open desert in west central Saudi Arabia (28°15'N, 41°40'E). After designation as a protected area in 1988, Mahazat was surrounded by a chain-link fence that excluded all domestic livestock. There are no permanent sources of drinking water for oryx in the reserve.

The climate of this region is characterized by hot summers and mild winters. Weather records for Mahazat for the last decade show that in June, the hottest month, daily maximum and minimum temperatures averaged 41.5 and 24.5 °C, respectively, whereas in January, these values were 23.4 and

10.6 °C (NWRC Annual Report, 1999). Annual precipitation in 1998, all of which fell between January and April, averaged 63.0 mm, whereas in 1999 rain fell twice in January and twice in March, totalling 47.4 mm.

The vegetation of Mahazat is dominated by perennial grasses, including *Panicum turgidum*, *Lasiurus scindicus*, *Stipagrostis* sp. and *Ochthochloa compressa*, and by small acacia trees (*Acacia* sp.) (Mandaville, 1990). Sporadically distributed among wadis, *Maerua crassifolia* trees are an important source of shade for oryx in summer.

Measurement of minimum fasting metabolic rate and TEWL in the laboratory

Measurement of basal metabolic rate (BMR), the minimum metabolic rate of postabsorptive animals at rest at temperatures within their thermal neutral zone and in their normal rest phase of the diurnal cycle (King, 1974; Blaxter, 1989), may be difficult to achieve in ruminants. As a result, most investigators measure minimum fasting metabolic rate as an approximation of BMR (Weiner, 1977; Blaxter, 1989). We determined minimal rates of oxygen consumption and of evaporative water loss during May 2000 for oryx that were postabsorptive (supplied with water but no food for 50 h prior to measurement), during the day (08:00–18:00 h), using standard flow-through respirometry and hygrometry methods (Gessaman, 1987; Williams, 1999; Williams and Tieleman, 2000). We selected 50 h as the fasting interval because domestic sheep (Robbins, 1993), white-tailed deer (*Odocoileus virginianus*; Silver et al., 1969), moose (*Alces alces*; Renecker and Hudson, 1986) and pronghorn antelope (*Antilocarpa americana*; Wesley et al., 1973) reached minimum metabolic rates after 48 h without food, because oryx lost more than 12 % of their body mass when deprived of food for this period and further mass loss could have influenced metabolic rates (Blaxter, 1989) and because, in preliminary trials, oryx that were fasted for 72 h were considerably more restless when placed in our chamber.

Constructed of angle-iron and sheets of galvanized steel, our metabolic chamber (142 cm×180 cm×45 cm) was equipped with a steel-mesh floor on which oryx stood over a layer of mineral oil into which the urine and feces fell, excluding both as a source of evaporative water during measurements. A small computer fan affixed to the ceiling of the chamber ensured mixing of gases during measurements. One end of the chamber served as an entrance which, when fitted with a rubber gasket, replaced and bolted to the chamber, rendered our system airtight. Prior to each measurement, we checked for air leaks around the lid using a solution of soap and water. The temperature within the chamber was controlled at 30±1 °C by placing it in a small thermostatically controlled enclosure. While measuring metabolic rate and TEWL, T_a within the chamber was monitored continuously with a 28-gauge thermocouple.

During experiments, air under positive pressure from a compressor coursed through two large (100 cm×21 cm) drying columns containing anhydrous CaSO₄ (Drierite), through a

Tylan mass-flow controller set at 120 l min⁻¹ (model 2925V; 0–400 l min⁻¹; calibrated against a primary standard traceable to the NIST in October 1999 by Flow Dynamics Inc., Arizona, USA), then into the chamber. Exiting air was sampled by pumps which routed air to a General Eastern dewpoint hygrometer (model M4) and to columns of Drierite and Ascarite before entering an Applied Electrochemistry oxygen analyzer (S3A-II) to determine the fractional concentration of oxygen in dry, CO₂-free air. Each oryx remained in the chamber for at least 3 h prior to measurements, and then, after it had remained calm for an additional hour, we recorded data for 20 min and calculated averages. We recorded the oxygen concentration, the dewpoint of exiting air, the temperature of the dewpoint hygrometer and T_a within the chamber each minute using a Campbell Scientific data logger (model 21X). Calculations of oxygen consumption were performed using equation 2 of Hill (Hill, 1972), and oxygen consumption was converted to heat production using the relationship 20.08 J ml⁻¹ O₂ (Schmidt-Nielsen, 1990).

Total evaporative water loss (TEWL; g day⁻¹) was calculated using the equation:

$$\text{TEWL} = [(\dot{V}_e \rho_{\text{out}} - \dot{V}_i \rho_{\text{in}})] \times 1.44 \times 10^{-3}, \quad (1)$$

where ρ_{in} and ρ_{out} are the absolute humidity (g H₂O m⁻³) of inlet air and outlet air, respectively, \dot{V}_i is the flow rate (ml min⁻¹) of air entering the chamber, as given by the mass-flow controller, and \dot{V}_e is the flow rate of exiting air. Absolute humidity (ρ ; g H₂O m⁻³) was determined using the equation:

$$\rho = 216.7 e_s / T_{\text{dp}} + 273.15, \quad (2)$$

where e_s is the saturation vapor pressure at a given dew point and T_{dp} is the temperature of the dew-point hygrometer (List, 1951). We calculated \dot{V}_e as follows:

$$\dot{V}_e = \dot{V}_i - [\dot{V}_{\text{O}_2}(1 - \text{RQ})] + \dot{V}_{\text{H}_2\text{O}}. \quad (3)$$

In this equation, \dot{V}_i (ml min⁻¹), the flow rate of air into the chamber, and \dot{V}_{O_2} (ml min⁻¹), the rate of oxygen consumption, are known, the respiratory quotient, RQ, is assumed to equal 0.71 (King and Farner, 1961; Robbins, 1993), and the rate of water loss, $\dot{V}_{\text{H}_2\text{O}}$ (ml min⁻¹) is calculated as:

$$\dot{V}_{\text{H}_2\text{O}} = \rho(\dot{V}_i + \dot{V}_{\text{CO}_2} - \dot{V}_{\text{O}_2}) / (1 - \rho), \quad (4)$$

where \dot{V}_{CO_2} is the rate of CO₂ production (ml min⁻¹; Williams and Tieleman, 2000).

Capture of oryx for field studies

To capture oryx during the summer of 1998, we took advantage of the fact that oryx forage at night and lie in the shade during the day. We waited for them to return to shade in the early morning, and then darted them with anesthetic (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). After immobilization of an oryx, we weighed it, took a background blood sample, injected it with doubly labeled water (DLW), then reversed the anesthetic. Infused into the jugular vein, the injectate (1.75 ml kg⁻¹ body mass) contained 99 % deuterium (²H) and 10 % oxygen-18 (¹⁸O).

Initial concentrations of ^2H in the body water averaged 185.1 ± 14.5 p.p.m. excess, whereas initial concentrations of ^{18}O averaged 245 ± 22.7 p.p.m. excess. Final concentrations of ^2H and ^{18}O averaged 128 ± 40 and 140 ± 48 p.p.m. excess, respectively. We transported the animal to a shaded holding pen, where it remained throughout the day, allowing isotopes to equilibrate. As evening approached, we took an initial blood sample, attached a radio collar and released the animal at the site of capture.

Our spring measurements during March–April 1999 were more difficult to obtain because oryx do not rest beneath shade trees at this time of year and are less approachable when foraging. Members of some herds allowed us to approach while feeding during the day; we opportunistically darted animals when they were within range, a procedure that biased our sample towards males because males tend to position themselves on the periphery of the herd. After successful immobilization, we then followed our previous methods for the use of DLW.

Equilibration of isotopes

In studies on ruminants, the time allowed for equilibration of isotopes has varied from 1 h in springbok (*Antidorcas marsupialis*; 40–45 kg; Nagy and Knight, 1994) and 5–8 h in black-tailed deer (*Odocoileus hemionus*; 45.4 kg; Nagy et al., 1990) to 6–8 h in the camel (*Camel dromedarius*; approximately 450 kg; Siebert and Macfarlane, 1971). Ostrowski et al. determined that isotopes equilibrate completely in the body water pool, including the rumen, of

oryx after 6 h (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). In the present study, we allowed 9–15 h for isotopes to equilibrate before taking an initial blood sample (Table 1).

Calculation of water influx

Assuming hydrogen isotopes exit the animal only in water molecules, water influx ($\text{mol H}_2\text{O day}^{-1}$) can be calculated as $r_{\text{H}_2\text{O}} = k_{\text{H}}N$, where N is moles of body water and k_{H} is the fractional isotope turnover per unit time (Lifson and McClintock, 1966; Nagy, 1975; Nagy and Costa, 1980). The fractional turnover of a hydrogen isotope in the body water pool is calculated as $k_{\text{H}} = (\ln H_i - \ln H_f) / t$, where $\ln H_i$ and $\ln H_f$ are the natural logarithms of the initial and final concentrations of a hydrogen isotope in the body water, respectively, and t is time in days. Versions of this equation have been applied to calculate water influx for mammals, including ruminants (King et al., 1975; King et al., 1978; Nagy and Costa, 1980; Nagy and Knight, 1994).

However, for ruminants, the use of the above equation can lead to an overestimate of water influx, because of loss of hydrogen isotopes by avenues other than in water (Midwood et al., 1989; Midwood et al., 1994), and an overestimate of water flux translates into an overestimate of energy expenditure. Methane production, for example, forms an additional route of isotope loss, because hydrogen from water in the body fluids is incorporated into methane during methanogenesis (Czerkawski and Breckenridge, 1974). In addition, labeled hydrogen in organic molecules that are

Table 1. Data for the doubly labeled water study on oryx

| Animal identity | Sex ^a | Mean body mass (kg) | Equilibration time (h) | Interval ^b (days) | Rate of change in body mass (% day ⁻¹) | Rate of water influx (ml day ⁻¹) | Rate of CO ₂ production (l day ⁻¹) |
|---------------------------|------------------|---------------------|------------------------|------------------------------|----------------------------------------------------|----------------------------------------------|-----------------------------------------------------------|
| Summer measurements, 1998 | | | | | | | |
| 125 | M | 101.8 | 11.4 | 7.56 | -1.3 | 1319 | 607 |
| 167 | F | 81.5 | 13.2 | 5.52 | -1.7 | 1010 | 490 |
| 109 | F | 87.4 | 10.9 | 10.50 | -1.2 | 1263 | 439 |
| Zah | F | 73.1 | 10.4 | 9.00 | -2.2 | 626 | 787 |
| 69 | M | 83.2 | 13.0 | 7.45 | -0.4 | 3425 | 448 |
| 128 | M | 67.5 | 9.4 | 9.38 | -2.7 | 216 | 395 |
| Mean | | 81.5 | 11.4 | 8.2 | -1.6 | 1310 | 527 |
| s.d. | | 11.7 | 1.5 | 11.4 | 0.8 | 1019 | 113 |
| Spring measurements, 1999 | | | | | | | |
| 136 | M | 105.4 | 8.9 | 9.58 | 0.01 | 3787 | 934 |
| 125 | M | 105.0 | 12.7 | 11.35 | -0.5 | 5169 | 1157 |
| 44 | F | 59.9 | 8.4 | 10.88 | -1.0 | 2572 | 764 |
| 45 | M | 82.2 | 15.1 | 11.09 | -1.3 | 2824 | 1246 |
| 91 | M | 91.5 | 12.7 | 11.05 | -1.4 | 2573 | 1096 |
| 116 | M | 90.0 | 8.6 | 10.58 | 0.3 | 3699 | 1111 |
| Mean | | 89.0 | 11.1 | 10.8 | -0.6 | 3438 | 1051 |
| s.d. | | 16.9 | 2.8 | 0.6 | 0.8 | 1006 | 135 |

^aF, female; M, male.

^bTime in days between initial and final blood sample.

exported from the body, such as in feces, will lead to an overestimate of water flux. We have derived the following equation for water influx of oryx:

$$r_{\text{H}_2\text{O}} = \frac{(k_{\text{H}}N) - (r_{\text{CH}_4} + r_{\text{H}})}{(f_1X) + (1 - X)}, \quad (5)$$

where r_{CH_4} is the equivalent moles of water attributable to methane production per day, r_{H} is the equivalent moles of hydrogen isotope lost in dry feces, f_1 is a fractionation factor ($^2\text{H}_2\text{O}$ vapor/ $^2\text{H}_2\text{O}$ liquid), assumed to equal 0.93 (Lifson and McClintock, 1966; Nagy and Costa, 1980), and X is an estimate of the proportion of the total water loss subject to fractionation, assumed to be 0.25 (Speakman, 1997).

From experiments *in vitro*, Czerkawski and Breckenridge (Czerkawski and Breckenridge, 1974) established that 50% of the hydrogen atoms of methane, produced during methanogenesis, are derived from body water, with the remainder coming from organic molecules. Hence, hydrogen loss as methane inflates k_{H} , and because two hydrogen atoms from body water are lost per methane molecule, the production of 1 mole of methane results in an overestimate of water flux by 1 mole. We have estimated the amount of methane produced by oryx (C ; mol day $^{-1}$) from the equation $C=0.56+0.00123F$ (where dry food intake F is in g day $^{-1}$), generated from data for cattle eating hay (Kriss, 1930). In captivity, the amount of dry food eaten by oryx can be approximated by $F=-400+20.0M$ (where M is body mass in kg) (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). On the basis of estimates of dry food intake, we calculated that an 80 kg oryx would produce methane at a rate of 2.04 mol day $^{-1}$; Midwood measured a rate of methane production of 1.2 mol day $^{-1}$ in sheep (60 kg) (Midwood et al., 1989).

Ruminants consume a diet high in fiber content, which results in the production of substantial fecal mass (Robbins, 1993). Isotopes of hydrogen can exchange with the hydrogen atoms of cellulose or other organic molecules in feces, leading to an overestimate of water influx. For sheep, Midwood et al. (Midwood et al., 1993) found a loss of deuterium from feces equivalent to 7.2 mmol H $_2$ O g $^{-1}$ dry feces. To estimate dry matter fecal production, we confined four oryx that ranged in body mass from 82.3 to 101.1 kg individually in pens (3 m \times 4 m) with concrete floors. We provided them with dry hay and water for 3–5 days prior to measurements until they reached a constant body mass. Thereafter, we measured hay consumption and fecal production for three consecutive days. Feces were dried in an oven at 70 °C to constant mass. Because dry matter fecal production was unrelated to body mass in these experiments ($F=4.99$, $P=0.16$, $N=4$), we used an average value for production of dry feces of 435.3 \pm 18.9 g day $^{-1}$ (mean \pm s.d., $N=12$ measurements). This yielded a value for r_{H} of 3.13 mol day $^{-1}$. For lambs weighing 35 kg, Midwood et al. (Midwood et al., 1993) measured a dry matter fecal production of 262 g day $^{-1}$. Our measurements of water flux accounting for methane production and for loss of hydrogen in dry feces were 5.0 \pm 1.2% lower than uncorrected values.

Our estimate of water influx depends on the moles of body water (N), a value sometimes estimated from the dilution space of hydrogen isotopes in studies on ruminants (King et al., 1978; Nagy and Knight, 1994). However, estimates of total body water using isotopes of hydrogen in ruminants can be 6–15% higher than estimates based on H $_2$ ^{18}O dilution space (Fancy et al., 1986). Calculations of percentage body water in oryx using ^{18}O dilution space yielded a mean value of 66.5 \pm 5.0% (mean \pm s.d., $N=12$). We used this value as an estimate of body water composition in our calculations of water flux and of energy expenditure because we were unsure of the exact amount of DLW injected into several individuals.

Calculation of rates of CO $_2$ production

In a validation study, Midwood et al. (Midwood et al., 1994) compared CO $_2$ production of four sheep over a period of 10 days with estimates provided by the DLW method and found a mean error of +3.6% when they accounted for isotope loss in methane and in fecal solids. If these authors had ignored corrections for isotope loss in methane and in feces, they would have underestimated CO $_2$ production by approximately 12%.

To estimate the rate of CO $_2$ production (mol CO $_2$ day $^{-1}$), we used the equation:

$$r_{\text{CO}_2} = \frac{(k_0N) - [(r_{\text{H}_2\text{O}} \times X \times f_2) + (1 - X)r_{\text{H}_2\text{O}}]}{2f_3}, \quad (6)$$

where k_0 is the fractional turnover of ^{18}O , f_2 , the fractionation of H $_2$ ^{18}O vapor relative to H $_2$ ^{18}O liquid, is 0.99, and f_3 , the fractionation of C $^{18}\text{O}_2$ gas relative to H $_2$ ^{18}O liquid, is 1.039 (Lifson and McClintock, 1966). Our equation simplifies to $r_{\text{CO}_2}=0.481(k_0N-0.9975r_{\text{H}_2\text{O}})$, where $r_{\text{H}_2\text{O}}$ is water flux corrected for methane production and for loss of hydrogen atoms in fecal solids (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). To convert CO $_2$ production to energy expenditure, we used 21.0 kJ l $^{-1}$ CO $_2$ (Nagy and Knight, 1994). Isotope concentrations were measured in triplicate at the Center for Isotopic Research at the University of Groningen, the Netherlands.

Estimation of plant water content

For determinations of water content for plants, we harvested shoots and stems (50–100 g wet mass) of the three most common grasses in the oryx diet (Spalton, 1999; S. Ostrowski, unpublished results), *Panicum trugidum*, *Lasiurus scindicus* and *Stipagrostis* sp., three samples each from three areas known to be utilized by oryx for grazing for a total of nine samples for each plant per month. During the summer of 1998, we sampled plants at night between 02:00 and 05:00 h when water content was potentially at its highest (Taylor, 1968) and when oryx were foraging, but in the spring of 1999 we sampled plants during the day because oryx foraged mostly during daylight at this time. For *Stipagrostis* sp., we sampled inflorescences because oryx select these structures when available (Tear et al., 1997). For the other plants, we hand-

gathered the greenest stems and leaves obtainable, a strategy that we assume mimics foraging by oryx (Edlefsen et al., 1960). Plants were placed in air-tight bags, weighed on site using a portable electronic scale (to ± 0.01 g) and then transported to our laboratory, where they were frozen at -20°C . Samples were subsequently dried at 70°C to constant mass and reweighed.

Statistical analyses

Values are presented as means ± 1 s.d. Means were compared using *t*-tests, with $P=0.05$ as the minimum level of significance. Plant moisture content was compared between seasons by two-way analysis of variance (ANOVA) after percentages had been arcsine-transformed (Zar, 1996).

Results

Laboratory measurements

Among females with a mean body mass of 89.2 ± 8.9 kg ($N=6$), minimal fasting rate of oxygen consumption averaged $19.0 \pm 1.51 \text{ h}^{-1}$, or $9160 \pm 732 \text{ kJ day}^{-1}$ (Table 2). Males, which weighed 79.0 ± 7.8 kg ($N=6$), had a rate of oxygen consumption of $18.0 \pm 1.21 \text{ h}^{-1}$, which was equivalent to $8674 \pm 565 \text{ kJ day}^{-1}$. The sexes did not differ significantly in body mass ($t=2.1$, $P>0.06$) or in rate of oxygen consumption ($t=1.3$, $P>0.2$). Combining data for sexes, oryx with a body mass of 84.1 kg had a minimal fasting rate of heat production of 8980 kJ day^{-1} .

TEWL was $898 \pm 126 \text{ g day}^{-1}$ for females, whereas for males, it averaged $829 \pm 262 \text{ g day}^{-1}$, values that were statistically indistinguishable ($t=0.6$, $P>0.5$). For males and females

together, TEWL was $870 \pm 181 \text{ g day}^{-1}$. Body temperature, taken immediately after measurement of metabolic rate, averaged $38.6 \pm 0.6^\circ\text{C}$.

Field measurements

Body masses of oryx during summer of 1998 averaged 81.5 ± 11.7 kg ($N=6$), whereas during spring of 1999 body mass averaged 89.0 ± 16.9 kg ($N=6$), values that do not differ significantly ($t=0.6$, $P>0.5$; Table 1). Body mass did not change appreciably during measurements for either year (Table 1).

During the summer, free-ranging oryx expended $11076 \pm 3070 \text{ kJ day}^{-1}$, whereas during spring of 1999 they expended energy at a rate nearly double to that during the summer, $22081 \pm 3646 \text{ kJ day}^{-1}$, values that differed significantly ($t=5.7$, $P<0.0001$) (Fig. 1A).

Water influx during the hot summer averaged $1310 \pm 1019 \text{ ml day}^{-1}$, whereas in spring, it was $3438 \pm 1006 \text{ ml day}^{-1}$, rates that differed significantly (Fig. 1B; $t=3.5$, $P<0.007$). Water influx rate (WIR; ml day^{-1}) for spring and summer combined was correlated with energy expenditure (FMR; kJ day^{-1}): $\text{WIR} = -115.4 + 0.15\text{FMR}$ ($F=7.6$, $P<0.02$, $N=12$).

Using a two-way ANOVA with unequal replication, plant water content varied significantly between seasons ($F=182.5$, $P<0.001$), with overall water content being lower during the summer of 1998, and was significantly different among species ($F=44.8$, $P<0.001$) with *Stipagrostis* sp. having less water than the other two species in both years (Table 3). The percentage water in *Panicum turgidum* and in *Lasiurus scindicus* did not differ significantly in 1998 or in 1999.

Table 2. Fasting metabolic rate and total evaporative water loss of Arabian oryx

| Animal identity | Sex | Body mass (kg) | Rate of O_2 consumption (h^{-1}) | Energy intake (kJ day^{-1}) | TEWL ($\text{g H}_2\text{O day}^{-1}$) | T_b ($^\circ\text{C}$) |
|------------------------|-----|----------------|------------------------------------------------------|----------------------------------------|------------------------------------------|----------------------------|
| 92 | F | 84.3 | 18.3 | 8854 | 807 | 39.1 |
| 80 | F | 95.8 | 21.00 | 10124 | 1089 | 38.9 |
| 156 | F | 103.0 | 20.90 | 10072 | 838 | 39.3 |
| 110 | F | 79.0 | 17.93 | 8645 | 766 | 38.8 |
| 158 | F | 89.8 | 17.89 | 8622 | 870 | 39.0 |
| 90 | F | 83.4 | 17.93 | 8641 | 1014 | 39.5 |
| Mean (female) | F | 89.2 | 19.00 | 9160 | 898 | 39.1 |
| s.d. | | 8.9 | 1.5 | 732 | 126 | 0.3 |
| 325 | M | 77.4 | 17.38 | 8374 | 913 | 38.7 |
| 295 | M | 78.1 | 19.93 | 9606 | 1035 | 38.1 |
| 331 | M | 82.2 | 18.44 | 8886 | – | 37.5 |
| 401 | M | 66.0 | 18.41 | 8874 | 922 | – |
| 381 | M | 80.8 | 16.76 | 8077 | 446 | 38.2 |
| 403 | M | 89.7 | 17.07 | 8227 | – | 38.0 |
| Mean (male) | M | 79.0 | 18.00 | 8674 | 829 | 38.1 |
| s.d. | | 7.8 | 1.2 | 565 | 261 | 0.4 |
| Mean (male and female) | | 84.1 | 18.60 | 8980 | 870 | 38.6 |
| s.d. | | 9.6 | 1.4 | 668 | 181 | 0.6 |

TEWL, total evaporative water loss; T_b , body temperature; F, female; M, male.

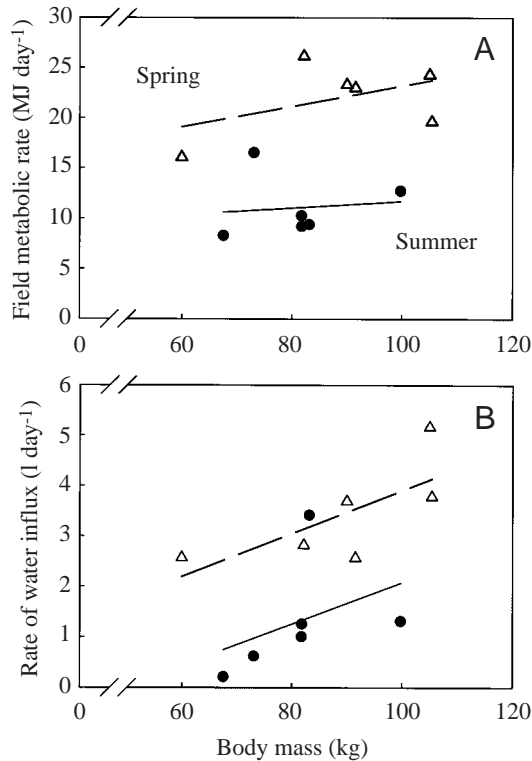


Fig. 1. (A) Field metabolic rate and water influx rate (B) of oryx in Mahazat as-Sayd during the summer of 1998 (filled circles) and during the spring of 1999 (open triangles). Lines were drawn using Linear Regression.

Discussion

Among some desert mammals, BMR was found to be reduced compared with values from more mesic species, with the result that putative arid-adapted species are thought to reduce their energy demand, conserve water and produce less heat that must be dissipated in a warm environment (MacMillen, 1983; Bennett, 1988; Williams et al., 1997). Oryx have a lower minimal fasting metabolic rate than many other Artiodactyla when compared with predictions of the equation provided by Hayssan and Lacy (Hayssen and Lacy, 1985), which yields a metabolic rate of $22.21 \text{ O}_2 \text{ h}^{-1}$ for an 84.1 kg oryx; measured values for oryx are approximately 16.7% lower than predicted.

The most recent analysis of the basal metabolic rate of mammals is that of Lovegrove (Lovegrove, 2000), who

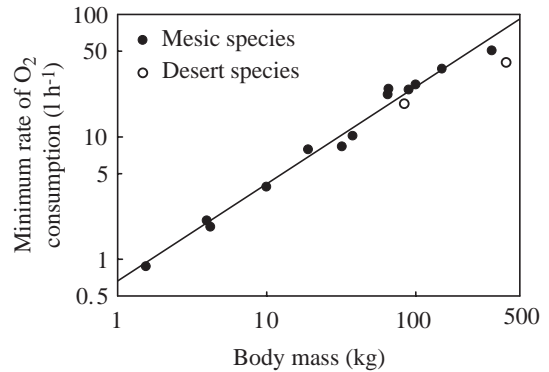


Fig. 2. Minimum rate of oxygen consumption of Artiodactyla. Data are presented in Table 4. Open circles represent the oryx (84.1 kg) and the camel (407 kg). See text for further details.

compiled so-called basal metabolic rates (BMRs) for 487 species. Because we disagreed with his approach of grouping animals by zoogeographic region as a meaningful unit of comparison, with his definition of a desert mammal (those for which 95% of the distribution occurred within the 500 mm rainfall isohyet) and with his definition of 'basal metabolic rate', which included animals measured at rest, regardless of their status of alimentation, we did not think it meaningful to compare metabolic rates of the oryx with Lovegrove's (Lovegrove, 2000) allometric equation for mammals from the Palearctic. Instead, we compiled data from original literature for minimum resting metabolic rate for 15 species (Table 4), two of which were desert species, the camel and oryx, and calculated the equation: $\log \dot{V}_{\text{O}_2} = -0.153 + 0.758 \log M$ (where \dot{V}_{O_2} is in l h^{-1} and M is in kg) (Fig. 2; $N=15$, $r^2=0.97$, $F=419.7$, $P<0.0001$). In our data set, we differentiated between species that were fasted before measurements and those that were not for future researchers who may want to use them (Table 4); it is well known that fasted ruminants have significantly lower metabolic rates than when they have recently fed (Renecker and Hudson, 1985; Blaxter, 1989). In addition, we did not have a phylogeny for these species and therefore did not explore the usage of statistical methods to correct for historical bias. Comparison between fasted and unfasted species showed no difference between slopes, as indicated by the insignificant interaction term in an analysis of covariance (ANCOVA; $F=0.43$, $P>0.5$); when we assumed a common slope, we found

Table 3. Water content of plants in the diet of Arabian oryx

| | 1998 ^a | | | | 1999 ^b | | | |
|---------------------------|-------------------|-----------|-----------|------|-------------------|----------|----------|------|
| | June | July | August | Mean | February | March | April | Mean |
| <i>Stipagrostis</i> sp. | 4.6±2.5 | 12.7±10.5 | 4.4±0.4 | 7.2 | 38.6±8.1 | 45.7±4.9 | 34.5±8.5 | 39.6 |
| <i>Panicum turgidum</i> | 45.4±3.4 | 44.5±5.3 | 41.4±5.5 | 43.8 | 47.1±4.9 | 51.9±5.5 | 49.5±4.4 | 49.5 |
| <i>Lasiurus scindicus</i> | 35.7±5.3 | 30.4±5.6 | 27.0±14.5 | 31.0 | 40.5±8.2 | 55.6±9.5 | 52.5±5.9 | 49.5 |

Values are means ± S.D. ($N=9$).

^aPlants collected at night when oryx were feeding during the summer.

^bPlants collected during the day when oryx were feeding in spring.

Table 4. *Fasting and resting metabolic rates of Artiodactyla*

| Species | Body mass (kg) | Rate of oxygen consumption (l h ⁻¹) | Source |
|---------------------------------------------------------------------|----------------|-------------------------------------------------|--------------------------------|
| Mouse deer ^a (<i>Tragulus javanicus</i>) | 1.613 | 0.869 | Whittow et al., 1977 |
| Dik-dik ^a (<i>Madoqua kirkii</i>) | 3.97 | 2.06 | Maskrey and Hoppe, 1979 |
| Blue duiker ^b (<i>Cephalophus monticola</i>) | 4.20 | 1.81 | Haim and Skinner, 1991 |
| Steenbok ^b (<i>Raphicerus campestris</i>) | 9.60 | 3.70 | Haim and Skinner, 1991 |
| Roe deer ^b (<i>Capreolus capreolus</i>) | 19.0 | 7.85 | Weiner, 1977 |
| Mountain goat ^a (<i>Oreamnos americanus</i>) | 32.0 | 8.32 | Krog and Monson, 1954 |
| Pronghorn antelope ^b (<i>Antilocarpa americana</i>) | 37.8 | 10.19 | Wesley et al., 1973 |
| Bighorn sheep ^b (<i>Ovis canadensis</i>) | 65.0 | 22.10 | Chappel and Hudson, 1978 |
| White-tailed deer ^b (<i>Odocoileus virginianus</i>) | 65.9 | 24.62 | Silver et al., 1969 |
| Oryx ^b (<i>Oryx leucoryx</i>) | 84.1 | 18.5 | This study |
| Wildebeest ^b (<i>Connochaetes taurinus</i>) | 90.0 | 24.18 | Rogerson, 1968; Lovegrove 2000 |
| Waterbuck ^a (<i>Kobus ellipsiprymnus</i>) | 100.0 | 26.67 | Taylor et al., 1969 |
| Eland ^a (<i>Taurotragus oryx</i>) | 150.0 | 35.88 | Taylor and Lyman, 1967 |
| Moose ^b (<i>Alces alces</i>) | 325.0 | 50.66 | Renecker and Hudson, 1986 |
| Camel ^a (<i>Camelus dromedarius</i>) | 407.0 | 40.38 | Schmidt-Nielsen et al., 1967 |

^aAnimals not fasted before trials.

^bAnimals fasted before measurements, usually for 48 h; steenbok and blue duiker fasted overnight.

that elevations were insignificantly different ($F=1.4$, $P>0.2$). Hence, at this stage, we report an equation for all data combined. Despite these limitations in the data, oryx had a fasting metabolic rate only 9.1 % lower than predicted by this equation, which suggests that they do not have an unusually low fasting metabolic rate. However, we note that oryx at the National Wildlife Research Center do not experience the high T_a values of Mahazat as-Sayd, have food and water provided *ad libitum* and do not travel the same distances in search of food as do oryx in Mahazat as-Sayd. Fasting metabolic rates of oryx in the field may differ from those we have measured for captive animals.

Evaporative water loss might be expected to be a physiological variable under strong selection among desert-dwelling mammals because, in most species, TEWL, the primary avenue of water loss, exceeds fecal and urinary water loss combined (Schmidt-Nielsen, 1979; Wilson, 1989; Tracy and Walsberg, 2000). In mammals ranging in size from bats (15.8 g) to elephants (3630 kg), Chew's (Chew, 1965) equation

predicts a TEWL of 2408.3 g H₂O day⁻¹ for an 84.1 kg oryx, whereas our measured value for oryx was 870.0 g H₂O day⁻¹, only 36.1 % of the predicted value.

The near-legendary ability of the domestic camel (*Camelus dromedarius*) to survive in desert conditions was investigated over four decades ago (Schmidt-Nielsen et al., 1956; Schmidt-Nielsen et al., 1957; Schmidt-Nielsen, 1979). Unfortunately, TEWL was not directly measured; instead, it was approximated from studies on water balance (Schmidt-Nielsen et al., 1957). For a single, hydrated, 260 kg camel during winter, when T_a values were below 15 °C, TEWL was estimated as 2262 ml H₂O day⁻¹. Mass-adjusting TEWL, we calculated values of 22.9 and 22.4 ml H₂O/day× $M^{0.826}$, respectively, for the camel and oryx, where the exponent 0.826 is the slope of the allometric equation for TEWL for mammals (Chew, 1965). We emphasize that measurements on the camel were made outdoors during winter at ambient temperatures below 15 °C, whereas those on the oryx were made in a chamber with a relative humidity of less than 30 % and at an

ambient temperature of 30 °C. Because the evaporative water loss of large mammals is often considerably higher at 30 °C than at 15 °C (Chew, 1965), the mass-adjusted TEWL for oryx could be lower than for the camel given an identical water vapor pressure gradient.

Because BMR makes up 25–45 % of the daily energy expenditure of a mammal, one might expect a positive relationship between BMR and FMR (Kleiber, 1961; Nagy, 1987; Ricklefs et al., 1996). However, for the marmot (*Marmota flaviventris*), a relatively low BMR did not translate into a reduced FMR (Salsbury and Armitage, 1994). The evolutionary and ecological significance of a diminution in BMR is still an unresolved issue, despite attempts to place variation in BMR within an ecological framework (McNab, 1986; Bennett, 1988; Lovegrove, 2000).

We report FMRs for the Arabian oryx, the largest desert ruminant so far measured using the DLW method, during two distinct periods, June–September, when grasses were parched and T_a values high, and March–April, when grasses were green. The difference in FMR between the two periods represents the largest disparity in FMR so far reported for a eutherian mammal; FMR in summer was 11 076 kJ day⁻¹ for oryx weighing 81.5 kg and nearly doubled after rains to 22 081 kJ day⁻¹ for oryx weighing 89.0 kg. The allometric equations of Nagy et al. (Nagy et al., 1999) predict FMRs of 22 787 kJ day⁻¹ for an 81.5 kg oryx (summer) and 24 417 kJ day⁻¹ for an 89.0 kg animal (spring). Our measurements of FMR were 48.6 % of these predicted levels during summer and 90.4 % after rains. Thus, it appears that oryx markedly reduce their energy expenditure during summer, probably by adjusting their behavior and physiology. At this time, they forage only at night when T_a values are moderate, lie completely inactive beneath shade trees during the daylight hours, conducting away body heat to reduce dependence on evaporative cooling to maintain body temperature, and range over smaller areas at night to forage (S. Ostrowski, unpublished results). In the spring, after rains when grasses were green and plentiful, oryx had a higher energy expenditure, an augmentation that may have resulted from increased costs of thermoregulation, because of cooler T_a values, and from increased activity costs, because they were moving greater distances to forage and because they were foraging for longer periods. In addition, as food intake increases, their minimum metabolic rate may increase, as it does for some desert birds and temperate-zone mammals (Rogowitz, 1990; Williams and Tieleman, 2000), but we have no data for oryx to support such a view. Assuming that fasting metabolic rate remains unchanged over the year, it accounted for 78.3 % of FMR during summer but for only 39.3 % of FMR during spring after rain.

Among similar-sized mammals, WIR can vary by an order of magnitude depending on taxon, season and diet (Nagy and Peterson, 1988). In general, herbivorous mammals have a high WIR, as much as three times that of terrestrial carnivores, because of the relatively high water content and low digestibility of a plant diet. On the basis of 28 measurements

on seven species, Nagy and Peterson (Nagy and Petersen, 1988) reported an allometric equation for herbivorous eutherian mammals that predict WIRs of 5680 ml H₂O day⁻¹ for a 81.5 kg oryx in summer and 6092 ml H₂O day⁻¹ for a 89.0 kg oryx in spring. Values for WIR in this study were 23.1 % of expectation for oryx in summer and 56.4 % for oryx in spring, when the water content of plants was high.

Prompted by the counterintuitive prediction that large desert mammals have a higher WIR than similar-sized non-desert mammals, based on the equations of Nagy and Peterson (Nagy and Peterson, 1988), we (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted) re-evaluated the relationship between body mass and water flux (WIR; l H₂O day⁻¹) among large ungulates in hot environments; $WIR = -0.885 + 0.922 \log M$ (where M is body mass in kg; $N = 10$). Using the slope of this equation, these authors calculated a mass-adjusted WIR of 99.3 ml H₂O/day × $M^{0.922}$ for the camel and 30.5 ml H₂O/day × $M^{0.922}$ for oryx in summer. Making the same correction for data from the present study gave a mass-adjusted WIR of 22.7 ml H₂O/day × $M^{0.922}$ during summer, and 54.8 ml H₂O/day × $M^{0.922}$ during spring. Oryx have a remarkably low WIR even during periods when grasses contain ample water, suggesting that this species has evolved mechanisms that reduce water expenditures.

With a predator-free environment and after several years of rainfall, the oryx population in Mahazat-as Sayd has grown to almost 400 since the initial re-introduction in 1989 (Ostrowski et al., 1998; Treydte, 2000). Concern over the likelihood of population declines during years of drought led to discussions about the most appropriate management strategy to reduce catastrophic mortality events and to minimize the probability of extinction. In computer simulations of population trajectories over the next 100 years, a management protocol that provided a reasonable probability of long-term persistence of oryx was to maintain the population at 70 % of the carrying capacity (Treydte, 2000; Treydte et al., 2001). To implement such a plan, one needs information about, among other things, the food requirements of oryx. Dry matter food intake can be ascertained from knowledge of the plant water content and the diet and from the water influx of oryx (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). During the summer, oryx consume a diet of 81.7 % *P. turgidum*, 6.1 % *L. scindicus*, 3.3 % *Stipagrostis* sp. and 8.9 % other plants such as the leaves of *Acacia* sp. (S. Ostrowski, J. B. Williams, E. Bedin and K. Ismail, manuscript submitted). Assuming 0.028 ml of oxidative water is produced from 1 kJ of energy expended (Schmidt-Nielsen, 1990), then during the summer oryx obtained 310.1 ml of metabolic water daily, 23.7 % of their total water intake. The remainder, 999.8 ml, must come from the plants that they eat. Assuming mean values for water content (Table 3), and a water content of other plants of 40 %, we estimated that oryx ate 2742 g of wet matter per day during summer, or 1742 g of dry matter. Because we did not know the proportions of various plants in their diet in spring, we assumed that plants were eaten in equal proportions and that all plants contained 46.2 % water, the average for the

three common grasses in Mahazat as-Sayd (Table 3). We calculated that oryx consumed 6102 g wet matter per day during spring, or 3283 g dry matter. Assuming that oryx expend energy at the higher rate for 5 months of the year and at the lower rate for the rest of the year, then each adult consumes approximately 858 kg of dry matter per year.

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