WATER INFLUX AND FOOD CONSUMPTION OF FREE-LIVING ORYXES (ORYX LEUCORYX) IN THE ARABIAN DESERT IN SUMMER

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We measured water-influx rate during the hot summer in free-ranging adult Arabian oryxes (*Oryx leucoryx*) in Mahazat as-Sayd, a 2,244-km² protected area in west-central Saudi Arabia. Oryxes obtained 2,294 ml/day of water in their food and from oxidative water, the latter amounting to 14.2% of total water influx. For ungulates living in hot environments, we constructed an allometric curve: log(water-influx rate [liters/day]) = $-0.885 + 0.922 \cdot \log(body mass [kg])$, ($r^2 = 0.77$, F = 26.8, P < 0.001, n = 10). The Arabian oryx had the lowest mass-specific water-influx rate (31.5 ml kg^{-0.922} day⁻¹), only 32% that of the camel (99.3 ml kg^{-0.922} day⁻¹), emphasizing the degree of evolutionary specialization in oryx. Between June and September, oryxes grazed primarily on 3 grasses, *Panicum turgidum, Lasiurus scindicus*, and *Stipagrostis*. *P. turgidum*, taken in largest quantity, had the highest moisture content, 35–45% per g of wet matter. Dry matter intake averaged about 3.1 kg during the summer months; plant intake varied inversely with moisture content.

Key words: allometry, antelope, Arabian oryx, Artiodactyla, desert, Oryx leucoryx, water influx

Desert environments are characterized by high ambient temperature, intense solar radiation, desiccating winds, scant rainfall, and low primary productivity. Because animals that occupy desert regions face constant desiccation, they must tightly regulate efflux of water to maintain positive water balance (Macfarlane 1968; Schmidt-Nielsen 1990). Many small desert rodents achieve positive water balance without drinking by reducing evaporative water loss (Mac-Millen and Lee 1967; Tracy and Walsberg 2000), by eliminating nitrogenous wastes with minimal water (Schmidt Nielsen and O'Dell 1961), and by remaining within a subterranean burrow during the day and foraging at night (Schmidt-Nielsen 1990).

A number of species of large ruminants live in semiarid and arid ecosystems, a sur-

prising 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), and that during dry periods grasses in deserts provide only small amounts of preformed water (Spalton 1999). A few wild ruminants reside permanently in arid and hyperarid deserts, the latter having the lowest ratio of precipitation relative to evaporative losses on earth (Meigs 1952). Of the 10 species of wild ruminants that occupy hot deserts, 9 are threatened (World Conservation Monitoring Centre 1996); the addax (Addax nasomaculatus) and scimitar-horned oryx (Oryx dammah) are nearly extinct (Newby 1980, 1984). Understanding the physiology of these large ungulates is a critical step in efforts to conserve them.

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The Arabian oryx (Oryx leucoryx), a desert antelope that once ranged throughout most of the Arabian Peninsula, was extirpated from the wild by 1972 (Henderson 1974). Before this time, conservationists captured a small number of animals and housed them in zoos (Grimwood 1962), with the intent of reintroducing captivereared individuals into native habitats, as was indeed done in Oman in 1982 (Stanley Price 1989). In 1989, Arabian oryxes were reintroduced into Mahazat as-Sayd, a protected area in Saudi Arabia 160 km northeast of Taif. Captive-reared animals acclimatized quickly to wild conditions without supplemental food and water; the population has increased significantly over the last decade (Ostrowski et al. 1998; Treydte et al. 2001). The oryx population in Mahazat as-Sayd provides an opportunity to investigate functional adaptations of this endangered species to its desert environment.

Circumstantial evidence, mostly from captive individuals, has led some authors to propose that a number of ruminants can live without drinking water. The list includes the dik-dik (Rhynchotragus kirki-Hoppe 1977), Cape eland (Taurotragus oryx), fringe-eared oryx (Oryx beisa callotis-Lewis 1977; Taylor 1969), and Grant's gazelle (Gazella granti-Taylor 1968a). However, apart from the fringe-eared oryx, all these species occupy semiarid habitats and would likely succumb to dehydration if challenged with arid or hyperarid conditions during the hot summer. Even the legendary camel (Camelus dromedarius), capable of surviving without drinking up to 6 weeks during cooler periods (Cole 1975; Schmidt-Nielsen 1990), must drink every 4 days during summer months (Cole 1975; Gauthier-Pilters 1958; Macfarlane et al. 1963; Schmidt-Nielsen 1964). Few studies have determined water intake of large ruminants under free-living conditions (Macfarlane et al. 1963; Nagy and Knight 1994). Measurements of water flux of the Arabian oryx are particularly interesting because this species survives in the Arabian Desert,

including the Rub al-Khali, one of the driest regions in the world (Meigs 1952), without access to drinking water. Stanley Price (1989) suggests that wild oryxes in Oman can maintain water balance as long as their diet contains at least 35% water when ambient air temperature is <31°C.

We test the hypothesis that Arabian oryxes have lower water-influx rates than do other large herbivores living in hot environments. Finally, we employ our data on water-influx rate and information on water content in the plants that oryxes eat to estimate food consumption.

MATERIALS AND METHODS

Our study area, Mahazat as-Sayd, consisted of a 2,244-km² tract of flat, steppe desert in westcentral Saudi Arabia (28°15'N, 41°40'E). After being designated as a protected nature reserve in 1988, Mahazat as-Sayd was surrounded by a fence to exclude domestic livestock. Other than temporary pools after infrequent rain, Mahazat as-Sayd provides no drinking water for oryxes. The climate of this region is characterized by hot summers and mild winters. 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 (S. Ostrowski, in litt.). Annual rainfall averaged 129.6 mm in 1996 and 84.3 mm in 1997.

The vegetation of Mahazat as-Sayd is dominated by perennial grasses, including *Panicum turgidum*, *Lasiurus scindicus*, *Stipagrostis*, and *Ochthochloa compressa* (Mandaville 1990). Small acacia (*Acacia tortillis*) and *Maerua crassifolia* trees, sporadically distributed along *wadis* (washes), are an important source of shade for oryxes in summer. Only 21% of the area is covered by plants (Treydte et al. 2001).

Determinations of water flux using isotopes of hydrogen depend upon an initial and final sample of body fluid, both of which should be in isotopic equilibrium with all compartments of the body-water pool (Lifson and McClintock 1966; Nagy and Costa 1980). In theory, any fluid can be sampled for determining water-influx rate (Nagy and Costa 1980). Because 1 of our goals was to estimate water-influx rate noninvasively midway though the experimental period by sampling water in feces, we compared the concentrations of tritium (³H) in blood and fecal water, after equilibration and when we took final samples.

Ambiguity exists about the time required for isotopes to equilibrate in the body water of herbivorous mammals. Estimates range from 1 h in the springbok (*Antidorcas marsupialis*—Nagy and Knight 1994); to 6–8 h in the camel (Siebert and Macfarlane 1971). Previously we showed that tritium equilibrated in the body-water pool after 6–8 h in oryx when isotopes were administrated intravenously (S. Ostrowski, in litt.). We allowed 9-11 h for isotopes to equilibrate in the present study.

Measurement of water flux in the field.—We attempted to minimize capture-stress by using the fact that during the day in summer oryxes lie in shade and forage only in the late evening and at night. Using our vehicle as a blind, we positioned ourselves near known shade trees around sunrise. When oryxes returned from foraging to lie in the shade, we injected them (n =6) with 4 mCi ³H using a CO₂-powered dart gun (GUT-50, Telinject, Römerberg, Germany). After being darted, each animal returned to its shade tree within 20 min and remained there until the evening, allowing sufficient time for 3H to equilibrate in body fluids. In the late afternoon, we injected the animal with a mixture of etorphine (mean dose = $2.5 \text{ mg} \pm 0.2 \text{ SE}$; M99, 4.9 mg/ml, C-Vet, Leyland, United Kingdom) and xylazine (dose = 25 mg; Rompun, 50 mg/ml, Bayer, Leverkusen, Germany), a drug combination that induced anesthesia within 10 min (Machado et al. 1983). When the oryx was anesthetized, we weighed it to ± 0.5 kg with a Salter scale (Salter Brecknell, Minneapolis, Minnesota) attached to a tripod, obtained a blood sample from the jugular vein, collected fecal pellets from the rectum, and attached a radiocollar (MOD-400, Telonics, Mesa, Arizona) around its neck. The anesthetic was then reversed with 6 mg diprenorphine (M50-50, 12 mg/ml, C-Vet) and 7.5 mg atipamezole (Antisedan, 5 mg/ml, Orion, Espoo, Finland), and animals were released.

We tracked oryxes by locating their radio signals every 2 days. Midway during the overall interval (3–4 days), we located each individual, and after we observed them to defecate, collected their feces (1–4 min after defecation). After brushing away any adhering soil from feces, we stored feces in airtight glass vials in a cool box until we could place them in a freezer about 3 h later.

For final samples, on average 7.7 days after the initial sample, we located each oryx at sunrise, followed it to its shade tree, again injected the same anesthetic with a dart gun, sampled blood and feces as before, reweighed it, reversed the anesthesia, and then released it.

Water was distilled from all samples using rapid vacuum sublimation (Vaughan and Boling 1961). In brief, samples were placed in a 50-ml flask, sealed, frozen in liquid nitrogen, and then placed under vacuum. A glass finger attached to the flask was then placed in liquid nitrogen. Water within the sample quickly sublimated into the finger, where it remained frozen. Samples were distilled overnight to assure complete dryness, thereby eliminating errors associated with fractionation during drying.

The ³H content of water distilled from samples was measured in triplicate on a Beckman 5800 liquid scintillation counter (Beckman Instruments, Fullerton, California) using the method of Williams (1987). After placing 50 μ l of distilled water in Beckman Ready-Safe[®] scintillation cocktail (Beckman Instruments), we counted ³H until a sigma error of <1% was reached.

Assuming ³H exits the animal only in water, water-influx rate (moles/day) can be calculated as $r_{H_2O} = k_H \times N$, where N is the moles of body water, and k_H is the fractional isotope turnover per unit time (Lifson and McClintock 1966; Nagy 1975; Speakman 1997). The fractional turnover of a hydrogen isotope in the body-water pool is calculated as $k_{\rm H} = (\ln[H_i] - \ln[H_f])/t$, where $ln(H_i)$ and $ln(H_f)$ are natural logs of the initial and final specific activities of ³H (cpm) in body water, respectively, and t is time in days. This equation has been used in a number of studies to calculate water influx for ruminants (Nagy and Knight 1994; Siebert and Macfarlane 1971; Speakman 1997). We have assumed that total body water of oryxes constitutes 0.66 of body mass, the value found by Williams et al. (2001) for oryxes using deuterium dilution space. For animals that changed body mass during the interval, we assumed a linear change in total body water and calculated N as $(N_1 + N_2)/$ 2 (Nagy and Costa 1980). The efficacy of hydrogen isotopes in monitoring water flux has been well documented; estimates are usually

within $\pm 10\%$ of mean value (Nagy and Costa 1980).

Loss of hydrogen isotopes by avenues other than water may lead to errors in the estimate of water influx when using the above-mentioned equation (Lifson and McClintock 1966; Nagy and Costa 1980). Methane production in ruminants forms an additional route of isotope loss, as do labeled hydrogens occupying positions in molecules other than water that are exported from the body, such as in feces and in milk. We report values for water influx using the standard equation of Lifson and McClintock (1966), and values for which we attempt to correct for isotope loss via methane production and feces, and for fractionation. We derived the following equation for water influx of oryxes:

$$r_{H_{2}O} = \frac{k_{H}N - (r_{CH_{4}} + r_{H})}{(f_{1}X) + (1 - X)}$$

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 (³H vapor/³H liquid), here assumed to equal 0.953 (Nagy and Costa 1980), and X is an estimate of the part of total water loss subject to fractionation, here assumed to be 0.25 (Midwood et al. 1994; Speakman 1997).

Hydrogen loss from methane inflates $k_{\rm H}$ and, as a result, water-influx rate (Midwood et al. 1989). Because 2 hydrogens from body water are lost when 1 mole of methane is produced (Czerkawski and Breckenridge 1974), a 1:1 relationship exists between the overestimate of moles of water lost and moles of methane produced. We have estimated moles of methane produced by oryxes as CH_4 (moles/day) = 0.56 + 0.00123 (mass of dry food [g]/day) on the basis of data from cattle eating grasses (Kriss 1930). In captivity, an 80-kg oryx eats about 1,200 g/day of dry food, and a 110-kg oryx, about 1,800 g/day (S. Ostrowski, in litt.). We have calculated dry matter intake of free-living oryxes on the basis of these data.

Ruminants consume a diet high in fiber, which results in the production of substantial fecal mass. Isotopes of hydrogen can exchange with hydrogens of cellulose or other organic molecules in feces, leading to a small overestimate of water influx. Midwood et al. (1994) found a loss of deuterium in feces of sheep equivalent to 7.2 millimoles H₂O/g dry feces. To estimate dry matter fecal production, we fed 4 captive oryxes hay (6-8% moisture, 10-13% crude protein, 23-25% crude fiber) and provided them with water. Each animal was weighed daily (± 200 g). Fecal pellets were collected for 3 consecutive days after body mass stabilized $(\pm 1\%)$, which required 6-7 days. Feces were dried at 70°C to constant mass and weighed using a Sartorius P310 scale (Sartorius, Göttingen, Germany) to an accuracy of 0.01 g. We found a dry matter fecal production of 435.3 \pm 18.9 g/day (*n* = 4 animals, 12 measurements), with an estimate of 3.13 moles/ day for loss of isotope in dry feces (r_H). Among the oryxes that we measured, fecal production was not related to body mass (F = 4.99, d.f. =1, 3, P = 0.16).

During summer, oryxes in Mahazat as-Sayd feed mainly on Stipagrostis, P. turgidum, and L. scindicus (H. Gillet, in litt.). To ascertain water content of plants in the oryx diet, we harvested shoots and stems (50-100 g wet mass) of each species from 3 areas known to be grazed by oryxes. We collected 9 plants of each species at night during June, August, and September, in 1998 and 1999, between 0200 h and 0500 h, when water content was potentially the highest (Taylor 1968b). For Stipagrostis we sampled inflorescences because oryx eat these structures when available (Tear et al. 1997). For the other 2 species, we hand-gathered the greenest stems and leaves, a strategy that we assume mimics foraging by oryx (Edlefsen et al. 1960). Plants were weighed at the site using a Sartorius P310 scale (Sartorius) to an accuracy of 0.01g, placed in airtight plastic bags, 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.

We measured water content of plants during summers of 1998 and 1999 but measured water flux of oryxes during summers of 1996 and 1997. Because phenology and water composition of grasses are strongly associated with rainfall (Ilius 1997), and because patterns of precipitation in Mahazat as-Sayd were similar in spring (March–May) in 1996 and 1998 (50.3 and 66.0 mm, respectively) and in 1997 and 1999 (18.8 and 15.6 mm, respectively), we assumed that plant water contents were similar in the summers of 1996 and 1998, and 1997 and 1999. No rain fell in our study area during summer of any of the 4 years. To compare water-influx rate among ungulates, we constructed an allometric equation based on 9 desert ruminant species living in hot arid environments. Because only 1 other study has been completed on water-influx rate of a free-living ungulate, the springbok (Nagy and Knight 1994), we included values for water influx for wild species farmed in natural environments or confined to outdoor pens. Where several estimates for water influx were available for the same species, we selected the 1 study that most closely paralleled our protocol.

Means are reported ± 1 SD. We assumed statistical significance at P < 0.05. Before testing for differences in percentages, we performed an arcsine transformation of data. To test for differences in moisture content among plant species, we used a model I three-way analysis of variance with species, year, and months as fixed factors (Zar 1984).

RESULTS

To use feces as a source of body water, the isotopic concentration of this material must reflect that of the body-water pool. When comparing ³H concentrations of final blood samples of wild oryxes with concentrations in water from feces removed from the rectum at the time of drawing of blood, we found no significant differences (t =0.19, P > 0.8, n = 6).

Water influx in oryxes during summer varied between 269.7 and 3,776 ml H_2O/day and averaged 1,956.6 \pm 1,220 ml H_2O/day

day for our 6 animals (Table 1). Because 1 oryx showed signs of capture stress and apparently did not eat much during the 6-day measurement interval (as evidenced by a total water intake of only 269.7 ml H₂O/day), we recalculated a mean water intake based on the other 5 animals. For this group with a mean body mass of 104.8 kg, water intake was 2,294 \pm 1,004 ml H₂O/day. Another oryx, a lactating female with a calf 7–10 days old, had a higher water influx than other oryxes. Females nursing calves may have higher water requirements (Maltz and Shkolnik 1984).

During summer, *P. turgidum* consistently had the highest moisture content, around 40% by weight of wet matter for both years, whereas *Stipagrostis* had the lowest values (Table 2). *L. scindicus* contained on average 30.2% water in 1998 and 30.3% in 1999. Water content differed among species (F =515.7, *d.f.* = 2, P < 0.001). The only significant interaction was for species times year (F = 6.8, *d.f.* = 2, P < 0.002), indicating that water content varied among species between years (Table 2).

DISCUSSION

Among similar-sized mammals, water flux can vary by as much as 1 order of magnitude, depending on taxon, season, and diet (Nagy and Peterson 1988). Compared

TABLE 1.—Water-influx rate, body mass, and study conditions for 6 wild Arabian oryxes in Mahazat as-Sayd, Saudi Arabia, during summer.

| Animal | Sex | Month | Mean ambient tempera- ture (°C) | Interval (days) | Mean body mass (kg) | Change in body mass (%/day) | Water influx ^a (ml/day) | ^a Water influx ^b (ml/day) |
|----------------|-----|-----------|--|--------------------|------------------------|-----------------------------------|---------------------------------------|--|
| 1 | F | June | 35.0 | 8.0 | 118.0 | -0.20 | 2,479.6 | 2,387.8 |
| 2 | Μ | August | 32.9 | 8.0 | 101.7 | -0.18 | 2,616.5 | 2,533.5 |
| 3 | F | August | 33.7 | 8.0 | 103.2 | -1.10 | 1,238.0 | 1,143.3 |
| 4 | Μ | September | 32.2 | 7.9 | 96.9 | -0.26 | 1,717.3 | 1,628.9 |
| 5 | F | September | 32.1 | 8.1 | 104 | 0.00 | 3,850.9 | 3,776.4 |
| 6 | М | September | 32.2 | 6.0 | 81.2 | -2.40 | 268.5 | 269.7 |
| \overline{X} | | * | 33.1 | 7.7 | 100.8 | -0.68 | 2,027.5 | 1,956.6 |
| SD | | | 1.1 | 0.8 | 11.9 | 0.91 | 1,225.4 | 1,220.2 |

^a Calculated according to Lifson and McClintock (1966).

^b Calculated according to Williams et al. (2001) with correction for methane production, isotope loss in feces, and fractionation.

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| | | Panicum turgidum | | Lasiurus | scindicus | Stipagrostis ^a | | | |
|-----------|--------------|------------------|------------|--------------|-------------|---------------------------|------------|--|--|
| | | \bar{X} | SD | \bar{X} | SD | \bar{X} | SD | | |
| June | 1998 1999 | 45.4 39.7 | 3.3 2.7 | 35.7 32.8 | 2.7 9.0 | 10.2 4.6 | 8.9 2.5 | | |
| August | 1998 1999 | 41.4 38.2 | 5.5 3.6 | 26.9 23.9 | 14.5 2.2 | 6.6 4.4 | 3.7 0.4 | | |
| September | 1998 1999 | 35.4 36.9 | 6.7 1.1 | 27.9 36.9 | 3.9 3.2 | 3.1 4.3 | 0.9 1.0 | | |

TABLE 2.-Moisture content expressed as percentage of wet mass of 3 important grasses in diet of Arabian oryxes in Mahazat as-Sayd, Saudi Arabia, during summer.

^a Stipagrostis foexiana, S. plumosa, and S. ciliata.

with carnivores, herbivorous mammals have higher rates of water intake because of the relatively high water content and low digestibility of their diet. Nagy and Peterson (1988) reported an allometric equation for herbivorous eutherian mammals, based on 28 measurements of 7 species, that predicts a water-influx rate of 6,937 ml H₂O/ day for a 104.8-kg oryx, 202% higher than what we measured. Nagy and Peterson's (1988) allometric equation for desert eutherians, derived from multiple measurements on 24 species, with the largest being the collared peccary (Dicotyles tajacu, 19.8 kg), predicts a water-influx rate of 8,942 ml H₂O/day for the Arabian oryx. Because oryxes are much larger than peccaries, extrapolation beyond the data should be viewed with caution (Zar 1984). Compared with herbivorous eutherians or with desert eutherians, oryxes appear to have low water-influx rates, a finding consistent with the hypothesis that oryxes have evolved mechanisms that result in a frugal water economy.

We noticed from equations of Nagy and Peterson (1988) that large desert mammals have a higher water flux than similar-sized nondesert mammals. Hence, we reevaluated the relationship between body mass and water flux in large herbivorous mammals in hot environments (Table 3). The allometric equation that describes this relationship is $\log(\text{water-influx rate [liters H_2O/day]}) =$ $-0.885 + 0.922 \cdot \log(body mass [kg]); (r^2 =$ 0.77, F = 26.8, P < 0.001, n = 10). Our data set included both free-living and semifree-living conditions. Dividing water-influx rate for each species by body mass^{0.922} is 1 way of standardizing comparisons, where 0.922 is the slope of our allometric curve. When we did this, we found that the oryx had the lowest normalized water-influx rate, 31.5 ml H₂O kg^{-0.922} day⁻¹ (Table 3).

Our data set for water-influx rate included camels that had access to drinking water, which may have influenced the slope of our regression. Thus, we also compared waterinflux rate among ungulates by dividing it by mass^{0.795}, where 0.795 is the slope of the allometric equation for water-influx rate for herbivorous eutherian mammals (Nagy and Peterson 1988). Again, we found that Arabian oryxes had the lowest mass-adjusted water-influx rate, 30.7% lower than that of the fringe-eared oryx, the species with the 2nd lowest mass-adjusted water-influx rate (Table 3).

With exceptional tolerance to heat and water deprivation, the camel is often regarded as the quintessential desert ungulate (Schmidt-Nielsen 1964; Yagil 1985). We found that mass-corrected water-influx rate for camels varied between 96 and 120.2 ml H_2O kg^{-0.922} day⁻¹, depending on the study (Macfarlane et al. 1963; Maloiy 1973; Siebert and Macfarlane 1971). With a masscorrected water-influx rate one-third to onefourth that of the camel, oryxes appear to conserve water more effectively.

In the oryx, low water turnover may be

TABLE 3.—Water-influx rates expressed as milliliters per day, as milliliters per day normalized to mass^{0.922} for large herbivorous mammals of arid and semiarid environments (this study), and as milliliters per day normalized to mass^{0.795} for herbivorous eutherian mammals (Nagy and Peterson 1988).

| | | | Water-influx rate | | | |
|---|----|--------------|-------------------------------|---|---|------------------------|
| Species | n | Mass (kg) | (ml H ₂ O/ day) | $\begin{array}{c} (ml \ H_2O \\ kg^{-0.922} \\ day^{-1}) \end{array}$ | $\begin{array}{c} (ml \ H_2O \\ kg^{-0.795} \\ day^{-1}) \end{array}$ | Source |
| Camelus dromedarius, Somali camela | 4 | 520 | 31,720 | 99.3 | 219.8 | Maloiy (1973) |
| Bos taurus, Boran cattle ^a | 6 | 417 | 31,692 | 121.6 | 261.8 | Maloiy (1973) |
| Taurotragus oryx, Cape eland ^b | 5 | 211 | 11,540 | 83 | 163.8 | King et al. (1978) |
| Connochaetes taurinus, wildebeest ^c | 1 | 175 | 9,275 | 79.3 | 152.8 | Maloiy (1973) |
| Oryx beisa callotis, fringe-eared oryx ^c | 1 | 136 | 3,944 | 42.5 | 79.4 | Maloiy (1973) |
| <i>Oryx leucoryx</i> , Arabian oryx ^d | 5 | 104.8 | 2,294 | 31.5 | 56.8 | This study |
| Alcelaphus buscelaphus, hartebeest ^c | 2 | 88 | 4,576 | 73.7 | 130.2 | Maloiy (1973) |
| Capra hircus, Somali goat ^a | 4 | 40 | 3,840 | 128 | 204.5 | Maloiy (1973) |
| Antidorcas marsupialis, springbok ^d | 6 | 36.8 | 1,600 | 57.5 | 91.0 | Nagy and Knight (1994) |
| Ovis aries, Ogaden sheep ^a | 12 | 31 | 3,317 | 139.8 | 216.3 | Maloiy (1973) |

^a Semi-free-living in equatorial desert with drinking water available.

^b Outdoor pen with food and water supplied.

° Semi-free-living in natural equatorial desert with no drinking water available.

d Free-living without access to drinking water.

attributable to a combination of behavioral and physiological adjustments. In summer, oryxes spend most of the day lying in the shade, restricting their feeding activities to the cool daylight hours and night (Stanley Price 1989). They often dig shallow depressions beneath shade trees, which presumably facilitates conductance of body heat to the soil surface when they lie down, rather than use evaporative cooling to maintain body temperature.

We estimated food consumption of oryxes in the field from water-influx rate and water content of their diet with the following equation:

$$Q = \frac{W_{tot} - W_{met}}{(aX_1 + bX_2 + cX_3 + dX_4)}$$

where Q = total wet mass of plant material consumed, W_{tot} = water influx (2,294 ml H₂O/day), W_{met} = metabolic water production (ml/day) calculated as 0.028 g H₂O/kJ of energy expended (Schmidt-Nielsen 1990), X₁, X₂, X₃, and X₄ are average water content (g/kg) in *P. turgidum*, *L. scindicus*, *Stipagrostis*, and other plants, respectively (Table 2), and a, b, c, and d are proportions of those plants in the diet. On the basis of a field metabolic rate of 11,467 kJ/day in summer (Williams et al. 2001), $W_{met} = 321$ ml or 14.4% of total daily water influx rate, a value consistent with the finding for the fringe-eared oryx, 16.4% (King et al. 1978). Thus, oryxes obtain 1,973 ml H₂O/day in the plants that they eat during summer (2,294 ml water – 321 ml metabolic water), which would require a consumption of 5.4 kg of wet plant material (3.1 kg dry mass).

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