

# Water and energy balance in Namibian desert sand-dune lizards *Angolosaurus skoogi* (Andersson, 1916)

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**Abstract.** Skoog's lizards (family Cordylidae) live on and in the slipfaces of shifting sand-dunes in the hyperarid Namib Desert. We measured field metabolic rate (FMR) and water flux (doubly labelled water), diet (stomach content analysis), chemical composition of food items (water, energy and mineral contents), evaporative water loss in the field, and standard metabolic rate (SMR) in the laboratory. These lizards had FMRs and food requirements that are about half those of other lizards, although their SMR was not notably low. Water intake rates in the field were high due to consumption of very succulent growing shoots of nara, a perennial shrub in the cucumber family that stays green all year round on underground water obtained via a long tap-root. Consumption of wind-blown, dry plant material (detritus, comprising about 20% of the dry matter in the average diet) may be related to mineral nutrition. Behavioural adaptations (reduced above-ground activity, which lowers food and energy requirements, and selection of succulent plant food) rather than physiological adaptations that reduce resource requirements, appear to be most important in permitting survival of this lizard in its bleak habitat.

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## Introduction

Skoog's lizard, *Angolosaurus skoogi* (Andersson, 1916), a member of the saurian family Cordylidae, occurs only on coastal sand-dunes in northern Namibia and southern Angola, Africa (Steyn, 1963). These dunes are mobile, and harbour little vegetation, so the animal biomass in this hyperarid dune sea is relatively low. Nevertheless, Skoog's lizards occur in surprisingly dense populations in some parts of the habitat, where they far outnumber all other vertebrates (Mitchell *et al.*, 1987).

How are these lizards able to exist in such a seemingly inhospitable place? This question has several important components, which include: what do they eat; how much food do they need and how do they get it; how much water do they need and how do they get it; how do they use their thermal environment to avoid overheating yet maintain acceptable body temperatures in this essentially shadeless habitat; how do they reproduce and where do they deposit their eggs; and how do they deal with predators? Several of these questions have already been addressed. *Angolosaurus skoogi* is primarily herbivorous, the population studied ingesting mostly the green, succulent tissues of the perennial curcubit plant called nara (*Acanthosicyos horridus*) that grows in portions of the dune sea (Pietruszka *et al.*, 1986). The lizards are diurnal, and are active only when environmental conditions permit them to attain and maintain relatively high body temperatures (35–40°C). They have characteristic postures thought to be thermoregulatory in function, and they dive into, and remain below the surface of dune slipfaces when inactive (Hamilton & Coetzee, 1969; Mitchell *et al.*, 1987; Seely *et al.*, 1988). Nara flowers and growing shoots are preferred foods, and are thought to provide the main source of water to the lizards, which do not normally have

access to free water at any time of the year (Mitchell *et al.*, 1987). Dry, wind-blown detritus and dry grass and other plants are also consumed, though the benefits of consuming other material when nara is available are not clear (Mitchell *et al.*, 1987).

Adaptations that facilitate maintenance of water and energy balance in desert habitats have been described for several species of reptiles living in other deserts (Nagy, 1988). The Namib desert may be much older than most other deserts (Crawford, 1981), so one might expect that reptiles living in this desert would possess more advanced or even novel adaptations, and some are known to do so (Louw & Holm, 1972). We studied water and energy metabolism of free-living *Angolosaurus skoogi*, by using doubly labelled water, in order to evaluate the hypothesis that these lizards have lower water, energy and food requirements than other desert lizards. In addition, we measured aspects of diet composition to determine whether consumption of nara might entail some penalty to the lizards, such as osmotic or ionic stress (Mitchell *et al.*, 1987), and to try to understand why the lizards consume dry detritus.

## Materials and methods

### Study site

We studied *Angolosaurus skoogi* lizards living in a single dune slipface at the same study site used by Pietruszka *et al.* (1986), Mitchell *et al.* (1987), and Seely *et al.* (1988). This site is located on the south bank of the Unjab river bed (usually dry) in the Skelton Coast National Park, Namibia, in southwestern Africa (20°09'S, 13°14'E). The cold Benguela current of the Atlantic Ocean is about 15 km to the west, and the air temperature is determined not so much by season but by whether the wind is blowing onshore or offshore. During our study, onshore winds and morning clouds moderated the minimum air temperature (measured just above ground level at the base of a nara plant using a minimum/maximum thermometer): mean 16.6°C, SD 2.0°C,  $n = 7$ . The clouds usually evaporated by 08.00 h, and daytime maximum air temperatures averaged  $32.1 \pm 1.6^\circ\text{C}$  ( $n = 7$ ). Maximum globe temperatures would have been at least 10°C higher (Seely *et al.*, 1988). During the study period, 5–18 January 1988, a trace of rain fell on the last day, after all sampling had been completed. No dew or precipitating fog occurred during our study.

The sand-dunes in this area are barchanoid, and move slowly to the north over the underlying gravel plain. The dominant plant in the study area is nara (*Acanthosicyos horridus*), a leafless member of the cucumber family, which has a long tap-root and occurs primarily along the edges of river courses. Other plants making up the less than 1% total vegetative cover include the low-growing perennials *Merremia guerichii* and *Suaeda plumosa*, which had some green tissues during our study, and the grasses *Stipagrostis hermannii* and *Brachiaria psammophila*, which were visibly dry and brown.

### Doubly labelled water (DLW)

To measure field metabolic rates (FMR) and water flux rates with doubly labelled water (Nagy, 1983), we captured, sexed, weighed, and marked 20 *Angolosaurus skoogi* by toe clipping and with water-soluble paint. We injected them with 0.307 ml of sterile water containing 95 atom % oxygen-18 and 0.1 mCi of tritium. After waiting at least 90 min for the isotopes to mix completely in body water (Nagy, 1980; Nagy & Costa, 1980), we took about 50 µl of blood from an infraorbital eye sinus, and the lizards were released where captured. Beginning 10 days later (during which time the study area was not disturbed by us), we attempted to recapture marked lizards. The 10 captured animals were weighed, their blood was sampled and they were released again. Samples were also taken from two uninjected lizards for measurement of background isotope levels. Blood samples, along with samples of the injection solution, were flame sealed in glass microhaematocrit capillary tubes, and stored on ice pending analysis in Los Angeles. Additional samples of plasma, along with urine and sap from succulent nara stems were flame sealed in capillary tubes pending analyses of osmotic concentrations.

### Diet

Twenty-one *Angolosaurus skoogi* were captured from dunes adjacent to our study dune for analysis of diet. Stomach contents were removed using a fire-polished glass tube as an oesophageal cannula, and the lizards were released unharmed. Four of the lizards had empty stomachs. Stomach contents of the remaining 16 lizards were sorted under a dissecting microscope and dried to constant mass in an oven at 65°C. The average diet, on a dry mass basis, was calculated using weighted

means of each diet item. Fresh samples of the diet items were collected from the study area into tared, sealable containers for subsequent measurements of water, energy and mineral contents. We took care to select only items that lizards could reach, and we collected items during the time of day that lizards might have eaten them. Samples of freshly voided faeces from recaptured lizards were collected opportunistically for chemical analyses. (These faeces could have been voided prematurely due to capture stress, and may have had higher water contents as a result.)

#### Evaporative water loss

In order to estimate the amount of water these lizards lost by evaporation while buried in the sand, we measured body mass losses of marked animals buried continuously for 24-h periods. [This procedure requires the assumption that the lizards did not defecate or urinate while submerged, which is reasonable because lizards usually defecated and urinated soon after emergence, using a stereotyped, tail-arching posture (Seely *et al.*, 1988), which accompanies opening of the cloacal vent, and which would be difficult to achieve while submerged.] Fine thread, 1 m in length and having a small piece of coloured plastic surveyor's tape on one end, was tied around the waists of six lizards. After being weighed, they were allowed to bury in a dune slipface, and their positions were marked with stakes. Exactly 24 h later, those that showed no evidence of having emerged since initial burial were recaptured, weighed, and released for a second 24-h measurement period.

#### Standard metabolic rate

Three *Angolosaurus skoogi* living on sand-dunes at the Samanab river bed 15 km north of our study site were collected and returned to Los Angeles for measurements of standard metabolic rate. The lizards were housed for several months in a terrarium containing Namib sand, with an incandescent light bulb providing a photothermal gradient  $10 \text{ h day}^{-1}$ . After being held without food for 2 days, they were placed individually in a flow-through gas exchange system kept at  $30 \pm 0.5^\circ\text{C}$ . Rates of  $\text{CO}_2$  production (STPD) during the inactive (nocturnal) phase of the diel cycle were measured using a Li-Cor 6251  $\text{CO}_2$  analyser and a Sigma mass flow controller. We assumed a respiratory quotient of 0.71 and an energy equivalent of

$27.7 \text{ kJ l}^{-1} \text{CO}_2$  (fat metabolism) for purposes of interconverting among units of standard metabolic rate.

#### Sample analyses

Blood samples were microdistilled to obtain pure water, which was then analysed for tritium by liquid scintillation counting, and for oxygen-18 by proton activation analysis (Wood *et al.*, 1975; Nagy, 1983; see also Speakman *et al.*, 1990). Body water volumes of injected animals, which are required in the calculations, were estimated as dilution spaces of injected oxygen-18 water. Rates of  $\text{CO}_2$  production and water flux were calculated using the equations for linearly changing body water volumes (Nagy, 1980; Nagy & Costa, 1980), and heat equivalents of  $\text{CO}_2$  volumes were calculated assuming a diet of plant matter yields  $21.7 \text{ J ml}^{-1} \text{CO}_2$  (Nagy, 1983).

Plasma, urine and nara sap samples were measured for osmotic concentration using a Wescor model 5100B vapour pressure osmometer. Samples of food and faeces were weighed fresh, dried to constant mass at  $65^\circ\text{C}$ , and reweighed to determine water content. The remaining dry matter was powdered in a Spex Mixer/Mill using only plastic utensils and containers to minimize metal contamination. Energy contents were determined with a Phillipson microbomb calorimeter, and metal concentrations were estimated with an Applied Research Laboratories optical emission spectrophotometer.

#### Statistics

Results are shown as means and standard deviations. Possible correlations between variables were examined by the method of least squares regression analysis (Dixon & Massey, 1969). Differences between means were tested for significance ( $P < 0.05$ ) using a two-tailed *t*-test, except where an *F*-test indicated that variances were heterogenous. In those cases, the Mann-Whitney U-test was used. Other statistical procedures used are described below.

#### Results

Of the 10 lizards we recaptured, four were females and six were males (Table 1). There were no statistically significant differences in body mass or mass-specific rates of  $\text{CO}_2$  production or water influx, so the results were pooled. Mean body mass

was 57.4 g, of which an average of 73.0% (SD = 2.0%,  $n = 13$ ) was body water. Most lizards lost slight amounts of body mass over the 11–13-day measurement periods, and the mean rate of body mass change differed significantly from zero ( $P < 0.005$ ,  $t$ -test). Because animals that are not maintaining constant body mass may have atypical feeding rates, FMRs and water influx rates, it is important to obtain estimates of these rates in steady state animals before comparing field results with other species. To do this, we first corrected the DLW results in Table 1 for individual animal differences due to body mass by regressing  $\log kJ \text{ day}^{-1}$  and  $\log \text{ml H}_2\text{O influx day}^{-1}$  on  $\log g$  body mass, then dividing the DLW data by  $g$  mass to the appropriate exponent. Both regressions were highly significant ( $F_{1,8} = 17.4$ ,  $P < 0.005$  for FMR and  $F_{1,8} = 10.9$ ,  $P < 0.025$  for water influx, via  $F$ -tests for significance of the regression), and yielded exponents of 1.06 for FMR and 1.48 for water influx rate. The mass-normalized results were then regressed against rate of change of body mass. Neither of these regressions was significant ( $P < 0.50$  via  $F$ -tests), indicating no detectable relationship between body mass change and the physiological variables within our data set. Thus, we could use the mean values shown in Table 1 to represent FMR and water influx rate of *Angolosaurus skoogi* lizards maintaining constant body mass in the field during January.

The 17 stomach contents examined were made up mostly of fresh, green nara (*Acanthosycios horridus*) stem tips (shoots) and flower parts (71.6% by dry mass of total diet). Eight stomachs contained only green nara shoots and flowers. Dry

nara flower petals made up 1.4% of the diet, so nara stem tips accounted for a total of 70.0% of the diet's dry mass. Dry leaves and stems of the grass *Stipagrostis hermannii* comprised 19.0% of the diet, and dry seeds (apparently also from *Stipagrostis hermannii*) accounted for 1.3% of the diet. These two items were apparently consumed as wind-blown detritus available at the base of dune slip faces. Faecal pellets, apparently from *Angolosaurus skoogi* but possibly from *Aporosaurus anchietae* lizards also living on the slipfaces, accounted for 6.1% of the diet, loose sand (not in faecal pellets) made up 0.03%, and aphids comprised 0.2% of the diet. The aphids may have been ingested incidentally along with nara shoots, as many nara plants in our study area were infested with these homopteran insects.

The water content of nara shoots was high, averaging  $4.04 \text{ g H}_2\text{O g}^{-1}$  dry matter, or 80% water, whereas the grass contained less than 15% water (Table 2). (The water content value in Table 2 for faeces was measured on freshly voided faeces from recaptured lizards. The faeces in stomach contents most probably was ingested after it had dried to below 20% water.) Energy contents of nara and grass are typical of other desert plants (Nagy & Shoemaker, 1975), but that of faeces is relatively low, probably because the faeces contained much sand. Faeces from captive *Angolosaurus skoogi*, which probably ingested less sand with their food than did free-living lizards, had higher energy contents [ $21 \text{ kJ g}^{-1}$  (Pietruszka *et al.*, 1986) and  $20.2 \text{ kJ g}^{-1}$  (B.C. Clarke & K.A. Nagy, unpublished observations)]. These faecal energy values yield an apparent assimilation value for energy of about

**Table 1.** Field metabolic rates (FMR), body masses, and water flux rates of Skoog's lizards *Angolosaurus skoogi* in summer (January) of 1988 in the Namib Desert.

Animal		Body mass		FMR		Water influx	
No.	Sex	Mean (g)	Change (% day <sup>-1</sup> )	(ml CO <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup> )	(kJ day <sup>-1</sup> )	(ml kg <sup>-1</sup> day <sup>-1</sup> )	(ml day <sup>-1</sup> )
2	F	48.2	-0.26	0.106	2.65	10.0	0.48
4	M	90.1	-0.17	0.114	5.36	11.0	0.99
8	F	47.5	-0.59	0.073	1.82	4.1	0.19
13	M	42.0	-0.74	0.099	2.17	12.2	0.51
14	M	92.9	-0.23	0.089	4.32	18.2	1.69
16	M	43.6	-0.17	0.058	1.32	9.5	0.41
17	F	41.6	-0.16	0.095	2.06	8.3	0.35
18	M	56.6	-0.13	0.108	3.17	16.3	0.92
19	M	75.4	+0.09	0.106	4.19	17.2	1.30
20	F	36.4	-0.30	0.141	2.67	16.5	0.60
Mean		57.4	-0.27	0.099	2.97	12.3	0.74
SD		21.0	0.24	0.023	1.28	4.6	0.47

**Table 2.** Composition of diet items and faeces, and estimated assimilation of dietary substances by *Angolosaurus skoogi*. Units shown are on a per gram dry mass basis, and means are given with standard deviation in parentheses.

Substance	<i>Acanthosycios horridus</i> shoots (n=2)	<i>Stipagrostis hermannii</i> stem, leaves (n=2)	<i>Angolosaurus skoogi</i> faeces (n=6)	Apparent assimilation*
Water (g)	4.04(0.0)	0.17*	1.70(0.9)	81
Energy (kJ)	19.9(0.9)	16.1(0.3)	14.4(3.9)	72
Potassium (mg)	33.0(3.4)	1.2(0.02)	26.2(10.5)	63
Calcium (mg)	4.3(0.2)	3.4(0.2)	3.1(1.0)	72
Phosphorus (mg)	3.3(0.04)	3.6(0.5)	20.2(2.4)*	-124*
Magnesium (mg)	4.2(0.0)	2.1(0.04)	5.1(1.5)	50
Sodium (mg)	0.18(0.02)	3.2(0.3)	5.3(3.3)*	-151*
Silicon (mg)	2.1(0.3)	5.5(0.4)	15.2(2.0)*	-103*
Iron (mg)	0.33(0.006)	1.1(0.4)	4.4(0.6)*	-233*
Aluminium (µg)	104(28)	533(150)	3050(1500)*	-503*
Zinc (µg)	47(13)	0(0)	115(45)	-14
Copper (µg)	14(0.1)	5.4(1.2)	47(8)*	-42*
Manganese (µg)	26(1.1)	94(24)	719(390)*	-580*
Boron (µg)	17(0.8)	14(2)	26(5)	41
Titanium (µg)	18(1.9)	82(44)	880(210)*	-963*
Chromium (µg)	0.07(0.09)	1.6(0.8)	12(3)*	-1100*
Strontium (µg)	2.5(0.03)	14(1)	29(4)*	-125*
Tin (µg)	0.5(0.2)	0.8(0.1)	1.3(0.4)	14
Lead (µg)	23(0.6)	7.3(1.2)	34(4.6)	36

\* Apparent assimilation = 100[(estimated amount of substance per g dry diet, assuming a diet of 80% *Acanthosycios horridus* shoots and 20% *Stipagrostis hermannii* leaves and stems) - (amount of substance per 0.372 g *Angolosaurus skoogi* faeces)] / (amount of substance per g dry diet); dry matter assimilation value of 62.8% assumed from B.C. Clarke & K.A. Nagy (unpublished observations).

\* n = 1.

\* Results affected by sand in faecal samples.

60%, which is probably more accurate than the 72% value shown in Table 2.

The high concentrations of silicon, sodium, iron, aluminum, manganese, titanium and other substances in the faeces are also probably due to sand contamination rather than to undigested residues from the food (Table 2). The electrolyte contents we measured in our plant samples are similar to those measured by Mitchell *et al.* (1987), although the K:Na quotients differ somewhat between studies. We estimated the apparent assimilation coefficients for the substances listed in Table 2 by assuming that the diet was approximately 80% nara and 20% *Stipagrostis*, and that 1 g dry matter of this diet yields 0.372 g dry faeces (B.C. Clarke & K.A. Nagy, unpublished observations). The negative assimilation values shown for 10 of the substances in Table 2 are probably due to the effects of sand in the faeces, along with the fact that our dietary intake calculations do not account for sand ingestion by the lizards. The elemental concentration values determined by emission spectrometry (Table 2) are relatively inaccurate and variable (as indicated by the high standard

deviations for many values), and are best viewed as approximations of the metal content of the samples.

The six lizards used to measure evaporative water loss during submersion weighed 31.1 g (range 15.4 - 46.7 g) and lost 0.251 g (range 0.177 - 0.314 g) of body mass per 24 h of burial in a slipface. As might be expected, log water loss rate was correlated with log body mass ( $P < 0.05$  via an *F*-test). The relationship is described by the equation  $\log(\text{g water lost day}^{-1}) = 0.91 \log(\text{g body mass}) - 2.0$ , with  $r^2 = 0.66$ , standard error of slope = 0.32, and SE of intercept = 0.48.

Osmotic pressures of plasma samples from free-living lizards averaged  $357 \pm 19$  mosM ( $n = 7$ ). Fresh urine samples had concentrations of  $313 \pm 50$  mosM ( $n = 9$ ), while samples of sap from nara shoots averaged  $491 \pm 8$  mosM ( $n = 3$ ).

Standard metabolic rates (SMR) of three *Angolosaurus skoogi* at a body temperature of 30°C averaged  $0.063 \pm 0.013$  ml  $\text{CO}_2$   $\text{g}^{-1} \text{h}^{-1}$ . Their body masses averaged  $28.7 \pm 20.3$  g. This SMR value is only about 30% of the value of 0.30 ml  $\text{O}_2$   $\text{g}^{-1} \text{h}^{-1}$  (equivalent to 0.21 ml  $\text{CO}_2$   $\text{g}^{-1} \text{h}^{-1}$ ) reported by

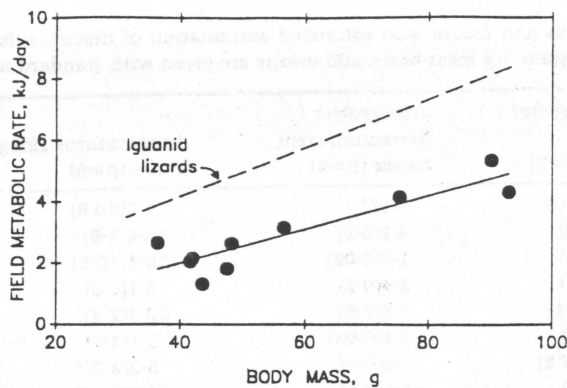


Fig. 1. Field metabolic rates of *Angolosaurus skoogi* (filled circles and solid line) are about half of those of iguanid lizards during their activity season (represented by dashed line; from Nagy, 1987).

Mitchell *et al.* (1987) for *Angolosaurus skoogi* weighing 15.6 g. We suspect that their lizards were not completely at rest and post-absorptive.

## Discussion

### Comparative energetics and water fluxes

The daily energy requirement of free-living *Angolosaurus skoogi* is remarkably low in comparison to that of most other lizards studied to date. Iguanid lizards of similar size have FMRs during their activity seasons (Nagy, 1982) that are much higher than the FMRs of *Angolosaurus skoogi* (Fig. 1). The FMR predicted for an iguanid lizard having a body mass of 57.4 g is 5.70 kJ day<sup>-1</sup> (Nagy, 1987). Thus, *Angolosaurus skoogi* have a mean FMR (2.97 kJ day<sup>-1</sup>, Table 1) that is only about half of that required by other lizards to exist for 1 day. This low energy requirement is clearly of adaptive value in an environment having sparse food resources.

How does *Angolosaurus* achieve such a low energy requirement? Several other species of lizards also have FMRs about half of those expected on the basis of their body mass. These include three species in the family Xantusiidae ('night lizards'; W.J. Mautz & K.A. Nagy, unpublished observations), and a Namib desert gecko (K.A. Nagy, M.K. Seely & R. Fuffenstein, unpublished observations). The low metabolic rates of night lizards have physiological as well as ecological and behavioural components. They have standard metabolic rates that are also only half those of other lizards, and they are reclusive, sedentary, and select relatively low body temperatures in the field (Mautz, 1979). The desert

gecko (*Rhoptropus afer*) also has a low standard metabolic rate (Peterson, 1990) along with its low FMR, but it is not particularly reclusive, sedentary, or thermophobic. *Angolosaurus skoogi* does not seem to share the reduced SMR of xantusiids and the gecko: our measurements of SMR are virtually the same as predicted SMR for equivalent-sized squamate reptiles (Andrews & Pough, 1985). Moreover, *Angolosaurus skoogi* probably maintains moderate to high body temperatures (between 25 and 40°C) throughout the day, whether above or below ground, during the season in which our measurements were made (Mitchell *et al.*, 1987). Thus, it appears that these lizards have low FMRs primarily because they are comparatively inactive in their natural habitats. Mark-release-resight studies (Mitchell *et al.*, 1987) suggest that individual lizards are active every third day, and may remain buried for 5 days or longer. Focal-animal studies of time-activity budgets are needed to evaluate the question of whether individual lizards remain underground for long periods of time compared to other lizard species.

Despite their low FMRs, water influx rates in Skoog's lizards were typical of other desert lizards. Their mean rate of water influx (Table 1) is about 80% of that predicted for a desert reptile of their average body mass (Nagy & Peterson, 1988), and there is much overlap of measured and predicted values for individual animals (Fig. 2). They achieved this rate of water consumption mostly by selecting a diet item that was unusually succulent. Nara shoots had a higher water content than many (though not all) plant foods consumed by another herbivorous desert lizard (*Sauromalus obesus*; Nagy, 1973), and nara was more succulent than all diet items consumed by the plant-eating desert lizard *Dipsosaurus dorsalis* (Mautz & Nagy, 1987). Again, a behavioural difference seems to account for the ability of Skoog's lizards to obtain surprising amounts of water.

'Water economy index' is the ratio of the total amount of water taken in each day to the amount of energy used that day (Nagy & Peterson, 1988). The lower this ratio, the less water an animal uses per unit of 'living'. Desert vertebrates tend to have lower WEI values than their non-desert relatives, reflecting adaptations to their arid habitat. Desert reptiles have WEI values averaging about 0.20 m H<sub>2</sub>O influx kJ<sup>-1</sup> metabolized. *Angolosaurus skoogi* lizards had a WEI value of 0.25, higher than most other desert lizards studied to date, and at the upper end of the theoretical range in WEI for herbivorous vertebrates that do not drink water. This indicates that behavioural adjustments (diet

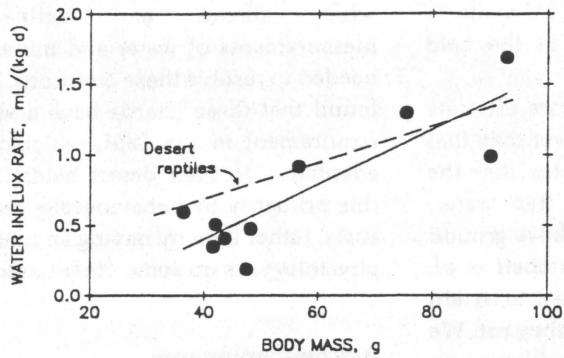


Fig. 2. Rates of water influx in free-ranging Skoog's lizards (filled circles and solid line) are similar to those of other desert lizards (represented by dashed line; from Nagy & Peterson, 1988).

selection) rather than physiological adaptations that reduce water requirements directly, are probably more important to these lizards.

#### Feeding rate

It is possible to estimate the feeding rate of an animal from measurements of both its FMR and its water intake rate, provided that the diet and its metabolizable energy and water yield are known, and the food was the only source of exogenous water. B.C. Clarke & K.A. Nagy (unpublished observations) have measured a mean dry matter assimilation of 62.8% in *Angolosaurus skoogi* lizards fed a diet similar to that in this study. Using energy content measurements of food and faeces from several studies (see above), we estimated that 60% of dietary energy, or 11.5 kJ g<sup>-1</sup> dry matter, was assimilated. Assuming that about 10% of this, or 1.2 kJ g<sup>-1</sup>, was voided as chemical potential energy in urinary solids (as with *Sauromalus obesus*; Nagy & Shoemaker, 1975), then the food provided 10.3 metabolizable kJ g<sup>-1</sup> dry matter. The amount of food needed to just meet metabolic energy expenditures would be 0.29g dry matter day<sup>-1</sup> [(2.97 kJ metabolized day<sup>-1</sup>)/(10.3 metabolizable kJ g<sup>-1</sup>)] for a 57.4-g lizard.

A diet of 80% nara shoots and 20% dead *Stipagrostis* would contain 3.27 ml H<sub>2</sub>O g<sup>-1</sup> dry matter (calculated from Table 2). Metabolic water produced from oxidation of the metabolizable energy in 1g of this food is about 0.40 ml g<sup>-1</sup> dry matter [based on conversion factors in Nagy (1983)], so total water yield of this diet is about 3.67 ml g<sup>-1</sup> dry matter. Thus, with a water influx rate of 0.74 ml day<sup>-1</sup> (Table 1), and assuming no drinking water was available, a 57.4-g lizard would have had to consume 0.20g dry matter

day<sup>-1</sup> of food. This estimate is 70% of that based on energy metabolism (above), and is in general agreement given the uncertainties in diet composition and the assumptions involved in this calculation.

A typical herbivorous iguanid lizard of the body mass of our lizards may be expected to consume about 0.57g (dry matter) of food per day (Nagy, 1987), so *Angolosaurus* lizards require only about 35–42% of the food iguanid lizards need to maintain homeostasis. This low food requirement may be considered to be a desert adaptation, and it appears to be due to the small amount of time these lizards spend active above ground. Although such behaviour may confer advantages in terms of reduced energy requirements, it may occasion disadvantages such as reduced breeding opportunities and loss of social and territorial status. Observations of reproductive and social behaviour would be especially interesting in light of this finding.

#### Water balance

The minimum rate at which a lizard must obtain water to achieve balance is determined by its minimum water loss rate. The mean water efflux rate calculated from hydrogen isotope data gathered in this study was 14.3 ± 4.2 ml kg<sup>-1</sup> day<sup>-1</sup>, or 0.82 ml day<sup>-1</sup> for a 57.4-g individual. Evaporative water loss measurements on submerged lizards in the field indicate that a lizard this size would lose 0.40 ml day<sup>-1</sup> if it stayed underground continuously.

Evaporation undoubtedly would be higher when lizards emerged during daylight hours. We can estimate faecal water loss from food intake rate (0.20–0.24g dry matter day<sup>-1</sup>), dry matter digestibility (62.8%), and faecal water content (1.70 ml g<sup>-1</sup> dry faeces, Table 2) to be about 0.14 ml day<sup>-1</sup>. This leaves 0.28 ml day<sup>-1</sup> for urinary water loss and evaporation while above ground. These lizards have been observed to void > 3 ml of urine when active in the field (Peitruszka *et al.*, 1986). It would take about 10 days for a 57.4-g lizard to accumulate that much urine, if the estimates in this study are correct. More time would be required if evaporative water loss above ground is much higher than that below ground. Casual observations of captive lizards suggest that they lose water rapidly when above ground, raising the possibility that reduced above-ground activity in the field may be more a consequence of high evaporative water loss than of low food availability in the habitat. Detailed laboratory

measurements of water losses must be made to permit a more detailed evaluation of the field water budget of these lizards.

The observation that the feeding rate estimate based on water intake (above) was lower than that based on energy metabolism indicates that the lizards we studied did not drink free water. Indeed, no free water was available above ground during our study. We agree with Mitchell *et al.* (1987) that *Angolosaurus skoogi* appear to obtain all the water they need from the nara they eat. We did not observe lizards drinking sap welling up on bitten-off stem stumps, as did Pietruszka *et al.* (1986), but this behaviour would not seem to be necessary to achieve water balance given that nara shoots themselves are 80% water.

Skoog's lizards may also obtain all the energy they need from nara, because the organic matter in growing shoots is mostly in soluble form, rather than in relatively indigestible fibre, as in more mature plant tissues. This fact raises the question of why these lizards seek out and consume dry, wind-blown detritus, which undoubtedly has a comparatively low energy yield, and may even require more water to excrete as moist faeces than it brings into the lizard (Nagy, 1972). Does *Stipagrostis hermannii* detritus contain some nutrient that is relatively unavailable in nara? The osmotic concentration of nara sap is high [491 mosM, similar to the value of 563 mosM measured by Mitchell *et al.* (1987)], and it will be osmotically stressful to the lizards. (Their plasma and urine osmotic concentrations were relatively high.) This suggests that nara may provide more than enough salts to the lizards. However, analyses of elemental contents of nara and grass (Table 2) indicate that sodium may be a nutrient that is more abundant in detritus.

#### Desert survival

We agree with Pietruszka *et al.* (1986) and Mitchell *et al.* (1987) that *Angolosaurus skoogi* lizards can survive in their hyperarid dune sea habitat primarily because they can eat nara shoots and flowers, which are very succulent and provide all necessary water to the lizards. The long tap-roots of nara bring subterranean water, that fell as rain in the distant mountains, to the surface in the form of succulent, easily digestible plant tissues. Potential drawbacks to this food source include its high osmotic concentration, and its possible nutritional deficiency (perhaps sodium). Its consumption may be necessitated by a high water requirement by the lizards due to high evaporative water losses

while abroad and active. Laboratory measurements of water and mineral budgets are needed to resolve these questions. In addition, we found that these lizards have a very low energy requirement in the field, which we view as an adaptation to their desert habitat. They achieve this primarily by behaviourally reducing activity costs, rather than by having an unusual metabolic physiology, as do some other desert lizards.

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