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FIELD METABOLIC RATE OF A DIURNAL DESERT GECKO, *Rhoptropus afer*

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Abstract: Doubly labeled water measurements of the field metabolic rate (FMR) of a diurnally-active, heliothermic, Namib Desert gecko reveal a surprisingly low daily energy requirement. FMRs averaged 230 J/d, which is only half of that expected for a 2.6-g diurnal lizard, and is also half that of two species of nocturnal desert geckos. *Rhoptropus afer* also has a low standard metabolic rate, indicating that this is a physiological, rather than a behavioral phenomenon. The resulting low food requirement (55% of predicted) adapts *Rhoptropus afer* to the relative scarcity of resources in its habitat. These lizards were able to maintain water balance in the field on their insect diet alone, without drinking water, despite exposing themselves to the very desiccating microenvironments that occur on granite outcrops during daylight hours. The remarkably low resource requirements of these geckos are not unique, however, occuring also in three nocturnal, arid-habitat species of xantusiid lizards.

Key words: Gekkonidae; field metabolic rate; food requirement; *Rhoptropus afer*; Namib Desert; doubly labeled water; ecological energetics; water flux; desert adaptation; water balance; drinking

INTRODUCTION

Reptiles and amphibians have very low food and energy requirements in comparison with birds and mammals, and this low cost of living apparently permits these ectotherms to exploit several ecological and natural history parameters that may be unavailable to endothermic animals (Pough, 1980, 1983). For example, small size and elongate shape make endothermy difficult due to thermoregulatory constraints, but these same properties may favor thermoregulation by ectotherms. Also, an ectotherm's greater ability to endure periods of low food and water availability may favor their occupation of habitats such as deserts.

If low food and energy requirements confer advantages to reptiles in general in some habitats, then it is reasonable to suggest that similar advantages may accrue to different families within the Class Reptilia. Do metabolic rates and food requirements also differ between species in different families in a manner that is expected from their life-style and habitat? Three species within the Family Xantusiidae are known to have low resting metabolic rates (RMR) and low field metabolic rates (FMR) in comparison with other families af lizards (Mautz, 1979; Mautz and Nagy, unpublished results). These xantusiids live in arid areas, are nocturnal, and are reclusive. Another family, the Gekkonidae, also contains species that live in deserts and are nocturnal, and they might be expected to have low energy requirements as well. Surprisingly, the FMRs of a nocturnal

Kalahari Desert gecko, Pachydactylus bibroni, and a nocturnal Negev Desert gecko, Ptyodactylus hasselquistii, were not notably low (Nagy and Degen, 1988; Nagy and Knight, 1989). These results suggest that these geckos may either have unexpectedly-high thermal profiles through a typical day, or they may be much more active than expected for a nocturnal lizard, or they may possess unusually high RMR, which may be a characteristic of the family. In order to test the latter hypothesis, we took advantage of an opportunity to measure FMRs of a diurnally-active desert gecko, Rhoptropus afer, in the Namib Desert. We expected their FMRs to higher than, or at least the same as, those of other diurnal lizards.

MATERIALS AND METHODS

We studied geckos (Rhoptropus afer Peters 1869) at the southern edge of their distribution in Namibia (Haacke and Odendaal, 1981). Our study site (23° 31′ S, 14° 59′ E) was adjacent to the southern bank of the Kuiseb River, 8.5 km NW of the Desert Ecological Research Unit at Gobabeb. The lizards were abundant on the relatively flat, exfoliating granite outcrops. Maximum daytime air temperatures during the study averaged 33.4 ± 3.3°C (n = 23), and minimum temperatures averaged 16.5 ± 2.3°C (n = 23) at Gobabeb. Light dew was measured on 2 January, the day of initial capture; precipitating fog was recorded on 6 and 9 January, and 0.7 mm of rain fell at 2200 on 17 January.

On the morning of 2 January 1988, we captured 22 geckos, injected them intraperitoneally with 14.5 ul of sterile water containing 95 atom % oxygen-18 and 4.8 uCi of tritium, weighed them, numbered them with water-soluble paint and felt-tipped marker ink, took a small (20 ul) blood sample from the infraorbital eye sinus (or a urine sample, if available) between two and three hours after injection, and released them where captured by 1330 h. Blood samples were taken from two uninjected geckos for measurement of background isotope levels, and a sample of injection solution was taken for subsequent calibration. Three weeks later, on 22 and 24 January, we attempted to recapture marked geckos. It soon became apparent that most marked geckos had shed their skins, along with our marks. (We found one gecko in the process of shedding painted skin, and we found bits of shed, painted skin on the ground.) Thereafter, we recaptured all geckos we saw, weighed them, and took a blood sample, in order to determine from the presence of enriched isotopes whether they were marked or not. Six injected animals were recaptured.

Blood, urine, and injection solution samples were flame-sealed in glass capillary tubes and kept on ice during transport to the University of California, Los Angeles for analysis. There, samples were microdistilled under vacuum to obtain pure water, which was analyzed for tritium using a Beckman LS 230 liquid scintillation counter, and for oxygen-18 by proton activation analysis (Nagy, 1983; Wood et al., 1975). Body water volumes of injected geckos were calculated as O-18 dilution space from O-18 concentrations in initial blood samples (Nagy, 1983).

Because we were unable to determine which initial sample went with each of the recaptured lizards, we estimated initial isotope concentrations for each lizard from its body mass, a regression of body water volume on body mass, and constants representing the dilution kinetics of both isotopes in body water (Nagy, 1983; Nagy et al. 1984). This involves the assumption that recaptured geckos maintained approximately constant body masses over the 3 wk measurement period, which seems reasonable because the recaptured lizards did not appear to be particularly thin or fat, and growth by these already-adult lizards should not have been great during the measurement period. The maximum errors associated with these assumptions and procedures should be about 5% for FMR and about 15% for water flux rates. The polarity of these errors should be random, so mean FMR and water flux values should be relatively accurate (Nagy, 1980; Nagy and Costa, 1980). We calculated rates of CO_2 production and water flux using the equations for constant body water volumes (Nagy, 1980; Nagy and Costa, 1980), and heat equivalents of CO_2 volumes were calculated assuming that an insect diet yields 25.7 joules per ml CO_2 (Nagy, 1983). The insectivorous diet of these geckos was confirmed by visual examination of stomach contents of several animals that died during final blood sampling.

Results are expressed as means along with standard deviations. Other statistical procedures used are described below.

RESULTS

The average body mass of the six recaptured lizards was 2.6 g (Table 1). Total body water volumes (O-18 dilution spaces) of all injected geckos averaged 74.0 ± 2.6% of body mass (n = 20). The mean field metabolic rate was 8.8 ml CO_2 per day (or 227 J/d, in units of energy metabolism), and water influxes averaged 51 ul/d (Table 1).

DISCUSSION

To address the question of whether Rhoptropus afer has a FMR typical of other lizards, we compared the mean FMR of R. afer with that predicted for a 2.6 g iguanid lizard (Nagy, 1987). Rhoptropus afer had FMRs (227 J/d) averaging only 47% of that expected (481 J/d), and the value for R. afer lies outside the 95% confidence interval of the prediction (327 to 706 J/d), indicating that the difference is statistically significant. All individuals had much lower costs of living than expected for equivalent-sized iguanid lizards (Fig. 1). This low energy, and hence food, requirement probably facilitates survival in the relatively-barren habitat that these lizards occupy.

Regarding the various modes of energy metabolism among lizards, four categories seem to be emerging. First, the iguanid lizard pattern of FMR being about 6% that of an equivalent-sized bird or mammal (Nagy, 1987) is shared by four species of lacertid lizards (Nagy et al. 1984; Nagy, 1987; Vernet et al. 1988), two nocturnal species of geckos (Nagy and Degen, 1988; Nagy and Knight, 1989), and one skink (Nagy and Knight, 1989), and may represent the general lizard pattern. The second mode is represented by three species of xantusiid ("night") lizards, which have FMRs about half of those of iguanid lizards (Mautz and Nagy, unpublished results). These xantusiids also have very low resting metabolic rates, suggesting a physiological mechanism underlying the low FMR. This mode may be shared by the lacertid Acanthodactylus pardalis (Vernet et al., 1988). The third mode is shown by the cordylid lizard Angolosaurus skoogi, which has a low FMR but an iguanid-like RMR (Nagy, Clarke, Seely, Mitchell, and Lighton, unpublished results). This suggests that behavioral mechanisms, such as reclusiveness or relative inactivity, account for their low FMR. Fourth, high FMRs coupled with iguanid-like RMRs occur in two species of teiid lizards (Anderson and Karasov, 1981 and 1988; Karasov and Anderson, 1984); a lacertid (Bradshaw et al., 1987), and a varanid lizard (Green et al., 1986). Behavioral differences (increased activity costs) are probably also the cause of the high FMRs in these lizards.

Rhoptropus afer appears to fall in the second category: low FMR and low RMR (physiological adjustment). Peterson (1990) found that R. afer has a standard metabolic rate that is only 51% of that predicted for a squamate reptile of equivalent size (Andrews and Pough, 1985), and is lower than any other gecko yet measured. Given that R. afer is diurnally-active, a sit-and-wait insect predator, and has body temperatures up to 38°C when active (Brain, 1962; Burrage, 1973; Odendaal, 1979; Werner, 1977), and that other diurnal, predatory squamate reptiles have RMRs that are significantly higher than nocturnal, fossorial and reclusive squamates (Andrews and Pough, 1985), it is very surprising to discover such a low cost of living for this species. These geckos are very alert, quick-moving and difficult to catch. Thus, their low metabolic rates do not correspond with sluggishness.

The water flux rates of individual *R. afer* tended to be lower than those of other desert reptiles (Fig. 2). The mean flux rate of 0.051 ml/d (Table 1) is 63% of that expected for a 2.6 g desert reptile, but this difference is not statistically significant (primarily because of the large variation among values used in deriving the predictive equation of Nagy and Peterson, 1988). Nevertheless, these results are consistent with the interpretation that *Rhoptropus afer* has comparatively low water requirements. This is especially interesting in light of the observations of Mautz (1982) that 1) about half of total water lost by desert lizards is by evaporation, and about half of the evaporative loss occurs through the skin, and 2) skin evaporation rate is highly dependent on temperature, wind velocity and humidity, so that cutaneous evaporation is potentially very high for a lizard basking on a rock during the day. We predict from these observations that the skin of *Rhoptropus afer* has an extraordinarily low permeability to water, and suggest that measurements of evaporative water loss be made on this species. *Rhoptropus* geckos, like the xantusiid lizards, have spectacles (clear scales) over their eyes, which probably reduce evaporative water losses substantially (Mautz, 1982), and contribute to very low water requirements.

Rates of food consumption may be estimated in two ways: that required to provide the metabolizable energy the lizards used, as measured with DLW, and that required to account for measured water intake rate. We assumed that the insect diet of R. afer was nutritionally similar to that of two species of insectivorous lizards in the southern Kalahari (Nagy et al., 1984), and that it yielded 15.1 kJ metabolizable energy and 3.39 ml of preformed plus metabolically-produced water per g of dry food mass. Both methods yield the same estimate of feeding rate: 15.0 mg dry food consumed per day. This estimate is only 55% of the feeding rate predicted for an insectivorous iguanid lizard of the same size (Nagy 1987), further illustrating the economical life of these geckos. The remarkably good agreement between these two estimates of feeding rate indicates that no additional water was ingested by the geckos during our study. Thus, these lizards apparently can maintain water balance without drinking water in the field.

Desertic conditions have prevailed in the Namib for a long period of time. Since the Cretaceous, arid to semi-arid conditions have dominated, although the extreme aridity is thought to have developed since the late Tertiary (Ward et al., 1983). This has provided a long time for the evolution of adaptations to this relatively cool, aseasonal coastal desert (Lancaster et al., 1984).

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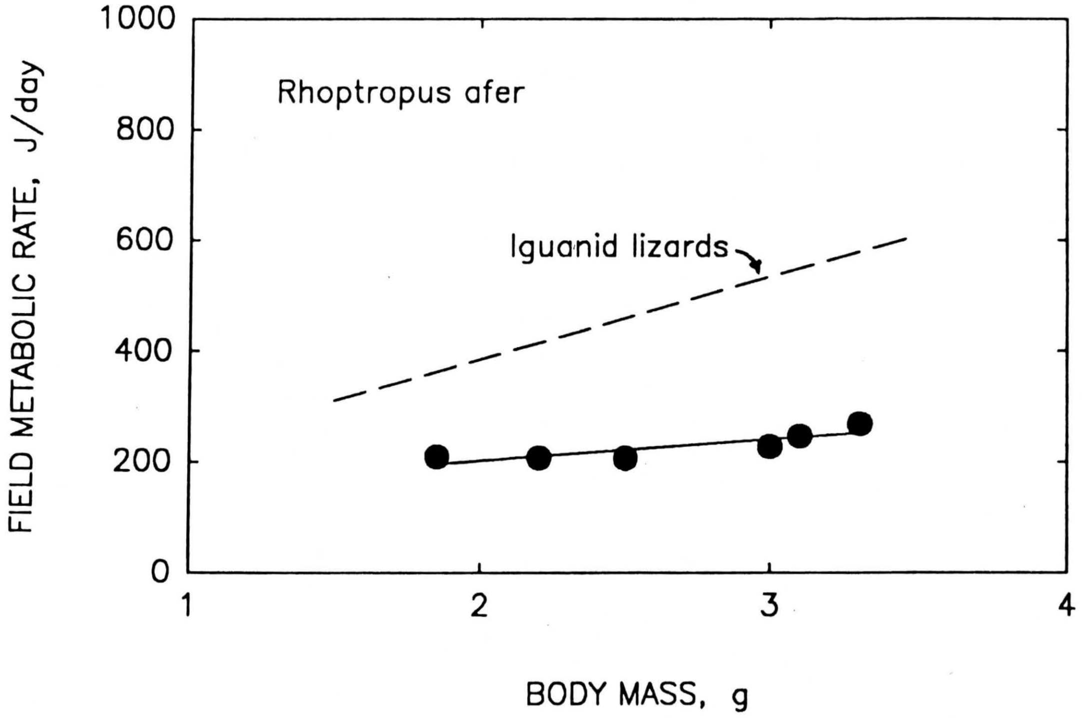
Table 1. Body mass, field metabolic rate and water influx rate in Namib Desert geckos *Rhoptropus afer* in mid-summer (January) 1988.

Animal	Body mass, (g)	Measurement time, (d)	FMR (ml CO_2 g^{-1} h^{-1})	FMR (ml CO_2 d^{-1})	FMR (J d^{-1})	Water influx (ml $kg^{-1}d^{-1}$)	Water influx (ml d^{-1})
1050	3.0	20.1	0.123	8.8	227	16.1	0.048
1054	1.85	20.1	0.183	8.1	209	18.7	0.035
D	3.3	22.3	0.132	10.4	268	12.8	0.042
G	2.2	22.3	0.152	8.1	207	20.0	0.044
I	3.1	22.3	0.129	9.6	246	32.5	0.101
K	2.5	22.3	0.133	8.0	206	14.6	0.037
Mean	2.6	21.6	0.142	8.8	227	19.1	0.051
S.D.	0.6	1.1	0.022	1.0	25	7.1	0.025

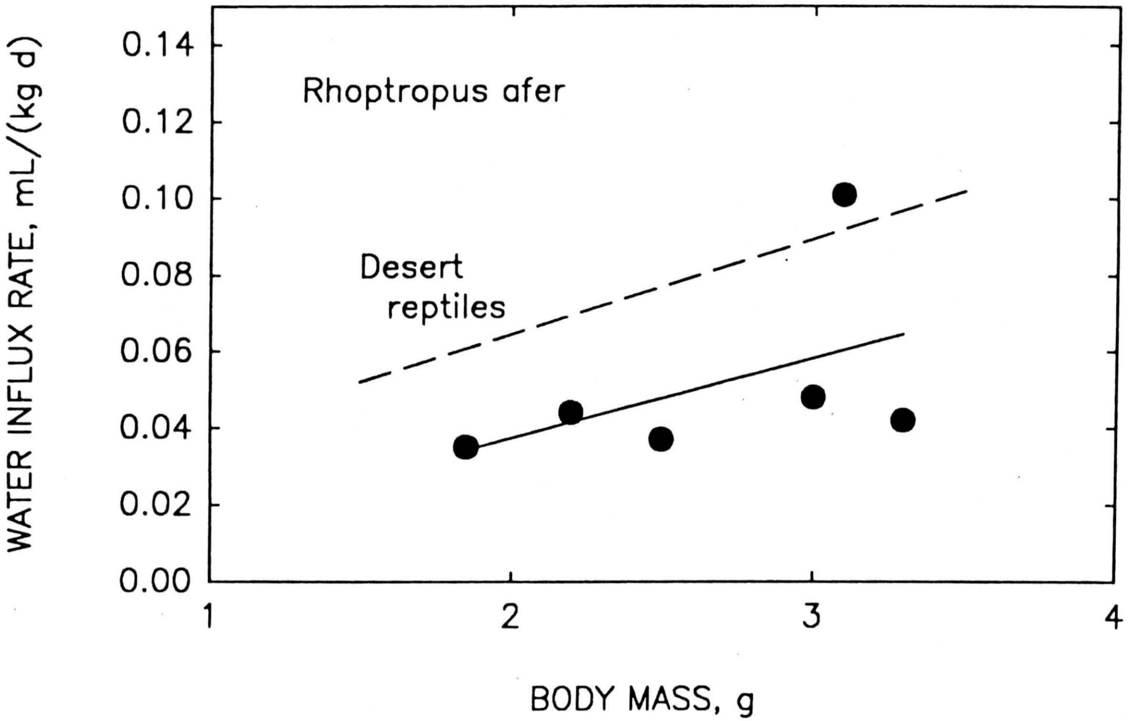
FIGURE LEGENDS

Fig. 1. Field metabolic rates of *Rhoptropus afer* (filled circles and solid line) are about half of those of iguanid lizards of similar size (dashed line, from Nagy, 1987).

Fig. 2. Rates of water influx in free-ranging Rhoptropus afer (filled circles and solid line) compared to those expected for desert reptiles of similar size (dashed line, from Nagy and Peterson, 1988).


Rhoptropus afer
Iguanid lizards
FIELD METABOLIC RATE, J/day
0
200
400
600
800
1000
1
2
3
4
BODY MASS, g

F. 2


Rhoptropus afer
Desert
reptiles
WATER INFLUX RATE, mL/(kg d)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
1
2
3
4
BODY MASS, g