SURPRISINGLY LOW FIELD METABOLIC RATE OF A DIURNAL DESERT GECKO, *RHOPTROPUS AFER*.—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 some microhabitats and lifestyles 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.

A major reason for the relatively low energy requirements of reptiles is that they have low body temperatures during much of a 24-h cycle in the field, whereas most endotherms maintain constant, high body temperatures (Nagy, 1987). Accordingly, one might expect nocturnal lizards to have lower field metabolic rates (FMRs) than diurnal lizards have, because active nocturnal lizards usually cannot achieve body temperatures as high as can diurnal lizards during their activity period. Thus, it was surprising to discover that the FMRs of a nocturnal Kalahari Desert gecko, *Pachydactylus bibroni*, and a nocturnal Negev Desert gecko, *Ptyodactylus hasselquistii*, were not notably low and were statistically indistinguishable from FMRs of diurnal iguanid lizards (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, they may be much more intensely active than expected for a nocturnal lizard, or they may possess unusually high concentrations or activities of metabolic enzymes, which may be a characteristic of the family. 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 its FMR (corrected for differences in body mass) to be higher than those of the nocturnal geckos, as a result of *R. afer* spending more time each day at higher body temperatures (Brain, 1962; Odendaal, 1979). Exposure to daytime climatological conditions of low humidity, solar radiation, and higher air temperatures should also increase evaporative water losses, and we expected water flux rates in *R. afer* to be elevated as well.

Methods.—We studied geckos (*Rhoptropus afer*) 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 were typical (Lancaster et al., 1984), averaging 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 Jan., the day of initial capture; precipitating fog was recorded on 6 and 9 Jan., and 0.7 mm of rain fell at 2200 on 17 Jan.

On the morning of 2 Jan. 1988, we captured 22 geckos, injected then intraperitoneally with 14.5 μl of sterile water containing 95 atom percent oxygen-18 and 4.8 μCi of tritium, weighed them, numbered them with water-soluble paint and marked them with felt-tipped ink, took a small (20 μl) 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 Jan., we returned to the site and recaptured two marked geckos, but it was apparent that most marked geckos had shed their skins, along with our marks. Thereafter, we recaptured all geckos we saw, weighed them, and took a blood sample, to determine from the presence of enriched isotopes whether they were marked or not. Four more injected animals were recaptured in this fashion.

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

TABLE 1. BODY MASS, FIELD METABOLIC RATE, AND WATER INFLUX RATE IN NAMIB DESERT GECKOS *Rhoptropus afer* (n = 6) IN MIDSUMMER (JAN.) OF 1988.

	Mean	SD	Minimum	Maximum
Body mass, g	2.6	0.6	1.8	3.3
Measurement period, days	21.6	1.1	20.1	22.3
Field metabolic rate:				
mL $CO_2 \cdot g^{-1} \cdot h^{-1}$	0.142	0.022	0.123	0.183
mL $CO_2 \cdot d^{-1}$	8.8	1.0	8.0	10.4
$J \cdot d^{-1}$	227	25	206	268
Predicted $J \cdot d^{-1}$	481*			
Actual FMR/predicted FMR	0.47			
Water influx rate:				
mL $\cdot kg^{-1} \cdot d^{-1}$	19.1	7.1	12.8	32.5
mL $\cdot d^{-1}$	0.051	0.025	0.035	0.101
Predicted mL $\cdot d^{-1}$	0.081*			
Actual WIR/predicted WIR	0.63			

* FMR predicted using eq. 38 for iguanid lizards from Nagy (1987), WIR predicted using eq. 19 for desert reptiles from Nagy and Peterson (1988).

concentrations in initial blood samples (Nagy, 1983).

Because we were unable to determine which initial sample went with each of the recaptured lizards, we used the single-sample, doubly labeled water (DLW) method (Nagy et al., 1984; Webster and Weathers, 1989). This method involves prediction of each recaptured animal's initial isotope levels from its initial body mass, using empirical regressions of initial isotope concentration on body mass, as calculated from results for the 22 injected geckos. A validation study of this method revealed only small errors: CO_2 production rate estimates averaged less than 0.5% different from either directly measured CO_2 production (Haldane method) or the two-sample DLW method (range −8.3–11.2%), and water flux rates estimated using the single-sample method averaged 1.5% lower than two-sample method results (range −13.7–2.0%; Webster and Weathers, 1989). The additional potential error in our study resulting from our assumption that initial body masses were the same as recapture body masses was evaluated by recalculating the DLW results using initial mass and body water values that were 10% higher and 10% lower than weight-maintenance values. This resulted in CO_2 production errors of less than 0.12%, water influx errors of less than 0.13%, but water efflux errors of +21.5% and −24.0%. Thus, the maximum errors associated with these assumptions and procedures should be less than 1% for FMR and water influx rates but up to 25% for water efflux 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.—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% (±SD) 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 μl/d (Table 1).

To address the question of whether *R. afer* has an FMR that is higher than that 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 averaging only 47% of that expected (481 J/d), and the value for *R. afer* lies outside the 95% confidence interval of the prediction (327–706 J/d), indicating that the difference is statistically significant.

The water influx rates of *R. afer* tended to be lower than those of other desert reptiles. 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). A comparatively low rate of water influx would be expected for a species having a low FMR and, hence, a low food requirement, because the main avenue of water intake in a desert reptile is its food (Nagy and Peterson, 1988).

Discussion.—Our hypothesis that the diurnal *R. afer* would have an FMR higher than those of two species of nocturnal geckos is clearly negated by these results. The FMRs of the nocturnal geckos did not differ significantly from those of diurnal iguanid lizards, and the FMR of *R. afer* not only did not exceed these values but it was significantly lower than expected. The differences between *R. afer* and the nocturnal geckos can be illustrated by comparing the body-mass-corrected FMR value (calculated assuming the scaling exponent of 0.8 for iguanid lizards is applicable to gekkonids): *R. afer*, 0.106 kJ g$^{-0.8}$ d^{-1}; *Ptyodactylus hasselquistii*, 0.204 kJ g$^{-0.8}$ d^{-1}; *Pachydactylus bibroni*, 0.239 kJ g$^{-0.8}$ d^{-1}.

What can account for the surprisingly low FMR of *R. afer*? When they are abroad, they are alert, sprint rapidly, and are difficult to catch with a noose, so the intensity of their activity does not seem unusually low. It is possible that they select unusually low body temperatures when inactive, but the scarcity of low environmental temperatures for long periods in the retreats available in their habitat makes this unlikely. More likely is the possibility that the metabolic machinery of *R. afer* differs from that of other lizards, allowing this species to function at a much reduced FMR. Three species of lizards in the family Xantuisiidae have resting (standard) metabolic rates that are about half those of most other lizards studied (Mautz, 1979), and their field metabolic rates are also about half of those expected (Mautz and Nagy, 1988). Resting metabolic rate typically accounts for about 30–60% of FMR in lizards (Peterson et al., 1990), so a 50% reduction in resting metabolism, alone, would not completely account for a 50% reduction in FMR. This suggests that these xantusiid lizards also have unusually low costs for activity.

Rhoptropus afer also has a resting metabolic rate that is about half or less of that expected for a similar-sized squamate or lizard (Peterson, 1990). Thus, it seems likely that the physiology and biochemistry of energy metabolism in this species differs from that of iguanid lizards, perhaps in a manner similar to that between mammals and reptiles, where large differences in mitochondrial densities and metabolic enzyme activities are known to occur (Else and Hulbert, 1981; Hulbert and Else, 1981). All species of xantusiid lizards thus far studied show reduced metabolic rates, suggesting low energy metabolism may be a property of that family. To date, *R. afer* is the only nonxantusiid lizard known to have low energy metabolism, and the observation that this is atypical of geckos suggests that the family Gekkonidae has much interesting diversity remaining to be explored. Such diversity may contribute importantly to understanding of the evolution of high metabolic rates and endothermy (Else and Hulbert, 1987).

Suggested measurements to help resolve these questions, pertaining to both *R. afer* geckos and to xantusiid lizards, include field determinations of 24-h behavior and body temperature patterns; the relation of SMR to body temperature; and the relative density of mitochondria and activities of key metabolic enzymes in muscle and liver tissues.

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REPRODUCTION AND BEHAVIOR OF WESTERN MUD SNAKES (FARANCIA ABACURA REINWARDTII) IN AMERICAN ALLIGATOR NESTS.—Mud snakes (Farancia abacura) frequent aquatic lowlands along the Atlantic Coastal Plain south through Florida, westward across the Gulf states, and northward up the lower Mississippi River Valley (Smith, 1938; McDaniel and Karges, 1983) where they prey primarily on aquatic salamanders (Amphiuma, Siren), and to a lesser extent on frogs and fish (Van Hyning, 1932; Meade, 1946; Clark, 1949). This species is behaviorally unusual in that it is one of the few snakes, aside from pythons, that exhibits maternal care during incubation (Meade 1937; Riemer, 1957; Shine, 1988). Among the few literature records of nesting in the wild is one by Deitz and Jackson (1979) who found a clutch of the eastern subspecies (F. a. abacura) in the nest of an American alligator (Alligator mississippiensis) in northcentral Florida. We report an additional four clutches of the western subspecies (F. a. reinwardtii) found at Lacassine National Wildlife Refuge (30°00′N, 92°50′W) in southwestern Louisiana and here provide a synopsis of known aspects of reproductive biology for mud snakes.

On 9 July 1985, an active alligator nest was discovered containing a clutch of 33 alligator eggs that we deduced were laid between 30 June and 5 July. The nest measured 170 × 160 × 58 cm and was constructed of maidencane (Panicum hemitomon). The eggs were covered by 30 cm of vegetation and had a core temperature of 30 C. This nest was examined again on 8 August. By that time, the nest had been depredated (probably by a raccoon, Procyon lotor). The nest was scattered into three clumps but partly rebuilt. No alligator eggs or eggshells were present. However, while searching for the latter, two clutches of western mud snakes were found about 1 m apart within the remaining structure (Table 1). A small female was captured and photographed at clutch 1-A and then