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Comparative Field Energetics of a Kalahari Skink (*Mabuya striata*) and Gecko (*Pachydactylus bibroni*)

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Many diurnal lizards maintain comparatively high body temperatures by means of behavioral thermoregulation. They should have higher daily integrated body temperatures, and hence higher daily energy and food requirements than nocturnal lizards, which have lower body temperatures when active. We tested this hypothesis with a diurnal skink and a nocturnal gecko, both of which are arboreal insectivores. Doubly labeled water measurements indicate that field metabolic rates (FMR), water flux rates, and feeding rates do not differ between these two sympatric Kalahari lizards. Our results suggest that geckos: 1) may have higher body temperatures during the daytime; 2) may be more active while abroad; 3) may be abroad longer each day; and, 4) may have different thermal effects on their energy metabolism than previously thought.

ENERGY use by ectothermic animals depends, in part, on body temperature (Bartholomew, 1982). Resting (or standard) metabolic rates of reptiles double or triple with a 10 C increase in body temperature until the temperature at which normal activity occurs is reached (Bennett and Dawson, 1976). Thus, the warmer a lizard is, the greater its energy expenditures for maintenance. Activity costs are additive to resting costs, and small, active, diurnal lizards have metabolic rates that are about three times higher than when they are at rest (Bennett and Nagy, 1977; Merker and Nagy, 1984). The energetic costs of staying warm and being active are such that a small, diurnal lizard typically spends about eight times more energy to be abroad and active for a day than it does to remain in a cool burrow all day (Merker and Nagy, 1984).

We hypothesized that these profound effects of temperature on the daily energy expenditures of lizards should be reflected, in general, as systematically lower field metabolic rates in nocturnal lizards as compared with diurnal lizards. We tested this hypothesis by comparing the field metabolic rates (FMR) of a sympatric diurnal skink and a nocturnal gecko. Both species are insectivorous, weigh between 15–20 g, and live on the trunks of acacia trees, replacing each other on the same trees at sunrise and sunset. Thus, the species are quite similar ecologically, with the main difference being the daily timing of the activity period.

MATERIALS AND METHODS

We studied adult skinks (*Mabuya striata*) and geckos (*Pachydactylus bibroni*) living on trees, rock walls and buildings in Nossob Camp, Kalahari Gemsbok National Park, South Africa, during 13–28 Oct. (austral spring) 1986. The trees in camp were the native species *Acacia eriloba* and *Boscia albitrunca* along with a few exotic *Prosopis chilensis*. Some lizards lived near an irrigated garden, and thus experienced a more mesic habitat than others we studied. We recorded locations of each lizard, evaluated the mass-corrected FMR and water influx results for any significant differences between individuals living close to, and far from, the garden, and found none (probability values (|*Ps*| > 0.35, Students t-values |t| = 0.50 and t = 0.38, respectively, degrees of freedom |df| = 4 for both) comparing the three skinks nearest the garden with the three more distant skinks, and *P* > 0.08 (t = 0.96, df = 7 for FMR) and *P* = 0.056 (Mann-Whitney U value |U| = 3, n = 5,4 for water influx), comparing the five geckos near the garden with four farther away. However, because these lizards may have experienced a somewhat lusher habitat inside the camp than lizards in the field, caution is advised in making comparisons of our results with those from other studies.

On 13 Oct. 1986, 12 skinks were captured in the morning, and 13 geckos were caught after dusk. All lizards were given an intraperitoneal injection of 0.101 ml of sterile water (containing 95 atoms % oxygen-18 and 30 microcuries of tritium) at the time of capture. Each lizard was weighed to the nearest 0.01 g and given an identification number (painted on its back). Some of the toes of the skinks, but not the geckos, also were clipped for future identification. One hour after injection, about 50 microliters of blood were taken from an orbital sinus, and the lizard was released at the point of capture. Two weeks later (27–28 Oct.), we recaptured six marked skinks and nine marked geckos. Each lizard was then weighed and a second blood sample was taken before re-release. When possible, we took urine samples rather than blood samples from recaptured lizards, in order to minimize trauma. Urine has been found to reach isotopic equilibrium with blood within several hours after injection (Nagy and Costa, 1980), so using urine samples rather than blood from recaptured lizards should introduce no error.

Samples from injected lizards, along with three samples from uninjected lizards (for measurement of isotope natural abundance levels) and a sample of the injection solution, were flame-sealed in glass capillary tubes and kept on ice during transport to the University of California, Los Angeles for analyses. We microdistilled samples to obtain pure water, which was then analyzed for tritium using a liquid scintillation counter, and for oxygen-18 by proton activation analysis (Wood et al., 1975; Nagy, 1983a). Rates of CO_2 production and water flux were calculated using the equations for linearly-changing 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 [J]/ml CO_2 (Nagy, 1983b). We corrected FMR data for differences among individual lizards' body masses using the mass exponent 0.80 (Nagy, 1982a). This exponent was calculated from iguanid lizard FMR data, but we used it for our skink and gecko data because exponents for scincid and gekkonid lizards presently are unavailable. Water flux data were corrected for mass differences using the mass exponent 0.91 for reptiles living in arid and semi-arid habitats (Nagy, 1982b).

Conversion of FMR data from units of CO_2 production to units of heat production, and estimation of feeding rates from FMR and water influx rate data require knowledge of the diet and its chemical composition. Both species of lizards are known to eat arthropods primarily (Huey and Pianka, 1977; Pianka and Huey, 1978; Pianka, 1986), and we confirmed this by analyzing stomach contents of all recaptured animals, along with eight unmarked skinks captured at the end of the study. A fire-polished glass cannula was gently inserted down a lizard's esophagus, and all of its stomach contents were massaged into the opening of the tube and removed. Prey items were identified using a dissecting microscope.

We measured minimum and maximum air temperatures with a Min-Max thermometer placed in continuous shade at ground level. Rainfall amounts were recorded using a standard meteorological rain gauge located within Nossob Camp.

Results are expressed as means along with 95% confidence intervals. Comparisons between mean values were done with Student's t-statistic, after confirming that distributions were homogeneous by means of the F-statistic (Afifi and Azen, 1979). For nonhomogeneous distributions, we used the Mann-Whitney U-statistic (Dixon and Massey, 1969).

RESULTS

The mean body mass of the recaptured skinks (19.5 g) was about 17% greater than that of the geckos (16.6 g), but this difference is not statistically significant (Table 1). Both species maintained essentially constant body masses on average. Thus, we used the mean values of physiological variables in Table 1 to represent steady-state conditions in free-living lizards.

Surprisingly, the field metabolic rates of skinks and geckos did not differ significantly (Table 1, Fig. 1). Water flux rates, on a whole-animal basis, were significantly greater in skinks than in geckos (Table 1). However, this difference was not significant when corrected for differences in body mass. Body water volumes, as estimated by the dilution space of injected oxygen-18 (Nagy, 1980), were significantly lower ($P < 0.01$) in skinks (66.0 ± 3.1% of live body mass, n = 6) than in geckos (76.7 ± 1.5%, n = 9).

Both species of lizards primarily ate arthropods. Three geckos had empty stomachs. Among the remaining six geckos, three (50% of total) contained only grasshoppers, one (17%) had eaten only a solphugid, and the stomachs of two others (33%) contained leg parts of arthropods along with much sand. Of the 14 skinks captured for diet analysis, six had empty stomachs. Among the remaining eight, two (25%) had eaten only moths, two (25%) ate only grasshoppers, one (13%) ate only leafhoppers, and three (37%) ate various other insects and shed lizard skin.

Minimum and maximum air temperatures in the shade at ground level averaged 20.0 ± 1.9 C (n = 11) and 33.7 ± 2.1 C, respectively. Daytime relative humidities ranged between 15 and 20%. A total of 8.4 mm of rain fell on 16 and 17 Oct., and trace amounts of rain fell on 19 and 22 Oct.

DISCUSSION

Comparative energetics.—It is clear that the FMR of the gecko is not lower than that of the skink (Table 1). Moreover, these two lizards have field energy requirements that are indistinguishable from those of iguanid lizards. The mean FMR of skinks (2.9 kilojoules [kJ]/d) is well within the 95% confidence interval of the prediction (1.6–3.5 kJ/d) of FMR for an iguanid lizard weighing 19.5 g, and the mean FMR of geckos (2.2 kJ/d) also is within the 95% confidence interval [CI] of the FMR prediction (1.4–3.1 kJ/d) for a 16.6 g iguanid lizard (Nagy, 1982a, 1987). This is surprising, in view of the strongly nocturnal activity period of geckos. Several questions for future research come to mind. The unexpectedly high FMR of geckos may be due, in theory, to: 1) high metabolic rates at night (possibly from unusually intense activity levels or long activity periods); 2) high metabolic rates during daylight hours from activity bouts while in daytime retreats; 3) high daytime metabolic rates from behavioral regulation of high body temperatures while in retreats; or, 4) high overall energy expenditures due to high levels of resting metabolism (thermal acclimation and acclimatization, Bartholomew, 1982).

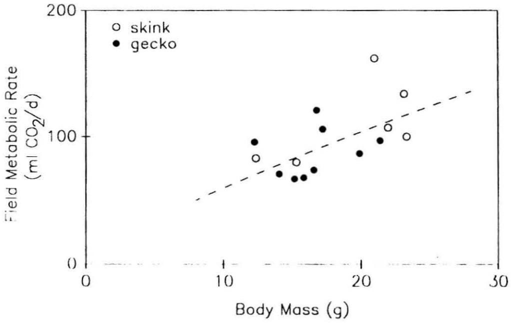

Fig. 1. Relationship between field metabolic rate and body mass for Kalahari Desert skinks (*Mabuya striata*) and geckos (*Pachydactylus striata*). Dashed line represents iguanid lizards (ml CO_2/d = $8.72g^{0.80}$, modified from Nagy, 1982).

We doubt that resting metabolism of *Pachydactylus* geckos is unusually high, because those of other geckos are not notably high (Bennett and Dawson, 1976; Withers, 1981; Andrews and Pough, 1985). We observed some evidence of geckos "basking" after sunrise by leaving their tails exposed to the sun, but serving to plug their burrows at the same time, much as the Austra-

TABLE 1. COMPARISON OF BODY MASSES, FIELD METABOLIC RATES AND WATER FLUX RATES OF SYMPATRIC SKINKS (*Mabuya striata*) AND GECKOS (*Pachydactylus bibroni*) IN THE KALAHARI DESERT. Values are means ± 95% confidence intervals.

	Skink (diurnal) (n = 6)	Gecko (nocturnal) (n = 9)	*t*-value, *P*[a]
Body mass			
Mean, g	19.5 ± 4.8	16.6 ± 2.1	1.55, n.s.
Change rate, $\%\cdot\text{day}^{-1}$	+0.4 ± 0.6	+0.1 ± 0.7	0.65, n.s.
Field metabolic rate			
ml $CO_2\cdot\text{day}^{-1}$	111 ± 33	87 ± 15	1.81, n.s.
$\text{kJ}\cdot\text{day}^{-1}$	2.9 ± 0.9	2.2 ± 0.4	1.82, n.s.
$\text{kJ}\cdot\text{g}^{-0.80}\cdot\text{day}^{-1}$[b]	0.27 ± 0.06	0.24 ± 0.04	0.87, n.s.
Water influx rate			
ml $H_2O\cdot\text{day}^{-1}$	0.64 ± 0.24	0.40 ± 0.09	2.71, <0.02
ml $H_2O\cdot\text{kg}^{-0.91}\cdot\text{day}^{-1}$[b]	23.4 ± 7.8	17.7 ± 5.2	1.53, n.s.
Water efflux rate			
ml $H_2O\cdot\text{day}^{-1}$	0.59 ± 0.21	0.38 ± 0.07	2.69, <0.02
ml $H_2O\cdot\text{kg}^{-0.91}\cdot\text{day}^{-1}$[b]	21.5 ± 6.7	16.8 ± 4.6	1.47, n.s.

[a] n.s. = not significant ($P > 0.05$); all data sets passed an F-test for homogeneity of variance. Degrees of freedom = 13 for all t-tests.
[b] Corrected for differences in body mass.

lian gecko *Diplodactylus conspicillatus* is thought to do (Pianka, 1986). Pianka and Huey (1978) observed an individual *Pachydactylus bibroni* basking in full sunlight early in the morning, at a body temperature of 32.8 C. These observations support explanation (3) above, but determination of daily time budgets and thermal regimes for both of these species is essential for a conclusive answer to this problem.

Comparative water relations.—Like FMR, water flux rates also are related exponentially to body mass in reptiles, with an exponent of 0.91 for reptiles living in arid and semi-arid habitats (Nagy, 1982b). Mass-corrected water flux rates of the skink and the gecko did not differ significantly (Table 1). Thus, part of the difference in whole-animal water fluxes is due to differences in body mass between species. Mass-corrected water influx rates in skinks and geckos were 114% and 86% of the mean, mass-corrected influx rate of 20.5 $\text{ml}\cdot\text{kg}^{0.91}\cdot\text{d}$ in arid and semi-arid reptiles (Nagy, 1982b).

Feeding rate.—Doubly labeled water results can be used to calculate rates of food intake in two ways. First, if the amount of dietary metabolizable energy is known, then the daily food ration can be calculated from FMR. Secondly, if the dietary yields of "preformed" water and "metabolic" water (formed in vivo during oxidative metabolism) are known, and if the animal does not drink any water, then the feeding rate required to account for the observed rate of total water influx can be calculated. This method gives an estimate of actual feeding rate, which can then be compared to the feeding rate required to achieve energy balance (above), in order to evaluate the daily performance of the lizard (Nagy, 1975). We used the values of 15.1 kJ of metabolizable energy and 3.39 ml of preformed plus metabolic water yielded per g of dry food, which were obtained from the diets of two other species of insectivorous, Kalahari lizards (Nagy et al., 1984).

The two feeding rate estimates for skinks are very similar: 0.192 g dry matter of food consumed per day to maintain energy balance, and 0.189g/d estimated from water influx rate. This agreement lends confidence to our food requirement estimates, and suggests that skinks may not have drunk any free water during our study period. For geckos, a larger difference exists between the two feeding rate estimates: 0.146 g/d to achieve energy balance, and 0.118 obtained according to water influx calculations. The observation that the water-influx-based rate is lowest suggests that geckos also did not drink water. Differences in species composition of the geckos diet could account for this discrepancy in feeding rate estimates: a diet containing less fat and more water would result in closer agreement between feeding rate estimates. The food requirement estimated herein for skinks is not significantly different from that expected for an iguanid lizard having the same body mass and diet (Nagy, 1987). A Kalahari gecko requires about the same amount of food each day as does a similar-sized iguanid lizard in the New World.

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