

# SEASONAL WATER INFLUX AND ENERGY EXPENDITURE OF FREE-LIVING FAT SAND RATS

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**ABSTRACT.**—Free-living fat sand rats (*Psammomys obesus*) consumed only saltbush (*Atriplex halimus*), did not drink water, and maintained constant body mass in summer and winter. Rates of water influx and energy expenditure of adults were greater in winter than in summer. Daily intake of dry matter by adults ranged from 9.3 (summer) to 11.0% (winter) of body mass; intake of fresh matter ranged from 24.7 (summer) to 32.0% (winter) of body mass. Water content of *A. halimus* consumed by adult fat sand rats was similar in the two seasons; therefore, the increase in water influx in winter was related mainly to a greater consumption of fresh matter. Mass-specific influx of water in winter was greater in juveniles than in adults, but mass-specific expenditure of energy was similar in the two cohorts. This indicated that juveniles selected leaves of *A. halimus* with greater water content than did adults. Intakes of dry matter and fresh matter by juveniles were 11.8 and 43.4% of their body masses, respectively.

The fat sand rat (*Psammomys obesus*) is a diurnal gerbillid rodent (Gerbillinae: Cricetidae) widely distributed in the Sahara–Arabian deserts (Walker et al., 1975). This rodent is herbivorous and is able to thrive by consuming only leaves and stems of plants belonging to the family Chenopodiaceae (Daly and Daly, 1973). In deserts of Israel, it feeds heavily or entirely on the saltbush *Atriplex halimus* and does not drink water (Degen et al., 1990; Frenkel and Kraicer, 1972).

*Atriplex halimus* has high water content, thus provides much water; however, this plant has a low yield of metabolizable energy and is high in electrolyte content (Degen et al., 1988; Kam and Degen, 1988). To reduce their electrolyte intakes, fat sand rats scrape the salt-containing cuticular and epicuticular layers from the leaf with their teeth before consuming it. Rats scrape relatively large amounts of tissue from dry leaves and smaller amounts from moist leaves (Degen, 1988; Kam and Degen, 1988). A similar leaf-scraping behavior was reported for the chisel-toothed kangaroo rat *Dipodomys microps*, a New World desert heteromyid that feeds on the saltbush *A. confertifolia* (Kenagy, 1972, 1973).

Because of the low yield of energy and high moisture content of *A. halimus*, fat sand rats must consume large amount of dry and fresh matter to satisfy their energy requirements. In this study, we used doubly labelled water to determine the seasonal water influx and energy expenditure, and the dry and fresh matter intakes for fat sand rats. Seasonal changes in availability of water are dramatic in desert habitats, but fat sand rats may have solved this potential problem by feeding solely on an evergreen shrub year-round.

## MATERIALS AND METHODS

The study was conducted in the Negev Desert near Sede Boqer (30°52'N, 34°47'E). This region is arid, having 250–300 biologically dry days per year and a precipitation: evaporation ratio of <0.2 (United Nations Educational, Scientific, and Cultural Organization, 1977). Rainfall occurs in winter and averages 90 mm annually with large differences in its temporal and spatial distributions. Dew amounts to 18 mm annually and occurs on about 190 nights (Zangvil and Druian, 1980). Temperatures are highest in August, with a daily mean of 25.3°C, and are lowest in January, with a daily mean of 9.7°C (Zangvil and Druian, 1983).

As adults, fat sand rats are solitary and each inhabits a complex burrow system with several openings, usually at the base of an *A. halimus* shrub (Orr, 1972). We examined shrubs and burrow entrances for signs of activities of fat sand rats. Active sites were characterized by stems of *A. halimus* shrubs freshly gnawed

by fat sand rats, fresh feces at the entrance of the burrows, clean burrow entrances, and freshly used paths. Fifty modified Havahart traps, baited with fresh leaves of *A. halimus*, were used to capture fat sand rats. Three to four traps were placed at burrow openings at each site judged to be inhabited by a fat sand rat. Traps were set before dawn and monitored at 1-h intervals.

Water influx and carbon dioxide production for fat sand rats were measured in winter (January–February) and in summer (July–August) 1986 in an area that had a high density of *A. halimus*. Captured animals were toe-clipped for identification and weighed to  $\pm 0.01$  g on a balance. Each animal was injected intraperitoneally with 0.5 ml water containing 97 atom %  $^{18}\text{O}$  (Yeda, Rehovot) and 1.85 MBq/ml of tritium (New England Nuclear). Two hours were allowed for equilibration of the isotopes with body fluids (Culebras et al., 1977; Karasov, 1981) after which time a blood sample was collected from the infraorbital sinus of the rat by use of hematocrit capillary tubes. The animals then were released at the capture site. Initial capturing of fat sand rats was done for 3 days during which time traps were not set at sites where fat sand rats had been captured previously. Animals were recaptured 3–21 days after injection and a second blood sample was collected. The animals were weighed and released.

Blood samples were refrigerated then micro-distilled to obtain pure water (Wood et al., 1975). Specific activity of tritium was determined by liquid scintillation spectrometry (Kontron). Duplicate 0.5-ml samples were added to 5 ml of Bray's solution and counted for 10 min. Counts were corrected for quenching by use of a series of quenched standards. Levels of  $^{18}\text{O}$  concentration were measured in triplicate by an autogamma-counting system (Packard) after converting  $^{18}\text{O}$  to gamma-emitting  $^{18}\text{F}$  by cyclotron-generated proton activation (Wood et al., 1975). Three samples from noninjected fat sand rats were similarly treated to determine background levels of isotopes.

Volume of total body water was estimated from the initial dilution of  $^{18}\text{O}$  and water flux was calculated from the subsequent decline in specific activity of tritium at recapture (Nagy and Costa, 1980). Rates of  $\text{CO}_2$  production were estimated from the declines in specific activities of tritium and  $^{18}\text{O}$  through time. We assumed that the total body water volume, as a fraction of body mass of the fat sand rats, remained constant over the measuring period and that any change in absolute total body water volume was linear (Nagy, 1980).

To convert  $\text{CO}_2$  production of fat sand rats to energy expenditure, we used the conversion factor of 21.7 J metabolizable energy/ml  $\text{CO}_2$ , as reported for rodents consuming vegetation (Karasov, 1982). Intake of dry matter of *A. halimus* was calculated by assuming 9.58 kJ of metabolizable energy/g dry matter (Kam and Degen, 1989). This method yields an estimate of the feeding rate required to achieve energy balance, a reasonable assumption because fat sand rats were maintaining constant body masses (Table 1). Production of metabolic water was calculated as 0.31 ml water/g dry matter consumed (Kam and Degen, 1989), and preformed water was calculated as water influx minus metabolic water. We assumed negligible influx of water vapor across lungs and skin of fat sand rats and that they did not drink water or lick dew. No free water was available in the vicinity of the study area and we never observed *Psammomys* to lick dew. Intake of fresh matter was calculated as intake of dry matter plus preformed water.

A Mann-Whitney *U*-test was used to compare influx of mass-specific water for different cohorts and between seasons. Mass-specific production of  $\text{CO}_2$  by juveniles and adults in winter was similar; these data were pooled and compared with adults in summer, also by use of a Mann-Whitney *U*-test. A paired *t*-test was used to compare body mass of rats initially trapped to that of recaptured rats. A level of  $P < 0.05$  was accepted as significant. Values are presented as  $\bar{X} \pm SD$ .

## RESULTS

Eleven fat sand rats (seven juveniles and four adults) were recaptured in winter and four fat sand rats (all adults) were recaptured in summer. Water flux was determined for all animals; however,  $\text{CO}_2$  production could not be measured for five juveniles and two adults in winter because specific activity levels of  $^{18}\text{O}$  in these rats were too close to background levels at recapture.

There was no significant difference between body masses of individuals captured initially and those recaptured in both seasons; therefore, fat sand rats were considered in near steady-state water and energy balances (Table 1). The total volume of body water as a fraction of body mass of juveniles and adults in winter was higher than that of adults in summer. Mass-specific water influx was highest for juveniles in winter and lowest for adults in summer. Mass-specific  $\text{CO}_2$  production of juveniles and adults in winter were similar and were higher than that of adults in summer (Table 1).

Estimated mass-specific intake of dry matter consisting of *A. halimus* by fat sand rats ranged from 0.093 g g body mass<sup>-1</sup> day<sup>-1</sup> for adults in summer to 0.118 g g body mass<sup>-1</sup> day<sup>-1</sup> for



(±SD) body mass, total body water, water influx and CO<sub>2</sub> production of fat sand rats in winter and in summer. Values in a row with different superscripts are significantly other (Mann-Whitney U-test, P < 0.05).

Season:	Winter		Summer
	Juvenile	Adult	Adult
	7	4	4
(%/day)	-0.02 ± 0.46	-0.01 ± 0.64	-0.03 ± 0.75
	80.0 ± 6.9	167.5 ± 13.4	165.6 ± 6.1
(ml/g)	0.754 ± 0.010 <sup>a</sup>	0.761 ± 0.003 <sup>a</sup>	0.718 ± 0.006 <sup>b</sup>
d)	28.4 ± 7.5 <sup>a</sup>	41.6 ± 4.3 <sup>b</sup>	30.2 ± 4.1 <sup>a</sup>
	0.351 ± 0.080 <sup>a</sup>	0.248 ± 0.008 <sup>b</sup>	0.182 ± 0.022 <sup>c</sup>
	2	2	4
	81.2 ± 2.3	175.7 ± 14.8	165.6 ± 6.1
	2.18 ± 0.02 <sup>a</sup>	2.03 ± 0.12 <sup>a</sup>	1.72 ± 0.39 <sup>b</sup>

whereas daily fresh-matter intake ranged from 0.247 g/g body mass to 0.434 g/g body mass in these groups, respectively. Estimated water content as a percent of fresh matter consumed was 72.6% for juveniles in winter, 64.9% for adults in winter, and 62.5% for adults in a summer (Table 2).

Responses of fat sand rats with other groups of eutherian mammals, their water intake and energy expenditure fell within the 95% confidence limits of predicted rates, respectively. Their water influx was similar to that predicted for herbivores of their order. Their water influx was similar to that predicted for herbivores of their order. Their water influx was similar to that predicted for herbivores of their order. Their energy expenditure tended to be higher than that predicted for eutherian mammals in general, and lower than that predicted for desert eutherian mammals (Table 3).

DISCUSSION

Water intake of fat sand rats was higher in winter than in summer. This was similar to that reported for fat sand rats (Degen et al., 1990) and the difference in seasonal water influx was the result of differences in preformed water of *A. halimus* consumed. Changes in water intake as a result of shifts from a relatively dry diet in summer and autumn to a wetter diet in winter and spring were reported in phasianids from the Negev Desert (Alkon et al., 1985; Kam et al., 1985) and sand partridges, *Ammoperdix heyi*—Alkon et al., 1985; Kam et al., 1985. A seasonal shift in diet was reported in several Negev Desert rodents (Bar et al., 1985). In addition, water influx reflecting dietary preformed water also was reported in

Estimated intakes of dry and fresh matter of *Atriplex halimus* by fat sand rats (*Psammomys obesus*) in summer. Included in the table are estimated intakes of metabolic and preformed water content of consumed *A. halimus* as a percent of fresh matter.

Season:	Winter		Summer
	Juvenile	Adult	Adult
Intake (g/day)	9.58	19.26	15.27
	0.118	0.110	0.093
Water (ml/day)	2.97	5.97	4.73
	0.037	0.036	0.029
Respiration (ml/day)	25.43	35.63	25.46
	0.318	0.213	0.154
Water matter (g/day)	35.01	54.89	40.73
	0.434	0.320	0.247
Water content (%)	72.6	64.9	62.5

TABLE 3.—Measured water influx and energy expenditure of fat sand rats (*Psammomys obesus*) in winter and in summer and the predicted water influx and energy expenditure for free-living animals of their body masses. Allometric prediction equations used were for groups of animals.

	Season:		Summer	Authority
	Cohort:	Winter		
	Juvenile	Adult	Adult	
<b>Water influx</b>				
Fat sand rats (ml/day)	28.4	41.6	30.2	This study
Herbivores (predicted)	23.1	41.5	41.1	Nagy and Peterson, 1988
Measured/predicted	1.23	1.00	0.74	
Rodents	10.8	21.1	20.9	Morris and Bradshaw, 1981
Measured/predicted	2.63	1.97	1.45	
Desert eutherians (predicted)	9.5	19.2	19.0	Nagy and Peterson, 1988
Measured/predicted	2.99	2.17	1.59	
Eutherian mammals (predicted)	11.7	21.5	21.3	Nagy and Peterson, 1988
Measured/predicted	2.43	1.94	1.42	
<b>Energy expenditure</b>				
Fat sand rats (kJ/day)	91.8	184.5	146.3	This study
Herbivores (predicted)	145.5	255.0	243.9	Nagy, 1987
Measured/predicted	0.63	0.72	0.60	
Desert eutherians (predicted)	101.8	186.8	177.3	Nagy, 1987
Measured/predicted	0.90	0.99	0.83	

pocket gophers (*Thomomys bottae*—Gettinger, 1984) and in antelope ground squirrels (*Amospermophilus leucurus*—Karasov, 1983), both species active during the day. However, all of these animals have a varied diet, feeding on seeds and dry vegetation that have a water content of ca. 8–10% of fresh matter, and on moist vegetation and animal matter that have a content of ca. 70–80% of fresh matter. The foods eaten by these rodents exhibit seasonal availability, thus influencing maintenance homeostasis of the consumers. This was not the case with fat sand rats that consumed only *A. halimus* year-round. *A. halimus* shows a large within-day variation of water content, and, although the plant is usually more moist in winter than in summer, there is large overlap in water content between seasons (Ilan, 1984). Intake of preformed water thus depends on the time of day that the *A. halimus* is consumed and in this way fat sand rats regulate their water influx to some extent. For example, in summer, foraging begins earlier in the day than in winter, a time when water content of the leaves is maximum (Ilan, 1984). Fat sand rats are in their burrows at midday. In contrast, in winter, foraging begins later in the day than in summer and fat sand rats are active at midday (Ilan, 1984).

Calculated water content of the *A. halimus* eaten by fat sand rats in the two seasons was similar, 64.9% in winter and 62.5% in summer. Thus, the increase in water influx in winter was not a consequence of the difference in preformed water in the diet, as reported for other animals, but rather mainly as a consequence of higher energy expenditure of rats in winter. Adult fat sand rats had ca. 18% greater expenditure of mass-specific energy in winter than in summer (1.05 kJ g<sup>-1</sup> day<sup>-1</sup> and 0.089 kJ g<sup>-1</sup> day<sup>-1</sup>, respectively); consequently, greater intake of *A. halimus* was a prime reason for greater water influx.

Juvenile fat sand rats consumed *A. halimus* that possessed a slightly higher water content than that eaten by adults, and juveniles had a higher mass-specific influx of water than adults. Ben-Chaouacha et al. (1983) reported a water influx of 0.383–0.406 ml g<sup>-1</sup> day<sup>-1</sup> in fat sand rats weighing 65–87 g and consuming chenopods. These fat sand rats were similar in body mass and had a similar water influx to juveniles in our study, which suggests Ben-Chaouacha et al. (1983) also measured juveniles. This also supports the conclusion that juveniles select leaves of higher water content than those selected by adults.

We calculated that fat sand rats must consume 24.7–43.4% of their body mass/day in fresh matter or 9.3–11.8% of their body mass/day in dry matter to obtain enough energy to fulfill their requirements. Ben-Chaouacha et al. (1983) estimated that fat sand rats consumed 50% of

their body mass/day in fresh matter, which was similar to our calculations for juveniles. Others reported that free-living fat sand rats consumed 32–100% of their body mass daily in fresh matter (Daly and Daly, 1973; Happold, 1984; Petter, 1961).

Generally, water influx of fat sand rats was similar to that predicted for herbivores of equal body mass, but tended to be higher than that predicted for eutherian mammals in general, rodents, and desert eutherians. This indicates that water influx often is a reflection of diet selection and that this measurement should be used with caution in assessing the adaptability of an animal to its environment. Furthermore, daily expenditure of energy tended to be lower than that predicted for herbivores and desert eutherians. This was rather surprising because *A. halimus* has a high fiber content and low efficiency of use of its energy for maintenance and growth (Degen et al., 1988; Kam and Degen, 1989) suggesting a relatively high energy expenditure for animals consuming this shrub. In contrast, seeds have a low fiber content, high digestibility, and high efficiency of use of energy, and granivorous rodents usually have lower metabolic rates than herbivorous rodents (McNab, 1986).

The predictive equations of energy expenditure for desert eutherians included several granivorous rodents, yet energy expenditure of fat sand rats was similar or tended to be lower than that predicted for these two groups. Fat sand rats exhibited an energy expenditure lower than that predicted for herbivores indicating that these rats are well adapted for consuming *A. halimus* as a staple in their diet. In addition, because water influx of fat sand rats tends to be higher than that predicted for herbivores, but their energy expenditure lower than that predicted, suggests that the *A. halimus* consumed by fat sand rats had a higher water content than vegetation consumed by other herbivores.

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## SEASONAL ENERGY, WATER, AND FOOD CONSUMPTION OF NEGEV CHUKARS AND SAND PARTRIDGES<sup>1</sup>

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**Abstract.** Chukars (*Alectoris chukar*) and Sand Partridges (*Ammoperdix heyi*), two ground-dwelling phasianids, are permanent residents of the Negev desert and are sympatric over much of their ranges. Sand Partridges (body mass = 150–250 g), however, inhabit only arid and very arid areas, whereas Chukars ( $m_b = 350\text{--}600$  g) are widely distributed and inhabit deserts only at the margins of their ranges. We compared some of the desert adaptations of these phasianids by measuring the seasonal field metabolic rates (FMR) and water influxes (using doubly labelled water), diet selection, and food requirements of free-living Chukars and Sand Partridges at a site where both species occurred. Both species showed adaptation in the form of low energy metabolism, which ranged from 43 to 81% of that expected for birds of similar body mass. During summer, Sand Partridges had lower energy expenditures ( $5.47 \text{ kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$ ) and water influxes ( $72.3 \text{ mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ) than did Chukars ( $6.42 \text{ kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$  and  $93.5 \text{ mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ , respectively), indicating more pronounced adjustments to arid conditions in the desert specialist. However, both species obtained more than half of their water influx in summer by drinking. Their summer diet was relatively dry, consisting mainly of seeds (80%) along with some green vegetation (18%) and, in Chukars, occasional arthropods. This situation changed abruptly after winter rains, which induced germination and reduced the availability of seeds. Chukars were unable to maintain energy balance in the face of low ambient temperatures and a diet (90% green vegetation) that contained much water but comparatively little energy, and they mobilized fat reserves to meet energy requirements. Most Sand Partridges left the study area after winter rains, apparently migrating to the lower elevation, warmer, and drier Arava (part of the Rift Valley). The winter rainy season appears to be the most stressful time of the year for both species. The adaptations to hot, dry conditions possessed by Sand Partridges may be accompanied by constraints on their abilities to cope with cool, wet conditions, and this may restrict them to arid and very arid habitats.

**Key words:** *Alectoris*; *Ammoperdix*; desert adaptation; desert partridge; diet selection; distribution; doubly labelled water; energy metabolism; feeding rate; field metabolic rate; granivore; migration; water flux; water relations.

### INTRODUCTION

Mammals that live in deserts, where water and energy availability may be important factors in determining their distributions, generally have lower energy expenditures (McNab 1979) and rates of water use (Nicol 1978) than their nondesert counterparts. Desert birds, too, apparently have lower energy (Dawson and Bennett 1973) and water (Degen et al. 1982) requirements than nondesert species.

However, because of their mobility, most avian species that inhabit deserts are not as tightly constrained as are mammals. For example, the Mourning Dove (*Zenaidura macroura*, Dawson 1976) and sand grouse (*Pterocles* spp., Thomas 1984), both diurnal species, inhabit extreme deserts but fly great distances to drink. Other excellent fliers such as the Pale Crag Martin (*Hirundo obsoleta*) and Little Green Bee-eater (*Merops orientalis*) also live in deserts and prey on flying insects that provide them with food high in energy and preformed water. Nocturnal predators such as owls and nightjars are inactive during the day and also hunt prey high in energy and preformed water.

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Thus, many avian species are able to inhabit the desert because of their mobility, their choice of food, and their temporal activity patterns.

Diurnal, terrestrial, granivorous birds with limited flying ability are less able to search large areas for food and water, and therefore may be more vulnerable to harsh desert conditions. Furthermore, seeds, their principal food during the summer, yield little preformed water at a time when the birds' water requirements for thermoregulation may be greatest. Thus, we would expect such species to conform to the patterns found in mammals, i.e., to have lower energy and water requirements than their nondesert counterparts.

We examined the energy and water fluxes of two, primarily granivorous, terrestrial phasianids, the Chukar (*Alectoris chukar*) and the Sand Partridge (*Ammodramus ammodramus*), both permanent residents in Israel. The Chukar (350–600 g body mass) is widely distributed in the southern and central Palearctic (Cramp and Simmons 1980) and has been successfully introduced into North America and elsewhere (Bohl 1971). In Israel, Chukars are found in a variety of habitats including Mediterranean, montane, steppe, and desert biomes (Dor 1975). Generally, they inhabit deserts only at the margins of their range or where the environment has been modified by man. By contrast, the Sand Partridge (150–250 g body mass), smaller and paler than the Chukar, is wholly restricted to arid and very arid habitats in southwestern Asia and northeastern Africa (Cramp and Simmons 1980). In Israel, it is found principally in the Negev and Judean deserts and the Lower Jordan Valley. Its range includes the Arava (part of the Rift Valley), the most extreme desert area of Israel, which has an annual precipitation of 50 mm or less and a daily average summer maximum air temperature of  $\approx 40^\circ\text{C}$ . Chukars and Sand Partridges are sympatric in Israel within an area approximately bounded by the 200- and 90-mm isohyets.

Given the difference in their geographic distributions, we reasoned that Sand Partridges would have relatively lower energy and water requirements than Chukars. We used doubly labelled water (DLW) to estimate seasonal field metabolic rates and water influxes of free-living birds of both species. We also calculated components of their energy and water intakes by using DLW measurements in conjunction with crop content analyses.

#### MATERIALS AND METHODS

This study was made from November 1982 to March 1984 in the vicinity of Sede Boqer ( $34^\circ 47' \text{ N}$ ,  $30^\circ 52' \text{ E}$ ) in the Negev desert highlands. This area is classed as arid, having 250–300 biologically dry days per year and a precipitation : evaporation ratio of  $< 0.2$  (UNESCO 1977). Rain falls during the winter and averages 104 mm annually, with large annual differences in total precipitation and in its temporal and spatial distributions. Dew occurs on about 190 nights per year and

daily relative humidity averages 58%. Maximum and minimum daily air temperatures range between  $40^\circ$  and  $9^\circ$  over the year and average  $32^\circ$  during August, the hottest summer month, and  $5^\circ$  in January, the coldest winter month (Zangvil and Druian 1983). Meteorological data concerning rainfall and air temperatures during the present study were provided by the Desert Meteorological Unit, Jacob Blaustein Institute for Desert Research, at Sede Boqer. Daily mean air temperature was calculated as the average of daily maximum and daily minimum air temperatures.

Birds were captured at several sites in Nahal Zin, an ephemeral river that contains several permanent pools of water. Onset of germination and growth of annual and perennial plants in Nahal Zin are closely linked to the winter rains, and plant production is largely determined by the amount and distribution of precipitation. As a result, large yearly fluctuations in primary production, especially of annual plants, are characteristic of the region (Evenari et al. 1982). The major period of plant growth is in winter and early spring and most herbaceous vegetation is dry and dormant by early summer. Most vegetation occurs along the river bed. The predominant perennial plants are the shrubs *Atriplex halimus*, *Nitraria retusa*, *Hammada scoparia*, *Anabasis articulata*, *Zygophyllum dumosum*, *Suaeda asphaltica* and *Artemisia herba alba*. In addition, a variety of herbs and geophytes occur.

#### *Bird capture and doubly labelled water measurements*

Chukars and Sand Partridges were captured in sorghum-baited wire mesh traps ( $90 \times 90 \times 60 \text{ cm}$ ) with two walk-in funnel entrances. Traps were checked regularly so that the maximum time a bird remained in a trap before processing was 30 min. All captured birds were marked with leg bands, and some were fitted with individually identifiable back tabs (Alkon 1982).

Birds were weighed to 0.1 g on a semianalytical field balance (K-Tron, Model 600) and injected intramuscularly with water containing 97 atom %  $^{18}\text{O}$  (Yeda, Rehovot) and 1.8 MBq/g of tritium (Radiochemical Center, Amersham). Chukars received injections of 1.5 g and Sand Partridges of 0.6 g; injection amounts were accurate to 0.1 mg. After allowing 45–60 min for the isotopes to equilibrate with body fluids (Degen et al. 1981), small ( $\approx 0.2 \text{ g}$ ) blood samples were collected from the basilic vein and the birds were released at the point of capture. In order to measure  $\text{CO}_2$  production rates and water fluxes of the birds by isotopic decline rates, blood samples were collected from birds recaptured and weighed at least 2 d after injection of the doubly labelled water.

Blood samples were centrifuged and sera removed. Part of the serum was used to measure tritium levels, and the rest of the serum plus the red blood cells were micro-distilled to obtain pure water to measure  $^{18}\text{O}$  levels (Wood et al. 1975). To determine the specific



activity of tritium, 0.05 mL of serum were added to 5 mL Bray's solution and counted in duplicate for 10 min in a liquid scintillation counter (LKB-Wallac, Model 1211). Counts were corrected for 6% serum dry matter content and for quenching using a series of quenched standards. Levels of  $^{18}\text{O}$  specific activity were measured in triplicate by an Autogamma counting system (Packard) after converting  $^{18}\text{O}$  to gamma-emitting  $^{18}\text{F}$  by cyclotron-generated proton activation (Wood et al. 1975). Three blood samples from noninjected birds of each species were treated similarly and were used to measure background abundances of  $^{18}\text{O}$  and tritium.

Total body water (TBW) volumes were estimated from the initial dilution of tritium, and water fluxes were calculated from the subsequent decline after release in specific activity of tritium (Degen et al. 1981).  $\text{CO}_2$  production rates were estimated from the declines over time in specific activities of tritium and  $^{18}\text{O}$  (Lifson and McClintock 1966, Nagy 1980). We assumed that fractional water contents of birds remained constant through time, and we calculated TBW at recapture as the product of body mass and fractional TBW of the animal at the time of injection. We also assumed that any change in absolute TBW volumes were linear through time. We converted rates of  $\text{CO}_2$  production of Chukars and Sand Partridges to rates of energy expenditure and metabolic water production on the basis of the proportions of seeds, vegetation, and insects in their diet in different seasons, using the factors 21.9 J and 0.658  $\mu\text{L H}_2\text{O}/\text{mL CO}_2$  for seeds, 21.7 J and 0.637  $\mu\text{L H}_2\text{O}/\text{mL CO}_2$  for green vegetation and 25.7 J and 0.660  $\mu\text{L H}_2\text{O}/\text{mL CO}_2$  for insects (Nagy 1983).

#### Diet

The study took place in a nature reserve where birds could not be killed to examine their crop contents. We managed, however, to remove surgically crop contents from five Chukars and five Sand Partridges captured in Nahal Zin in 1983–1984 and to release these birds with no apparent effect on their subsequent behavior. Crop contents of an additional 115 Chukars and eight Sand Partridges that were shot by hunters in the vicinity of Nahal Zin in 1981–1982 were analyzed. Data on 84 of these latter Chukar crops have been reported previously (Alkon et al. 1985), and we have added data from the other 36 crops in this report. No Sand Partridges were captured for diet analyses in spring, and we estimated their diet on the basis of water and energy intake rates (see Estimation of Food Intake).

Crop content analysis followed the methods of Korshgen (1980), which was described by Alkon et al. (1985). We separated the dietary components into seeds, green vegetation (leaves, herbaceous seedlings, fruits, and other plant material) and insects. Seeds and vegetation were also collected in the field, and their water and dry matter contents were measured by drying to constant mass at 70°. Energy densities of the seeds were measured using a Phillipson microbomb calorimeter.

TABLE 1. Gross energy content (bomb calorimetry) and water content (by drying) of seeds consumed by Chukars and Sand Partridges.

Species	Energy content (kJ/g dry matter)	Water content (mL/g fresh matter)
<i>Polygonum arenastrum</i>	19.8	0.089
<i>Reaumuria mirtella</i>	16.4	0.079
<i>Erodium ciconium</i>	21.3	0.048
<i>Calendula aegyphaca</i>	21.0	0.058
Gramineae	18.8	0.047
<i>Trigonella arabica</i>	15.9	0.074
<i>Amaranthus</i> sp.	16.7	0.075
<i>Medicago</i> sp.	19.7	0.069
<i>Triticum</i> sp.	18.6	0.071
Graminae	15.8	0.062
No. 2*	17.8	0.087
No. 39*	18.5	0.087
Mean ( $\pm$ SD)	18.4 $\pm$ 1.9	0.071 $\pm$ 0.014

\* No. 2 and No. 39 are unidentified seeds.

Earlier studies have shown that the diet of Chukars depends mainly on plant phenological conditions and not on chronological factors (Alkon et al. 1982, 1985). We therefore noted the time of rainfall during 1981–1982 and 1983–1984 when the birds were collected for crop content analyses, so that data from the time of rains and emergence of green vegetation could be applied to the present study. We then divided the year according to the type of food available, as follows: spring, summer, pre-winter rain and post-winter rain.

#### Feeding rate

We estimated the rate of food consumption necessary to provide exactly the amount of energy used by the birds daily for metabolism. (Metabolism was measured with doubly labelled water.) Actual feeding rates should have been (1) higher than this estimate when the birds were growing or storing energy as fat (positive energy balance), or (2) lower than this estimate when fat stores were being depleted (negative energy balance).

The metabolizable energy yields per gram of dry matter of the various diets were calculated as the sum of the yields from the seed, vegetation, and insect portions of the diets. Metabolizable energy in seeds was  $\approx 14.8$  kJ/g (total energy content averaged 18.4 kJ/g dry matter [Table 1], of which  $\approx 80.4\%$  was metabolizable, based on measurements by Pinshow, Degen and Alkon [1983] for partridges fed a diet composed mainly of crushed seeds). We assumed that metabolizable energy in the dry matter fraction was 10.9 kJ/g for green vegetation, and that insects yielded 20.3 kJ/g, as determined for desert rodents eating these diets (Karasov 1982, 1983). Dry matter intake rates required for maintenance of energy balance were calculated as field metabolic rate (kilojoules per day) divided by metabolizable energy in the diet's (kilojoules per gram) dry matter. Rates of ingestion of the three dietary com-

ponents (seeds, vegetation, insects) were also calculated in this manner.

#### *Water intake*

The rates of dietary water intake (preformed water in the food plus metabolic water produced from oxidation of chemical potential energy in the food) were calculated for each food type from rates of dry matter consumption (above) and measurements of food composition. Seeds contained 0.076 mL of preformed water per gram of dry matter (calculated from Table 1) and yielded 0.445 mL of metabolic water per gram of dry matter, calculated as follows: [(water formed/CO<sub>2</sub> produced) ÷ (heat produced/CO<sub>2</sub> produced)] · (metabolizable energy/seed dry mass) = [(0.000658 mL/mL) ÷ (21.9 J/mL)] · (14 800 J/g), for a total water yield of 0.521 mL/g dry matter.

Preformed water per unit dry matter of vegetation was 3.00 ± 0.15 mL/g (*n* = 13) in summer and before winter rains, and 3.81 ± 0.19 mL/g (*n* = 13) after winter rains and in spring. The metabolic water yield of vegetation dry matter was ≈ 320 mL/g, calculated as follows: [(water formed/CO<sub>2</sub> produced) ÷ (heat produced/CO<sub>2</sub> produced)] · (metabolizable energy/vegetation dry mass) = [(0.000637 mL/mL) ÷ (21.7 J/mL)] · (10 900 J/g), so total water yields from consumption of vegetation were ≈ 3.32 mL/g of dry matter during dry periods and 4.13 mL/g during moister periods. We assumed that preformed water per unit insect dry matter was 2.33 mL/g (Edney 1977). Metabolic water yield of insect dry matter would be ≈ 0.521 mL/g, calculated as follows: [(water formed/CO<sub>2</sub> produced) ÷ (heat produced/CO<sub>2</sub> produced)] · (metabolizable energy/insect dry mass) = [(0.000660 mL/mL) ÷ (25.7 J/mL)] · (20 300 J/g), for a total of 2.85 mL/g of insect dry matter consumed. Dietary water intake was calculated as the product of dry matter intake and water yield of the food.

This procedure is also based on the assumption that animals were eating just enough food to achieve energy balance. During those seasons when partridges were approximately in energy balance, these estimates of dietary water intake should be close to actual dietary intake rates. Because tritiated water measured total water intake (dietary + drinking + a small amount of vapor input), we estimated drinking rates by subtracting dietary intake from the total measured isotopically.

#### *Estimation of food intake*

It is possible to estimate the diet proportions of an animal from its rates of CO<sub>2</sub> production and water influx, provided that it does not drink water, it is maintaining energy balance, it consumes only two types of foods, and the water and metabolizable energy yields of the two foods differ substantially and are known (Degen et al. 1986). We used this method to calculate the proportions of seeds and green vegetation consumed by Sand Partridges in spring, a season for which

crop contents were not available. Sand Partridges were not seen drinking in spring, and they did not consume insects at other times of the year, so we assumed they ingested only seeds and green vegetation. Under these conditions, field metabolic rate (kilojoules per day) equals the sum of metabolizable energy in the dry matter of seeds consumed ([14.8 kJ/g] · [g/d]) and metabolizable energy in the dry matter of green vegetation consumed ([10.9 kJ/g] · [g/d]). Similarly total water influx (millilitres per day) equals the sum of the water yield of seed dry matter consumed ([0.521 mL/g] · [g/d]) and the water yield of the dry matter equivalent of green vegetation ingested ([4.13 mL/g] · [g/d]). Simultaneous solution of these equations yields rates of consumption of seeds and vegetation.

#### *Statistical analyses*

Comparisons between Chukars and Sand Partridges were made allometrically to account for differences in body mass (*m<sub>b</sub>*, in grams). FMRs were expressed per *m<sub>b</sub>*<sup>0.61</sup>, using the exponent reported for free-living birds (Walsberg 1983), and water fluxes were expressed per *m<sub>b</sub>*<sup>0.75</sup>, using the exponent for caged birds (Pinshow et al. 1983).

Analysis of variance was used to test for significant differences (*P* < .05) among seasons within and between species. We also used the Student-Newman-Keuls test (Steel and Torrie 1960) where applicable.

#### RESULTS

In the winter of 1982–1983, rainfall totalled 141 mm. The first substantial rainfall was 7.2 mm, and fell on 23 October 1982. In the winter of 1983–1984, total precipitation was only 56 mm, with the first substantial rainfall (12.6 mm) occurring on 15 January 1984. The mean daily air temperatures were similar in December 1982 and December 1983 (10.2° vs. 11.1°C). In December 1982 green vegetation was abundant, but, by contrast, vegetation was dry and dormant the next December (1983).

Fifty individual Chukars and 50 individual Sand Partridges were captured, and of these 26 Chukars and 38 Sand Partridges were recaptured at least once for CO<sub>2</sub> production rate and water flux measurements. Some individuals were captured in several seasons and some were recaptured more than once within a season. After winter rainfall, few Sand Partridges were present in the study area and none was captured. In 1982–1983 no birds were captured during the breeding season, and in 1983–1984 birds in our study area did not pair off for breeding (Carmi-Winkler 1985).

#### *Crop content analyses*

Seeds comprised 80% and green vegetation 18% of dry matter in Chukars' crop contents in the summer (Table 2). This shifted to 8% seeds and 90% green vegetation after winter rains. Chukars consumed some insects (2.1–6.7% of dry matter intake) but none was

TABLE 2. Diet composition of Chukars and Sand Partridges at various seasons from 1981 to 1984. Values are means  $\pm$  SD.

	Spring	Summer	Winter pre-rain	Winter post-rain
<i>Alectoris chukar</i>				
<i>n</i>	15	34	37	34
% total dry matter				
Seeds	52.9 $\pm$ 36.0	79.7 $\pm$ 27.4	58.2 $\pm$ 35.4	7.5 $\pm$ 22.5
Vegetation	44.4 $\pm$ 38.0	18.2 $\pm$ 27.8	35.1 $\pm$ 37.0	90.4 $\pm$ 22.8
Insects	2.7 $\pm$ 7.4	2.1 $\pm$ 5.6	6.7 $\pm$ 14.3	2.1 $\pm$ 6.7
Metabolizable energy (kJ/g dry matter)	13.2	14.2	13.8	11.4
Water yield (mL/g dry matter)	2.23	1.10	1.71	3.21
Energy equivalent (J/mL CO <sub>2</sub> )	21.9	21.9	22.1	21.8
<i>Ammoperdix heyi</i>				
<i>n</i>	0	4	9	0
% total dry matter				
Seeds	63.4	80.3 $\pm$ 24.0	85.8 $\pm$ 30.4	...
Vegetation	36.6	19.7 $\pm$ 24.0	14.2 $\pm$ 30.4	...
Insects	0	0	0	...
Metabolizable energy (kJ/g dry matter)	13.4	14.0	14.3	...
Water yield (mL/g dry matter)	1.85	1.07	0.92	...
Energy equivalent (J/mL CO <sub>2</sub> )	21.8	21.9	21.9	...

found in crops of Sand Partridges. Sand Partridges consumed 80–86% seeds and 14–20% green vegetation during the summer and the pre-rain period. We calculated that Sand Partridges consumed 63% seeds and 37% green vegetation during the spring.

#### Body mass and water content

Chukars weighed about twice as much as Sand Partridges (Table 3). The lower mean body masses of the summer samples for both species were due to recruitment of juveniles into the marked population.

Total body water (TBW) volume in Chukars ranged from a mean of 63% of body mass before the rains to 68–73% following rains (Table 3). There were no significant differences among spring, summer, and pre-rain means, but the post-rain TBW content was significantly ( $P < .01$ ) higher. In Sand Partridges, TBW in the spring was significantly higher than before the rains (68 vs. 62%,  $P < .01$ ). These results indicate that

partridges of both species had lower fat contents following the rainy periods.

#### Field metabolic rates

In Chukars, CO<sub>2</sub> production rates following winter rains were significantly higher than in the other seasons (Table 4). They increased from 1.28 mL·g<sup>-1</sup>·h<sup>-1</sup> before the rains in 1982 to 1.69 mL·g<sup>-1</sup>·h<sup>-1</sup> after the rains (December 1982), an increase of 32%, and from 1.07 mL·g<sup>-1</sup>·h<sup>-1</sup> in spring 1983 to 1.55 mL·g<sup>-1</sup>·h<sup>-1</sup> after the rains (March 1984), an increase of 45%. In Sand Partridges, CO<sub>2</sub> production rates increased from 1.45 mL·g<sup>-1</sup>·h<sup>-1</sup> in summer 1983 to 1.80 mL·g<sup>-1</sup>·h<sup>-1</sup> before the rains (December 1983), an increase of 24%. Allometric comparisons between species showed that there was a significant difference in CO<sub>2</sub> production rates only in summer 1983 when Chukars had a 17% higher rate than Sand Partridges ( $P < .01$ ) per  $m_b^{0.61}$ . Rates of energy expenditure showed similar patterns

TABLE 3. Body mass ( $m_b$ ) and total body water volume (TBW; as percentage of  $m_b$ ) of free-living Chukars and Sand Partridges in different seasons and mean seasonal air temperatures ( $T_a$ ). Values are means  $\pm$  SD.

Seasons	Pre-rain (Nov 82)	Post-rain (Dec 82)	Spring (Apr 83)	Summer (Aug 83)	Pre-rain (Dec 83)	Post-rain (Mar 84)
Mean $T_a$ (°C)	13.2	10.2	18.5	25.3	11.1	14.6
Chukars						
<i>n</i>	8	12	5	15	14	5
$m_b$ (g)	456 $\pm$ 45	449 $\pm$ 77	534 $\pm$ 67	374 $\pm$ 52	437 $\pm$ 60	446 $\pm$ 34
TBW (%)	63.2 $\pm$ 2.3	68.4 $\pm$ 2.8	67.3 $\pm$ 2.9	66.7 $\pm$ 1.8	62.9 $\pm$ 2.7	72.6 $\pm$ 2.4
Sand Partridges						
<i>n</i>	3	...	7	29	17	...
$m_b$ (g)	214 $\pm$ 3	...	205 $\pm$ 10	159 $\pm$ 19	196 $\pm$ 17	...
TBW (%)	61.9 $\pm$ 2.9	...	67.6 $\pm$ 1.5	67.3 $\pm$ 2.0	64.0 $\pm$ 2.8	...

TABLE 4. Seasonal CO<sub>2</sub> production rates in free-living Chukars (*Alectoris chukar*) and Sand Partridges (*Ammoperdix heyi*). Values (means ± SD) with same superscripts within each species do not differ from each other.

		CO <sub>2</sub> production per unit body mass				
Season	Date	<i>Alectoris chukar</i>		<i>Ammoperdix heyi</i>		P†
		n*	CO <sub>2</sub> (mL·g <sup>-1</sup> ·h <sup>-1</sup> )	n*	CO <sub>2</sub> (mL·g <sup>-1</sup> ·h <sup>-1</sup> )	
Pre-rain	Nov 82	2 (2)	1.278 ± 0.219 <sup>a</sup>	2 (2)	1.411 ± 0.189 <sup>a</sup>	NS
Post-rain	Dec 82	5 (3)	1.689 ± 0.418 <sup>b</sup>			
Spring	May 83	3 (3)	1.070 ± 0.053 <sup>a</sup>	5 (4)	1.622 ± 0.185 <sup>ab</sup>	<.01
Summer	Aug 83	14 (11)	1.228 ± 0.262 <sup>a</sup>	37 (23)	1.453 ± 0.215 <sup>a</sup>	<.01
Pre-rain	Dec 83	23 (9)	1.331 ± 0.291 <sup>a</sup>	14 (9)	1.796 ± 0.699 <sup>b</sup>	<.01
Post-rain	Mar 84	2 (2)	1.554 ± 0.472 <sup>ab</sup>			

		CO <sub>2</sub> production per unit metabolically active body mass				
Season	Date	<i>Alectoris chukar</i>		<i>Ammoperdix heyi</i>		P†
		n*	CO <sub>2</sub> (mL·g <sup>-0.61</sup> ·h <sup>-1</sup> )	n*	CO <sub>2</sub> (mL·g <sup>-0.61</sup> ·h <sup>-1</sup> )	
Pre-rain	Nov 82	2 (2)	13.75 ± 2.70 <sup>a</sup>	2 (2)	11.25 ± 1.69 <sup>ab</sup>	NS
Post-rain	Dec 82	5 (3)	19.89 ± 4.93 <sup>c</sup>			
Spring	May 83	3 (3)	12.14 ± 1.11 <sup>a</sup>	5 (4)	12.89 ± 1.62 <sup>a</sup>	NS
Summer	Aug 83	14 (11)	12.13 ± 2.51 <sup>a</sup>	37 (23)	10.41 ± 1.51 <sup>b</sup>	<.01
Pre-rain	Dec 83	23 (9)	14.03 ± 3.02 <sup>ab</sup>	14 (9)	14.33 ± 5.94 <sup>a</sup>	NS
Post-rain	Mar 84	2 (2)	17.12 ± 5.73 <sup>bc</sup>			

\* Values in parentheses are numbers of individuals measured and *n* represents number of measurements.

† *P* represents level of significance in comparisons between species within seasons.

(Table 6). For subsequent calculations, we combined data for 1982 and 1983–1984 pre- and post-rain periods.

#### Water fluxes

No difference was found between water influx and water efflux within any season within either species, indicating that the birds were generally in water balance. In Chukars, water influx increased by 2–3 fold after rains (Table 5). In Sand Partridges, water influx was lowest before rains in 1982. Water influxes, corrected for body size difference, were generally higher in Chukars (Table 5) except in spring. For subsequent

calculations, we combined results for the winter periods in 1982 with 1983–1984.

Rates of dietary water intake (preformed plus metabolic), calculated from the steady-state feeding rates, reflected the seasonal differences in diet composition of Chukars (Table 6). In the spring and post-winter rains, predicted dietary water intake was about the same as actual total water intake (measured with tritiated water) in both species. This indicates that the birds did not drink free-standing water. Measured water influxes in summer and pre-winter rains were much higher than influxes predicted for steady-state feeding, with the difference due to drinking water from pools (which we observed).

TABLE 5. Seasonal water influxes in free-living Chukars (*Alectoris chukar*) and Sand Partridges (*Ammoperdix heyi*). Values (means ± SD) with same superscripts within each species do not differ from each other.

		Water influx per unit body mass				
Season	Date	<i>Alectoris chukar</i>		<i>Ammoperdix heyi</i>		P†
		n*	H <sub>2</sub> O (mL·kg <sup>-1</sup> ·d <sup>-1</sup> )	n*	H <sub>2</sub> O (mL·kg <sup>-1</sup> ·d <sup>-1</sup> )	
Pre-rain	Nov 82	2 (2)	98.3 ± 22.2 <sup>a</sup>	4 (3)	70.0 ± 11.1 <sup>a</sup>	NS
Post-rain	Dec 82	5 (3)	206.2 ± 42.3 <sup>b</sup>			
Spring	May 83	4 (3)	96.0 ± 23.8 <sup>a</sup>	5 (4)	118.4 ± 16.4 <sup>b</sup>	NS
Summer	Aug 83	14 (11)	121.2 ± 17.9 <sup>a</sup>	38 (23)	115.2 ± 20.5 <sup>b</sup>	NS
Pre-rain	Dec 83	29 (9)	116.9 ± 21.3 <sup>a</sup>	16 (9)	100.5 ± 21.4 <sup>b</sup>	<.05
Post-rain	Mar 84	6 (4)	272.1 ± 112.7 <sup>b</sup>			

		Water influx per unit metabolically active body mass				
Season	Date	<i>Alectoris chukar</i>		<i>Ammoperdix heyi</i>		P†
		n*	H <sub>2</sub> O (mL·kg <sup>-0.75</sup> ·d <sup>-1</sup> )	n*	H <sub>2</sub> O (mL·kg <sup>-0.75</sup> ·d <sup>-1</sup> )	
Pre-rain	Nov 82	2 (2)	82.1 ± 19.9 <sup>a</sup>	4 (3)	47.4 ± 7.9 <sup>a</sup>	<.05
Post-rain	Dec 82	5 (3)	178.1 ± 36.3 <sup>b</sup>			
Spring	May 83	4 (3)	80.4 ± 19.4 <sup>a</sup>	5 (4)	79.5 ± 11.3 <sup>b</sup>	NS
Summer	Aug 83	14 (11)	93.5 ± 12.6 <sup>a</sup>	38 (23)	72.3 ± 12.3 <sup>b</sup>	<.01
Pre-rain	Dec 83	29 (9)	94.0 ± 17.5 <sup>a</sup>	16 (9)	67.4 ± 14.4 <sup>b</sup>	<.01
Post-rain	Mar 84	6 (4)	220.0 ± 89.4 <sup>b</sup>			

\* Values in parentheses are numbers of individuals measured and *n* represents number of measurements.

† *P* represents level of significance in comparisons between species within seasons.

### Feeding rates

Rates of food consumption, both dry and fresh matter, were lowest during summer for both species (Table 6). The rate of fresh matter consumption by Chukars was very high after the rains (more than six times that in summer), when the diet of Chukars switched from primarily seeds to primarily succulent, green vegetation (Table 2).

### DISCUSSION

#### Desert adaptations

Most previous studies of desert birds have focused on the summer, and the birds' abilities to survive during hot, dry conditions (Degen et al. 1983, Goldstein and Nagy 1985). In this study, we found that Chukars and Sand Partridges did quite well during summer, but surprisingly, the period after winter rains was apparently the most difficult for both species.

During the warm part of the year, both Chukars and Sand Partridges had much lower metabolic rates and water influxes than expected for birds in general. Low energy and water requirements are considered to be adaptive in desert animals (Nicol 1978, McNab 1979). The field metabolic rate expected for a bird that does not forage in flight is  $12.8 \text{ kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$  (Walsberg 1983). Chukars and Sand Partridges had FMRs that were 43–58% of this value (Table 6). The allometry of water influx in free-living birds has not yet been reported, but Pinshow et al. (1983) found that water influx in caged birds is related to body mass by the exponent 0.75. Chukars and Sand Partridges had field water influxes in spring, summer, and pre-rain periods that ranged between 47 and 94  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ . These are much lower than water influxes in nondesert birds such as Silvereyes, *Zosterops lateralis* (450–700  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; Rooke et al. 1983), House Martins, *Delichon urbica* (303  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; Bryant and Westertep 1980), Purple Martins, *Progne subis* (306  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; Utter and LeFebvre 1973), Starlings, *Sturnus vulgaris* (390  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; Ricklefs and Williams 1984), and Jackass Penguins, *Spheniscus demersus* (121  $\text{mL} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ ; Nagy et al. 1984).

#### Species comparisons

Chukars and Sand Partridges were able to increase or maintain their fraction of body solids during the warm seasons, so they were consuming enough energy and water to meet or exceed their needs. This was not the case after winter rains, however. Chukars reduced their fraction of body solids, apparently because they were not consuming enough energy to meet their metabolic costs, and were making up the difference by using body fat stores. The higher body water content of Chukars after rains indicates a lower body fat content (Alkon et al. 1982, 1985). Water balance was probably not a problem because the Chukars were eating primarily vegetation, which was very succulent, and their

TABLE 6. Field metabolic rates, feeding rates, and water influxes in Chukars and Sand Partridges during various seasons.

	Spring	Summer	Winter pre-rain	Winter post-rain
<i>Alectoris chukar</i>				
<i>n</i>	4	14	31	11
Body mass (g)	498	359	422	482
Field metabolic rate,				
kJ/d	280	232	297	416
$\text{kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$	6.34	6.41	7.43	9.61
% of predicted	49	50	58	75
Feeding rate (estimated)				
g dry matter/d	21.2	16.3	21.5	36.5
g fresh matter/d	59.2	25.9	48.4	164
Water influx (mL/d)				
Total	47.8	43.5	48.9	117
Dietary (calculated)	47.2	17.9	36.8	141
Water drunk	0.6	25.6	12.1	...
<i>Ammoperdix heyi</i>				
<i>n</i>	5	38	20	0
Body mass (g)	203	156	204	...
Field metabolic rate,				
kJ/d	174	119	188	...
$\text{kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$	6.78	5.46	7.32	...
% of predicted	52	43	57	...
Feeding rate (estimated)				
g dry matter/d	13.0	8.5	13.1	...
g fresh matter/d	31.8	14.0	19.5	...
Water influx (mL/d)				
Total	24.0	17.9	19.3	...
Dietary (calculated)	24.0	9.1	12.0	...
Water drunk	0.0	8.8	7.3	...

water influxes were quite high. We suspect that Chukars were losing body solids because they could not find enough seeds, which are energy-dense compared to green vegetation, to provide adequate energy before their crops were full of bulky vegetation. Numbers of seeds available are reduced in Negev desert soils after rains because many of them germinate (Loria and Noy-Meir 1980). Caged Chukars were unable to maintain energy balance on green vegetation alone (Degen et al. 1984). Similar results were found with Wood Pigeons, *Columba palumbus* (Kenward and Sibly 1977), and Bobwhite, *Colinus virginianus* (Robel et al. 1979).

The Sand Partridges that left our study area after winter rains may have migrated east toward the Arava (part of the Rift Valley), where lower elevation, lower rainfall, and warmer temperatures would exert less thermal stress on the birds. Farmers in the Arava commonly report increases in Sand Partridge numbers after winter rains (M. Kam, A. A. Degen, and K. A. Nagy, *personal observation*).

Sand Partridges appear to be better adapted to hot, dry conditions than are Chukar partridges. In sum-



mer, Sand Partridges had significantly lower energy and water requirements than did Chukars, on a mass-corrected basis. The FMR of Sand Partridge in summer was only  $1.5 \times$  basal metabolic rate (BMR), compared with  $1.9 \times$  BMR in Chukars (BMR data for Chukars and Sand Partridge from Frumkin 1983). The low FMR of Sand Partridges in summer ( $5.5 \text{ kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$ ) is comparable to that of the similar-sized (145-g) Gambel's Quail, *Callipepla gambelii* ( $4.4 \text{ kJ} \cdot \text{g}^{-0.61} \cdot \text{d}^{-1}$ ), another desert specialist that occurs in the Colorado desert in California (Goldstein and Nagy 1985).

Previous studies comparing Chukars and Sand Partridges have shown that Sand Partridges tolerate dehydration better (Degen 1985), maintain brain temperature better under heat stress and dehydration (Kleinhaus et al. 1985), have a higher upper critical temperature (Frumkin 1983), and can better use saline water (Levgoren et al. 1986). Although water influxes in summer were quite low in Chukars and Sand Partridges, both species apparently required water for drinking, as has been suggested by Degen et al. (1983, 1984). Thus, like Gambel's Quail (Goldstein and Nagy 1985), these partridges may be restricted to desert areas near water sources in summer. With drinking water available, the less specialized Chukar apparently can live sympatrically with the more specialized Sand Partridge in the Negev desert.

However, after winter rains, the cool, mesic conditions coupled with low-quality food resources are stressful to both species, but apparently less so for Chukars. We suggest that Sand Partridges may be unable to inhabit cooler, more mesic areas, and are restricted to warm deserts. Sand Partridges do occur in drier parts of the Negev and Judean deserts where Chukars are not present (Degen et al. 1983).

#### Field feeding rates

The amount of food (dry matter) consumed by a Chukar partridge weighing 413 g (weighted mean body mass) over a year was calculated by assuming daily food consumption rates (from Table 5) over the spring (61 d), summer (183 d), pre-rain (61 d) and post-rain (60 d) periods. Annual food consumption by a Sand Partridge weighing an average 180 g was also estimated, by assuming that its feeding rate in the post-rain period was the same as during the pre-rain period. A single Chukar consumed  $\approx 7.8$  kg of dry matter per year, of which  $\approx 60\%$  was seeds,  $37\%$  was vegetation, and  $3\%$  was insects. A Sand Partridge consumed  $\approx 3.9$  kg of food (dry matter) annually, with  $79\%$  of this being seeds and  $21\%$  vegetation. By comparison, Gambel's Quail (body mass 145 g) consumes at least 3.0 kg of dry matter annually, of which  $73\%$  is seeds,  $25\%$  is vegetation, and  $2\%$  is arthropods (estimated from results of Goldstein and Nagy 1985).

Thus, all three species of desert-dwelling phasianids consume  $\approx 20$  times their body mass in food (dry matter) each year. This information should be useful to

conservationists and wildlife managers (two of these three species are considered to be game birds in various countries), as well as to some farmers who consider these birds to be pests that eat their crops.

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## ENERGY EXPENDITURE AND WATER FLUX IN THREE SYMPATRIC DESERT RODENTS

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### SUMMARY

(1) The golden spiny mouse, *Acomys russatus* (Muridae), the common spiny mouse, *Acomys cahirinus*, and the bushy-tailed jird, *Sekeetamys calurus* (Gerbillidae), are similar in body size and are sympatric in many rocky areas in Israeli deserts. They differ in that *A. russatus* and *S. calurus* inhabit extremely arid areas where *A. cahirinus* is absent, and *A. russatus* is diurnal, whereas the other two species are nocturnal.

(2) We estimated their field metabolic rates and water fluxes with doubly-labelled water, and determined diets, feeding rates, and activity periods during spring in order to evaluate questions concerning their desert adaptations and their different geographical distributions. We devised a method for determining the proportions of two food types (e.g. leaves and insects) consumed by non-drinking, free-ranging animals, using doubly-labelled water measurements and diet composition analyses.

(3) All three species maintained water and energy balances, and had similar mass-specific water influxes (about  $0.13 \text{ ml g}^{-1} \text{ d}^{-1}$ ), while consuming different proportions of dry, mature vegetation and insects. We estimated that insects provided 38% of the total dry matter intake for *A. cahirinus*, 62% for *A. russatus* and 87% for *S. calurus*. *A. cahirinus* (38.3 g body mass) had the highest daily energy flux of the three species and expended  $1.35 \text{ kJ g}^{-1} \text{ d}^{-1}$  during its 10.5-h activity period. *A. russatus* (45.0 g) expended  $1.06 \text{ kJ g}^{-1} \text{ d}^{-1}$  during its 9-h activity period and *S. calurus* (41.2 g) expended  $1.07 \text{ kJ g}^{-1} \text{ d}^{-1}$  during its 10.5-h activity period.

(4) Water influxes of these three species were intermediate between those of other rodents, suggesting that behavioural diet selection can be as important as physiological water conservation in adapting to desert life. Their energy expenditures were lower than those predicted for rodents of their body mass, which is consistent with the notion of low energy expenditures among desert-adapted rodents. The ratio of water influx to dry matter intake (ml:g) was 1.3 in *A. cahirinus*, as compared with 1.9 in *A. russatus* and 2.5 in *S. calurus*. Thus we assumed more water was available for evaporative cooling in the latter two species and concluded that this could explain, at least in part, their different geographical distributions.

### INTRODUCTION

The composition of rodent communities has been widely investigated (Grant 1972; Brown 1975; Ricklefs 1976; Rosenzweig 1977; Abramsky 1981). It is generally agreed that

similar species cannot coexist in the same habitat and that either one species will exclude the other or one will evolve an adaptation that will eliminate or reduce the competition between them. Sympatric species may share some resources, but presumably the overlap is not sufficient to eliminate one of them (Ricklefs 1976).

The golden spiny mouse, *Acomys russatus* (Wagner 1840) (Muridae), the common spiny mouse, *A. cahirinus* (Desmarest 1891), and the bushy-tailed jird, *Sekeetamys calurus* (Thomas 1892) (Gerbillidae) are similar in body size and are sympatric in many rocky areas in Israeli deserts. *A. cahirinus* is widely distributed from eastern and northern Africa to Iran. *A. russatus* and *S. calurus* have more restricted distributions and are found primarily in eastern Egypt, including the Sinai, and the Negev desert, the Arava and the Judean desert of Israel (Harrison 1972; Dor 1975). The three species inhabit natural crevices among rocks and do not dig burrows (Shkolnik 1971; Z. Zook Ramon & A. Haim unpublished).

These rodents differ in three important respects: (i) *A. russatus* and *S. calurus* inhabit extremely arid areas where *A. cahirinus* is absent (Haim 1969); (ii) *A. russatus* is diurnal, whereas the other two species are nocturnal (Haim 1969; Shkolnik 1971); and (iii) *S. calurus* hops bipedally, whereas the other two species are quadrupedal (our observations).

We determined energy expenditure and water flux of these three species, and quantified their diets under free-living conditions. These variables were examined in relation to the desert adaptations and the different distributions of these rodents.

## MATERIALS AND METHODS

### *Study site*

The study was done during March and April of 1984, on the steep, rocky eastern slope of Mount Yishay near Ein-Gedi (35°23'N, 31°28'E) in the Judean desert. We estimated that rocks and boulders covered greater than 95% of the surface. The area supports a sparse natural vegetation of Saharo-Arabian plants (Zohary 1980). Our study area was dominated by small shrubs of *Zygophyllum dumosum*, *Salsola vermiculata* and *Fagonia* spp. The leaves available for consumption were mature and dry, containing only about 10% water.

The region is hot and dry with an annual rainfall of 50–70 mm, all occurring in the winter. Dew is infrequent, occurring on seven or eight nights per year. Mean maximum and minimum daily air temperatures average 40 °C and 26 °C, respectively, in July and August, the hottest months, and 21 °C and 13 °C, respectively, in January, the coldest month (Mane 1958; Katsnelson 1959). During our study, maximum and minimum temperatures averaged 31 °C and 18 °C, respectively, all days were sunny with no cloud cover and there was no dew.

### *Animal capture and doubly-labelled water measurements*

One hundred rodent traps, either Sherman or Havahart, were set in five rows that covered 4800 m<sup>2</sup>. The traps were checked every 3 h for 2 days. Captured rodents were toe-clipped for identification and weighed to 0.01 g on a semi-analytical field balance (K-Tron, Model 600). Each animal was then injected intraperitoneally with 0.15 ml of water containing 97 atoms % <sup>18</sup>O and 50 μCi tritium per ml. After allowing 2 h for equilibration of the isotopes with body fluids (Culebras *et al.* 1977; Karasov 1981), a blood sample was collected from the infraorbital sinus with a hematocrit capillary tube, and the animal was weighed again and then released at the capture site. Animals were

recaptured and weighed 3–8 days later, second blood samples were collected and the animals were released.

Blood samples were refrigerated until analysed. They were first micro-distilled (Wood *et al.* 1975) to obtain pure water. Tritium levels were determined by liquid scintillation spectrometry (LKB-Wallac, model-1211 Rackbeta) and  $^{18}\text{O}$  levels by a Gamma-Romatic counting system (Packard) after converting  $^{18}\text{O}$  to gamma-emitting  $^{18}\text{F}$  by cyclotron generated proton activation (Wood *et al.* 1975).

Total body water volume of the animal was calculated from the dilution space of  $^{18}\text{O}$ , water flux was estimated using the decline over time in specific activity of tritium, and  $\text{CO}_2$  production was estimated using the declines over time in specific activities of tritium and  $^{18}\text{O}$  (Lifson & McClintock 1966; Nagy 1980; Nagy & Costa 1980).

#### *Calculation of energy expenditure and food intake*

We were working in a nature reserve, and therefore could not kill animals for stomach content analyses. However, during the study one animal of each species was accidentally killed and their stomach contents were analysed as outlined by Bar, Abramsky & Gutterman (1984). The analyses revealed that all three individuals had eaten only insects and dry, mature vegetation. In addition, previous studies have shown that these three species are omnivorous (Happold 1984).

Based on our analyses and Happold's (1984) report, we assumed that the species ate insects and dry, mature vegetation. We used published values for diet composition and metabolizability in our calculations. We assumed that dry, mature vegetation contained 0.111 g preformed water and 9.0 kJ metabolizable energy per g dry matter, and that 21.7 J of energy and 0.637  $\mu\text{l}$  metabolic water were produced per ml  $\text{CO}_2$  production. For insects, the factors we used were 2.333 g preformed water and 20.3 kJ metabolizable energy per g dry matter, and 25.7 J of energy and 0.660  $\mu\text{l}$  metabolic water generated per ml  $\text{CO}_2$  production. These conversion factors were derived from feeding experiments done on insectivorous desert lizards (Nagy 1983), herbivorous desert lizards (Nagy 1972; Nagy & Shoemaker 1975), and omnivorous desert rodents (Karasov 1982, 1983) fed insects and natural plant diets.

We calculated the proportions and amounts of insect and plant matter consumed from field measurements of  $\text{CO}_2$  production and water influx.  $\text{CO}_2$  production per g dry matter was calculated as

$$\text{insects: } 20\,300 \text{ J g}^{-1} / 25.7 \text{ J (ml CO}_2\text{)}^{-1} = 789.9 \text{ ml CO}_2 \text{ g}^{-1} \quad (1)$$

$$\text{vegetation: } 9000 \text{ J g}^{-1} / 21.7 \text{ J (ml CO}_2\text{)}^{-1} = 414.7 \text{ ml CO}_2 \text{ g}^{-1} \quad (2)$$

Then we assumed that the rodents did not drink free water during our study (no rain fell and there was no dew), and calculated the combined preformed and metabolic water produced per g dry matter as

$$\text{insects: } 2.333 \text{ ml g}^{-1} + 0.521 \text{ ml g}^{-1} = 2.854 \text{ ml g}^{-1} \quad (3)$$

$$\text{vegetation: } 0.111 \text{ ml g}^{-1} + 0.264 \text{ ml g}^{-1} = 0.375 \text{ ml g}^{-1} \quad (4)$$

Therefore, combining eqns (1), (2), (3) and (4):

$$789.9X + 414.7Y = \text{ml CO}_2 \text{ production}$$

$$2.854X + 0.375Y = \text{ml H}_2\text{O influx}$$

where  $X = g$  dry matter of insects consumed, and  $Y = g$  dry matter of vegetation consumed. Solving for  $X$  and  $Y$ , we calculated the mass of insect and vegetation consumed to satisfy the energy expenditure and water influx of each species.

Analysis of variance was used to test whether or not means were different among the three rodents. A level of  $P < 0.05$  was chosen as significant, and means were separated by Student Neuman-Keuls test (Steel & Torrie 1960).

## RESULTS

Five *A. cahirinus*, five *A. russatus* and four *S. calurus* were recaptured at least once and of these four, four and one, respectively, were recaptured twice. *A. cahirinus* and *S. calurus* were trapped at night (19.00 hours to 05.30 hours; one *S. calurus* was trapped at 08.00 hours) and *A. russatus* was trapped during the day (06.00–10.00 hours and 14.00–19.00 hours; one was trapped at 21.00 hours). From trapping times, we assumed that *A. cahirinus* and *S. calurus* were active  $10.5 \pm 1.5$  h day<sup>-1</sup>, and that *A. russatus* was active for  $9 \pm 1.5$  h day<sup>-1</sup>. Mean air temperatures during the active periods were 22 °C for the two former species and 27 °C for the latter.

*A. russatus* tended to be heavier than the other two species (Table 1), but differences among them were not significant. Total body water volume as a percentage of body mass did not differ among species and ranged between 64.3% and 67.1%. There was no difference between water influx and water efflux within any species and body masses did not increase or decrease significantly between captures, indicating that the rodents were maintaining steady-state water and energy budgets. In addition, there was no difference in water influx among the three species and values ranged between 0.126 and 0.144 ml H<sub>2</sub>O per g body mass per day.

CO<sub>2</sub> production, on a mass-specific basis, was more than 30% higher in *A. cahirinus* (2.36 ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) than in either *A. russatus* (1.78 ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) or *S. calurus* (1.75 ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>) (Table 1). Daily energy expenditure (*DEE*) was calculated as 1.352 kJ g<sup>-1</sup> day<sup>-1</sup>, 1.057 kJ g<sup>-1</sup> day<sup>-1</sup> and 1.067 kJ g<sup>-1</sup> day<sup>-1</sup> for *A. cahirinus*, *A. russatus* and *S. calurus*, respectively (Table 2). Therefore, mass-specific *DEE* was approximately 27% higher in *A. cahirinus* than the other species. We estimated that insects provided 58% of the total energy intake in *A. cahirinus*, 79% in *A. russatus* and 94% in *S.*

TABLE 1. Body mass ( $m_b$ ), total body water volume (*TBW*) as %  $m_b$ , water efflux (*WE*), water influx (*WI*) and CO<sub>2</sub> production in free-living *Acomys cahirinus*, *Acomys russatus* and *Sekeetamys calurus* (values are means, with S.D. in parentheses)

Species	<i>Acomys cahirinus</i>	<i>Acomys russatus</i>	<i>Sekeetamys calurus</i>
Number of measurements	9*	9*	5†
$m_b$ (g)	38.27 (5.12)	45.04 (5.10)	41.23 (2.22)
$m_b$ change (% day <sup>-1</sup> )	+0.04 (1.38) <sup>a</sup>	-0.43 (1.64) <sup>b</sup>	-0.72 (1.69) <sup>b</sup>
<i>TBW</i> (% $m_b$ )	65.77 (0.88)	67.09 (6.55)	64.25 (3.71)
<i>WE</i> (ml day <sup>-1</sup> )	5.06 (0.75)	5.75 (2.56)	6.09 (1.13)
<i>WI</i> (ml day <sup>-1</sup> )	5.04 (0.73)	5.65 (2.36)	5.89 (0.93)
<i>WE</i> (ml g <sup>-1</sup> day <sup>-1</sup> )	0.134 (0.023)	0.128 (0.056)	0.148 (0.031)
<i>WI</i> (ml g <sup>-1</sup> day <sup>-1</sup> )	0.134 (0.027)	0.126 (0.052)	0.144 (0.027)
CO <sub>2</sub> (ml g <sup>-1</sup> h <sup>-1</sup> )	2.36 (0.29) <sup>a</sup>	1.78 (0.42) <sup>b</sup>	1.75 (0.41) <sup>b</sup>

\* On five individuals.

† On four individuals.

Means with different superscripts, a and b, are different from each other.

TABLE 2. Estimated daily energy expenditure (*DEE*), dry matter intake (*DMI*), water influx (*WI*) and fresh matter intake in free-living *Acomys cahirinus*, *Acomys russatus* and *Sekeetamys calurus*. The proportions of insects and vegetation are given for each measurement and values in parentheses are percentage of total. Water influx is proportioned into preformed (*pre*) and metabolic (*met*) water.

Values are daily means

Species	<i>Acomys cahirinus</i>	<i>Acomys russatus</i>	<i>Sekeetamys calurus</i>
<i>DEE</i> (kJ g <sup>-1</sup> day <sup>-1</sup> )	1.352 (100.0)	1.057 (100.0)	1.067 (100.0)
Insects (kJ g <sup>-1</sup> day <sup>-1</sup> )	0.786 (58.1)	0.830 (78.5)	1.001 (93.8)
Vegetation (kJ g <sup>-1</sup> day <sup>-1</sup> )	0.566 (41.9)	0.227 (21.5)	0.066 (6.2)
<i>DMI</i> (g day <sup>-1</sup> )	10.16 (100.0)	6.61 (100.0)	5.66 (100.0)
Insects (g day <sup>-1</sup> )	3.87 (38.1)	4.09 (61.7)	4.93 (87.1)
Vegetation (g day <sup>-1</sup> )	6.29 (61.9)	2.52 (38.3)	0.73 (12.9)
<i>WI</i> (ml g <sup>-1</sup> day <sup>-1</sup> )	0.134 (100.0)	0.126 (100.0)	0.144 (100.0)
Insects <i>pre</i> water (ml g <sup>-1</sup> day <sup>-1</sup> )	0.090 (67.3)	0.095 (75.6)	0.115 (80.2)
Insects <i>met</i> water (ml g <sup>-1</sup> day <sup>-1</sup> )	0.020 (15.1)	0.021 (16.9)	0.026 (17.9)
Vegetation <i>pre</i> water (ml g <sup>-1</sup> day <sup>-1</sup> )	0.007 (5.2)	0.003 (2.2)	0.001 (0.6)
Vegetation <i>met</i> water (ml g <sup>-1</sup> day <sup>-1</sup> )	0.017 (12.4)	0.007 (5.3)	0.002 (1.3)
Fresh matter intake (g day <sup>-1</sup> )	19.88 (100.0)	16.42 (100.0)	17.25 (100.0)
Insects (g day <sup>-1</sup> )	12.89 (64.8)	13.62 (82.9)	16.44 (95.3)
Vegetation (g day <sup>-1</sup> )	6.99 (35.2)	2.80 (17.1)	0.81 (4.7)
Moisture in diet (%)	48.9	59.7	67.2
<i>WI/DMI</i> (ml H <sub>2</sub> O per g DM)	1.32	1.91	2.54

*calurus*. Of the dry matter intake, 38% was insects in *A. cahirinus*, 62% in *A. russatus* and 87% in *S. calurus* and of the fresh matter these values were 65%, 83% and 95%, respectively (Table 2). The water content of the total diet was 48.9% for *A. cahirinus*, 59.7% for *A. russatus* and 67.2% for *S. calurus*. Insects provided most of the water for all three species (Table 2).

We estimated metabolic rates during periods of activity (Table 3) as follows. We assumed that metabolic rates during inactivity periods were at resting levels. Basal metabolic rates (*BMR*), measured as O<sub>2</sub> consumed, have been reported for *A. cahirinus* and *A. russatus* (Shkolnik & Borut 1969) and for *S. calurus* (S. Haim unpublished) for animals collected from Ein-Gedi near the present study area. These measurements were made after only 4 h of food deprivation (A. Shkolnik & A. Haim unpublished), so they probably include some cost for digesting and assimilating food. We assumed that these values represent resting metabolism (*RMR*), and converted them to units of energy using 20.08 J per ml O<sub>2</sub> consumed (Kleiber 1975). Energy expenditures during the daily periods of inactivity were calculated from time budgets, and metabolic expenditures while active were calculated by subtraction of *RMR* from *DEE*. Over a 24-h period, *DEE* ranged from

TABLE 3. Daily energy expenditure (*DEE*), resting metabolic rate (*RMR*), and time-energy budgets of free-living *Acomys cahirinus*, *Acomys russatus* and *Sekeetamys calurus*

Species	<i>Acomys cahirinus</i>	<i>Acomys russatus</i>	<i>Sekeetamys calurus</i>
<i>DEE</i> (kJ g <sup>-1</sup> day <sup>-1</sup> )	1.352	1.057	1.067
<i>RMR</i> (kJ g <sup>-1</sup> day <sup>-1</sup> )	0.530*	0.386*	0.371†
Cost while active (kJ g <sup>-1</sup> day <sup>-1</sup> )	0.822	0.671	0.696
Activity time (h day <sup>-1</sup> )	10.5	9.0	10.5
<i>DEE/RMR</i>	2.55	2.74	2.88
Cost while active/ <i>RMR</i>	4.55	5.64	5.29

\* Calculated from Shkolnik & Borut (1969).

† Calculated from A. Haim (unpublished).



$2.55 \times RMR$  to  $2.88 \times RMR$  for the three species, and metabolic expenditures during the activity period ranged from  $4.55 \times RMR$  to  $5.64 \times RMR$ .

## DISCUSSION

Many desert granivorous rodents can survive on a seed diet without drinking water under laboratory conditions. These rodents have evolved effective water-conserving mechanisms, notably high urine concentration, dry faeces and low evaporative water loss (Schmidt-Nielsen 1964; Christian 1979; Withers, Louw & Henschel 1982; MacMillen 1983). In contrast, omnivorous desert rodents cannot survive on a dry diet without drinking water (MacMillen & Hinds 1983). Granivores can therefore inhabit deserts through their physiological adaptations and omnivores, herbivores, insectivores and carnivores through their diet selection.

Analyses of stomach contents of the three species we studied revealed that they were eating insects and dry, mature vegetation at the time of the study. These findings are similar to previous food habit studies of these species (Happold 1984). Our observations were made on one individual from each species and therefore definite conclusions on diet selection cannot be made. However, based on the ratio between water influx and dry matter intake, both *A. russatus* and *S. calurus* consumed diets of higher water content, thus more insects than dry, mature vegetation, than did *A. cahirinus*.

In order to evaluate the field water relations of the three rodent species we studied, we compared their water influxes with those of other rodents, most of which live in arid habitats. The allometric equation derived from regression analyses indicates that water influx ( $\text{ml day}^{-1}$ ) =  $0.21 m_b (\text{g})^{0.90}$  (summarized by Morris & Bradshaw 1981), where  $m_b$  is body mass. The species we studied had 1–13% lower water influxes than those predicted for rodents of their body mass: *A. cahirinus*,  $0.190 \text{ ml g}^{-0.90} \text{ day}^{-1}$  (90% of predicted); *A. russatus*,  $0.183 \text{ ml g}^{-0.90} \text{ day}^{-1}$  (87% of predicted); and *S. calurus*,  $0.207 \text{ ml g}^{-0.90} \text{ day}^{-1}$  (99% of predicted). However, examination of individual species listed by Morris & Bradshaw (1981) reveals that granivorous rodents tended to have lower water influxes (e.g. *Perognathus formosus*,  $0.092\text{--}0.158 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ; *Dipodomys merriami*,  $0.159\text{--}0.186 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ; *Perognathus fallax*,  $0.203 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ), whereas omnivorous rodents had somewhat higher rates than other rodents (e.g. *Pseudomys albocinereus*,  $0.183\text{--}0.315 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ; *Meriones shawii*,  $0.220\text{--}0.258 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ; *Mus musculus*,  $0.290\text{--}0.327 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ; *Rattus fuscipes*,  $0.402 \text{ ml g}^{-0.90} \text{ day}^{-1}$ ).

This comparison suggests that, although granivorous rodents tend to have lower water influxes in the field than do omnivorous rodents, there is much overlap, and the distinct differences present in captive rodents in the laboratory are not so apparent in the field. The three species we studied fell between, but overlapped with, omnivorous and granivorous rodents in general. We suggest that 'granivorous' desert rodents do not necessarily restrict their diet to seeds, and that behavioural adaptations (e.g. diet selection) can be as effective as physiological adaptations that conserve water, in permitting rodents to survive and reproduce in deserts. Indeed, seasonal studies have shown that desert rodents can have high rates of water intake by selecting succulent foods (Grubbs 1980; Morris & Bradshaw 1981; Karasov 1983). Thus, water influxes in the field, and water-conserving capabilities in captivity, may be poor predictors of the habitat distribution of rodents.

Nocturnally active *A. cahirinus* had a 28% higher energy expenditure, on a mass-specific basis, than the congeneric, but diurnal, *A. russatus*. *A. cahirinus* probably

had higher costs for temperature regulation than did *A. russatus* since air temperatures during the night were lower than during the day. Also, *A. cahirinus* was active longer and ate more plant matter than did *A. russatus*. (The ratios of *DEE* to *RMR* and cost while active to *RMR* were lower for *A. cahirinus* primarily because the *RMR* for *A. cahirinus* is about 40% higher than that for the other two species (Shkolnik & Borut 1969; Haim & Borut 1981; Daily & Haines 1981).)

Clearly, it was more expensive in terms of energy for the nocturnal species to exist than it was for the diurnal species. It is puzzling, therefore, that the nocturnal niche appears to be preferred by both species of *Acomys*. Shkolnik (1971) found that *A. russatus* became nocturnal when *A. cahirinus* was removed from the habitat, and he suggested that *A. cahirinus* may force *A. russatus* to become diurnal where both species occur together. It may be that factors such as predation pressure, which are not measured in the currency of energetics or water relations, make the diurnal activity period disadvantageous.

*S. calurus* was active for 10.5 h each night, as was *A. cahirinus*, consumed primarily insects and had a 27% lower metabolic rate than *A. cahirinus*. This may be explained by the foraging mode and behaviour of *S. calurus*. The bipedal locomotion of *S. calurus* may reduce its locomotion costs (Dawson & Taylor 1973; Dawson 1976; Thompson *et al.* 1980), permitting it to forage more economically than the quadrupedal *A. cahirinus*.

In comparing energy expenditures of these three rodents with other rodents studied so far, we used the allometric regression equation of Grodzinski & Wunder (1975), where  $DEE$  ( $\text{kJ g}^{-1} \text{day}^{-1}$ ) =  $8.56 m_b$  ( $\text{g}$ )<sup>-0.46</sup>. Although the equation was established for captive animals, the daily energy expenditures of the three species were still lower than the average daily metabolic rates predicted for rodents of their body mass: *A. cahirinus* was 15.6% lower, *A. russatus* was 28.8% lower and *S. calurus* was 31.0% lower (Table 4). This is consistent with the notion of low energy expenditures among desert-adapted rodents (Schmidt-Nielsen 1964).

The energy intake of *A. cahirinus* was higher than that of the other two species and their insect intake was the lowest. Metabolizable energy is greater for insects than for dry, mature vegetation per unit mass of dry matter, but not per unit mass of fresh matter. If stomach volume is a limiting factor in the total fresh matter intake, than *A. cahirinus* needs a larger fraction of dry matter intake than the other two species. This was reflected by the ratio of water influx to dry matter intake ( $\text{ml:g}$ ) which was 1.3 for *A. cahirinus* as compared with 1.9 for *A. russatus* and 2.5 for *S. calurus*. In more arid areas, *A. cahirinus* would have to increase their ratio of water influx to energy intake, but then perhaps, they could not consume enough dry matter to meet energy requirements. This could explain

TABLE 4. Expected daily water influxes ( $WI_{ex}$ ) and expected daily energy expenditure ( $DEE_{ex}$ ) compared to measured values ( $WI_m$  and  $DEE_m$ , respectively) in *Acomys cahirinus*, *Acomys russatus* and *Sekeetamys calurus*.  $WI_{ex}$  ( $\text{ml day}^{-1}$ ) was calculated as  $0.21 m_b^{0.9}$  (Morris & Bradshaw 1981) and  $DEE_{ex}$  ( $\text{kJ g}^{-1} \text{day}^{-1}$ ) was calculated as  $8.56 m_b^{-0.46}$  (Grodzinski & Wunder 1975);  $m_b$  (body mass) in g

Species	<i>Acomys cahirinus</i>	<i>Acomys russatus</i>	<i>Sekeetamys calurus</i>
$WI_m$ ( $\text{ml day}^{-1}$ )	5.04	5.65	5.89
$WI_{ex}$ ( $\text{ml day}^{-1}$ )	5.58	6.46	5.97
$WI_m/WI_{ex}$ (%)	90.3	87.5	98.7
$DEE_m$ ( $\text{kJ g}^{-1} \text{day}^{-1}$ )	1.352	1.057	1.067
$DEE_{ex}$ ( $\text{kJ g}^{-1} \text{day}^{-1}$ )	1.601	1.485	1.547
$DEE_m/DEE_{ex}$ (%)	84.4	71.2	69.0

their different distributions, i.e., the ability of *A. russatus* and *S. calurus* to inhabit extreme deserts where *A. cahirinus* is absent.

It is possible that these three rodent species can coexist partly because they use somewhat different food and time resources. *A. russatus* is diurnal, whereas the other two species are nocturnal, and although *A. cahirinus* and *S. calurus* feed at similar times, *S. calurus* consumes substantially more insects and less vegetation than does *A. cahirinus*. However, more detailed information is required on the insects consumed by the three species and the rate of renewal of the insects from day to night before questions concerning competition and coexistence can be answered.

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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 ( $[P_s]$ ) > 0.35, Student's  $t$ -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 lush 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 micro-distilled 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<sub>2</sub> 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<sub>2</sub> volumes were calculated assuming that an insect diet yields 25.7 joules [J]/ml CO<sub>2</sub> (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<sub>2</sub> 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 ( $66.0 \pm 3.1\%$  of live body mass,  $n = 6$ ) than in geckos ( $76.7 \pm 1.5\%$ ,  $n = 9$ ).

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 soliphugid, 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  $20.0 \pm 1.9$  C ( $n = 11$ ) and  $33.7 \pm 2.1$  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

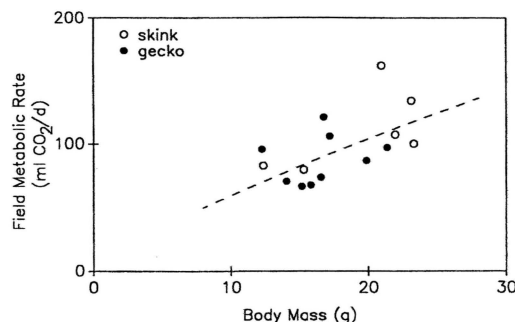


Fig. 1. Relationship between field metabolic rate and body mass for Kalahari Desert skinks (*Mabuya striata*) and geckos (*Pachydactylus striata*). Dashed line represents iguanid lizards ( $\text{ml CO}_2/\text{d} = 8.72\text{g}^{0.80}$ , modified from Nagy, 1982).

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).

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  $\pm$  95% confidence intervals.

	Skink (diurnal) (n = 6)	Gecko (nocturnal) (n = 9)	t-value, P <sup>a</sup>
<b>Body mass</b>			
Mean, g	19.5 $\pm$ 4.8	16.6 $\pm$ 2.1	1.55, n.s.
Change rate, %·day <sup>-1</sup>	+0.4 $\pm$ 0.6	+0.1 $\pm$ 0.7	0.65, n.s.
<b>Field metabolic rate</b>			
ml CO <sub>2</sub> ·day <sup>-1</sup>	111 $\pm$ 33	87 $\pm$ 15	1.81, n.s.
kJ·day <sup>-1</sup>	2.9 $\pm$ 0.9	2.2 $\pm$ 0.4	1.82, n.s.
kJ·g <sup>-0.80</sup> ·day <sup>-1b</sup>	0.27 $\pm$ 0.06	0.24 $\pm$ 0.04	0.87, n.s.
<b>Water influx rate</b>			
ml H <sub>2</sub> O·day <sup>-1</sup>	0.64 $\pm$ 0.24	0.40 $\pm$ 0.09	2.71, <0.02
ml H <sub>2</sub> O·kg <sup>-0.91</sup> ·day <sup>-1b</sup>	23.4 $\pm$ 7.8	17.7 $\pm$ 5.2	1.53, n.s.
<b>Water efflux rate</b>			
ml H <sub>2</sub> O·day <sup>-1</sup>	0.59 $\pm$ 0.21	0.38 $\pm$ 0.07	2.69, <0.02
ml H <sub>2</sub> O·kg <sup>-0.91</sup> ·day <sup>-1b</sup>	21.5 $\pm$ 6.7	16.8 $\pm$ 4.6	1.47, n.s.

<sup>a</sup> 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.

<sup>b</sup> 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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## DO DESERT GECKOS CONSERVE ENERGY AND WATER BY BEING NOCTURNAL?<sup>1</sup>

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Body temperature has a very large effect on the rate of energy metabolism of ectothermic animals. Nocturnal lizards, which have low body temperatures when they are active at night, may have lower daily energy requirements than do diurnal lizards, which maintain high body temperatures while active during daylight hours. We tested the hypothesis that the nocturnal desert gecko *Ptyodactylus hasselquistii* has lower energy and water needs than do diurnal desert lizards by comparing doubly labeled water measurements of field metabolic rates (FMRs) and water fluxes for both groups. The FMRs and water influx rates of the geckos were statistically indistinguishable from those of diurnal iguanid lizards. We suggest that field observations of daily time and activity budgets, and thermal regimes, be made to permit evaluation of this surprising finding.

### INTRODUCTION

Ectothermic animals, such as lizards, use very little food and energy in comparison with endothermic animals of the same body size. Field metabolic rates and feeding rates of iguanid lizards are only about 5% of those of birds or mammals (Nagy 1982a). A large part of this difference is apparently due to the differing daily thermal regimes of endotherms and ectotherms. Consider a diurnal, 100-g bird and a diurnal, 100-g lizard living in the same habitat and having the same diet. The bird maintains a high body temperature continuously and must increase its heat production to stay warm at night as ambient temperature falls. However, the lizard's metabolic rate drops rapidly at dusk because it ceases being active and because its body temperature cools to that of its sur-

roundings. This 20-fold difference in energy requirements suggests that population densities of lizards can be 20 times higher than those of similar-sized endotherms in the same trophic level, and that lizards may be better adapted than endotherms to situations of low food supply, such as during seasonal droughts or in desert habitats.

Because much of the difference between the energy requirements of lizards and endotherms is due to different daily profiles of body temperature, we hypothesized that differences may also exist among species of lizards that have different daily thermal regimes due to different activity patterns. Diurnal lizards maintain near-mammalian body temperatures during their activity period by shuttling between sun and shade (Cowles and Bogert 1944). In contrast, nocturnal lizards are active at much lower body temperatures (Templeton 1970). We had an opportunity to test the hypothesis that nocturnal desert lizards have lower energy and water requirements than do diurnal desert lizards by making doubly labeled water measurements (Nagy 1975) of field metabolic rate (FMR) and water flux in geckos and comparing these results with predicted rates for iguanid lizards of the same body mass and similar ecological niche.

### MATERIAL AND METHODS

We studied a population of geckos (*Ptyodactylus hasselquistii guttatus*) living on

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and around a small, abandoned outbuilding near Sede Boqer (30° 52' N, 34° 57' E, 475 m above sea level) in the Negev Desert highlands, Israel. This area is classified as arid, having 250–300 biologically dry days per year and a precipitation:evaporation ratio of <0.2 (Unesco 1977). Rain occurs during winter and averages 104 mm annually, with much variation in total annual precipitation and its temporal and spatial distribution. Dew occurs on about 190 nights per year, and average relative humidity in the daytime is 58% (Zangvil and Druian 1983). This moisture comes primarily from the Mediterranean Sea via the prevailing onshore breeze. Air temperatures at the study site were recorded during the study using a minimum/maximum thermometer placed in continuous shade at ground level inside the building. Minimum temperatures averaged  $22.7 \pm 3.8$  C ( $\pm$  95% confidence interval), and maximum temperatures averaged  $34.5 \pm 5.4$  C.

*Ptyodactylus* geckos are insectivorous and are primarily nocturnal (Werner 1965; Perry and Werner 1981). During daylight hours of August 5 and 7, 1983, we captured 13 geckos by hand and with nooses on poles. Each lizard was given an intraperitoneal injection of 0.030 ml of

sterile water containing 95 atoms % oxygen-18 and 10  $\mu$ Ci of tritium. Each gecko was weighed to the nearest 10 mg, sexed (on the basis of head width and length measurements, when sex was not otherwise obvious due to the presence of eggs in utero or enlarged hemipenes), and marked with a number on its belly and back. After 1 h (for injected isotopes to equilibrate completely in body water), a small (ca. 50  $\mu$ l) blood sample was taken from an orbital sinus, and the gecko was released where captured. After 12–14 days, each lizard was recaptured, weighed, and a second blood sample was taken before rerelease. When possible, we took urine samples (voluntarily contributed) rather than blood samples from recaptured lizards in order to minimize unnecessary trauma.

Samples from injected lizards, along with samples from two uninjected lizards (for measurement of isotope background levels) were flame-sealed in heparinized glass capillary tubes, marked with tape, and kept on ice until they were microdistilled under vacuum at Sede Boqer. The distilled samples were transported to the University of California, Los Angeles, where they were analyzed for tritium via liquid scintillation counting, and for oxy-

TABLE 1  
BODY MASSES AND RATES OF ENERGY METABOLISM AND WATER FLUX IN FREE-RANGING *Ptyodactylus hasselquistii* GECKOS AT SEDE BOQER IN THE NEGEV DESERT DURING SUMMER (August 1983)

	Males (N = 6)	Females (N = 5)	Overall <sup>a</sup> (N = 13)
Body mass (g) . . . . .	9.71 $\pm$ 2.36	9.58 $\pm$ .84	9.09 $\pm$ 1.24
Mass change rate (%/day) . . . . .	+47 $\pm$ .68	+50 $\pm$ .92	+41 $\pm$ .39
Body water (%) . . . . .	72.6 $\pm$ 4.9	73.2 $\pm$ 5.1	72.9 $\pm$ 2.3
Energy metabolism (kJ/day) . . . . .	1.11 $\pm$ 0.31	1.50 $\pm$ 0.62	1.19 $\pm$ 0.28
Predicted metabolism (kJ/day) (95% CI range) <sup>b</sup> . . . . .	1.38 (.95–2.01)	1.36 (.93–1.99)	1.30 (.90–1.91)
Ratio: actual/predicted . . . . .	.82	1.10	.91
Water influx rate (ml/day) . . . . .	.29 $\pm$ .08	.35 $\pm$ .17	.29 $\pm$ .07
Predicted influx (ml/day) (95% CI range) <sup>b</sup> . . . . .	.30 (.17–.51)	.30 (.17–.50)	.28 (.16–.48)
Ratio: actual/predicted . . . . .	1.00 $\pm$ .34	1.19 $\pm$ .51	1.03 $\pm$ .22

NOTE.—Values are means  $\pm$  95% confidence intervals.

<sup>a</sup> Includes two juveniles of undetermined sex. There were no statistically significant differences between males and females in any of the measured variables ( $P > .05$  via a Student's *t*-test where variances were homogeneous, and via a Mann-Whitney *U*-test where variances were heterogeneous [body mass data only]).

<sup>b</sup> Antilogarithmic transformation yields asymmetric CI ranges around the predicted values.



gen-18 by proton activation analysis (Wood et al. 1975; Nagy 1983). Total body water volumes were estimated as the dilution spaces of injected oxygen-18 (Nagy 1980), rates of CO<sub>2</sub> production and water flux were calculated using the equations for linearly changing water volumes (Nagy 1980; Nagy and Costa 1980), and heat equivalents of CO<sub>2</sub> volumes were calculated assuming that an insect diet yields 25.7 J/ml CO<sub>2</sub> (Nagy 1983).

Results are given as means ± 95% confidence intervals. Comparisons between means were made using Student's *t*-statistic for data sets that had homogeneous variances, according to an *F*-test ( $P \leq .05$ ). Where variances were not homogeneous, we used the Mann-Whitney *U*-statistic, accepting the  $P \leq .05$  level of significance.

RESULTS

Among the 13 recaptured geckos, five were females and six were males, thereby presenting us with the opportunity to test for differences in measured variables between sexes. Mean body masses of males and females did not differ significantly (table 1). Although reproductively active males tend to be larger, have enlarged heads, and are sexually dimorphic in coloration when compared to females (Perry and Werner 1981), our sample included males that were not reproductively active and so were difficult to distinguish visually from females. None of the measured variables differed significantly between sexes, so the data were combined with measurements from two juvenile geckos of undetermined sex, and overall means were calculated.

The geckos averaged 9.1 g body mass (table 1). They were growing slowly during the 2 wk of measurements, as indicated by the observations that rates of body mass change differed significantly from zero ( $P < .05$  via two-tailed *t*-test), and that the 95% confidence intervals for mass change rate did not include zero (table 1). Total body water volumes were typical for lizards, averaging 72.9% of live mass.

Rates of carbon dioxide production were  $0.191 \pm 0.058$  ml (g·h)<sup>-1</sup> in males,  $0.254 \pm 0.094$  in females, and  $0.213 \pm 0.040$  ml (g·h)<sup>-1</sup> overall, including the

two juveniles. Field metabolic rates (FMRs, calculated by converting CO<sub>2</sub> produced per hour to kilojoules produced per day) averaged 1.19 kJ/day overall (table 1). Rates of water influx averaged 0.29 ml/day (table 1) and were slightly higher than were rates of water efflux, as expected for growing animals.

To address the question of reduced energy and water metabolism in geckos, we calculated rates of heat production and water influx expected for diurnal lizards of the same mean body mass as each of our three groups of recaptured geckos (males, females, and combined; table 1) and compared actual rates with the 95% confidence intervals (CI) of predicted values. We used the allometric regression equation (and the associated equation for the 95% CI of

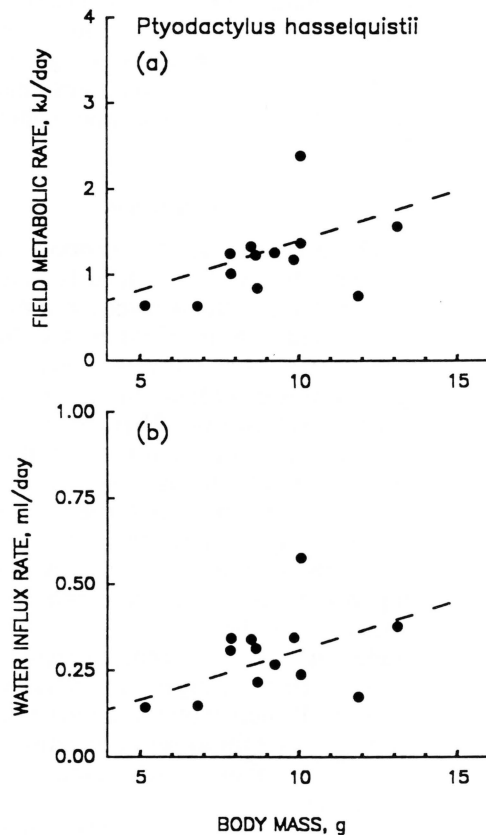


FIG. 1.—Comparison of measured rates of (a) energy metabolism and water influx (b) in free-living Negev Desert geckos with predicted values for diurnal lizards (dashed lines, from Nagy 1982a, 1982b).

the prediction) for FMR in iguanid lizards during the spring and summer activity season (Nagy 1982a, 1987). All species used in deriving that equation are diurnal, and most are insectivorous and inhabit deserts. To predict water influx for a diurnal desert lizard of a given body mass, we used the scaling equation derived from field measurements on arid and semiarid reptiles (Nagy 1982b), most of which are insectivores, and all of which are diurnal. The associated equation for the 95% CI of the prediction of water influx ( $y_p$ ) is 95% CI  $\log y_p = \log y_p \pm 0.223 [1.06 + 0.089 (\log x - 1.478)^2]^{0.5}$ , where  $x$  is body mass in grams.

Negev geckos have FMRs and water influx rates that are statistically indistinguishable from those of diurnal lizards having otherwise similar niches. In no group (males, females, or overall) do measured rates differ significantly from predicted rates (table 1). Some geckos had FMRs and water influx rates that were higher than predicted, and others had lower rates (fig. 1).

#### DISCUSSION

These results do not support our hypothesis that nocturnal lizards have lower energy, water, and food requirements than do diurnal lizards. Field metabolic rates and water flux rates in Negev Desert geckos were essentially the same as if these lizards were diurnal. There are several potential explanations for the remarkably high FMR of geckos. These are (1) our study animals may have been more diurnal than expected, (2) they may have had much higher body temperatures over a 24-h period than we expected for a nocturnal species, (3) they may have had much higher activity costs than expected due to more intense or longer daily activity bouts, and/or (4) their metabolic rates may have compensated for lower body temperatures by means of thermal acclimatization (Bartholomew 1982).

Frankenberg (1976, 1978, 1979) and Frankenberg and Werner (1979) have shown that the three subspecies of *Ptyodactylus hasselquistii* in Israel vary from being essentially nocturnal in the south-

ern, desert-dwelling form (*P. h. hasselquistii*) to essentially diurnal in the northern, cool-habitat form (*P. h. puisieuxi*). The subspecies we studied in the Negev, *P. h. guttatus*, is "diurnonocturnal," in keeping with its geographically intermediate habitat, but it varies between having nocturnal or mostly diurnal activity periods depending on season. We did not make daily time-budget observations on marked animals because such disturbance (observers inside the outbuilding) undoubtedly would have affected gecko behavior and hence FMR and water flux measurements. However, quick spot checks of our marked animals after dark indicated that they were nocturnally active. They were probably somewhat active in late afternoon and early evening as well (Frankenberg 1979). Accordingly, they would have had ample opportunity to achieve relatively high body temperatures late in the day. In fact, *P. h. guttatus* living at Sede Boqer are known to bask and maintain relatively high body temperatures in the afternoons in summer (Werner and Goldblatt 1978).

Whether these geckos have unusually long or intense activity periods or whether they have thermally acclimatized metabolic rates is not known. Frankenberg's (1978, 1979) results and our own casual observations suggest that these geckos are rather sedentary sit-and-wait predators that do not move around a great deal while abroad. Only a few other geckos have been subjected to laboratory studies of temperature effects on energy metabolism, and these did not show thermal acclimatization to any remarkable extent (Bennett and Dawson 1976).

We suspect that the primary reason that *Ptyodactylus* geckos had such high FMRs is because they behaviorally selected rather high body temperatures during the day, especially while they were inactive at the beginning of the day. Appropriate field observations concerning this question would be especially interesting. If geckos do select warm rather than cool body temperatures, and have relatively high energy, water, and food requirements as a result, this calls into question the preconception that low resource requirements are always adaptive for a desert animal.

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## FIELD ENERGETICS AND FORAGING MODE OF KALAHARI LACERTID LIZARDS<sup>1</sup>

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**Abstract.** We examined the energetic costs associated with foraging mode in the widely foraging lizard *Eremias lugubris* (mean mass 3.83 g) and the sit-and-wait lizard *Eremias lineocellata* (3.27 g). These lizards are broadly sympatric in the Kalahari desert. Individuals of both species were probably abroad every day, but the wide forager was abroad for much shorter periods (2.75 h/d vs. 10.25 h/d). Nevertheless, the widely foraging species had significantly higher field metabolic rates (800 vs. 544 J/d, as measured with doubly labeled water), feeding rates (metabolizable energy of 1165 vs. 739 J/d), production rates (365 vs. 195 J/d) and water influx rates (0.285 vs. 0.156 mL/d). Measurements were made before the reproductive season began; there were no significant differences in these measures between sexes within either species.

Resting metabolic rates (measured as O<sub>2</sub> consumed) were similar at 37°C (0.240 vs. 0.252 mL·g<sup>-1</sup>·h<sup>-1</sup>) and at 26° (0.094 vs. 0.103 mL·g<sup>-1</sup>·h<sup>-1</sup>), the field active and nocturnal burrow temperatures, respectively, of both species. Field metabolic rates, on a 24-h basis, were 3.1× resting in *E. lugubris* and 2.2× resting in *E. lineocellata*. Energy expenditures during the activity period were 12.0× resting in the wide forager and 2.8× resting in the sit-and-wait predator. Foraging efficiency (metabolizable energy gained while foraging/total energy spent while foraging) was higher in the wide forager (2.0) than in the sit-and-wait predator (1.6). However, when foraging efficiency is expressed as metabolizable energy gained/activity cost (above resting cost), the wide forager (2.2) was less effective than the ambush predator (2.6), apparently because the cost of searching is substantial for *E. lugubris* but negligible for *E. lineocellata*. The hourly cost of foraging was much higher for *E. lugubris* (almost 5× that of *E. lineocellata*) but the hourly benefit of foraging for *E. lugubris* was even higher (nearly 6× that of *E. lineocellata*). Thus *E. lugubris* made a greater profit on its investment (46 vs. 36% each day), and the wide forager grew nearly twice as fast as did the sit-and-wait predator during this study. On an annual basis, variation in food availability or differences in predation rate may alter the relative fitness of these foraging modes.

**Key words:** activity cost; cost-benefit analysis; daily energy expenditure; doubly labeled water; ecological energetics; *Eremias*; field metabolic rate; foraging efficiency; Kalahari desert; metabolic rate; production rate; water flux.

### INTRODUCTION

A major task that animals face is to obtain enough food to provide the energy needed for survival and reproduction. Finding, capturing, and ingesting food itself requires an expenditure of energy above that required for maintenance, growth, and other activities. The harder an animal works to get food, the more food it needs to achieve energy balance. Some animals use a widely foraging mode of getting food, which is probably more costly than the sit-and-wait mode used by other animals. Theoretical aspects of these foraging modes have been discussed by Schoener (1971), Gerritsen and Strickler (1977), Norberg (1977), Regal

(1978), Vitt and Congdon (1978), Andersson (1981), and Janetos (1982), but empirical studies of the energetics of foraging mode are few.

Among lizards, foraging costs and benefits of foraging have been analyzed in comparisons involving the sit-and-wait iguanids and the widely foraging teiids (Anderson and Karasov 1981, Andrews 1983). Widely foraging teiids have a higher foraging efficiency (metabolizable energy gain/energy expenditure during foraging) than do the sit-and-wait iguanids. However, these interesting comparisons are confounded by morphological, physiological, sensory, and behavioral differences associated with a major phylogenetic divergence, so observed differences in foraging efficiency may not be due to foraging mode alone.

We were able to compare the energetic costs (energy

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expended) and benefits (energy gained) in a sit-and-wait lizard and in a widely foraging lizard that belong to the same genus (*Eremias*: Lacertidae). These lizards are diurnal insectivores, and they live syntopically on sand dune ridges in the Kalahari desert (Huey et al. 1977, Pianka et al. 1979, Huey and Pianka 1981). They afford a unique opportunity to examine the comparative energetics of foraging mode in the virtual absence of phylogenetic differences. We measured field metabolic rates (FMR) using doubly labeled water (Lifson and McClintock 1966, Nagy 1980), and estimated foraging costs as the difference between field metabolic rates of field active and resting individuals. The latter was determined from resting metabolic rates in the laboratory and measurements of time budgets and thermal regimes in the field. We defined the benefit of foraging as the rate of metabolizable (useable) energy gain. Because metabolizable energy is used primarily for respiration with any excess energy appearing only as production of new biomass, we equated benefit with the sum of measured field metabolic rate and production rate. Results of behavioral and physiological studies of these lizards are reported elsewhere (Huey et al., *in press*; Bennett et al., *in press*).

#### MATERIALS AND METHODS

##### *Description of study area*

This study was conducted in late November 1981 (spring in the Southern Hemisphere). Adult lizards had recently emerged from brumation but had not yet begun reproductive activities. The study area was a north-east-facing stabilized sand-ridge and was located  $\approx 14$  km northeast of Twee Rivieren, Kalahari Gemsbok National Park, Republic of South Africa. This site lies within the "dune region" of the southern Kalahari (Leistner 1967) and was a small section of area "L" of Pianka (1971) and Pianka and Huey (1971). Vegetation at this site is described by Pianka and Huey (1971). Dominant plants include a variety of perennial grasses as well as numerous shrubs (*Acacia mellifera*, *A. hebeclada*, *Lycium hirsutum*, and *Rhigozum trichotomum*) and a few trees (*Boscia albitrunca*, *Acacia giraffae*, and *A. haematoxylon*). Perennial plants cover  $\approx 10\%$  of the area (Pianka and Huey 1971). Annual rainfall for the region is  $\approx 170$  mm (Leistner 1967).

##### *Doubly labeled water study*

On each of three successive days, we captured lizards on a different section of a  $500 \times 50$  m plot within the study area. The site of each capture was marked. Lizards were individually weighed, toe-clipped, painted with an identifying number, and injected intraperitoneally with 0.015 mL of water containing  $^3\text{H}$  at 12 MBq/mL and 97 atoms  $^{18}\text{O}$  per hundred atoms total O. Lizards were then released at the location of initial sighting. Because of the small body sizes of these lizards, we did not take blood samples for measurement

of the initial isotope activities. Instead, we captured, weighed, and injected an additional 6 *E. lugubris* and 11 *E. lineocellata* and then sampled their blood a minimum of 1 h later. Results from these lizards were used to estimate initial isotope activities of released lizards (see below). The additional lizards were then autopsied to determine sex, reproductive condition, diet, body water content, and body energy content as follows. Lizards were killed by cervical section, a mid-ventral incision was made in the abdomen, and the gonads were examined and measured. Contents of the stomach were removed and sorted, and the approximate volume of each diet component was estimated as percentage of total volume. Stomach contents were returned to the body cavity and were included in subsequent analyses of body composition. Body water content was determined as live body mass minus body mass after oven drying to constant mass at  $65^\circ\text{C}$ . The dry remains were pulverized in a Spex Mixer-Mill and the resulting powder was measured for energy content using a Phillipson microbomb calorimeter. All lizards used in these analyses were captured during the middle or late part of their activity periods, so they had ample opportunity to fill their stomachs before autopsy.

After an interval of 8–10 d, during which time the injected lizards were not disturbed by us, we revisited the study area and recaptured 20 of 32 injected *E. lugubris* and 16 of 20 *E. lineocellata*. We reweighed, sampled the blood, and autopsied each lizard (as described above). The volumes of blood samples obtained from two recaptured *E. lugubris* were too small for accurate isotopic measurements, so sample size for doubly labeled water measurements for this species was 18. Minimum and maximum air temperatures at 1 m in shade were recorded during the study, and averaged  $15^\circ$  and  $39^\circ$ , respectively.

Isotope levels were determined by liquid scintillation spectrometry (for  $^3\text{H}$ ) and proton-activation analysis (for  $^{18}\text{O}$ ) (Wood et al. 1975, Nagy 1980) using water that was distilled from blood samples. Field metabolic rates were calculated according to Eq. 2 in Nagy (1980) as modified from Lifson and McClintock (1966). Initial body water volumes of recaptured lizards were calculated from their initial body masses using a least-squares linear regression of body water on body mass determined from autopsy results. Total body water (TBW) contents [ $\text{H}_2\text{O}$  (g)/live mass (g)] of lizards autopsied at the time of injection did not differ significantly ( $P > .05$ , two-tailed  $t$  test) from those of animals recaptured 8–10 d later. Results were pooled by species and the following least-squares regressions were calculated:  $\text{TBW (g)} = 0.175 + (0.714 \times \text{live mass [g]})$  ( $r = 0.977$ ,  $df = 24$ ,  $F_{\text{regression}} = 3392$ ,  $P < .001$ ) for *E. lugubris*, and  $\text{TBW (g)} = 0.129 + (0.697 \times \text{live mass [g]})$  ( $r = 0.995$ ,  $df = 25$ ,  $F_{\text{regression}} = 2297$ ,  $P < .001$ ) for *E. lineocellata*. These regressions differ significantly in intercept (ANCOVA;  $F_{(1,51)} = 25.9$ ;  $P < .001$ ) but not in slope ( $F_{(1,51)} = 0.83$ ;  $P > .05$ ). Initial isotope



concentrations ( $^3\text{H}_1$ ] and [ $^{18}\text{O}_1$ ], corrected for background) and TBWs sampled 1 h after injection were used to calculate the constants  $C_{(^3\text{H})}$  and  $C_{(^{18}\text{O})}$  from the equations  $C_{(^3\text{H})} = [^3\text{H}_1] (\text{TBW [g]})$  and  $C_{(^{18}\text{O})} = [^{18}\text{O}_1] (\text{TBW [g]})$ , respectively. Mean  $C$  values for each isotope did not differ significantly between species, so overall means were calculated. Coefficients of variation were 5.02% for  $C_{(^3\text{H})}$  and 3.98% for  $C_{(^{18}\text{O})}$ . The regression equations above were used to calculate initial water volumes of recaptured lizards from their initial body masses. These TBW values were then used to calculate initial isotope concentrations in recaptured lizards from the appropriate constant. The maximum errors associated with this procedure should be  $\approx 5\%$  for field metabolism (Nagy 1980) and  $\approx 15\%$  for field water flux estimates (Nagy and Costa 1980). The polarity of these errors is random, so mean values should be relatively accurate, but variances may be falsely high.

Stomach contents provided information on types and relative volumes of prey eaten by each species. Samples of representative prey taxa were then collected in the study area and later analyzed for water and energy content. Live dietary items were pooled in proportion to their occurrence in the diet of each *Eremias* species, dried at  $65^\circ$  to determine water content, and the dry matter was then analyzed in triplicate for energy content (Phillipson microbomb calorimeter).

#### Behavioral and thermal measurements

Observations of daily behavior patterns, body temperatures, and burrow temperatures were made in order to partition FMR measurements into costs of resting and activity. Times of first emergence in the morning and last retreat into burrows later in the day for both species were determined independently by four observers during six separate days, and mean emergence and retreat times were calculated. Three marked individuals of each species were watched continuously throughout one day in order to ascertain whether individual lizards were abroad during the entire activity period determined (above) for the two populations. The intensity of activity and approximate distances traveled by these lizards were also recorded. To assess whether individual lizards were active on successive days, we captured five *E. lugubris* and six *E. lineoocellata*, painted unique marks on them, and immediately released them where captured. The following day, we intensively searched the study area and recorded the number of these individuals that were seen abroad.

Cloacal temperatures of four to six active lizards of each species were measured using a quick-registering Schultheis thermometer. These measurements confirmed the previous estimate (Huey et al. 1977) of  $37^\circ$  for field-active body temperature in both *E. lugubris* and *E. lineoocellata* while abroad. Three *E. lugubris* and four *E. lineoocellata* were followed until they retreated into their burrows. Then, these burrows were

fitted with thermocouples, and temperatures at the bottom of the burrows were recorded approximately hourly for the next 24 h. We assumed that the body temperatures of lizards in burrows were the same as burrow temperatures. We excavated two other lizards in burrows, and their body and burrow temperatures supported this assumption. The burrows of *Eremias* lizards were shallow (all  $< 13$  cm deep), so lizards occupying them had little opportunity to alter their temperatures by selecting various depths of soil.

#### Resting oxygen consumption

We measured resting metabolic rates on eight *E. lugubris* (average mass  $\pm \text{SE} = 4.09 \pm 0.25$  g) and eight *E. lineoocellata* ( $4.02 \pm 0.30$  g). Lizards were flown to the United States where they were housed in terraria and provided with ample water and food (termites and crickets). Photoperiods were adjusted to simulate Kalahari times. Incandescent lights permitted temperature regulation for 10 h/d. At other times body temperatures dropped to  $26^\circ$ , which approximates the average body temperature of these lizards during spring nights in nature.

Metabolic measurements were made within 2 wk of capture on healthy and vigorous lizards. Because we wished to use metabolic data in field energy budgets rather than to estimate "standard metabolic rates" (Bennett and Dawson 1976), oxygen consumption was measured on fed, alert animals during normal night and day periods and at normal field body temperatures in closed-chamber respirometers. This protocol eliminated the need to adjust metabolic rates to account for the energy-producing effect of food and for the cost of posture. At the beginning of a sampling period, animals were placed individually in plastic metabolic containers, which were fashioned from electrophoretic staining trays (500 mL in volume) and had removable lids, sealed with Lubri-seal (Arthur H. Thomas Company, Philadelphia, Pennsylvania). Air samples were withdrawn through a three-way stopcock valve. The chambers, with lids ajar, were placed in a controlled-temperature cabinet for at least 12 h. Lids were then sealed for 1 h, and 20-mL samples of air were withdrawn from each chamber at the beginning and end of this period. Carbon dioxide and water vapor were removed from the air samples as they were injected with a Razel syringe pump at  $\approx 10$  mL/min into an Applied Electrochemistry Model S3A Oxygen Analyzer. Oxygen consumption was calculated following Bennett and Gleason (1976); all reported volumes are corrected to STP conditions. Fractional oxygen levels in the chambers never declined below 20.3% during these experiments (ambient air = 20.96%). Animals were reweighed at the conclusion of these experiments.

Oxygen consumption was determined at the following times and body temperatures (see Results): night ( $26^\circ$ – $27^\circ$ , 0000–0100 BST = Botswana Standard Time for both species) and day ( $36^\circ$ – $37^\circ$ , 1000–1100 BST for



TABLE 1. Body mass and rates of growth, energy metabolism, water flux, and ingestion in free-ranging *Eremias* lizards living in the Kalahari desert during spring, along with resting metabolism of captive lizards. Two-tailed *t* test; NS = not significant ( $P > .05$ ).

	<i>E. lugubris</i>			<i>E. lineocellata</i>			<i>t</i> test
	$\bar{x}$	SE	<i>N</i>	$\bar{x}$	SE	<i>N</i>	
Body mass (g)	3.83	0.24	18	3.27	0.28	16	NS
Mass change (g/d)	+0.072	0.005	18	+0.035	0.003	16	$P < .05$
Mass change (%/d)	+1.87	0.26	18	+1.06	0.30	16	$P < .05$
Growth rate (J/d)	365	49	18	195	31	16	$P < .01$
Field metabolic rate							
CO <sub>2</sub> released (mL/d)	31.2	2.8	18	21.2	2.6	16	$P < .02$
(J/d)	800	72	18	544	67	16	$P < .02$
Resting metabolic rate (O <sub>2</sub> consumed)							
(mL · g <sup>-1</sup> · h <sup>-1</sup> ) at 37°C	0.240	0.015	8	0.252	0.017	8	NS
at 34°	0.213	0.013	8				
at 26°	0.094	0.007	8	0.103	0.004	8	NS
Field feeding rate							
Metabolizable energy (J/d)	1165	101	18	739	68	16	$P < .005$
Fresh mass (mg/d)	353	31	18	151	14	16	$P < .005$
Field water flux							
Influx (mL/d)	0.285	0.0016	18	0.156	0.008	16	$P < .005$
Efflux (mL/d)	0.231	0.013	18	0.140	0.007	16	$P < .005$
Body water (% of fresh mass)	76.0	0.3	26	74.0	0.5	27	$P < .005$

both species; and at 34°–35°, 1400–1500 BST for *E. lugubris*). Animals were observed continuously during the diurnal measurement periods. Data from any lizard that moved spontaneously for a total of 10 s or more during the hour's measurement were excluded from the analysis.

#### Energy budget and feeding rate calculations

Gas volumes were converted to joules assuming R.Q. = 0.75 and 25.7 J/mL CO<sub>2</sub> (determined for a fed, insectivorous lizard; Nagy 1983). Energy production rates were calculated from changes in body energy content using the equation: energy production per unit time (J/d) =  $\{([\text{live mass}_f \text{ (g)}] \times [\text{dry matter (g)/live mass}_f \text{ (g)}] \times [\text{energy per unit dry matter}_f \text{ (J/g)}]) - ([\text{live mass}_i \text{ (g)}] \times [\text{dry matter (g)/live mass}_i \text{ (g)}] \times [\text{energy per unit dry matter}_i \text{ (J/g)}])\} / \text{time (d)}$ , where the subscripts *i* and *f* refer to initial and final captures. Metabolizable energy ingestion = energy respired + energy stored in the body. Total (gross) energy ingestion = metabolizable energy ingestion/assimilation efficiency. Assimilation efficiency  $\{[(\text{energy ingestion}) - (\text{energy voided in feces and urine})] / \text{energy ingestion}\}$  was assumed to be 0.81 (Nagy 1982). Feeding rates were converted from joules to grams of dry matter and grams of fresh matter using measured energy contents and water contents of diets. Feeding rates calculated from energy fluxes were used to estimate rates of water input via preformed water in the diet and oxidation (metabolically produced) water for comparison with total water influxes measured with tritiated water. Preformed water input (mL) =  $[\text{fresh food consumed (g)}] \times [\text{H}_2\text{O content of fresh food (mL/g)}]$  and metabolic water production (mL) =  $[\text{energy used (J)}] \times [\text{H}_2\text{O}$

formed per unit energy used (0.0257 mL/J)] (calculated from results of Nagy 1982).

## RESULTS

### Body mass, production, reproductive condition

The mean body mass of *E. lugubris* (3.83 g) used in this study was slightly, but not significantly, higher than that of *E. lineocellata* (3.27 g, Table 1). Energy contents of a sample of lizards captured at the beginning of the study were 17.1 kJ/g dry matter (SE = 0.6, *N* = 6) in *E. lugubris* and 18.1 kJ/g (SE = 0.3, *N* = 6) in *E. lineocellata*. *E. lugubris* captured at the end of the study contained 17.7 kJ/g (SE = 0.8, *N* = 6) and *E. lineocellata* contained 18.9 kJ/g (SE = 0.2, *N* = 6). Differences in energy content within species are not significant ( $P > .05$ , two-tailed *t* test), but the difference between species is significant ( $P < .01$ , *df* = 22, two-tailed *t* test on means of pooled values).

*Eremias lugubris* grew significantly faster than *E. lineocellata* during our study: individual *E. lugubris* added almost two times more chemical potential energy to their bodies each day than did *E. lineocellata* (Table 1). Neither body mass nor growth rate differed between sexes within either species ( $P$ 's  $> .05$ , two-tailed *t* tests). Autopsy results showed that all lizards in this study were prereproductive: testes were small (maximum size 5.0 × 3.0 mm), epididymes were not yet enlarged, and ovarian follicles were still undeveloped (maximum diameter 1.8 mm).

### Field and resting metabolism

*Eremias lugubris* had a higher mean field metabolic rate than the sit-and-wait predator *E. lineocellata*

(Table 1). This difference was confirmed by analysis of covariance of the regressions of  $\log_{10}$  field metabolic rate on  $\log_{10}$  body mass for both species. The regressions differed significantly in intercept ( $F_{(1,32)} = 4.78$ ;  $P < .05$ ) but not in slope ( $F_{(1,32)} = 0.48$ ;  $P > .05$ ). FMR did not differ between males and females within either species ( $P$ 's  $> .05$ , two-tailed  $t$  tests).

Oxygen consumption of resting, fed lizards was greater at 37°C than at 26°, and mean  $Q_{10}$  was  $\approx 2.3$  (Table 1). There were no significant differences between species ( $P$ 's  $> .05$ , two-tailed  $t$  tests). Resting metabolic rates of *Eremias* lizards were similar to those of other lizards at comparable temperatures (Bennett and Dawson 1976).

#### Diet and feeding rate

Stomach contents indicated that the mean diet of *E. lineocellata* ( $N = 11$  stomachs) comprised 25.0% (by volume) flies, 25.0% spiders, 18.6% beetles, and  $< 10\%$  each of grasshoppers, earwigs, ants, termites and cockroaches. *E. lugubris* ( $N = 6$ ) stomachs averaged 79% termites and  $< 10\%$  each of lepidoptera larvae, hemiptera, leafhoppers, ants and scorpions. These diets are similar to those determined for the same species in the southern Kalahari in 1969–1970 by Huey and Pianka (1981). The stomachs of *E. lugubris* generally contained much more material than did those of *E. lineocellata*, as they did in Huey and Pianka's (1981) study. Stomach contents accounted for up to 24% of total body mass in some *E. lugubris* we autopsied. Samples of prey species, pooled to represent dietary mixtures, contained 78%  $H_2O$  ( $N = 1$ ) and 17.5 kJ/g dry matter ( $SE = 0.4$  for triplicate measurements) for the diet of *E. lugubris*, and 71%  $H_2O$  and 19.8 kJ/g dry matter ( $SE = 0.4$ ) for the diet of *E. lineocellata*. Termites (*Hodotermes* sp.), a major prey item for *E. lugubris*, contained 81%  $H_2O$  and 18.5 kJ/g dry matter ( $SE = 0.4$ ).

Daily rates of metabolizable energy intake (= growth + respiration) were about  $1.6 \times$  higher in the wide forager as compared with the sedentary predator (Table 1). Feeding rates, when expressed as daily consumption of live prey mass, were even higher in *E. lugubris* by comparison ( $2.3 \times$  those of *E. lineocellata*, Table 1), as a consequence of the higher water content and lower energy content of the diet of *E. lugubris*.

Water influx rates, calculated from estimates of feeding rates along with diet water contents, did not differ significantly from those measured in the field (using  $^3H$ ) for *E. lugubris* ( $0.296 \pm [SE] 0.026$  vs.  $0.285 \pm 0.016$  mL/d, respectively,  $P > .05$ , paired  $t$  test). This agreement lends confidence to our estimates of feeding rate, and suggests that *E. lugubris* did not drink rainwater that fell during the study and that rates of water vapor input were low in these lizards. In *E. lineocellata*, however, water influxes estimated from feeding rates were significantly lower than isotopically mea-

sured influxes ( $0.121 \pm 0.012$  vs.  $0.156 \pm 0.008$  mL/d, respectively,  $P < .005$ , paired  $t$  test), suggesting that *E. lineocellata* either drank water in the field or, less likely, they had a very large exchange of water across skin wetted by rain. *E. lineocellata* could have ingested rainwater before it evaporated from vegetation or soaked into the sand, because they were abroad during the afternoon when rain showers occurred, but *E. lugubris* had retreated to burrows by then.

#### Water balance

Both *Eremias* species were in positive water balance during our study: rates of water input exceeded rates of water loss (Table 1). The lizards were growing and the proportion of their bodies that was water did not change during the study (above). Water flux rates were significantly higher in *E. lugubris* (Table 1). Body water contents (percentage of live mass) were significantly higher in *E. lugubris* than in *E. lineocellata* (Table 1).

#### Time budgets and thermal regime

Individual lizards were probably abroad every day during our study. All five *E. lugubris* and six *E. lineocellata* that were painted and released were seen abroad the following morning. Two of these were in the process of shedding their old skins with our paint markings, indicating that these lizards continue to be active even during ecdysis. This conclusion is further supported by the fact that, within a few hours, we recaptured 71% of injected lizards that had been marked and released 8–10 d earlier. Given that 2 of 11 lizards (18%) shed skins within 24 h of our painting them (above), it is probable that most of the 29% of injected lizards that we did not recapture after 8–10 d had shed their paint marks, making it difficult to distinguish them from unmarked lizards. Many lizards were seen in the process of shedding while abroad and active during our study. Frequent shedding is not surprising in rapidly growing lizards, such as those we studied.

Continuous, detailed observations of individual lizards, supplemented with records of general lizard abundances during various parts of the day, indicated that *E. lugubris* had a much shorter activity period than did *E. lineocellata*. For *E. lugubris*, average emergence time was  $\approx 0800$  BST, time of retreat was  $\approx 1045$ , and duration of activity period was only 2 h 45 min. For *E. lineocellata*, emergence time was near 0745, retreat time was  $\approx 1800$ , and daily time abroad was 10 h 15 min.

Body temperatures of active lizards were 37°–38° (our observations and those of Huey et al. 1977). From our 24-h burrow temperature recordings, we estimated that *E. lugubris* would have a body temperature averaging 34° during the 7 h 15 min it spent in its burrow during daylight hours, and both species would average  $\approx 26^\circ$  in their burrows at night.

## DISCUSSION

*Daily energy expenditures*

Field metabolic rates measured with doubly labeled water represent total daily costs of living. We partitioned total costs by estimating daily resting costs in the field from laboratory measurements of resting metabolism and field time budgets, and then calculating activity costs by subtraction. An important assumption underlying these calculations is that lizards were actually at rest when in their burrows.

The widely foraging lizard *E. lugubris* was clearly working much harder when abroad than was the ambush predator *E. lineocellata*. Although *E. lugubris* spent only one-quarter of the time abroad that *E. lineocellata* did each day, *E. lugubris* spent nearly twice as much energy each day for activity (above resting costs). This difference is emphasized by the calculation that the metabolic rate of active *E. lugubris* was  $12\times$  resting, as compared with  $2.8\times$  resting in *E. lineocellata* (Table 2). The metabolic intensity of active *E. lugubris* in the field approached their maximum aerobic capacity of  $13.4\times$  resting at  $37^\circ\text{C}$  (Bennett et al., *in press*). The  $12\times$  resting value in Table 2 may be an overestimate, because the assumption that burrowed lizards were continuously at rest is probably incorrect to some (unknown) extent. One *E. lugubris* that was closely watched while it entered its burrow near midday kicked sand from its burrow and stuck its head out the entrance several times during the following half-hour. The cost of this activity in a burrow would, however, appear in our calculations as an increased cost while abroad. We estimated the effect of this on our calculations by assuming that *E. lugubris* were respiring at  $2\times$  resting for 4 h while burrowed at  $34^\circ$ , and recalculating field activity costs while abroad. In this case, *E. lugubris* would have a metabolic rate while abroad that is  $9.7\times$  resting at  $37^\circ$ , which is still much higher than that of *E. lineocellata*.

The field metabolic rates of these two lacertid lizards (Table 1) were similar to those of iguanid lizards. *Eremias lugubris* was 122% ( $273 \text{ J}\cdot\text{g}^{-0.8}\cdot\text{d}^{-1}$ ) and *E. lineocellata* was 94% ( $211 \text{ J}\cdot\text{g}^{-0.8}\cdot\text{d}^{-1}$ ) of the mean, mass-corrected value of  $224 \text{ J}\cdot\text{g}^{-0.8}\cdot\text{d}^{-1}$  for iguanid lizards during the activity season (Nagy 1982). By comparison, field metabolic rates of widely foraging teiid lizards are much higher ( $360 \text{ J}\cdot\text{g}^{-0.8}\cdot\text{d}^{-1}$  in *Cnemidophorus tigris* [Anderson and Karasov 1981] and  $288\text{--}444 \text{ J}\cdot\text{g}^{-0.8}\cdot\text{d}^{-1}$  in *Cnemidophorus hyperythrus* [Karasov and Anderson 1984]). The greater daily expenditures of *Cnemidophorus* spp. apparently are due to longer activity periods and higher body temperatures than *E. lugubris*, and not because *Cnemidophorus* are more intensely active when abroad.

The cost of activity for *E. lineocellata* ( $2.8\times$  resting) is similar to that of other sit-and-wait lizards:  $2.5\text{--}3.1\times$  resting for *Sceloporus occidentalis* (Bennett and Nagy 1977),  $1.5$  for *Callisaurus draconoides* (Anderson

TABLE 2. Daily energy expenditures of *Eremias* lizards during spring in the Kalahari desert. RMR = resting metabolic rate (calculated from values in Table 1).

	<i>E. lugubris</i> (3.83 g)	<i>E. lineocellata</i> (3.27 g)
Metabolic expenditure per day		
In burrow		
Energy resting at $26^\circ\text{C}$ (J)	97	89
[Time resting at $26^\circ$ (h/d)]	[14.0]	[13.75]
Energy resting at $34^\circ$ (J)	114	
[Time resting at $34^\circ$ (h/d)]	[7.25]	
Abroad		
Resting metabolism (J)	49	163
Activity cost above RMR (J)	540	292
Total energy while abroad (J)	589	455
[Total time abroad (h/d)]	[2.75]	[10.25]
Total field metabolism (J)	800	544
Total field/total resting	3.1	2.2
Total abroad/resting abroad	12.0	2.8

and Karasov 1981) and  $3.0\text{--}3.6$  in *Sceloporus virgatus* (Merker and Nagy 1984). However, metabolic rates of active *E. lugubris* ( $12\times$  resting) are much higher than those of three widely foraging teiid lizards:  $3.3$  for *Cnemidophorus tigris* (Anderson and Karasov 1981),  $3.9$  for *Cnemidophorus murinus* (Bennett and Gleeson 1979), and  $2.6\text{--}2.7$  for *Cnemidophorus hyperythrus* (calculated from data of Karasov and Anderson 1984). The comparatively low metabolic intensities of active *Cnemidophorus* lizards may correspond with their longer activity periods ( $3.5\text{--}9$  h vs.  $2.75$  h for *E. lugubris*) and their higher body temperatures ( $40^\circ$  vs.  $37^\circ$  for *E. lugubris*) and correspondingly higher resting metabolic rates (which lower factorial increment values). More important, distances moved per hour abroad are lower in *Cnemidophorus* spp. than in *E. lugubris* ( $96$  m/h by *C. murinus* [Bennett and Gorman 1979],  $45\text{--}106$  m/h by *C. hyperythrus* [Karasov and Anderson 1984], and  $180$  m/h by *C. tigris* [Anderson and Karasov 1981] vs.  $315$  m/h by *E. lugubris* [Huey and Pianka 1981]). Thus, *E. lugubris* is more intensely active while abroad than are the teiid lizards. Activity costs for *E. lugubris* are approached only by those of female *Sceloporus virgatus* during the time of rapid growth of reproductive tissues ( $8.3\times$  resting; Merker and Nagy 1984).

*Foraging costs, benefits, and profits*

We can compare the energetic costs, benefits, and profits of the two foraging modes these lizards used by making some simplifying assumptions. These are (1) that the lizards were inactive and did not feed while in their burrows, and (2) that they were foraging (looking for food) the entire time they were abroad. These assumptions allow us to estimate the cost of activity as the difference between resting metabolism and total

TABLE 3. Energetic cost, benefit, and profit of foraging by *Eremias* lizards. These calculations assume that lizards were foraging the entire time they were abroad, and that lizards were inactive and did not feed while in burrows.

	<i>E. lugubris</i> (widely foraging)	<i>E. lineoocellata</i> (sit-and-wait)
Benefit of foraging		
J useable energy obtained/h foraging	424	72
mg fresh food consumed/h foraging	128	15
Cost of foraging		
Total J spent/h foraging	214	44
J activity cost (above resting)/h foraging	196	28
Benefit : cost ratio (foraging efficiency)		
$\frac{\text{J useable energy obtained/h foraging}}{\text{Total J spent/h foraging}}$	2.0	1.6
$\frac{\text{J useable energy obtained/h foraging}}{\text{J activity cost/h foraging}}$	2.2	2.6
Profit		
Hourly		
J net energy gain/h foraging	210	28
Daily		
Absolute: J production/day	365	195
Relative: $\frac{\text{J production/day}}{\text{J total metabolic cost/day}} \times 100$	46%	36%

metabolism, and to designate activity cost as the cost of foraging. These assumptions are invalid to some unknown degree, because some field observations suggest that burrowed animals may not have been completely at rest, and because active lizards were probably concerned with other things in addition to foraging (see Schoener, 1969). We considered the gross benefit of foraging to be the rate of intake of metabolizable (useable) energy and the profit or net benefit of foraging to be the growth rate. Costs, benefits, and profits of foraging can be examined using a variety of time units. To facilitate comparison of foraging modes between species, we examined costs and benefits on an hourly basis (the time scale of most optimal foraging models) and profits on both a daily and an hourly basis.

*Eremias lugubris* was spending much more energy while it was foraging widely than was *E. lineoocellata* when it was sitting and waiting. The metabolic intensity (total energy spent per unit foraging time) of *E. lugubris* was nearly 5 × that of *E. lineoocellata* (Table 3). However, *E. lugubris* obtained metabolizable (useable) energy nearly 6 × faster than did *E. lineoocellata*. Thus, both the net energy gain ([useable energy input] - [total energy spent]) per unit foraging time (see Schoener 1974), as well as the benefit : cost ratio (foraging efficiency) during foraging (useable energy input/ total energy spent while foraging) were higher for the wide forager (Table 3). The foraging efficiency of *E. lineoocellata* (1.6) is similar to, but slightly higher than, those of other sit-and-wait lizards: 1.0–1.4 in *Sceloporus virgatus* (Merker and Nagy 1984) and 1.1–1.5 in *Callisaurus draconoides* (Anderson and Karasov

1981). *Eremias lugubris* had a foraging efficiency identical with that of the widely foraging teiid lizard *Cnemidophorus tigris* (2.0, Anderson and Karasov 1981). Foraging efficiency values tend to reduce relative differences between the two foraging modes compared to the large differences seen in absolute costs or benefits. Nevertheless, the foraging efficiency values presently available for lizards fall into two distinct groups. An advantage of this ratio is its independence from other factors, such as body size, thermal regime, and taxon, that complicate comparisons of absolute energy fluxes.

An interesting way of expressing foraging efficiency is the ratio of useable energy gained while foraging to the energy spent above and beyond maintenance costs while foraging. This value can be viewed as the benefit per unit of physical effort. In this sense, *E. lineoocellata* (2.6) was a more effective forager than *E. lugubris* (2.2, Table 3). This difference suggests that an important component of foraging—searching—can be very cheap (energetically) or quite expensive, depending on foraging mode. The wide forager spends energy to search by transporting its eyes, ears and Jacobson's organ through the habitat. However, the ambush predator can search with virtually no energetic cost above resting by simply keeping its eyes and ears open; its primary foraging costs are for prey capture and ingestion only.

The profits of foraging can alternatively be judged on a daily basis rather than per hour of foraging. Although daily measurements are influenced by differences in amounts of time spent foraging, they are more ecologically relevant as estimates of overall profit made by the two species. Both *Eremias* species made ener-

getic profits during our studies, but the wide forager earned nearly twice as much as did the sit-and-wait predator (Table 3). As a result, the wide forager grew faster and had a somewhat larger body mass (Table 1). However, the wide forager invested more energy in making its profit. When profits were calculated relative to investments [(production/d)/(total energy metabolized/d)], *E. lugubris* still earned higher "interest" than did *E. lineocellata* (Table 3).

#### *Implications for optimal foraging theory*

Models of optimal foraging predict adjustments in the foraging behavior of individuals in response to environmental changes or patterns (Schoener 1971, Norberg 1977, Janetos 1982). Our data involve fixed, interspecific comparisons and cannot, therefore, be used to test those models. Nevertheless, our results have implications for certain assumptions of foraging theory.

In most models of foraging, an optimal diet is defined as one that maximizes a predator's net energy gain per unit time spent foraging. The profitability of potential prey varies with energetic (or nutritional) value, associated costs (time and energy) of handling and eating, and probability of escape (Schoener 1971). Interestingly, *E. lugubris* has a much higher rate of net energy gain than does *E. lineocellata* (Table 3) even though *E. lugubris* specializes on prey (termites) that have relatively low energy value (3.52 kJ/g fresh mass, whereas the energy value of prey for *E. lineocellata* averages 5.74 kJ/g). Despite their low energetic value, termites might make profitable prey items for several reasons: (1) Termites forage in groups and thus are a clumped resource, (2) termites are slow and relatively defenseless against a lizard, which reduces handling costs and escape probabilities, and (3) termites have a high water content, which might be important to a lizard's water balance.

The marked difference in rates of energy gain (Table 3) between *E. lugubris* and *E. lineocellata* suggests that foraging mode has an important impact on energetics. In particular, widely foraging seems to be the more profitable foraging mode (herein, see also Anderson and Karasov 1981, Andrews 1983). If lizards are attempting to maximize net energy gains (a central postulate of basic foraging theory), why doesn't the sit-and-wait *E. lineocellata* switch to wide foraging? Similarly, why haven't iguanid lizards switched to wide foraging? Many reasons can be suggested for this apparent contradiction with assumptions of foraging theory, and we focus on three.

First, the limited stamina of *E. lineocellata* may constrain its foraging behavior. *Eremias lineocellata* was unable to maintain a wide-foraging pace (0.5 km/h, Huey and Pianka 1981) for >10–15 min on a laboratory treadmill, but *E. lugubris* could easily do so for at least 30 min (Huey et al., *in press*). (This marked interspecific difference in stamina can be traced to car-

diovascular adjustments [Bennett et al., *in press*]). Thus, even if wide foraging is energetically more advantageous than is ambush foraging, *E. lineocellata* may be physiologically restricted to a sit-and-wait foraging mode. In other words, *E. lineocellata* (and perhaps iguanid lizards) might be physiologically constrained from foraging "optimally."

Second, our study was conducted at one season and at one locality, and temporal (seasonal, year-to-year) or spatial variation in food abundance or prey type, or both, might influence the relative advantages of different foraging modes. The apparent energetic advantage of wide foraging during our study (Table 1) might be reversed during other times or at other localities, especially those characterized by low food abundance (Norberg 1977). The possibility that temporal or spatial variation in food abundance could promote the coexistence of predators with different foraging modes needs to be investigated.

Finally, the apparent energetic advantage of wide foraging (Table 3) may be a red herring that distracts our attention from a fundamental point: the evolution of behavior should be sensitive to all factors that influence fitness (e.g., Schoener 1971, Pulliam 1976, Milinski and Heller 1978, Krebs et al. 1981), not just to rate of energy gain. Wide foraging may result in higher energetic gains, but it also may result in higher rates of mortality (Broadley 1972, Gerritsen and Strickler 1977, Vitt and Congdon 1978, Huey and Pianka 1981). Models that attempt to evaluate competition between species with different foraging modes will have to address the complicated interactions involving energy gain and risk of predation.

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