FIELD ENERGETICS AND FORAGING MODE OF KALAHARI LACERTID LIZARDS[1]

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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 lineoocellata* (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_2 consumed) were similar at 37°C (0.240 vs. 0.252 mL·g^{-1}·h^{-1}) and at 26° (0.094 vs. 0.103 mL·g^{-1}·h^{-1}), 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. lineoocellata*. 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. lineoocellata*. The hourly cost of foraging was much higher for *E. lugubris* (almost 5× that of *E. lineoocellata*) but the hourly benefit of foraging for *E. lugubris* was even higher (nearly 6× that of *E. lineoocellata*). 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

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 northeast-facing stabilized sand-ridge and was located ≈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 ≈10% of the area (Pianka and Huey 1971). Annual rainfall for the region is ≈170 mm (Leistner 1967).

Doubly labeled water study

On each of three successive days, we captured lizards on a different section of a 500 × 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 ^3H at 12 MBq/mL and 97 atoms ^{18}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. lineoocellata* 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 midventral 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°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. lineoocellata*. 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° and 39°, respectively.

Isotope levels were determined by liquid scintillation spectrometry (for ^3H) and proton-activation analysis (for ^{18}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 [H_2O (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: TBW (g) = 0.175 + (0.714 × live mass [g]) ($r = 0.977$, df = 24, $F_{regression} = 3392$, $P < .001$) for *E. lugubris,* and TBW (g) = 0.129 + (0.697 × live mass [g]) ($r = 0.995$, df = 25, $F_{regression} = 2297$, $P < .001$) for *E. lineoocellata*. 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 ($[^3H_1]$ and $[^{18}O_1]$, corrected for background) and TBWs sampled 1 h after injection were used to calculate the constants $C_{(3H)}$ and $C_{(18O)}$ from the equations $C_{(3H)} = [^3H_1]$ (TBW [g]) and $C_{(18O)} = [^{18}O_1]$ (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 $C_{(3H)}$ and 3.98% for $C_{(18O)}$. 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° 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° 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 $\pm$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°, 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 ≈ 10 mL/min into an Applied Electrochemistry Model S3A Oxygen Analyzer. Oxygen consumption was calculated following Bennett and Gleeson (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°–27°, 0000–0100 BST = Botswana Standard Time for both species) and day (36°–37°, 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 ($P > .05$).

	E. lugubris			*E. lineoocellata*			
	$\bar{x}$	SE	N	$\bar{x}$	SE	N	t test
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_2 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_2 consumed)							
($mL \cdot g^{-1} \cdot h^{-1}$) 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_2 (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) = ({[live mass$_f$ (g)] × [dry matter (g)/live mass$_f$ (g)] × [energy per unit dry matter$_f$ (J/g)]} − {[live mass$_i$ (g)] × [dry matter (g)/live mass$_i$ (g)] × [energy per unit dry matter$_i$ (J/g)]})/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 {[(energy ingestion) − (energy voided in feces and urine)]/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) = [fresh food consumed (g)] × [H_2O content of fresh food (mL/g)] and metabolic water production (mL) = [energy used (J)] × [H_2O 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. lineoocellata* (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. lineoocellata*. *E. lugubris* captured at the end of the study contained 17.7 kJ/g (SE = 0.8, N = 6) and *E. lineoocellata* 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. lineoocellata* during our study: individual *E. lugubris* added almost two times more chemical potential energy to their bodies each day than did *E. lineoocellata* (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. lineoocellata*

(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 ≈ 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. lineoocellata* ($N = 11$ 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. lineoocellata,* 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. lineoocellata.* 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× 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× those of *E. lineoocellata,* 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 ^{3}H) for *E. lugubris* (0.296 ± [SE] 0.026 vs. 0.285 ± 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. lineoocellata,* however, water influxes estimated from feeding rates were significantly lower than isotopically measured influxes (0.121 ± 0.012 vs. 0.156 ± 0.008 mL/d, respectively, $P < .005$, paired t test), suggesting that *E. lineoocellata* either drank water in the field or, less likely, they had a very large exchange of water across skin wetted by rain. *E. lineoocellata* could have ingested rainwater before it evaporated from vegetation or soaked into the sand, because they were abroad during the afternoon when rainshowers 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. lineoocellata* (Table 1).

Time budgets and thermal regime

Individual lizards were probably abroad every day during our study. All five *E. lugubris* and six *E. lineoocellata* 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. lineoocellata.* 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. lineoocellata,* 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° 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. lineoocellata*. Although *E. lugubris* spent only one-quarter of the time abroad that *E. lineoocellata* 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× resting, as compared with 2.8× resting in *E. lineoocellata* (Table 2). The metabolic intensity of active *E. lugubris* in the field approached their maximum aerobic capacity of 13.4× resting at 37°C (Bennett et al., *in press*). The 12× 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× resting for 4 h while burrowed at 34°, and recalculating field activity costs while abroad. In this case, *E. lugubris* would have a metabolic rate while abroad that is 9.7× resting at 37°, which is still much higher than that of *E. lineoocellata*.

The field metabolic rates of these two lacertid lizards (Table 1) were similar to those of iguanid lizards. *Eremias lugubris* was 122% (273 J·g$^{-0.8}$·d^{-1}) and *E. lineoocellata* was 94% (211 J·g$^{-0.8}$·d^{-1}) of the mean, mass-corrected value of 224 J·g$^{-0.8}$·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 J·g$^{-0.8}$·d^{-1} in *Cnemidophorus tigris* [Anderson and Karasov 1981] and 288–444 J·g$^{-0.8}$·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. lineoocellata* (2.8× resting) is similar to that of other sit-and-wait lizards: 2.5–3.1× resting for *Sceloporus occidentalis* (Bennett and Nagy 1977), 1.5 for *Callisaurus draconoides* (Anderson

and Karasov 1981) and 3.0–3.6 in *Sceloporus virgatus* (Merker and Nagy 1984). However, metabolic rates of active *E. lugubris* (12× 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 2.6–2.7 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 (3.5–9 h vs. 2.75 h for *E. lugubris*) and their higher body temperatures (40° vs. 37° 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], 45–106 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× 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 2. Daily energy expenditures of *Eremias* lizards during spring in the Kalahari desert. RMR = resting metabolic rate (calculated from values in Table 1).

	E. lugubris (3.83 g)	E. lineoocellata (3.27 g)
Metabolic expenditure per day		
In burrow		
Energy resting at 26°C (J)	97	89
[Time resting at 26° (h/d)]	[14.0]	[13.75]
Energy resting at 34° (J)	114	
[Time resting at 34° (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

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.

	E. lugubris (widely foraging)	E. lineoocellata (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)		
$\dfrac{\text{J useable energy obtained/h foraging}}{\text{Total J spent/h foraging}}$	2.0	1.6
$\dfrac{\text{J useable energy obtained/h foraging}}{\text{J activity cost/h foraging}}$	2.2	2.6
Profit		
Hourly		
J net energy gain/h foraging	210	28
Daily		
Absolute: J production/day	365	195
Relative: $\dfrac{\text{J production/day}}{\text{J total metabolic cost/day}} \times 100$	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. lineoocellata* (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. lineoocellata* (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. lineoocellata* 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. lineoocellata* 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. lineoocellata* 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. lineoocellata* may constrain its foraging behavior. *Eremias lineoocellata* 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. lineoocellata* may be physiologically restricted to a sit-and-wait foraging mode. In other words, *E. lineoocellata* (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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