FIELD ENERGETICS AND FORAGING MODE OF KALAHARI LACERTID LIZARDS

KENNETH A. NAGY
Laboratory of Biomedical and Environmental Sciences, 900 Veteran Avenue, University of California, Los Angeles, California 90024 USA

RAYMOND B. HUEY
Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195 USA

AND

ALBERT F. BENNETT
School of Biological Sciences, University of California, Irvine, California 92717 USA

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 (400 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, consumed) were similar at 37°C (0.240 vs. 0.252 ml. g -1 h -1) and at 26°C (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 x resting in E. lugubris and 2.2 x resting in E. lineoocellata. Energy expenditures during the activity period were 12.0 x resting in the wide forager and 2.8 x 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 x that of E. lineoocellata) but the hourly benefit of foraging for E. lugubris was even higher (nearly 6 x 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 influx.

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 (1979), and Regel (1978), Vitt and Congdon (1978), Anderson (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...
expenditure 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 invertebrous and they live syntopically on sand dune ridges in the Kalahari desert (Huery et al., 1977, Pianka et al. 1979, Huery 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 production of new biomass, we equated benefit with gain. Because metabolizable energy is used primarily for respiration with any excess energy appearing only as production of new biomass, we equated benefit with gain.

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 14 km northeast of Tweep 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 Huery (1971). Vegetation at this site is described by Pianka and Huery (1971). Dominant plants include a variety of perennial grasses as well as numerous shrubs (Acacia mellifera, A. beclada, Lycium hirsutum, and Rhigozum trichotomum) and a few trees (Boscia albitrunca, Acacia giraffe, and Z. haemanthoxylon). Perennial plants cover 10% of the area (Pianka and Huery 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 m pplot within the study area. The site of each capture was marked. Lizards were individually weighed, toe-clipped, painted neurally with 0.015 mL of water containing 3H at 12 noon. 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 Phillips 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 weighed, 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 18O) (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 [H2O (g)/live mass (g)] of lizards autopsied at the time of injection did not differ significantly (P > 0.05, 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 x live mass (g) (r = 0.977, df = 24, F24,0.05 = 1793, P < 0.001) for E. lugubris, and TBW (g) = 0.129 + 0.697 x live mass (g) (r = 0.995, df = 25, F25,0.01 = 2397, P < 0.001) for E. lineoocellata. These regressions differ significantly in intercept (ANCOVA, F1,29 = 25.9; P < 0.001) but not in slope (F1,29 = 0.83; P > 0.05). Initial isotope
concentrations ([H] and [PO_4^2-]), corrected for background, and TBWs sampled 1 h after injection were used to calculate the constants C_w and C_m, from the equations C_m = [H] (TBW [g]) and C_w = [PO_4^2-] (TBW [g]). Mean C values for each batch were chosen as 0.05% from 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°C 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 (above) for the two populations. Periods determined (above) 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 4.09 ± 0.23 g) and eight *E. lineoocellata* (4.02 ± 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°C, 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 eight 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 (503 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 Radel 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 S.T.P. conditions. Fractional oxygen levels in the chambers never declined below 20.3% during these experiments (ambient air = 20.96%). Animals were weighed at the conclusion of these experiments.

**Oxygen consumption was determined at the following times and body temperatures (see Results): eight (26°C-27°C, 0000-0100 BST) Bostswana Standard Time for both species, and day (36°C-37°C, 1000-1100 BST) for...**
Growth rate (J/d) 365 49 18 195 3

TARLE I. Body mass and rates of growth, energy metabolism, water flux, and ingestion in free-ranging
Field feeding rate (metabolically produced) water for comparison with
Body mass (g) 3.83 0.24 18 3.27 0.28 16 NS

Field metabolic rate
CO₂ released (mL/d)

Resting metabolic rate (O₂ consumed)

Metabolizable energy ingestion

Field water flux

Efflux (mL/d)

Body water (4% of fresh mass)

both species; and at 34°-35°, 1400-1500 BST for
Animals were observed continuously during
The mean body mass of E. lugubris (3.83 g) used in
This study contained 17.7 kJ/g (SE ± 0.6, N = 6) in E. lineoocellata. E. lugubris captured at the end of the study contained 17.7 kJ/g (SE ± 0.6, 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 > 0.05, two-tailed test), but the difference between species is significant (P < 0.01, 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 significantly between sexes within either species (P's > 0.5, two-tailed tests). Autopsy results showed that all lizards

Field and resting metabolism

Eremias lugubris had a higher mean field metabolic rate than the sit-and-wait predator E. lineoocellata.
Growth and lower energy content of the diet of E. lugubris, leafhoppers, ants and scorpions. These diets are similar to those determined for the same species in the field (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 lipoptera 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 Huay and Pianka (1981). The stomachs of E. lugubris generally contained much more material than those of E. lineoocellata, as they did in Huay 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 contents (percentage of live mass) were significantly higher in E. lugubris, 22.1% compared with the sedentary predator E. lineoocellata, averaging 19.8 kJ/g dry matter that fell during the study and that rates of water input were low in these lizards. In E. lugubris, did not drink 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 abundance 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 ± 0800 BST, time of retreat was ± 1045, and duration of activity period was only 2 h 45 min. For E. lineoocellata, emergence time was near 0745, retreat time was ± 1800, and daily time abroad was ± 10 h 15 min. Body temperatures of active lizards were 37°-38° (our observations and those of Huay et al. 1977). From our 24-h barrow 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 ± 20° in their burrows at night.

Table 1. This difference was confirmed by analysis of covariance of the regressions of log,, field metabolic rate on log,, body mass for both species. The regressions differed significantly in intercept (F1,10 = 4.78, P < .05) but not in slope (F1,10 = 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°C, and mean Q10 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).
**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 ambusher *E. lineoocellala*. Although *E. lugubris* spent only one-quarter of the time abroad that *E. lineoocellala* 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 12.2× resting, as compared with 2.8× resting in *E. lineoocellala* (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 resting in burrows for 4 h while burrowed 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°C, which is still much higher than that of *E. lineoocellala*.

The field metabolic rates of these two lacertid lizards (Table 1) were similar to those of iguanid lizards. *Emydoidea blandingii* was 122% (273 J g⁻⁰.⁸ d⁻¹) and *E. lineoocellala* 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 murinus* [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* is more intensely active when abroad.

The cost of activity for *E. lineoocellala* (2.8× resting) is similar to that of other sit-and-wait lizards, 3.1× resting for *Sceloporus occidentalis* (Bennett and Nagy 1977), 1.5 for *Callichirus dracoconis* (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°V vs. 37°C for *E. lineoocellala*) 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 1981], and 180 m/h by *C. tigris* [Anderson and Karasov 1981] vs. 315 m/h by *E. lugubris* [Huey and Pianka 1981]). Thus, *E. lineoocellala* is more intensely active while abroad than are the teiid lizards. Activity costs for *E. lineoocellala* are approached only by those of female *Sceloporus virgatus* during the time of rapid growth of reproductive tissues (3.8× 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 metabolic expenditure per day

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

| Energy (J) | RMR at 26°C | RMR at 34°C | Abroad
|-----------|-------------|-------------|-----------
| *E. lugubris* ovullaria (3.83 g) | 97.0 | 97.0 | 14.0
| (3.27 g) | (10.25) | (13.75) | (7.23) |

**Foraging costs, benefits, and profits**
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.

<table>
<thead>
<tr>
<th>E. lugubris</th>
<th>E. incognita</th>
</tr>
</thead>
<tbody>
<tr>
<td>(widely foraging)</td>
<td>(sit-and-wait)</td>
</tr>
<tr>
<td><strong>Benefit of foraging</strong></td>
<td></td>
</tr>
<tr>
<td>J useable energy obtained/h foraging</td>
<td>424</td>
</tr>
<tr>
<td>J fresh food consumed/h foraging</td>
<td>128</td>
</tr>
<tr>
<td><strong>Cost of foraging</strong></td>
<td></td>
</tr>
<tr>
<td>Total J spent/h foraging</td>
<td>214</td>
</tr>
<tr>
<td>J activity cost (above resting)/h foraging</td>
<td>196</td>
</tr>
<tr>
<td><strong>Benefit: cost ratio (foraging efficiency)</strong></td>
<td></td>
</tr>
<tr>
<td>J useable energy obtained/h foraging</td>
<td>2.0</td>
</tr>
<tr>
<td>J activity cost/h foraging</td>
<td>2.2</td>
</tr>
<tr>
<td><strong>Profit</strong></td>
<td></td>
</tr>
<tr>
<td>Hourly: J net energy gain/h foraging</td>
<td>210</td>
</tr>
<tr>
<td>Daily: Absolute: J production/day</td>
<td>365</td>
</tr>
<tr>
<td>Relative: J production/day × 100</td>
<td>46%</td>
</tr>
</tbody>
</table>

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, 1980). 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. incognita 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. incognita (Table 3). However, E. lugubris obtained metabolizable (useable) energy nearly 6× faster than did E. incognita. 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. incognita (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 striatus (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 comparison 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. incognita (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 metabo- lized/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, Nor- berg 1977, Huey 1982). Our data involve diverse, 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) val- ue, associated costs (time and energy) of handling and eating, and probability of escape (Schoener 1971). In- terestingly, 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) and 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 ener- getics. In particular, widely foraging seems to be the more profitable foraging mode (herein, see also An- derson 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. lugubris switch to wide foraging? Sim- ilarly, why haven't iguanid lizards that specialize on prey (termites) that have a much higher rate of net energy gain, 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 ad- dress the complicated interactions involving energy gain and risk of predation.

Acknowledgments
This research was supported primarily by National Science Foundation grant DEB 81-09667 to R. B. Huey. Secondary funding was from Department of Energy Contract DE-AM03- 76SF00012 to the University of California (K. A. Nagy) and from National Science Foundation PCM 81-02313 and Na- tional Institutes of Health KO4 AM00351 to A. F. Bennett. The Datsun-Nissan Company (T. Dreyer, Promotions Man- ager) generously provided a Datsun 4x4 Bakkie for the field research. We are very indebted to Dr. G. DeGraf of the United Nations Park and to Warden E. Lehfeldt of the Kaf- fai/Gembok National Park for permission to conduct these studies and for their many efforts which made our research possible. W. D. Haacke, M. Haacke, and L. Wessels provided generous funding to the University of California, Lawrence, Kansas, USA.

Literature Cited
Lifson, N., and R. McClintock. 1966. Theory of use of the
Janetos, A. C. 1982. Active foragers vs. sit-and-wait pred-
Leistner, 0. A. 1967. The plant ecology of the southern
Huey, R. B., and E. R. Pianka. 1981. Ecological conse-
Kleiber, M. 1961. The fire of life. John Wiley and Sons,
Genitsen, J., and J. R. Strickler. 1977. Encounter proba-
Broadley, D. G. 1972. The horned viper Bitis caudalis (A. Smith) in the central Kalahari. Botswana Notes and Rec-
Gerritsen, J., and J. R. Strickler. 1977. Encounter proba-
bilities and community structure in zooplankton: a math-
ematical model. Journal of the Fisheries Research Board of Canada 34:71-82.
Huy, R. B., and E. R. Pianka. 1981. Ecological conse-
Huy, R. B., E. R. Pianka, and A. Hoffman. 1977. Sea-
Jennion, A. C. 1982. Active foragers vs. sit-and-wait pred-
Katavolos, W. H., and R. A. Anderson. 1984, in press. In-
terhabitat differences in energy acquisition and expenditure in lacertid lizards. Animal Behaviour.
Kleiber, M. 1961. The fire of life. John Wiley and Sons,
New York, New York, USA.
del, New York & London.
Leistner, O. A. 1967. The plant ecology of the southern
Lifson, N., and R. McClintock. 1966. Theory of the use of the
Milinski, M., and R. Heller. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (Gaster-
sey, USA.
Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of food-sourcing meth-
logical systems. Ohio State University Press, Columbus, Ohio, USA.
Pulliam, H. R. 1976. The principle of optimal behavior and the theory of communities. Pages 311-332 in P.O.R. Ban-
Rogal, F. P. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capaci-
ties. Pages 181-202 in N. Greenberg and P. D. Machean, editors. Lizards, snakes, and mammals: an analysis of activity and mental capabil-
ties. New York: Plenum.
1974. Temporal resource partitioning and the compression hypothesis. Proceedings of the National Acad-
emy of Sciences (USA) 71:4169-4172.
Vitt, L. J., and J. D. Couplon. 1978. Body shape, repro-
tutes of Mental Health, Rockville, Maryland, USA.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.
Koedoe in press.