Contrasts in Energy Intake and Expenditure in Sit-and-Wait and Widely Foraging Lizards

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Summary. Daily energy metabolism and water flux were measured with doubly labeled water in the free-living insectivorous lizards Cnemidophorus tigris (mean body mass 15.7 g) and Callisaurus draconoides (8.6 g) in June 1979 in the Colorado Desert of California. C. tigris was an active forager; it spent 91% of its 24-h activity period in movement. C. draconoides was a sit-and-wait predator; it spent less than 2% of its 10-h activity period in movement. C. tigris had significantly higher rates of field energy metabolism and water influx (210 J g⁻¹ day⁻¹, 36.8 µmol H₂O g⁻¹ day⁻¹, N = 19) than C. draconoides (136, 17.1, N = 18). There were no significant differences between the sexes within either species.

The extra costs of free existence were calculated from differences between field metabolic rates and maintenance costs estimated from laboratory respirometry. Rates of energy metabolism during the field activity period were about 1.5 × resting levels at 40°C (~field active body temperature) for C. draconoides and 3.3 × resting levels at 40°C (~field active body temperature) for the more active C. tigris. Feeding rates calculated from water influx data were 13.3 mg g⁻¹ day⁻¹ for C. tigris and 5.8 mg g⁻¹ day⁻¹ for C. draconoides. Though C. tigris had a high rate of energy expenditure, its foraging efficiency metabolizable energy intake was higher than C. draconoides' energy expended.

Introduction

The analysis of costs and benefits is a fruitful approach in ecological studies which are concerned with the allocation of time and energy for particular organismal processes (Heinrich 1972; 1975; Carpenter and MacMillen 1976; DeBenedictus et al. 1978; Walberg 1978). It is assumed that the general foraging mode a species exhibits has evolved through natural selection and that each foraging mode has particular costs and benefits in terms of time, energy, water, or some other ecologically important variable. A convenient dichotomy in describing foraging behaviors is sit-and-wait and active foraging (Schoener 1971). One would expect that the energetic costs of foraging would be higher for the active forager since movement results in a two- to ten-fold increase in energy metabolism for terrestrial vertebrates (Schmidt-Nielsen 1972; Taylor 1973). In lizards, where activity metabolism can account for up to 60% of total daily metabolism (Bennett and Nagy 1977; Bennett and Gleeson 1979), differences in foraging style might result in significant differences in total daily energy requirements. Furthermore, unless it had a higher rate of food intake per hour foraging, a lizard employing an energetically more expensive foraging method might have to spend more time foraging than a lizard which had lower foraging costs.

We explored these ideas by measuring the rates of energy expenditure and food consumption of two free-living, insectivorous lizards: Cnemidophorus tigris (Teiidae), a widely foraging lizard, and Callisaurus draconoides (Iguanidae), a sit-and-wait predator. These species lent themselves to comparison because they could be found in the same habitat, were similar in body size, and thermoregulated at similar body temperatures (see Results). Doubly labeled water (Lifson and McClintock 1966) was used to measure their rates of energy expenditure and food consumption. Since the most visible difference between these lizards which would affect energy utilization was that due to foraging style, they made excellent subjects for an exploration of the energetic costs and benefits of sit-and-wait versus active foraging.

Materials and Methods

Study Site

The study site was a 200 m × 300 m plot about 1.6 km northwest of Desert Center, Riverside County, California at an elevation of 260 m. Cover at the site was dominated by Larrea tridentata, Oenothera tenuifolia, Ambrosia dumosa, and Helianthus rigidus. Most annuals and perennials had set seed prior to the study period in June 1979. Mean minimum and maximum air temperatures (10 cm in the shade) at that time were 23°C (at dawn) and 38°C (midafternoon), respectively. (Subsurface soil temperatures at various depths, recorded with a 10-channel multichannel Rustrak recorder, are reported in Results.)

Commonly seen lizards on the site were Uta stansburiana, Urosaurus ornatus, Cnemidophorus tigris, and Diposo-saurus dorsalis. Callisaurus draconoides were post-reproductive; no males autopsied (N = 10) had yolked follicles or ovovivipal eggs. We did not autopsy C. tigris females; C. tigris males were not displaying courtship behavior.

Behavior

Objectives of behavioral observations were to determine 1) the number of days per week individuals of each species were active on the surface, 2) the number of hours per day each species was active, and 3) the proportion of the daily activity period each species spent stationary and in movement.

Lizards were moosed and deep-clawed temperatures were measured with a Wescor quick-reading thermometer. Body temperature data were not used if animals f celebr prior to capture. Animals were toe clipped, painted with an identification number, and later released at point of capture.

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Calliusurus draconoides exhibited high fidelity to small home ranges (~0.25 ha) so seven individuals were monitored for five consecutive days each to determine if they were active every day. Cremadophorus tigris was active most of the time and had larger home ranges (~1.0 ha), so we could not be confident that not finding an animal on one day meant it was not active that day. For the purposes of this study C. tigris was assumed to be active every day. Daily activity periods were determined by monitoring the presence and/or abundance on the plot of both species from 0600 h to 1845 h Pacific Standard Time (PST) on 22 days during June.

The procedure for studying behavior of the lizards differed slightly between species. For both species lizard searches were begun by walking slowly and watching carefully for stationary lizards. Normally a lizard was seen from 5 to 15 m distant, and if the lizard did not appear to be disturbed by the observer (did not flee) then the animal's behavior was recorded for the next 15 to 30 min. For C. draconoides a stopwatch was used to record time spent in movement and behavioral notes were written. Whereas C. draconoides observations were begun only if the lizard was stationary or not obviously moving due to human disturbance, C. tigris was often first sighted in transit from one shrub to another or as it moved beneath a shrub. Furthermore, the observer could not remain stationary (as in observing C. draconoides) while watching C. tigris. It was necessary to walk in a path parallel to that of the lizard in order to keep it in sight for more than a few minutes. When C. tigris were beneath bushes the observer remained motionless or walked slowly into a preferred observing position. The C. tigris at this locality were observed with remarkable ease; individual lizards appeared disturbed by observers very rarely. One method repeatedly employed to test a lizard's wariness of the observer was to stand in the wind and to causing the lizard to exit the shrub and to watch its reaction. Almost invariably the lizard took no notice of the observer, sometimes walking between the latter's feet. Because C. tigris moved almost continuously and required constant visual attention by the observer, a tape recorder was employed for all observations. A stop watch was used when transcribing the tapes; times spent in locomotion, sitting, digging, climbing, basking, etc., were quantified.

### Field Metabolism and Feeding Rates

Field metabolic rates were measured using the doubly labeled water method (Lilien and McClintock 1966, Congdon et al. 1978) validated this method for another lizard, Sceloporus. Wild lizards in our study were anesthetized and given a 50–100 ul intraperitoneal injection containing 55% 18O and 1.0 mCi of H2 per ml. After 3 h, a blood sample (50–75 ul) was taken from the infraorbital sinus, each animal was weighed to the nearest 0.01 g, and then released at the point of capture. Labeled H2O equilibrated in <1 h in C. tigris (W. H. K., personal observation). Lizards were recaptured at least 2 weeks later (mean=13.8 days), weighed, and a second blood sample was taken. Numbers of 25 injected C. tigris and 18 of 26 C. draconoides were recaptured.

Blood samples were distilled and the water was analyzed for 18H activity by liquid scintillation spectrometry. 18O content was measured by proton activation (Wood et al. 1975). CO2 production was calculated by using the linear body mass change equation of Lilien and McClintock (1966) as modified by Nagy (1975). Initial body water contents were calculated from the dilution of 18O. Final body water contents were estimated based on the mean percent of body mass which was water in the initial group (C. tigris, 73.8%; C. draconoides, 72.5%). CO2 production rates were converted from ml CO2 g⁻¹ h⁻¹ to kJ g⁻¹ dy⁻¹ using the relationship 25.7 J (ml CO2)⁻¹ (Nagy in press).

### Feeding Rates of the lizards were calculated using equation 2 of Nagy (1975). Total water influx, calculated from the turnover of 18H, was corrected for metabolic water production by using the conversion factor 0.026 ml H2O (kJ metabolized)⁻¹ (Schmidt-Nielsen 1975).

### Resting Metabolism

Resting metabolism of C. draconoides was measured in the laboratory using direct manometric technique with a single-valve Gilson Differential Respirometer. Animals were captured in late September 1979 and were maintained on a 12 L:12 D photoperiod with a heat lamp for basking. They maintained body mass on a daily diet of Tenebrio larvae. Within 2 weeks after capture measurements of O2 consumption were carried out at temperatures and times of day equivalent to the daily thermal cycle: 40°C at midnight phase and 30°C at midphase. Individual, nonstarved lizards were placed in 225 ml capacity jars. All lizards rested quietly within 5–10 minutes. Rubber stoppers placed in the mouth of each jar had two holes, one for connection to the respirometer and another for administration of the CO2 absorbant, a 5% KOH solution, into a 1.0 ml capacity cup. An equal size reference jar was used for each experimental jar. Animals were allowed to thermally equilibrate in the water bath of the respirometer for 1.5 h, with the top of the KOH-administering tube open to the atmosphere to allow maintenance of normal O2 levels. To ensure complete thermal equilibration inside the jar, the tube was stopped and measurement of O2 consumption was not initiated for another 30 minutes. O2 consumption was monitored for a minimum of 20 three-minute periods for each animal. Measurements were standardized to STPD conditions.

Numerical results are given as mean ± standard deviation (N= number of animals). The test (p<0.05) was used for tests of difference between means.

### Results

#### Behavior

Of the seven C. draconoides we monitored for daily activity, each was seen on each of five consecutive days. Of 31 C. tigris observed and/or captured during the study only two males were seen for three days, and the other 29 individuals were seen for one day only. Repeated efforts to locate individual C. tigris on consecutive days were unsuccessful. This difficulty was in part due to the unpredictability of the day to day location of individuals of this highly mobile species. For our analysis it was assumed that C. tigris, like C. draconoides, were active every day.

The length of the daily activity period was more easily determined for C. draconoides than for C. tigris. Calliusurus began to appear on the surface in abundance at 0630 h and could be seen until ~1800 h. On two very hot days (3 days maximum at 10 cm in shade=43.5°C) during the period lizards were labeled, C. draconoides were absent from the surface 1.5–2.0 h in the early afternoon. The daily activity period of Calliusurus during the study was estimated to be ~10 h. Cremadophorus tigris usually were first seen after 0645 h (19 of 22 days) but time of first sighting was sometimes before 0630 h (3 of 22 days). Fourteen C. tigris were seen to enter burrows late in the morning and not exit, ending their morning activity period at a mean time of 1000 h (range 0800–1100 h). Only three C. tigris were seen active past 1100 h, and these were lingering in the shade of the largest ironwood trees (Olneya). Activity in the afternoon was irregular. On only seven of 19 afternoons were any C. tigris seen on the surface, generally between 1600 and 1800 h and principally from 1630 to 1730 h. Total mean daily activity period for C. tigris was estimated to be ~5 h, only one-half that of C. draconoides.

The proportion of time during the daily activity period spent in movement also differed between the two species. Cremadophorus tigris spent 91.1% (range 76.6% to 100%, N=18 observation periods for 540 min total) of its time active in movement and C. draconoides 1.5% (range 0 to 8.7%, N=40 observation periods totalling 600 min). Male C. draconoides spent significantly more time in movement (2.9±2.8%, N=11) and moved significantly greater distances (9.8±8.6 m per 15 min) than did female C. draconoides (0.96±1.0%, N=27 and 2.7±3.8 m respectively (p<0.005). There were no significant differences between male and female C. tigris in time spent in movement or in distance.
Table 1. Body mass and rates of O₂ consumption and CO₂ production in Callianus draconoides and Cnemidophorus tigris. Values are mean (standard deviation, N)

<table>
<thead>
<tr>
<th></th>
<th>Callianus draconoides</th>
<th>Cnemidophorus tigris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laboratory, resting *</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ml O₂ g⁻¹ h⁻¹</td>
<td>0.148 (0.05,6)</td>
<td>0.150 (0.05,11)</td>
</tr>
<tr>
<td>35°C</td>
<td>0.299 (0.05,7)</td>
<td>0.270 (0.05,11)</td>
</tr>
<tr>
<td>40°C</td>
<td>9.52</td>
<td>15.66</td>
</tr>
<tr>
<td>Field</td>
<td>5.28 (0.96,18)</td>
<td>8.16 (1.44,19)</td>
</tr>
<tr>
<td>ml CO₂ g⁻¹ day⁻¹</td>
<td>8.63</td>
<td>15.66</td>
</tr>
</tbody>
</table>

* C. tigris resting O₂ consumption from Asplund (1970).

Energy Metabolism

There were no significant sexual differences in either field or laboratory metabolism within either species. Wild C. tigris had significantly higher mass specific field metabolic rates than wild C. draconoides (p<0.001) (Table 1). The difference is marked when the values are corrected for body mass differences: C. tigris, 0.36 kJ g⁻¹ day⁻¹; C. draconoides, 0.21 kJ g⁻¹ day⁻¹.

The extra costs of free existence were estimated from differences between laboratory and field metabolic rates. The field-active body temperature of C. draconoides was 40.4 ± 1.5°C (Fig. 1) which they maintained for ~10 h day⁻¹ (above). The remainder of the day we assumed they spent buried in the sand with body temperatures equal to the near-surface soil temperature in the shade (Fig. 2). Wild C. tigris had a mean field active body temperature of 41.0 ± 1.2°C (Fig. 1) which they maintained for ~5 h day⁻¹. The remainder of the day they spent in burrows about 13 cm deep (range 9-20 cm; R.A. A., personal observation) at body temperatures equal to the soil temperature at that depth (Fig. 2). The daily cost of resting in burrows or buried in the sand was estimated by integrating temperature-dependent metabolic rates calculated from measured Q₁₀'s (Table 1) over the temperature cycle each species experienced. Results are shown in Table 2. Field metabolic rates were 30% above maintenance for C. draconoides and 60% above maintenance for C. tigris. Callianus draconoides allocated 23.5% of total field costs to activity and C. tigris allocated 37.5%.

The average rate of energy expenditure during the activity period (Rₐ) was estimated by first assuming that the extra cost of free existence was confined to the activity period and then by adding that cost to maintenance costs during the activity period. This assumption is realistic since activity is probably minimal for animals with reduced body temperatures in burrows buried in the sand at night. The Rₐ for C. tigris was 22.5 J g⁻¹ (h active)⁻¹, whereas Rₐ for C. draconoides was 8.9 J g⁻¹ (h active)⁻¹. Rₐ of C. tigris, expressed as a multiple of resting metabolism at field-active body temperature, was more than twice the Rₐ of C. draconoides, expressed in the same manner (Table 2). This analysis involves the assumption that animals were active every day. This was essentially confirmed for C. draconoides (above) and if C. tigris had not been active every day, its Rₐ would be larger than calculated here.

Water Influx and Feeding Rate

Since no rain fell and no free water was available during the study, the lizards' water influx potentially resulted from three sources: 1) metabolic water production 2) preformed water in the food (food water) 3) water vapor influx. To calculate feeding rate from total water influx data, both the portion of total water influx due to preformed water influx and the mean water content of the prey must be known (Nagy 1975). Metabolic water production was calculated as described in Methods; further analysis of the data indicated that influx due to vapor exchange was
Table 2. A comparison of resting and field metabolic expenditure for \textit{Cnemidophorus dracoideos} and \textit{Cnemidophorus tigris}.

| Metabolic cost; g m\(^{-1}\) day\(^{-1}\) | Free-living in field | Total field | Field active
| --- | --- | --- | ---
| Maintenance in laboratory | Total | Resting near surface | Active in field | Total | Total maintenance | Active at 40°C |
| \textit{C. dracoideos} | 14 h at 26-40°C cycle | 10 h at 40°C | 46.6 | 58 | 104.6 | 46.6 | 89.1 | 135.7 | 1.3 | 1.5 |
| \textit{C. tigris} | 19 h at 30-40°C cycle | 5 h at 40°C | 96.5 | 34 | 130.5 | 96.5 | 113.2 | 209.7 | 1.6 | 3.3 |

Table 3. Body mass change, water influx, and calculated feeding rates of free-living \textit{Cnemidophorus tigris} and \textit{Cnemidophorus dracoideos}. Values are mean (standard deviation).

<table>
<thead>
<tr>
<th>Mean (\text{body mass} ) g</th>
<th>(d) body mass (\text{mg g}^{-1} \text{day}^{-1})</th>
<th>Water influx, ul g(^{-1}) day(^{-1})</th>
<th>Food intake</th>
<th>Dry mass (\text{mg g}^{-1} \text{day}^{-1})</th>
<th>Metabolizable energy (\text{J g}^{-1} \text{day}^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{Cnemidophorus tigris}</td>
<td>(N=19)</td>
<td>15.66</td>
<td>-0.04</td>
<td>(4.4)</td>
<td>36.8</td>
</tr>
<tr>
<td>\textit{Cnemidophorus dracoideos}</td>
<td>(N=18)</td>
<td>8.63</td>
<td>-2.5</td>
<td>(3.5)</td>
<td>17.1</td>
</tr>
</tbody>
</table>

* 95% confidence interval excludes zero * computed as described in Methods + calculated by subtraction

negligible, as described below. We assumed that arthropod prey had an average water content of 70% (Edney 1977) and a chemical potential energy content of 23 kJ (g dry mass)\(^{-1}\) of which about 75% was metabolizable (Harwood 1979). Feeding rates were calculated as (total \(\text{H}_2\text{O}\) influx - metabolite \(\text{H}_2\text{O}\) influx) / (2.34 ml \(\text{H}_2\text{O}\) per gram dry mass) (Table 3). There were no significant sexual differences in field water influx within either species.

Water vapor influx appeared negligible for the following reasons. When feeding rates of \textit{C. tigris} were calculated, metabolizable energy intake (229 g \(^{-1} \text{day}^{-1}\)) was within 10% of energy expenditure (210 g \(^{-1} \text{day}^{-1}\); Table 2). Such energy balance was the expected result in the \textit{C. tigris} which, on average, maintained body mass (Table 3). Had water vapor influx been larger, feeding rates calculated in the above manner would have overestimated total metabolism. The calculated metabolizable energy intake rate of \textit{C. dracoideos} was only 75% of their rate of energy expenditure (Tables 2, 3). Thus their mass loss (Table 3) can be explained by inadequate energy intake.

Discussion

\textbf{Energy Expenditure}

On a mass corrected basis, \textit{C. tigris} had a higher field metabolic rate than that measured for any lizard yet studied. Its field metabolism (0.36 kJ g \(^{-0.60} \text{day}^{-1}\)) was 62% greater than that predicted for a similar-sized iguanid lizard (0.224 kJ g \(^{-0.60} \text{day}^{-1}\); Nagy in press). The field metabolic rate of \textit{C. dracoideos} was within 6% of the predicted rate. Nagy's data were solely doubly labeled water measurements of lizard field metabolism. Bennett and Gorman (1979) used a time-energy budget method to estimate field metabolism of an insular tropical teiid, \textit{Cnemidophorus marinus}, and that estimate (0.31 kJ g \(^{-0.64} \text{day}^{-1}\)) was 15% below that measured for \textit{C. tigris}. Other time-energy budget estimates of lizard field metabolism range 0.09-0.44 kJ g \(^{-0.64} \text{day}^{-1}\) (McNab 1963; Alexander and Whiffield 1968; Wilson and Loew 1974; Dutton et al. 1975; Tinkle and Hadley 1975; Turner et al. 1976; Bennett and Gorman 1979). The methods used in these time-energy budget studies have differed and there has been no published validation of these techniques for estimating lizard field metabolism. Other studies of energy utilization by lizards involved estimations or measurements of feeding rate in field or laboratory and may include costs of tissue production in addition to respiration (Licht and Jones 1967; Mueller 1970; Kitchell and Windell 1971; Avery 1971, 1978).

A convenient way to standardize further field metabolic rate measurements for comparative purposes is to express them as a multiple of the daily maintenance costs (King 1975; Bennett and Nagy 1977). Maintenance costs are determined by the 24 h thermal regime of the lizard (Table 2). Expressed in this manner field metabolism of the very active \textit{C. tigris} was not very different than that of the relatively inactive \textit{C. dracoideos}. Values of field metabolism of both species, expressed in this manner, were lower than that of \textit{Sceloporus occidentalis} which had a field metabolism 2.0 to 2.5 times maintenance (Bennett and Nagy 1977). The comparatively lower value for \textit{C. tigris} is due to the fact that it was active for only two-thirds of the time that \textit{S. occidentalis} was thought to be active. However, \textit{C. dracoideos} was active slightly longer each day than \textit{S. occidentalis} so the lower value of the former might be due, in part, to a difference in intensity of activity.

We observed \textit{C. dracoideos} and found them to be more active for more than 95% of their activity period. While Bennett and Nagy (1977) provide no observational data, their estimates of field activity costs suggest that \textit{S. occidentalis} was more active than this. \(R_a\) for \textit{S. occidentalis} was calculated to be 2.5 to 3.0 times resting metabolism at field active body temperature.
while for *C. dracoides* it was only 1.5% *Cnemidophorus tigris* had the highest *R* made 3.3 times resting metabolism. The difference in *R* cannot be attributed to body size effects since *C. tigris* is the larger of the three and the cost of transport decreases with increased body size (Taylor 1973).

Assuming *C. tigris* were active for 5 h day−1 and moved at a rate of 0.18 km h−1 (above), they traveled almost 1 km day−1. The minimal cost of transport for a lizard of its size is about 56 g j m−2 (Taylor 1973), so locomotion cost *C. tigris* minimally 56 g j m−2. This is 27% of total daily metabolism and 72% of the activity component of daily metabolism. Some other components of their activity cost are the cost of digging (which is high in mammals- Vleck 1979), alertness, and climbing in shrubs.

**Costs and Benefits of Foraging**

The foraging styles of *C. dracoides* and *C. tigris* are radically different. One of the intriguing findings of this study was the relative success of the widely foraging strategy of the teiid. Its mass specific net rate of energy intake per hour active was higher than *C. dracoides* and, in terms of the benefits and costs of foraging, *C. tigris* was apparently more efficient.

A 16 g *C. tigris* had a rate of energy expenditure while foraging for 22.5 J g−1 h−1. During its 5 h of daily activity it captured and ingested 213 mg dry mass of arthropod or about 3.7 metabolizable kj. Its foraging efficiency during those 5 h (metabolizable energy in energy out) was 2.0. Its net rate of energy intake (metabolizable 1 g−1 h−1 consumed minus 1 g−1 h−1 expended) was 23.8 J g−1 h−1.

To make a similar calculation for *C. dracoides* requires the assumption that they were foraging the entire time they were active. This is difficult to assess in a sit-and-wait predator but we did observe feeding attempts by *C. dracoides* throughout the day. An average *Callisaurus* (9.0 g) expended 9 g−1 h−1 while active on the surface. During its 10 h of daily activity it ingested 52 mg dry mass of arthropod or about 900 metabolizable J. Its foraging efficiency was 1.1. Even if one were to assume *Callisaurus* ate enough to maintain constant mass, 71.4 mg dry mass day−1, it would still have a foraging efficiency (1.3) lower than *C. tigris*. Its mass specific net rate of energy intake would also be lower (4.7 J g−1 h−1).

Interestingly, the relative feeding costs and efficiencies of these two animals support a major assumption in Norberg's (1977) feeding model. His model was developed for animals with high energetic costs of foraging but which also have a less energy-consuming search method. He considered a cheap method to be one with a total energetic cost of 1.5 to 3.0 times basal metabolism; the cost calculated for *C. dracoides* in this study was 1.6 times resting metabolism. The more expensive method was considered to be 1.5 to 17 times basal metabolism and the foraging cost of *C. tigris* here was about 3.3 times resting metabolism. His major assumption was that the efficiency of a search method is higher, the higher the energy consumption linked to it. He did not define "efficiency" but if we assign it the meaning given here, then the assumption would hold for the sit-and-wait foraging method of *C. dracoides* and the active foraging method of *C. tigris*.

The large difference in foraging costs for these two lizards could result in differing responses to decreases in prey availability. Vitt and Omland (1977) suggested that the low midday activity of *C. tigris* during the summer might be related to the movement of fossorial invertebrates deeper into the substrate as soil surface temperatures increased during the day. They argued that the benefits of foraging did not outweigh the costs during the afternoon hours. But the costs for *C. dracoides* are much lower than for *C. tigris*. If arthropod abundance did decrease then the prey capture rate of both species might decrease. *Callisaurus dracoides* expends only 50% more energy active and alert on the surface than it would resting buried in the sand near the surface midday (*T*; *in the shade ~40° C). In contrast, *C. tigris* expends 234% more energy actively foraging on the surface than it would if it rested in a burrow (*T*; *in the shade ~418° C; Fig. 1) and rested midday. *Callisaurus dracoides* commits much less energy, in a relative sense, than does *C. tigris* during a period when foraging success may be poor. One might predict that *Callisaurus* would forage longer during the hot afternoon. However, without information on arthropod abundance or prey capture rates during hot versus cooler periods, this remains speculative.

In fact, another hypothesis explaining *C. tigris* summer midday resting is that soil surface temperatures become too high for *C. tigris* to both move across open spaces as it forages and also to regulate its body temperature at or below about 43° C (Asplund 1968).

Whatever the case, this study more generally demonstrated that the foraging mode employed by a lizard can have a significant effect on its total energy budget. Differences in foraging style do have different energetic costs and this should have important implications for the foraging economics of lizards with different foraging tactics. Furthermore, in animals which employ more than one tactic, the relative costs of each tactic may be an important factor determining which is employed under various conditions.

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