Ecology of the Beaded Lizard, *Heloderma horridum*, in a Tropical Dry Forest in Jalisco, México

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**Abstract.**—Activity patterns, diet, resource use, and thermal biology were investigated with the use of radiotelemetry in a population of Mexican beaded lizards in a tropical dry forest in coastal Jalisco, Mexico. Fifteen *H. horridum* ranging in mass from 36 to 1600 g were captured and marked within a 36 ha area. Growth rates of up to 15.5 mm/yr were observed. Diet consisted of eggs of spiny-tailed iguanas and other reptiles, and bird eggs and nestlings. Shelters were used in arroyos, on hillsides, and the forest floor. Trees were often used as shelters during the wet season. Mean home range size was 21.6 ha. Beaded lizards had a primary peak of surface activity at 1800 h, and a smaller peak at 0900 h. Seasonal differences in daily activity times were noted. Peak seasonal activity (17 d/mo) occurred in May and gradually decreased through the summer to a low of 1 d/mo in January. Beaded lizards, on average, spent 67 min above ground and traveled 236 m per activity bout, resulting in approximately 120 h/yr invested in surface activity. Minimum and maximum body temperatures recorded for resting *H. horridum* were 17.7 C (January) and 37.2 C (June). Mean monthly body temperatures ranged from 19.9 C in December to 28.5 C in July. Activity temperature range was 22.5–36.0 (x = 29.5 C). Activity temperatures were lower during the wet (x = 27.0) than during the dry (x = 30.2) season. *Heloderma horridum* is a more active, semiarboreal lizard than is *H. suspectum*, the only other living Helodermatid.

**Resumen.**—Patrones de actividad, dieta, uso de recursos, y temperatura fueron investigados en una población de escorpiones (*Heloderma horridum*) mediante el uso de radiotelemetría, en una selva baja caducifolia cerca de la costa de Jalisco, México. Quince individuos de *H. horridum* (con un rango del peso de 36 a 1600 g) fueron capturados y marcados en un área de 36 hectáreas. Se observó una tasa de crecimiento de hasta 15.5 mm/año. Los escorpiones se alimentan de huevos de la iguana negra y algunas lagartijas, y huevos y crías de pájaros. El ámbito hogareño promedio fue 21.6 ha. Se encontraron refugios en arroyos, acantilados rocosos, árboles, y en el suelo. Los escorpiones escalan y se trepan a los árboles especialmente en la época lluviosa. Los picos de actividad diurna en *H. horridum* fueron a las 0900 y 1800 horas, observándose diferencias estacionales en los tiempos de actividad. El pico de actividad (17 días/mes) ocurrió en mayo y gradualmente disminuyó durante el verano, hasta 1 día/mes en enero. En promedio, los escorpiones estuvieron 67 minutos fuera de los refugios y se movieron 236 m en cada periodo de actividad (aproximadamente 120 horas por año). El rango de temperatura corporal media en descanso fue de 19.9 C en diciembre a 28.5 C en julio. En actividad, la temperatura corporal media de los escorpiones fue de 29.5 C (22.5–36.0); siendo más baja durante la época lluviosa que durante la época seca. *H. horridum* es más activo y más arborícola que *H. suspectum*, el único otro miembro de la familia Helodermatid.

The Helodermatidae contains two extant species of stout-bodied venomous lizards with large, powerful jaw muscles and bead-like osteoderms underlying dorsal scales. They inhabit desert and dry subtropical regions of the southwestern United States, western Mexico, and Guatemala (Bogert and Martín del Campo, 1956; Campbell and Vannini, 1988; Campbell and Lamar, 1989). Both helodermatid species are predators on young and eggs of vertebrate nests. Recent work on *H. suspectum*, the Gila monster, has shown it to be a diurnal predator with a relatively low activity temperature of 29 C and a low investment of time and energy to activity (Low et al., 1967, 1986; Coombs, 1977; Porzer, 1981; Beck, 1990). The Gila monster's low resting metabolic rates and slow, infrequent surface activity contrasts with its surprisingly high capacity for aerobic activity (John-Alder et al., 1983). The Mexican beaded lizard or escorpión, *Heloderma horridum*, is the larger, more ancestral species (Pregill et al., 1986). It is encountered most frequently after summer rains in México and has long been known to be a good climber. Information on the natural history of beaded lizards is given in Bogert and Martín del Campo (1956). Álvarez del Toro (1982), Pregill et al. (1986), and Campbell and Lamar (1989). In most aspects of its ecology, however, *H. horridum* remains poorly known; published information on its diet, patterns of activity, thermal biology, and habitat use is either scanty or nonexistent. How might patterns of activity and thermal biology of beaded lizards be influenced by the
seasonality of their tropical dry forest environments? How does the ecology of *H. horridum* compare with that of *H. suspectum*?

We present results of a field study in a lowland tropical deciduous forest in Pacific coastal México designed to address these questions.

**Methods**

**Study Area.**—The study area is on the Estación de Biología Chamela (EBCH), a 16 km² biological reserve of the Universidad Nacional Autónoma de México (UNAM), located less than 5 km from the Pacific coast at approximately 19°30′N, 105°03′W in the state of Jalisco, México. The reserve is in a lowland tropical deciduous "dry" forest with a marked seasonality in precipitation (Fig. 1). Eighty percent of the mean annual precipitation of 748 mm (29.4 in) at EBCH falls during a four-month wet season between early July and early November; the mean annual temperature is 24.4°C, mean monthly maxima are 29.1–32.0, and mean monthly minima 14.8–22.9 (Bullock, 1986; Lott et al., 1987). Elevation ranges from 10 to 584 m.

Two major habitat types occur at the station (see Perez, 1982; Lott, 1985; Lott et al., 1987). An upland dry-deciduous forest occurs on dissected hilly terrain with numerous small drainages. It has a 4–15 m tall canopy with a well-developed understory of shrubs and dense herbaceous cover during summer and autumn months. A taller riparian semideciduous forest, developed on the larger arroyos, has a more open understory. The two habitat types are referred to by Lott et al. (1987) as upland forest and arroyo forest. They are, respectively, the "selva baja caducifolia" and "selva mediana subperenifolia a subcaducifolia" of Miranda and Hernández (1963).

**Study Procedures.**—Lizards were located primarily by searching the numerous trails and arroyos. Sightings of *Heloderma* were also made for us by station personnel. Individuals were weighed to the nearest 2 g with Pesola spring scales, measured (snout-to-vent [SVL], tail length, tail circumference), and uniquely toe-clipped for future identification. Only one toe was clipped on each animal, at the second joint. Fecal samples were collected when possible and contents were identified using a reference collection of potential prey items.

Locations, movements, and body temperatures of lizards were monitored using calibrated, temperature-sensing implantable radiotransmitters (IMP-200L, Telonics, Mesa, Arizona). The radios were surgically implanted by anesthetizing the lizards with ketamine hydrochloride, cutting a 3 cm transverse incision in the venter through the dermis and peritoneum 20–25 scale rows anterior to the vent, and placing a paraffin-coated radio into the peritoneal cavity. At 23 g, each radio weighed less than 4% of the body weight of its host. Incisions were closed with chromic gut suture. Six lizards were outfitted with radiotransmitters and monitored as follows: No. 1, July 1986–October 1987; No. 6, May–
Table 1. Mean body mass (g) and dimensions (mm) of adult *H. horridum* at EBCH. SDs are given in parentheses.

<table>
<thead>
<tr>
<th>Sex</th>
<th>N</th>
<th>Mass</th>
<th>SVL</th>
<th>Tail length</th>
<th>Total length</th>
<th>Tail circumf.</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>8</td>
<td>833 (351)</td>
<td>383 (36)</td>
<td>288 (31)</td>
<td>671 (67)</td>
<td>92.5 (18.6)</td>
</tr>
<tr>
<td>F</td>
<td>5</td>
<td>667 (212)</td>
<td>346 (32)</td>
<td>265 (26)</td>
<td>609 (53)</td>
<td>93 (9.8)</td>
</tr>
</tbody>
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After a 48 h recovery/observation period, lizards were released at the site of capture. They were not disturbed after their initial release except for an occasional body weight measurement and body temperature calibration check with a Schultheis thermometer. They were followed on the study site with a TR2 receiver and directional H-configuration antenna (Telonics). The radiotransmitters had a battery life of over 10 mo and a range of 0.2–6.0 km, depending upon topography and shelter characteristics (e.g., below ground in a canyon vs. in a tree on a ridge). The field study periods were 20 June–3 August 1986; 10–15 January 1987; 4 May–24 July 1987; 12–21 October 1987; 13–23 January 1988; 8–21 May 1988; 28 August–10 September 1988; 28 December 1988–4 January 1989; and 1–10 March 1989, totaling 185 days.

Locations of radio-implanted animals were checked each day in the morning and late afternoon. In 90% of cases exact locations of individuals were pinpointed and shelters marked with flagging. When thick understory prevented human travel without destruction of vegetation, locations were determined by triangulation from 10 m-high observation towers. The accuracy of the triangulation technique (±15 m radius) was determined by placing radiotransmitters at five known locations and independently determining their positions by triangulation from the observation towers.

Distances traveled were directly measured from some individuals. When a transmitting individual could not be followed directly, the straight-line distance between two consecutive shelter locations was measured and a correction factor added to account for non-linear movements of the active lizard. The correction factor (0.25 ± 0.08, obtained from 24 direct observations) was determined by the following: ADT – SLD/ADT, where ADT = actual distance traveled by lizard from point A to B, and SLD = straight-line distance from A to B.

Body temperatures of *Heloderma horridum* were monitored from the pre-calibrated radios throughout each day usually at bi-hourly intervals, often more frequently. Time of emergence of lizards from shelters onto the surface was identified by noting from the radiotransmitter the relatively rapid change in body temperature as a lizard left the nearly-constant temperature environment of its shelter. Environmental temperatures were measured with a Miller and Weber ("Schultheis") quick reading, cloacal thermometer, and from pre-calibrated temperature sensing radiotransmitters. Terminology pertaining to thermal biology follows that of Pough and Gans (1982).

Statistical procedures (Chi-square, correlation coefficient r, and two-tailed students t test) on data that met assumptions of normality and equity of variances follow Zar (1984). Means are followed by ±1 SD. Home ranges were calculated for lizards with a minimum of 15 sightings over 10 mo using the convex polygon method (Jennrich and Turner, 1969; Rose, 1982).

RESULTS AND DISCUSSION

Fifteen *H. horridum* were captured within an area of approximately 36 ha. Body mass ranged from 33 (juvenile) to 1600 g (adult male) and SVL ranged from 147 to 444 mm (Table 1). Growth rates in SVL over periods of at least 9 mo averaged 10.8 mm/yr (±3.9, range = 5.6–15.5, N = 5).

Snout–vent length is tightly correlated with tail length (r = 0.98, P < 0.001, N = 15) and less so with body weight (r = 0.79, P < 0.001, N = 15). Individual body weights fluctuated considerably throughout the activity season (April–October) and throughout the year. *Heloderma horridum* can lose a large percentage of its body mass and gain it back quickly after a few successful foraging bouts. One adult showed a 30% weight gain (stomach empty) between August 1986 and May 1987. Over the activity season, mean increase in body mass was 100 ± 80 g (N = 5). Moreover, lizards were able to quickly rehydrate with the first rains following the dry season, resulting in a substantial increase in body weight. One 880 g lizard gained 52 g of water after a light June rain of 1.5 mm.

*Food Habits.*—The diet of *H. horridum* at Chama consisted of reptilian and avian eggs, and young birds. In 14 fecal samples collected from 10 beaded lizards, remains of reptilian eggshells (10 of 14), feathers (8 of 14), and insects (5 of 14) were found. Six fecal samples contained remains of both reptile eggs and feathers.

We were able to identify the tough-shell remains of the spiny-tailed iguana, *Ctenosaura pectinata*, in 6 fecal samples. In addition, we ob-
served numerous *H. horridum* tracks at *Ctenosaura* nest sites, and found eggshells apparently exhumed by *Heloderma* (although most *Ctenosaura* eggs eaten by beaded lizards were probably swallowed whole). A peak in *Heloderma* activity coincides with the nesting season of *Ctenosaura* at EBCH (López-Valenzuela, 1981). Based on these observations we conclude that during May and June *H. horridum* derives a substantial portion of its diet from eggs of the spiny-tailed iguana. *Heloderma* also uses the excavated *Ctenosaura* nest sites as shelters. Most of the *Ctenosaura* nesting sites were located in sandy banks of arroyos and the friable soils of road banks and semi-open slopes. In March 1989 a *Ctenosaura pectinata* (approximately 300 g) and a 900 g *H. horridum* shared the same ground shelter.

Six of 14 fecal samples contained other, unidentified reptile eggshells; Chamela residents have observed beaded lizards excavating the eggs of other reptiles near the study area. In the species records by Casas-Andreu (1982) for the southwest coast of Jalisco inclusive of EBCH, there are three species of turtles, 23 egg-laying lizards, and 30 egg-laying snakes.

Feathers from the White-tipped dove (*Leptotila verreauxi*) were identified in 3 *H. horridum* fecal samples; 5 contained other, unidentified feathers and avian eggshells. The selection of nest sites by doves, chachalacas (*Ortalis poliocephala*), and trogons (*Trogon citreolus*) makes their nests especially vulnerable to foraging beaded lizards. Doves lay their eggs on the ground, trogons are tree-hole nesters, and chachalacas build crude platform nests in trees and large shrubs. Beaded lizards are capable of scaling vertical trunks of trees and spend a significant part of their time in trees (see below). We observed lizards foraging in areas where chachalacas and trogons were nesting. Crushed chachalaca eggshells were found at the base of a tree where a radio-equipped lizard was active, and Chamela residents have also informed us that *H. horridum* eats the eggs and young of these and other birds. Beaded lizards have also been observed raiding the nests of Beechey’s jay (*Cissilopa beecheyi*) in Nayarit, México (J. W. Hardy, cited in Pregill et al., 1986).

The insect parts that we found in *Heloderma* fecal samples were primarily small (<2 mm) adult coleopteran, hymenopteran, and orthopteran exoskeletons that were probably ingested “unintentionally” while the lizards were feeding on vertebrate nests. In some cases, however, beaded lizards may intentionally feed on coleopteran larvae. We found 10 beetle larvae between 20 and 30 mm long in the stomach of a road-killed *H. horridum* near Alamos, Sonora in August 1989, and Pregill et al. (1986) reported coleopteran larvae in two museum specimens of *H. horridum*.

Throughout its range *Heloderma horridum* feeds on juvenile mammals in nests (Bogert and Martín del Campo, 1956; Alvarez del Toro, 1982). Although no mammal remains were found in fecal samples of beaded lizards at EBCH, many of the 70 mammal species in the Chamela forest (species accounts in Ceballos and Miranda, 1986) provide potential meals for *H. horridum*. Sixteen rodents, the single lagomorph *Sylvilagus cunicularis*, the armadillo (*Dasypus*), the tlacuache (*Didelphis*), and 33 species of bats (*Chiroptera*) are potential *H. horridum* prey on the study site.

**Home Range, Habitat and Shelter Use.**—The mean home range of five *H. horridum* was 21.6 ha (Fig. 2). There was substantial overlap in the home ranges of these individuals. Some shelters in this region of overlap (Fig. 2) were used by more than one lizard at different times, and on two occasions in May 1987 two lizards (sexes unknown) were observed together, but were not engaged in outward physical interactions. Male–male combat was observed in this area in September 1984 (Beck and Ramírez-Bautista, 1991). Elevation within adjacent home range areas ranged from 90 to 150 m. Both vegetation types, upland and arroyo forest, were visited by beaded lizards, but the dense forest of slopes and uplands was used more frequently.

Most beaded lizard shelters occurred along the slopes of the numerous small gullies that crisscross the forest (Fig. 3). Because these gullies are such a dominant feature of the landscape at EBCH (Fig. 1), they did not seem to be selected as shelter sites out of proportion to their abundance. Arroyos, rocky slopes, and the forest floor, including both the dense and more open understory vegetation, all provide suitable substrata for *Heloderma* shelters (Fig. 3).

A typical *H. horridum* ground shelter was an abandoned burrow with a 15 cm-diameter opening and a tunnel extending inward 1–2 m, situated along a gully bank or slope above a small drainage and often at the base of a tree (Fig. 3). *Heloderma horridum* rarely digs its own shelters, unless it is excavating a nest that it later uses as a shelter. The directional exposure of 71 ground shelter entrances was not significantly different from random ($\chi^2 = 3.76, df = 3, P > 0.05$). Lizards inside underground shelters were usually 1.0–1.5 m from the entrance. During the surface-active season, lizards remained within shelters for an average of 2.3 ± 1.4 d (N = 106) before moving to another shelter.

Beaded lizards also used trees as shelters, especially during rainy periods. Of 16 tree shelters identified, 13 were used during or shortly
after rain, 11 of which were during the wet season months of July through October (Fig. 3). Both hollow branches and trunk sections 2–8 m above ground (mean approximately 3.5 m) served as tree shelters.

Activity Patterns.—*Heloderma horridum* exhibits a diurnal activity pattern with a strong peak of activity in the afternoon between 1600 and 2000 h and a smaller morning peak between 0700 and 1000 h (Fig. 4). During the rainy season at Chamela, the bimodal activity peaks of *H. horridum* were more separated than during the dry season. Beaded lizards had an earlier morning activity peak, and a second peak later in the afternoon and early evening (Fig. 4). The limited nocturnal activity in *H. horridum* at EBCH occurred predominantly during rainy periods (Fig. 4). Álvarez del Toro (1982) noted that *H. h. alvarezi* in Chiapas are active toward dusk and shortly thereafter (not in the morning) and that during rain they may emerge from burrows earlier in the day.

Rate of travel of 5 beaded lizards observed directly during 24 separate activity bouts ranged

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**Fig. 2.** Shelter locations and home ranges of 6 *H. horridum* monitored with radiotelemetry at Chamela. Data were insufficient to estimate home range for lizard No. 14. Large drainages are indicated but many of the smaller gullies are not. See text for specific observation periods.

**Fig. 3.** Frequency distribution of *H. horridum* shelter types on the study site; N = 97. Trees were used more frequently during the wet season.
from 0.7 to 7.0 m/min ($\bar{x} = 3.5 \pm 1.7$). During surface activity, beaded lizards traveled distances ranging from 15 m to nearly 1 km ($\bar{x} = 236 \pm 153$ m; $N = 116$; Fig. 5). Assuming a travel rate of 3.5 m/min, mean duration was approximately 67 minutes. While foraging, beaded lizards often followed the slopes and bottoms of the numerous small drainages that cut through upland forest.

*Heloderma* surface activity at EBCH peaked near the end of the dry season. Animals were most frequently sighted in early May, although considerable activity continued throughout June and July, gradually decreasing in September and October (Fig. 6). Lizards were frequently encountered on the surface after rains, especially at the onset of the rainy season in July. They were active on the surface on 47% of the days they were monitored during May through July, traveling an average of 252 m for each day active. By September and October radio-equipped lizards were active on only 33% of the days they were monitored, traveling an average of 242 m/day active. In January, they were active 17% of the days they were monitored and traveled an average of 45 m/day active. Some surface activity in the local population most likely occurs during every month of the year (Fig. 6).

We obtained an annual estimate of 25.3 km traveled over 121 h of surface activity for *H. horridum* at EBCH; missing data on distances traveled and days active were filled in by extrapolating from adjacent months (Fig. 6). This may be an underestimate of the actual annual activity because lizards were not monitored 24 h/day and some activity (e.g., short trips where lizards returned to the same shelter) may have gone undetected.

Non-foraging behaviors such as habitat selection, mate searching, nest site selection, and male combat probably comprise a significant portion of surface activity, but they were not quantified for *H. horridum* in this study. We were unable to test for differences in activity among ages and sex. In captive *H. horridum alvarezi* in Chiapas, México, male-female pairing takes place during October through November, male-male combat occurs from September to November, and eggs are laid between November and December (Álvarez del Toro, 1982; Ramírez-Ve-
láquez and Guichard-Romero, 1989). At EBCH male–male combat has been observed in September (Beck and Ramirez-Bautista, 1991); recently hatched juveniles emerge in July (Ramirez-Bautista, unpubl.; this study). Quantifying the competing time and energy requirements of these various activities and life history stages should be a primary challenge for future research.

**Thermal Biology.**—Mean monthly body temperatures of *H. horridum* while resting in shelters ranged from 19.9 C in December to 28.5 C in July (Fig. 7). Extremes in body temperatures ranged from 17.7 C (below-ground in January) to 37.2 C (thermal inertia after activity in June).

Body temperatures of *H. horridum* resting in below-ground shelters typically fluctuated very little over the course of a 24 h period (Fig. 8A). At such times body temperatures were highly correlated with temperatures 0.5 m underground (r = 0.95, P < 0.001), but were not correlated with surface (r = 0.04, P > 0.10) or air (r = 0.06, P > 0.10, df = 143) temperatures. When an animal moved to a new shelter, body temperature changes depended on the thermal characteristics of the new shelter. Lizards using shelters in trees showed considerable fluctuation in body temperature over 24 h (Fig. 8B). They had body temperatures more highly correlated with air (r = 0.55, P < 0.01) and ground surface (r = 0.64, P < 0.001) temperatures than with temperatures 0.5 m underground (r = 0.25, P > 0.10, df = 47). The general pattern, however, was for body temperatures of *Heloderma* to remain strikingly constant while the lizards were inside shelters, which could be over a week at a time during the activity season and longer at other times of the year.

The activity temperatures of *H. horridum* (Fig. 9) ranged from 22.5–36.0 C, and averaged 29.5 ± 3.2 C (N = 96), which was significantly higher than mean body temperature when at rest (inside shelters) during the activity season (t = 190.3, P < 0.001, df > 100). Activity temperatures during the wet season were significantly lower than during the dry season (t = 7.51, P < 0.001, df = 94; Fig. 9). Beaded lizards frequently left their shelters during and shortly after rainstorms, and were exposed to cooler surface and air temperatures at these times.

During heavy September rains in 1988, two radio-implanted lizards remained in tree shelters, leaving the shelters only after precipitation ended. Beaded lizards were observed sunbasking after heavy rains, and in January. One lizard monitored while sun basking in a tree after a heavy September rain maintained body temperature between 28.2 and 29.4 C (t = 28.8 ± 0.48 C, N = 12) between 1415 and 1620 h (body temperatures were sampled every 10 min).

Air temperature fell from 28.4 to 26.8 C during the same period.

**Comparisons with *H. suspectum***.—Information for *H. s. cinctum* in the Mojave Desert in southwestern Utah is from Beck (1986, 1990), and that for Sonoran Desert populations (*H. s. suspectum*) in Arizona and Sonora, México is from Lowe et al. (1986) and unpublished data.

*Heloderma horridum* exhibits a peak of activity in the late afternoon, and a smaller peak in the morning (Fig. 4). In contrast, the pattern for the desert-dwelling *H. suspectum* is scaled toward sunrise, with peak activity in the morning and a smaller peak in the late afternoon and early evening. Most of our observations of nocturnal
activity in *H. horridum* from localities in México other than Chamelita were made during summer rains (5 of 7). Similarly, a majority of adult *H. suspectum* observed in southeastern Arizona was active during or after summer night rains (4 of 5). Our data on the timing of activity of *H. horridum* and *H. suspectum* confirm that helodermites are indeed primarily diurnal, and not nocturnal as is often believed (see also Lowe et al., 1967, and Lardner, 1969).

The primary activity season for *H. horridum* at EBCH is the 8 month period from early April to mid November, during which about 88% of yearly surface activity takes place. The remaining 12% is an on-surface presence during a part of each of the remaining months of the year. Gila monsters reach their peak of surface activity during the early dry season. In the warm subtropical Sonoran Desert this peak is during March–April, but the activity season continues through the summer rains (middle July onward). *Helodermis suspectum* in the Sonoran Desert has an activity season nearly as long as *H. horridum* in Jalisco, and surface activity occurs during every month of the year. In contrast, the activity season for *H. suspectum* in the colder Mojave Desert in Utah (under a winter rainfall-dominated regime) extends from mid April to mid July and is only half as long as that of *H. horridum*.

The activity temperatures of *H. horridum* (\( T \approx 29.5 \), range = 22.5–36.0 C) are very similar to those observed in *H. suspectum* in Utah, Arizona, and Sonora. *Heloderma horridum* in Jalisco is exposed to far less annual temperature change than is, for example, *H. suspectum* in southwestern Utah. Gila monsters in the Mojave Desert in Utah spend over 83% of the year at or below a body temperature of 25 C, whereas body temperatures of *H. horridum* in Jalisco fell within this thermal zone less than 40% of the year (Fig. 7).

During subsurface inactivity in January, the coldest month, the body temperature of *Heloderma suspectum* reached as low as 10.6 C in southern Arizona (and undoubtedly lower), which is 7.1 C below the extreme of 17.7 that was experienced by *H. horridum* underground in January at Chamelita. The supercooling limit for *H. suspectum* is \(-3.89\) C (Lowe et al., 1971); supercooling information for *H. horridum* is not available. In the Sonoran Desert, individuals of *H. suspectum* emerge in late morning at deep body temperatures as low as 12.7 to 17.3 C for sunbasking during February–March, and rarely in December–January. It is unlikely that *H. horridum* exhibits surface activity at body temperatures below 17 C. During the warm months of June and July the two species exhibit similar body temperatures.

The maintenance of a higher body temperature throughout the year by *H. horridum* results in a substantial increase in resting metabolic rate and hence greater maintenance energy costs than is the case for *H. suspectum*. Metabolic rate is reduced considerably in *Heloderma* at low temperatures; the Q_{10} of 3.0 between 25 and 15 C (Beck and Lowe, unpubl.) provides a significant energy saving for winter-dormant *H. suspectum*. Neonatal and older juvenile helodermites occasionally consume the equivalent of their body weight in a single meal. Adult Gila monsters require only one equivalent of their body weight in food per year to satisfy main-
Fig. 8. Thermal relationships of radio-implanted *H. horridum* over 24 h periods in May 1987 (A), and September 1988 (B). Body temperatures of beaded lizards in ground shelters (A) remained constant except during brief above-ground activity bouts (arrows). Lizards inside tree shelters in September (B) exhibited wider fluctuations in body temperature.

Maintenance energy demands; this may be accommodated by 3–4 large meals/yr. To compensate for greater maintenance energy costs, *Heloderma horridum* must have a relatively higher net energy gain. The Mexican beaded lizard might therefore have a greater investment in surface activity than does the Gila monster.

Our estimate of minimum annual surface ac-
Fig. 9. Distribution of body temperatures during activity exhibited by 6 radio-implanted and 7 hand-captured *H. horridum* during the wet (mean = 27.0°C) and dry (mean = 30.2°C) seasons. Each observation is the body temperature of a lizard during a single activity bout; when several activity temperatures were obtained during one activity bout, the mean of those temperatures was used. The relationship between activity temperature and environmental temperatures is shown above. Mean activity temperature for the entire year was 29.5°C.

tivity at 121 h/yr for *H. horridum* is considerably higher than an estimate of 75 h/yr for *H. suspectum* in the Sonoran Desert in Arizona (exclusive of basking), and is nearly twice a generous estimate of 65 h/yr for *H. suspectum* in the Mojave Desert in south-western Utah. During September and October, *H. horridum* traveled over 10 times as far as a typical *H. suspectum*
in southwestern Utah at the northern extreme of the family distribution.

Our data suggest that *H. horridum* is indeed more active than is *H. suspectum*. Potential prey biomass and species diversity at Chamela is considerably higher than in desert habitats of *H. suspectum* to the north. Suitable prey species may be more abundant for *H. horridum* during late summer and autumn, a time when *H. suspectum* exhibits reduced activity. Moreover, reproductive behaviors (male combat, mate searching, nest site selection) that normally occur in late summer and early autumn may contribute to the continued activity that we observed in beaded lizards during September and October.

Although *H. horridum* in Jalisco invests about twice the time into surface activity as do the northernmost populations of the Gila monster, its overall investment in activity is still low. During May, the month with peak activity, beaded lizards at Chamela traveled an average of 4.1 km over 19.6 h of surface activity. The remainder of their time—over 95% of daylight hours—was spent in shelters.

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Glioxylosis and Swimming Performance in Juvenile American Alligators

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ABSTRACT.—Swimming speed of juvenile American alligators increased between 15 and 20 °C but not between 20 and 30 °C. Speed declined with time during the 4 min trials. Post-exercise lactate concentration increased with temperature and with duration of swimming. The rate of lactate formation during exercise increased with temperature and was higher in the first min of exercise than in the subsequent 3 min. Once the effects of temperature, body mass, and body length were removed, there was no relationship between the intensity of glycolysis and the distance covered in 1 min of swimming. In contrast, the alligators that swam the greatest distance in 4 min had the lowest lactate concentration. Thus, the relationship between the intensity of glycolysis and distance traveled varies with the duration of exertion in these animals during induced swimming.

Because crocodilians swim like fish, gallop like mammals, and exhibit an unusual "high walk" during routine terrestrial locomotion, their locomotor behavior and mechanics have intrigued biologists for many years (Manter, 1940; Colbert et al., 1946; Zug, 1974; Fish, 1984; Turner et al., 1985). It is implicit in such studies of locomotion that the results seen at the level of behavior are directly or indirectly traceable to, and dependent upon, underlying physiological processes. There is ample evidence linking locomotor behavior and locomotor physiology in reptiles and amphibians. For example, species with high locomotor stamina usually possess a high aerobic capacity whereas species with low endurance typically exhibit a low rate of oxygen consumption and a high reliance on glycolysis during intense exercise (Bennett, 1982; Taigen and Pough, 1985; Gatten et al., 1992). In spite of our extensive knowledge of the association between locomotor physiology and behavior among species of reptiles or amphibians, there is very little evidence to support the contention that this linkage between physiological capacity and behavioral ability exists among individuals of a single species. For example, individual toads with a high rate of oxygen consumption during exercise did not exhibit better locomotor performance than individuals with a low aerobic capacity either in laboratory trials (Walton, 1988) or in field tests (Wells and Taigen, 1984; Walton, 1988). Likewise, there was no direct association between sprint speed and limb muscle glycolytic