Ecology and Behavior of the Gila Monster in Southwestern Utah

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ABSTRACT.—Activity patterns, behavior, food habits, and thermal biology were investigated by radiotelemetry in a population of banded Gila monsters in southwestern Utah. Twenty-seven Gila monsters were observed within a 2 km² area. They fed on eggs and young mammals taken from nests. Quantities as large as 210 g, eaten in a single meal, did not appear to be envenomated. Activity peaked between late April and mid June, from 0800 to 1200 h. Distances traveled during activity bouts averaged 210 m (approximately 50 min), although individuals occasionally traveled over 1 km. Lizards were active on less than 10 days/month during their 90-day activity season, spending over 95% of their time below ground in shelters. This low energetic investment in activity is contrary to traditional descriptions of activity of lizards that forage on patchy prey. Gila monsters had a relatively low activity temperature (θ = 29.4 C) and at rest spent over 83% of the year at body temperatures of 25 C or below. Lizards occasionally basked near shelters in the spring. Several shelters were reused, some by more than one lizard, occasionally concurrently. Intraspecific interactions, including male combat, observed near shelters suggest that these helodermatids have a structured social system. Analysis of a 3-h fight between two large males revealed similarities with varanid lizard and crotaline snake combat, as well as similarities to combat in captive helodermatids.

Heloderma suspectum and H. horridum are the only extant members of the Helodermatidae, a family whose fossil record extends from the late Eocene of France and the late Cretaceous in North America (Pregill et al., 1986). Their current geographic distribution is limited largely to hot desert regions of the southwestern United States and desert, thornscrub, thornforest and tropical deciduous forest regions of western Mexico and Guatemala (Campbell and Vannini, 1988).

The venom and other unique qualities of helodermatids have interested herpetologists for many years (Bogert and Martin del Campo, 1956), but because these lizards rarely appear on the surface, field study over extended periods has been difficult. Recent work in Arizona has shown H. suspectum to be a secretive diurnal predator with a relatively low activity temperature, and a dietary specialization on eggs and young in vertebrate nests (Porzer, 1981; Jones, 1983; Lowe et al., 1986).

Finding nests, a widely distributed food source, should require a "widely searching" foraging mode (Huey and Pianka, 1981). Previous studies of lizard energetics have shown that "widely searching" predators allocate a greater portion of their respiratory energy to activity than to "sit and wait" predators (Anderson and Karasov, 1981; Huey and Pianka, 1981; Andrews, 1984; Nagy et al., 1984). One might predict that Heloderma would have similarly high activity costs during its activity season, yet little has been reported on actual distances traveled by free-ranging Gila monsters over extended periods, or on their energetic investment in activity. Their ability to take large meals and low energy demand while inactive (Beck, 1986) might make frequent searching for food unnecessary.

Here I present results of a 3-yr field study of Heloderma suspectum cinctum at the northern periphery of its range in southwestern Utah. I provide information on activity, food habits, habitat use, thermal biology, and behavior that sheds light on the social behavior, ecology and evolution of this species. I describe male-male aggressive behavior and discuss its physiological implications.

METHODS

Study Area.—The study site, a N-S oriented canyon, is in a Mojave/Great Basin Desert transition area near St. George, Washington County, Utah. Three km north of its mouth, the canyon opens into a sandy valley, 0.8 km wide and 1.7 km long, bounded by Navajo Sandstone cliffs to the W, N and E. Portions of the cliffs are capped with basaltic lava flows. Lava and sandstone boulders, strewn along the slopes of the cliffs and valley floor, provide shelters for Heloderma. The valley floor is largely composed of reddish-pink sand dunes deposited from the surrounding cliffs, and is dissected by several small washes. Considerable foraging activity

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occurs on these sandy areas. Elevation varies from 940 m at the valley floor to 1000 m along the canyon rim. The study area encompasses approximately 200 ha. Dominant vegetation includes creosote bush (Larrea tridentata), sand sage (Artemisia filifolia), and blackbrush (Coleogyne ramosissima). Annuals can be abundant from April through mid June.

Thermographs housed in a weather station installed near a center of Gila monster activity on the study site continuously recorded temperatures at 1.5 m above and 5, 25, and 75 cm below the surface. Additional substrate and ambient temperatures were recorded with handheld Shultheis and Tel-Tru (Germanow-Simon Co.) thermometers.

**Study Procedures.**—Preliminary fieldwork was conducted from 5 May–16 June, 1982, followed by two seasons utilizing radiotelemetry. Five Gila monsters captured on the study site were implanted with radio transmitters in May and June 1983, and monitored, usually daily, through September. Transmitters with fresh batteries were reimplanted into two lizards in October; these were monitored periodically through winter and spring, 1984. Daily observations resumed in mid April and continued through mid June 1984.

Gila monsters were located by following trackways in sandy areas. Animals were measured (snout–vent length [SVL], tail length, and tail circumference), placed in cloth bags and weighed (nearest 2 g) with Pesola spring scales. Lizards were toe-clipped for identification, and usually released shortly after capture. Fecal samples were collected from lizards that were retained. Body temperatures were determined with a Shultheis thermometer inserted 5 cm into the gut through the cloaca, and with radio transmitters.

Temperature-sensing radio transmitters were used to monitor lizard locations and to record body temperatures. The radio transmitters (IMP-200-L, Telonics) were hermetically sealed, paraffin-coated units weighing 23 g (6 x 2 cm). They had a battery life of 8–10 mo with a transmission range of 0.3 to 5.8 km, depending upon the terrain. Transmitter pulse rates varied with temperature; they were calibrated in a water bath and were accurate to within ±0.3 C.

Lizards were anesthetized with Ketalar (ketamine HCL) prior to radio implantation surgery. A transverse incision was made through the ventral surface to the right of the midline, 25–30 scale rows anterior to the vent. Transmitters were soaked in isopropyl alcohol then in Ringer's solution before implantation in the peritoneal cavity. Incisions were closed with gut suture and coated with Colotten. Lizards were released at the point of capture within one week after surgery. Transmitters were removed through an incision adjacent to the previous one using similar surgical procedures. Radio-implanted lizards were monitored with a portable receiver (Telonics, TR-1) and hand-held directional antenna.

Foraging paths, sequential relocations and shelters were marked on aerial photos of the study site. Shelters were marked with cairns for future identification. Several temperature samples were taken from each radio-equipped lizard, usually daily; time and behavior of the lizard (active, basking, or inside shelter) were recorded for each temperature sample.

Gila monster trackways in sandy areas were examined daily. Marked individuals left characteristic trackways that could be identified up to several h later. Distances traveled were paced off; date, location, and areas visited by lizards were recorded and marked on maps. Rate of travel was determined by timing Gila monsters; the actual (not straight line) distances traveled were measured and divided by time.

Data on diet were gathered by observing foraging, following trackways and noting nests invaded, and examining feces. Prey remains in feces were identified using a mammal guard hair key (Mayer, 1952) and a reference collection.

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). Means are followed by ±1 SD.

**Results and Discussion**

A total of 27 Gila monsters was captured, marked and measured on the 2.0 km² site (Appendix 1). Most (52%) were large adults, >320 mm SVL. Thirteen lizards (48%) were over 325 mm SVL, a size that Bogert and Martin del Campo (1956) thought *H. suspectum* rarely attains. Only one immature (221–260 mm SVL) and no juveniles (<220 mm SVL) were observed during the study.

Some of the Gila monsters on the study site had been marked and measured between 1975 and 1977 (Coombs, 1977), so data on growth for periods of up to 7 yr were obtained. Growth in body length was relatively slow in adults, averaging 4.8 mm/yr in individuals initially under 300 mm SVL, and 2.1 mm/yr in larger lizards (Table 1). Growth rates of 7–10 mm/yr have been reported for captive adult Gila monsters (Bogert and Martin del Campo, 1956; Tinkham, 1971).

**Food Habits.**—The diet of *H. s. cinctum* in Utah, based on four direct observations and 20 fecal samples, consists of infant cottontails (*Sylvilagus auduboni*, 42% of observations), desert tortoise (*Xerobates agassizi*) eggs (29%), young ground
squirrels (*Ammospermophilus leucurus*, 8%), young rock squirrels (*Spermophilus variegatus*, 8%), mourning dove (*Zenaida macroura*) eggs (8%), and carrion (young *Dipodomys merriami*, 4%). Large quantities can be ingested during a single feeding. A 650 g lizard consumed 210 g of young cottontail rabbits at 1100 h on 27 May, 1983, and another Gila monster (640 g) consumed 4 young rabbits (160 g total) at 1115 h on 12 June, 1983. On 3 June 1982 at 1230 h, a Gila monster excavated and consumed a desert tortoise nest of four eggs. The eggs were broken by the lizard and their contents lapped up along with a considerable quantity of sand.

On each occasion the lizards spent 5-15 min excavating the nests, and all young or eggs inside were consumed. This feeding behavior contrasts with that reported in northwestern Arizona for *H. suspectum*, which consumed an average of only 46% of eggs available at each of 24 Gambel’s quail nests (Jones, 1983).

Prey eaten by Gila monsters in the field were not obviously envenomated. The young cottontails, 35-45 g each, were swallowed without the characteristic chewing motions of envenomation, even when the rabbits were struggling lightly (Fig. 1). Pregill et al. (1986) suggest that venom injection by *Heloderma* is an adaptation for preying on large, bulky vertebrates in periodically cool environments, and that the skull morphology evolved from use of the massive jaws to kill and partially process large, defenseless prey (but see Greene, 1988). My field observations of Gila monsters eating relatively bulky mammalian prey do not support the hypothesis of a feeding role for the venom apparatus. As discussed by Lowe et al. (1986), the venom and delivery system of extant helodermatids most likely serves a primary role in defense.

**Thermal Biology.**—Mean monthly body temperatures of Gila monsters, excluding those during activity, ranged from 28.0 C in July 1983, to 12.3 C in late December 1983 (Fig. 2). When a lizard was inside a shelter, its body temperature typically fluctuated less than 1.0 C over a 24 h period.

Gila monsters spent more than 83% of the year at body temperatures of 25 C or less, and over 50% of the year at or below a body temperature of 20 C (Fig. 2). Body temperatures of lizards resting inside shelters were significantly correlated with surrounding air and soil temperatures ($r^2 = 0.36$, 0.17, 0.58, and 0.36 for air temperature at 1.5 m, and soil temperatures at 5, 25, and 75 cm below the surface, respectively). Winter body temperatures ranged from 11.3-15.2 C. These fall within the range experienced by other hibernating reptiles (1-15 C; Gregory, 1982). Soil temperatures at 75, 25, and

**Fig. 1.** Adult male *Heloderma suspectum cinctum* eating a young 40 g cottontail (*Sylvilagus auduboni*) from a nest in June, 1983. Four rabbits were swallowed alive without envenomation.

**Fig. 2.** Body temperatures of Gila monsters by month while at rest inside shelters and, on the far right of the figure, during surface activity. Dashed line indicates body temperature experienced during fighting, but not in other surface activities. Horizontal lines indicate means, vertical lines indicate ranges, and boxes indicate ±2 SE of the mean. Numbers above indicate sample sizes.
Table 1. Growth of free-living Gila monsters in Utah. Pre-1980 data are from Coombs (1977, and unpubl. data).

<table>
<thead>
<tr>
<th>Lizard number</th>
<th>Initial date</th>
<th>SVL (mm)</th>
<th>Final date</th>
<th>SVL (mm)</th>
<th>Months elapsed</th>
<th>Growth (mm)</th>
<th>Growth rate (mm/yr)</th>
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<tr>
<td>PC8</td>
<td>Jun 1977</td>
<td>295</td>
<td>May 1982</td>
<td>330</td>
<td>35</td>
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<td>PC6</td>
<td>Jun 1975</td>
<td>287</td>
<td>May 1982</td>
<td>331</td>
<td>44</td>
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<td></td>
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<tr>
<td>PC18</td>
<td>Jun 1976</td>
<td>310</td>
<td>May 1983</td>
<td>343</td>
<td>33</td>
<td>4.8</td>
<td></td>
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<tr>
<td>PC3</td>
<td>Jun 1975</td>
<td>290</td>
<td>May 1982</td>
<td>317</td>
<td>27</td>
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<tr>
<td>PC14</td>
<td>Jun 1982</td>
<td>343</td>
<td>Jun 1984</td>
<td>348</td>
<td>5</td>
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<td></td>
</tr>
<tr>
<td>PC4*</td>
<td>Jun 1976</td>
<td>291</td>
<td>May 1980</td>
<td>298</td>
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<td></td>
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<td>3</td>
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<td>339</td>
<td>Jun 1982</td>
<td>345</td>
<td>6</td>
<td>1.0</td>
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<td>355</td>
<td>May 1982</td>
<td>360</td>
<td>5</td>
<td>0.7</td>
<td></td>
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</tbody>
</table>

* Lizard PC4 lost 63% of its tail in 1977, which may have curtailed its growth rate.

5 cm depth were 7.0–15.3 C, 2.0–16.5 C, and −2.5–30.5 C respectively, between December 1983 and March 1984. Air temperatures ranged from −8.5 to 26 C during the same period.

Because Gila monsters are inactive for such long periods, thermal biology during such times may play an important role in their energetics. Helodermatids have unusually low metabolic rates (Beck and Lowe, unpubl. obs.), and the Q10 for metabolic rate between 20 and 25 C is 2.9 for *H. s. cinctum* (Beck, 1986). Reduced metabolic rate at low body temperatures presents a significant energy saving during periods of inactivity and/or reduced body temperature.

Body temperature during activity ranged from 17.4–36.8 C (mean of 29.3 C ±0.51, N = 41; Fig. 2). The lowest activity temperature (17.4 C) occurred during an aggressive interaction at an ambient temperature below 12 C. The lowest body temperature during normal foraging activity was 24.1 C; the activity range for this species is probably closer to 24.1–36.8 C. Activity occurred between 10.0–34.0 C ambient temperature and 20.5–32.0 C substrate temperature. Environmental temperatures correlate less strongly with body temperatures during activity ($r^2 = 0.11$ and 0.22 for ground surface and air temperature, respectively) than with body temperatures while inside shelters. Activity temperatures observed in this study indicate that, in comparison with other lizards (Brattstrom, 1965; Avery, 1982), the Gila monster has a relatively low activity temperature range, especially for a diurnal, desert lizard (Lowe et al., 1986). Other workers have reported similar activity temperatures for *H. suspectum* in Arizona and Utah (Schwartzman and Ohmart, 1976; Coombs, 1977; Porzer, 1981; Lowe et al., 1986).

Occasional basking behavior was observed at shelters from March through early May. A lizard typically exited within the first h after sunlight hit the shelter entrance and pressed the ventral surface against the ground, flattening the body. It entered and exited the shelter several times throughout the morning (Fig. 3). One animal observed for several days in late April and early May 1984 maintained a mean body temperature of 28.5 C (±0.2 C, N = 147) during basking periods, despite considerably lower environmental temperatures (Fig. 3). Basking behavior did not precede foraging or follow feeding, but some interesting intraspecific interactions occurred at this time (see below). With the onset of hotter weather in mid May, basking became much more rare.

Shelters.—All shelters used by Gila monsters were in rocky areas. Of 79 shelters, 59% were in loose Navajo Sandstone and 41% were on basaltic lava slopes or flows. Some animals in these black lava areas show considerable color matching to the darker habitat background (Beck, 1985). Most shelters were natural cavities, at times slightly modified by digging of the resident lizard. Tortoise (*Xerobates agassizii*) shelters and woodrat (*Neotoma lepida*) mounds (8% and 10%, respectively) were also used as shelters. Sixty-seven percent of shelter entrances faced E, SE, or S; the few facing NW or NE (2%) were used only during June and July. Four shelters used for overwintering faced S.

One shelter in a lava flow was excavated in mid September, 1983. The lizard was 1 m below the surface and 2 m from the shelter entrance. Based on soil temperatures and radio-implanted animals, lizards were estimated to be 1.0–1.5 m below the surface in shelters used during the winter (late November through mid March).

Fifteen shelters (19%) were reused, five by more than one lizard and three by two or more concurrently. During May and June 1982, one shelter was used by at least six Gila monsters. This shelter is in an area where considerable activity has been observed since 1975 (Coombs, 1977). Many lizards return to this area in late April and early May. Communal “dens” were not used for overwintering.

Home ranges of two males and one female with sufficient relocation data were 66.2, 32.6,
and 5.6 ha, respectively; their sequential shelter use is shown in Fig. 4.

Activity Patterns and Energetics.—Gila monsters are largely diurnal, not nocturnal as earlier believed (Bogert and Martín del Campo, 1956; Behler and King, 1979; Avery, 1982). Sixty-eight percent of the activity on the Utah study site occurred between 0830 and 1230 h (Fig. 5). In other parts of its range *H. suspectum* is also largely diurnal (Lowe et al., 1986), although nocturnal activity does occur. In southern Arizona *H. suspectum* is predominantly diurnal from March through May, crepuscular from June through September, and diurnal again from October.
through November (Lardner, 1969). Porzer (1981) and Jones (1983) reported crepuscular activity in *H. suspectum* in southern and northwestern Arizona, respectively.

Sixty-four percent of activity on the study site occurred from late April to early July (Fig. 6), and 77% of the total distance traveled by Gila monsters was recorded during that time. Gila monsters near Tucson, Arizona exhibited a similar activity peak during spring and early summer; from 1959–1964, 64% of surface activity (based on time of collection) was observed between mid March and mid June (see Fig. 5 in Lardner, 1969).

Radio-implanted lizards were active on an average of 9 days/mo during the 90-day activity season between mid April and mid July (Fig. 7). The maximum number of days/mo that any
lizard was surface-active was 14, during June 1983. Later that summer (August–September) the same lizard remained at a single shelter for nine consecutive weeks with no detectable above-ground movements.

Above-ground travels of Gila monsters ranged from short trips of a few m around shelter entrances to journeys of more than 1 km (mean = 213 ± 13 m, N = 150; Fig. 8). Rate of travel averaged 0.25 km/h ± 0.03 (N = 10), with a duration of approximately 51 min for an average activity bout. The greatest distances traveled by any lizard during the activity season were: 1190 m between 15–30 April (lizard PC14); 3555 m during May (PC14); 3150 m during June (PC18); and 2000 m between 1–15 July (SC2) (Fig. 9). Summing these distances gives a maximum of 10.6 km traveled during the activity season. This value probably overestimates the

![Figure 5](image_url) **Fig. 5.** Hourly distribution of Gila monster activity observed on the study site for all months combined (a) and by months of the activity season (b).

![Figure 6](image_url) **Fig. 6.** Mean biweekly activity observed on the study site based on trackway and telemetry data from 5 radio-implanted and 13 marked *Heloderma suspectum* during 1982, 1983 and 1984.

![Figure 7](image_url) **Fig. 7.** Number of days radio-implanted Gila monsters were active during months that they were monitored.
actual distance traveled by individual Gila monsters on the study site because it is based on the greatest distances traveled by any radio-equipped lizard during the activity season. I use it as an estimate of surface activity here because some activity may have gone unrecorded (e.g., trips where lizards returned to the same shelter), since lizards were not monitored 24 h/day. Given that 10.6 km represents 64% of annual surface activity, my estimate for the yearly distance traveled by a Gila monster on the study site is 10.6 km/0.64, or 16.6 km/yr. Assuming an average speed of 0.25 km/h, the estimated time spent in surface travel is 66.4 h/yr.

I observed Gila monsters digging in their shelters on a few occasions, and digging into reptile and mammal nests while foraging. One animal dug inside its shelter for a total of 7 h during late April and early May, 1984. The contribution of digging to the activity budget of the Gila monster is probably significant, but was not quantified in this study.

*Heloderma suspectum* specializes on the young and eggs in vertebrate nests, prey that are widely distributed in space. This requires search of a relatively large area, a foraging mode usually described as “widely searching” (Huey and Pianka, 1981). Studies on other lizards have shown that widely-foraging species have higher activity costs than do “sit and wait” predators, which typically wait for mobile prey to come within appropriate striking distance before initiating ambush and pursuit (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Lizards in this study occasionally traveled long distances, up to 1 km, while searching for prey (nests). Energy demands increased to

1.5–3 times over resting levels (Beck, 1986). Such energy expenditures match those reported in other widely searching lizards during their activity periods (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Activity was infrequent however, and large meals were eaten.

During the activity season, Gila monsters spend more than 97% of the time in shelters, and allocate less than 13% of their maintenance energy budget to surface activity (Beck, 1986). The energetic costs of searching for food are more than offset by long periods spent inactive. Thus, in terms of total time and energy allocated to activity during its activity season, the Gila monster ranks below “sit and wait” lizards, which allocate 25–35% of maintenance energy (respiration) to activity (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Reptiles that search their environment for each prey item can have low activity costs if activity bouts are infrequent and large meals are eaten. The assumption that a “widely searching” foraging mode requires a high energetic investment in activity is valid for smaller species that
Fig. 10. Behavioral sequences during combat as described in text: (A) Dorsal Straddle; (B) Lateral Head Shove while other lizard responds with Neck Arch; (C) Head Raise; (D) Circling.
are active on a daily basis, but not for *Heloderma suspectum*.

Food storage is directly proportional to mass (M^{0.9}; Calder, 1984), and in squamate reptiles metabolic rate (MR) is proportional to M^{0.80} (Andrews and Pough, 1985). The amount of time an animal can subsist between meals is proportional to storage/MR or M^{0.20}. Larger animals can thus subsist longer between meals. The relative large body size, low resting metabolic rate, and ability to take large meals make frequent foraging activity unnecessary for Gila monsters, and greatly reduces their activity costs. These traits contribute to the ability to exploit a food resource, the contents of vertebrate nests, upon which few other reptiles specialize. Three large meals, comparable in size to some taken by lizards in this study, can supply the yearly main-
tenance energy demands of an adult male Gila monster (Beck, 1986). Knowledge of the activity and energetics of additional large-bodied, less active species may help to refine current ideas of lizard energetics that have been formulated largely from smaller species that are active daily during their activity seasons.

**Intraspecific Interactions.** — From late April through late May some shelters were shared by as many as six Gila monsters concurrently in a rocky area at the north end of the study site. This area is not a “den” site where the reptiles congregate in the fall, overwinter, and emerge in the spring; rather, while some lizards may overwinter in this area, others return after overwintering about 1 km away. One large radio-equipped male, PC14, returned to this area in April 1984 after emerging from its winter shelter at the south end of the canyon, fought with another male, and then may have mated. The lizard’s sequential movements and shelter locations are described below (see also Fig. 4, shelters #20–34, and Appendix 2). This lizard had foraged successfully shortly after spring emergence; his late-fall body mass of 720 g (6 Nov., 1983) had increased to 880 g after defecating 40 g of *Sutulinus auduboni* remains on 17 April 1984. On 20 April, PC14 traveled more than 1 km to the NW (21, Fig. 4), into a shelter previously used by female PC20 in June, 1983. By 26 April, PC14 had moved another 450 m onto a S-facing lava slope at the N end of the study site and into a shelter (23, Fig. 4) used 1 June, 1983 by PC18, another large male (shelter #6, Fig. 4). He spent most of the morning and early afternoon in the shelter, emerging periodically to bask (Fig. 3). By 1516 h his body temperature had increased to 33.6 C and he fought with an unmarked male, PC25, at the shelter entrance. Selected photographs of the fight, which lasted nearly 3 h, comprise Figs. 10 and 11.

Nine of the ten major behavioral acts recorded in a combat interaction between two captive male *Heloderma suspectum* by Demeter (1986) were exhibited by these two lizards, as follows: Dorsal Straddle (Fig. 10A); Frontal Head Nudge (Fig. 10B, C); Lateral Head Shove (Fig. 10B); Neck Arch (Fig. 10C); Tail Wrap (Fig. 10A); Lateral Head Bite; Lateral Tail Thrash; Dorsal Head Pin; and Roll.

Seven additional major behavioral acts were identified in these Gila monsters, as follows. Head Raise: raising of head and stiffening of front limbs by inferior lizard following a Neck Arch; done in response to head nudge and shove by the other lizard (Fig. 10C). Circling: moving in a semi-circular path around another lizard (Fig. 10D). Body Twist: while in Dorsal Straddle, twisting of body by the inferior lizard and placing the gular region against the neck of the superior lizard so that the bodies are entwined. The superior lizard responded with a Neck Arch (Fig. 11A). Lateral Rocking: rocking motion from side to side while in Dorsal Straddle, often resulting in a Roll. Initiated by the inferior lizard; apparently serves to remove superior lizard by forcing separation. Dorsal Body Press: turning and pressing the dorsal body surface of the superior lizard against the dorsum of the inferior lizard.Performed under boulders where the superior lizard pressed the inferior lizard downward by pushing against a boulder with the forelimbs. High Stand: standing side by side, each lizard performing head raise. Scoop: pressing the snout under another lizard, scooping it upward.

Thirteen individual “bouts” were observed. A bout refers (as in Demeter, 1986) to a repeated series of movements by the combatants between initial physical contact and separation. A typical bout lasted 10 min (range = 4–15 min) and each consisted of three distinct sequences. (1) Upon approach, lizards performed Head Nudge, Shove, Neck Arch, and Head Raise, often switching roles. (2) The aggressor mounted the other lizard in a Dorsal Straddle. The lizards repeatedly performed Tail Wrap, unwrapping tails at intervals. The inferior lizard typically responded to a Dorsal Straddle with a Neck Arch, while the superior lizard performed a Dorsal Head Pin. The superior lizard also performed a Tail Thrash in a few bouts. Sequence 2 lasted the longest of the three, and considerable struggling ensued. The inferior lizard often walked with the superior lizard clinging to his dorsum. Lateral Rocking could separate the lizards but, if not separated, they usually proceeded into a Body Twist. (3) The inferior lizard initiated a Body Twist, and the two lizards remained in that position until one gained the superior position in a Dorsal Straddle or they broke apart, sometimes from the force exerted during twisting (Fig. 11A–D). Circling sometimes preceded sequence 1 above.

The objective during each bout was apparently to gain and maintain a superior position in the Dorsal Straddle. The inferiorly-positioned lizard initiated a Lateral Roll or Body Twist apparently in an effort to break the Dorsal Straddle and gain the top position. In one bout, however, the superior lizard initiated a change of positions that immediately resulted in separation.

After 2.5 h the lizards separated and PC25 moved upslope under a lava boulder. PC14 followed and crawled around several boulders adjacent to PC25. After 15 min PC14 crawled upslope and back into the shelter he had used earlier in the day. PC25 followed PC14 into the same shelter 3 min later, at 1824 h. Later that
evening PC25 left the shelter. He was next seen above ground at 1019 h the following morning, moving upslope 3 m southeast from PC14’s shelter. PC25 continued upslope and was not seen again on the lava slope.

PC14 remained at the shelter throughout the following day (27 April). He emerged periodically to bask at the shelter entrance (see Fig. 3) and made one 20 min round trip downslope at 1320 h. On 28 April at 1225 h, PC14 was rubbing his cloacal area on several lava boulders and grasses approximately 5 m W of his shelter. Later in the day he moved into a new shelter (24, Fig. 4), 20 m downslope to the SW.

On 29 April, PC14 spent most of the morning basking intermittently at his shelter entrance (Fig. 3). At 1525 h another Gila monster (PC26, sex unconfirmed) crawled into the shelter with PC14. Initially considerable hissing ensued, then the two lizards positioned themselves side by side facing the shelter entrance. They remained in the shelter together the rest of the evening, at least 6.5 h, separating periodically as PC14 dug vigorously inside the shelter. PC26 left the shelter sometime after 2200 h and was not seen again. The following morning PC14 was still in the shelter. On 1 May he weighed 732 g, having lost 150 g since 17 April. He remained at the shelter until 2 May, and on the lava slope through 14 May. By 28 May PC14 had returned to the S end of the canyon (34, Fig. 4).

Male-male fights in Heloderma suspectum have been previously observed in captivity (Gates, 1956; Demeter, 1986; Lowe, pers. comm.) and in the field (Lowe et al., 1986), although detailed accounts of combat sequences have not been published for free-ranging animals. Gates (1956) observed two captive Gila monsters “fighting over a female, the third occupant of the cage” in June, 1955. He removed one of the fighting lizards and later observed copulation in the two remaining cagemates. Combat behavior reported by Demeter (1986) in captive H. suspectum was strikingly similar to the fight between freeranging PC14 and PC25. A typical sequence in the captive lizards began with (1) Head Nudging and Shoving and Neck Arching, followed by (2) a Dorsal Straddle with an occasional Lateral Head Bite and Tail Thrash, and (3) a Roll that resulted in the animals disengaging and beginning a new sequence (Demeter, 1986). A major difference in the combat reported here was the Body Twist, which typically followed the Dorsal Straddle.

Validation of behaviors exhibited by captive reptiles from actual field observations is rare, and in this case serves to illustrate the stereotyped nature of fighting in male H. suspectum. Lowe et al. (1986) observed similar, stylized postures in the field, noting that fights can sometimes erupt into “vicious brawls,” although such behavior is more common in captive individuals that do not have the same options for retreat as do free-ranging animals.

Elements of the combat ritual of H. suspectum resemble grappling postures of varanid combat (Carpenter et al., 1976; Davis et al., 1986), and arching and entwining postures of crotaleine snake combat (Shaw, 1948; Lowe et al., 1986; Gillingham, 1987), but differ strikingly from aggressive behaviors (displays of posturing and head bobs, chases) observed in other lizard families (Carpenter and Ferguson, 1977; Demeter, 1986).

Combat interactions in squamate reptiles are usually interpreted to be tests of dominance. The “winner” is able to display superior physical strength, usually by forcing the subordinate to the ground until the subordinate initiates an escape response (Auffenberg, 1981; Gillingham, 1987). The winner is usually the larger animal. The resident may also have an advantage, although it can be supplanted by a larger intruder (Gillingham, 1987). The radio-implanted Gila monster (PC14) had been on the lava slope the previous year, and for three days before the fight with PC25. It was most likely the resident. Although they were fairly close in size (PC25’s exact size was not recorded) PC14 (SVL 343 mm, TL 498 mm) appeared slightly larger. Carpenter et al. (1976) interpreted the winner of bouts in Varanus gilleni as the male in the superior position at the end of each bout sequence. Using this criterion, PC14 won 8 bouts and PC25 won 5. On two occasions during the fight, PC25 retreated and PC14 pursued, although PC25 was still willing to partake in another bout as PC14 approached. It is not possible to know with certainty which, if either, was the winner of the combat. Because he was the resident, and the perceived “winner” of the majority of the bouts, PC14 most likely “won” the fight. Moreover, PC14 remained near the shelter for several days after PC25 had left the immediate area.

The cloacal rubbing behavior of PC14 near its early May shelters on the lava slope is noteworthy. It is likely a form of chemical communication used by H. suspectum, possibly to aid in establishment of the social hierarchy in communal areas. Varanus komodoensis may communicate using scent signals associated with fecal material deposited near thermoregulatory sites and along trails (Auffenberg, 1981).

The interaction between PC14 and PC26, the Gila monster that entered PC14’s shelter 3 days after the fight, is difficult to interpret fully. Only the snouts of the lizards were visible at the shelter entrance. While PC14 was not digging, they lay side by side with little movement. Their
interaction was considerably less aggressive than was the combat between PC14 and PC25. No biting or struggling was observed. PC14 and PC26 may have mated in the shelter. They were oriented in a position similar to a typical Heloderma mating posture (Gates, 1956). This interpretation is consistent with the hypothesis that male squamate reptiles fight in order to gain access to females. Copulation after combat has been commonly observed in captive reptiles (Gates, 1956; Carpenter and Ferguson, 1977).

These behavioral observations confirm that Gila monsters have a definite social system. These seemingly solitary lizards are not roaming aimlessly when searching for potential mates or foraging sites. Common shelter use and seasonal movements that bring individuals back to communal areas, establishment of dominance through male-male combat, and scent marking are all elements of a structured social system.

During combat, lizards appeared to approach the limits of their physical endurance, especially during the Dorsal Straddle, Tail Thrash and Body Twist. Their struggles during the three-hour fight left them nearly 20 m from their starting point. Ambient temperature was low (10 C) during most of the fight; by the time they had completed the struggle, both lizards were slow in righting themselves, and PC14's body temperature had dropped from 33.6 to 17.3 C. At 1630 h, light was falling.

The Varanoidea (Helodermatidae and Varanidae, Pruell et al., 1986) are unique among lizards in their high capacities for sustained aerobic activity (Bennett, 1983; John-Alder et al., 1983). At 25 C, Heloderma suspectum can sustain aerobic activity at a higher oxygen consumption rate than any other lizard measured (John-Alder et al., 1983). It has been suggested that aerobic endurance should be best developed in active lizards that search for widely distributed prey (Pough, 1983). Although the Varanoidea fit this description (Bennett, 1983), the Teiidae, which includes highly active, widely foraging predators, have aerobic capacities more typical of less active iguanids (Bennett, 1983; but see Garland, 1988).

The high aerobic capacities of helodermatids probably have little to do with locomotor efficiency and foraging. In the laboratory they are able to sustain a maximum aerobic speed of 0.7–1.0 km/h within their preferred temperature range (John-Alder et al., 1983), but typically forage at one third that pace. Heloderma does not rely on speed as a predator escape response; unlike most lizards, it is incapable of high-speed sprints. Secretive habits, cryptic coloration, and venom are its defenses against predators (Lowe et al., 1986; Greene, 1988).

The high endurance capacity of H. suspectum may be a pleisiomorphy from its ancestral varanoid stock, and may play a minor role in the ecology of this species today, but there are some interesting implications when viewed in the context of the intensive male-male combat rituals. Helodermatids and varanids are unique among lizards in having combat interactions that involve intensive grappling postures that potentially test the limits of physical endurance (Murphy and Mitchell, 1974; Carpenter, et al., 1976; Davis et al., 1986; Demeter, 1986; Lowe et al., 1986). In anurans, winners of male-male fights, which often take the form of intensive "wrestling matches," enjoy higher reproductive success (Wells, 1977, 1979; Pough, 1983). Those with greater endurance may thus have higher reproductive success. If male reproductive success in helodermatids and varanids is related to success in combat, selection for physical endurance during intraspecific combat may have played a role in the evolution of high aerobic capacities in lizards.

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Literature Cited


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APPENDIX 1

Body masses and lengths of Heloderma suspectum circumcinctum captured on the study site. Data provided are: lizard no., mass (g), SVL, and TL (mm). PC23, 145, 233, 348; SC1, 273, 290, 424; SC3, 451, 291, 431; PC22, 346, 300, 436; PC4, 338, 291, 446; PC21A, 265, 293, 447; PC13, 450, 306, 453; PC16B, 352, 310, 459; PC17, 350, 309, 460; PC6, 512, 331, 465; PC1, 314, 466; PC21B, 345, 328, 468; PC3, 462, 317, 472; PC16A, 480, 324, 476; PC19, 336, 477; PC11, 310, 478; PC9, 672, 345, 482; PC5, 320, 485; PC2, 326, 487; PC8, 535, 330, 493; SC2, 688, 339, 494; PC14, 880, 343, 498; SC5, 575, 342, 502; PC10, 610, 338, 508; PC18, 790, 343, 508; SC4, 469, 348, 513; PC20, 532, 360, 529. Mean values: mass, 479 g; SVL, 320 mm; and TL, 471 mm.

APPENDIX 2

Dates of sequential shelter use (day/month/yr) by Gila monsters as shown in Fig. 4. Numbers preceding dates below correspond to numbers next to shelters in Fig. 4.

