

Seasonal Patterns of Body Condition, Hydration State, and Activity of Gila Monsters (*Heloderma suspectum*) at a Sonoran Desert Site

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ABSTRACT.—Animals in nature use synergistic behavioral and physiological responses to cope with variation in resource availability. We used a combination of traditional tools (i.e., radiotelemetry, body-condition measurements, plasma osmometry, and direct observation) and contemporary techniques (i.e., implanted temperature loggers and portable ultrasonography) to identify seasonal patterns of body condition, hydration state, and surface activity of 16 free-living Gila Monsters during two active seasons. Despite seasonal drought each year, Gila Monster snout-vent length increased during the study; yet body mass, tail volume, and hydration state decreased. Generally, surface activity was associated with rainy periods, and males were significantly more active than females but only during the reproductive season. Our results indicate that Gila Monsters combine flexible behavioral patterns (i.e., the timing and duration of surface activity), resource storage and economical use, and tolerance of substantial physiological disturbance to endure seasonal resource limitations at a site in the Arizona-Upland subdivision of the Sonoran Desert.

Success of animals in hot deserts in part relies on elegantly integrated behavioral and physiological responses to maintain homeostasis despite limited and highly seasonal water and food availability. Reptiles are considered especially well suited for life in deserts because of low metabolic demands and low evaporative water loss (EWL) rates (Pough, 1980; Huey, 1982; Avery, 1982; Bradshaw, 1997). Although we have identified these and other behavioral and physiological processes used by reptiles to survive, our understanding of long-term integrated responses to resource variation in nature is still lacking. The Desert Tortoise (*Gopherus agassizii*) provides a rare example of such an integrated understanding because it has received considerable attention from biologists for decades because of its conservation status (Nagy and Medica, 1986; Peterson, 1996a,b; Tracy et al., 2006). The Desert Tortoise uses a survival approach that relies on low water and energy demands (Nagy and Medica, 1986; Henen et al., 1998), long-term water and energy storage (Peterson, 1996b), careful microclimate selection including extensive refuge use (Bulova, 2002), and tolerance of significant perturbations to water and energy balance caused by drought (Peterson, 1996a). Other reptiles demonstrate characteristics required for a similar

survival strategy in resource-limited environments, yet the collective behavioral and physiological responses used in nature are known for few species.

The Gila Monster (*Heloderma suspectum*) is a large (adult body mass = 350–700 g and snout-vent length; SVL = 260–360 mm), long-lived (>20 yr), and venomous lizard (Bogert and Martin del Campo, 1956; Beck, 2005) that provides an ideal model for long-term integrative behavioral and physiological studies. Gila Monsters experience limited and seasonal water and food availability because the species is geographically distributed predominantly in the Sonoran Desert of Arizona and Mexico, with populations on the fringe of the distribution extending slightly into adjacent deserts (extreme eastern Mojave Desert and western Chihuahuan Desert) (Beck, 2005). Although most published field studies on the species have been conducted outside the core (i.e., Sonoran Desert) distribution (e.g., Washington County, Utah: Beck, 1990; Grant County, New Mexico: Beck and Jennings, 2003; Clark County, Nevada: Gienger and Tracy, 2003), several characteristics of the species have been established. Gila Monsters use shelters extensively (Arizona: Lowe et al., 1986; Utah: Beck, 1990; New Mexico: Beck and Jennings, 2003; current Arizona site: Gallardo, 2003), store energy caudally (Bogert and Martin del Campo, 1956; Beck, 2005), and have relatively low preferred and activity body temperatures (28–29°C) compared to other desert lizards (Utah: Beck, 1990; New Mexico: 2005). Laboratory studies have also identified a suite of intrinsic characteristics

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that include a high aerobic capacity (John-Alder et al., 1983; Beck et al., 1995), a resting metabolic rate lower than predicted for its size (Beck and Lowe, 1994), the use of cloacal evaporative water loss to reduce body temperature when above 35°C (DeNardo et al., 2004), and the ability to use the urinary bladder as a reservoir from which water can be reabsorbed into circulation (Davis and DeNardo, 2007). Despite a relatively thorough understanding of specific behaviors and physiological capabilities of Gila Monsters, the synergistic benefits of these responses under natural conditions have not been studied.

We studied the behavior and physiology of a Gila Monster population in the Sonoran Desert of Arizona for two active seasons (March through September, when weekly surface activity is >5% of the time, unpubl. data). We combined traditional tools used in physiological ecology (e.g., radiotelemetry, body-condition measurements, plasma osmometry, and direct observation) with contemporary techniques (e.g., implanted automated body temperature loggers and portable ultrasonography) to identify seasonal patterns of surface activity and refuge use, body temperature (T_b), body condition, and hydration state of 16 Gila Monsters in nature.

MATERIALS AND METHODS

Study Site and Weather Conditions.—The study site is an undeveloped 3-km² area located in the Arizona Upland subdivision of the Sonoran Desert in Pinal County, Arizona (32°36'09N, 111°07'48W, 800–1,100-m elevation). Several isolated rocky buttes and hills of Precambrian granite and schist extend south-to-north along the eastern edge of the site and sandy bajada, intersected by intermittent washes, extends from the hillsides to the north and west. The vegetation is a dense heterogeneous matrix of tree-form legumes (*Prosopis grandulosa*, *Olneya tesota*, and *Parkinsonia* spp.), cacti (*Cereus giganteus*, *Opuntia* spp., *Ferrocactus cylindraceus*, and *Mammillaria* spp.), and shrubs (*Ambrosia dumosa*, *Acacia greggii*, *Larrea tridentata*, *Celtis pallida*, and *Calliandra eriophylla*). Mammal burrows are abundant, distributed across the site, and provide important subterranean refugia for Gila Monsters (Beck and Jennings, 2003; Gallardo, 2003).

To monitor weather, we recorded rainfall (≥ 2 mm) continuously using an automated rainfall gauge (model RG3-M, Onset Computer, Bourne, MA) and air temperature (T_{air} ; $\pm 0.2^\circ\text{C}$) hourly using an automated temperature logger (Stow-Away Tidbit, Onset Computer, Bourne, MA). Weather data were recorded at a central

location, and we reduced direct solar irradiation of the temperature logger by shading the logger in an open-ended PVC tube and suspending it from a tree branch 1 m above the ground.

We calculated total weekly precipitation, total active-season precipitation (mid-March to September), total monsoon precipitation (mid-July through mid-September), and proportion of precipitation attributable to the monsoon each year. We used hourly T_{air} to calculate weekly mean maximum and minimum T_{air} (= mean of daily T_{air} maxima and minima for each week).

Radiotelemetry.—Between March and May 2003, we collected 16 (10M : 6F) adult Gila Monsters from the field site, transported them to the laboratory at Arizona State University (ASU), and intracoelomically implanted each with an approximately 24-month radiotransmitter (13 g model SI-2, Holohil Systems, Ltd., Carp, Ontario, CA) and a miniature temperature logger (Thermochron iButton, model DS1921G, Maxim Corp., Dallas, TX) using methods similar to those used previously in the lab for rattlesnakes (Taylor et al., 2004). After surgery, but prior to recovery from anesthesia, we collected body-condition measures (see below) and then returned lizards to their site of capture within 48 h of surgery.

We used radiotelemetry to locate Gila Monsters approximately weekly during two active seasons (1 April to 1 September 2003 and 2004). During both years, we substantially increased radiotelemetry efforts during a 7–10-day sampling period at the beginning of each month from May through August to increase the likelihood of locating all individuals on the surface for body-condition measurements (see below). We did not collect measurements in early April because lizards emerged from overwinter quiescence in March and often remained at or near their overwinter locations for several weeks (unpubl. data), and we chose not to disturb the animals during these sensitive locations.

Gila Monsters have very limited activity during the hot and dry months (Porzer, 1981; Beck, 1990, 2005); therefore, we were unable to locate animals on the surface during June 2003 and 2004. We were also unable to collect measurements from some individuals during other collection periods (see below).

Growth Rate, Body Condition, and Hydration State.—We collected these data primarily in the field during 7–10-day sampling periods at the beginning of each month when Gila Monsters located using radiotelemetry were on the surface. Additionally, we collected some data in the laboratory at ASU during four sampling periods: upon first capture (April to May 2003); at the beginning of the 2004 active season; and

at the end of each active season (September 2003 and 2004). We used these lab sampling periods to obtain SVL and mass data that were more precise than what could be collected in the field. During lab sampling, we used a cloth measuring tape to measure SVL (± 1 mm) while lizards were anesthetized and an electronic scale to measure body mass (± 0.1 g; Acculab GS-2001, Edgewood, NY). In the field, we measured body mass (± 10 g) using a 1,000-g capacity spring scale (Pesola, Switzerland). Because body mass can vary drastically (15–35%) in Gila Monsters following a meal (Beck, 1990), drinking bout (Davis and DeNardo, 2007), or defecation, we modified our processing protocol in 2004 to also measure tail volume (± 1 mL). We did this by submerging the tail up to the cloaca into a water-filled graduated cylinder and then measuring water displacement by determining the amount of water needed to refill the cylinder after having the tail removed from it. Because Gila Monsters store energy reserves caudally (Bogert and Martin del Campo, 1956; Beck, 2005) and this reserve is not influenced by fecal elimination or water intake (Davis and DeNardo, 2007), tail volume measurements serve as an effective index of energy storage.

In addition to energy balance, water balance is also important to Gila Monsters (DeNardo et al., 2004; Davis and DeNardo, 2007). Thus, we assessed two aspects of the lizards' hydric condition in 2004. First, we used plasma osmolality (milliosmolar/kg; mOsm/kg) as an indicator of individuals' hydration states. We measured this by collecting 0.2 mL of blood from the caudal vein of each lizard using a heparinized 1-mL syringe and storing samples in 1-mL screw-top vials in a cooler until transported back to the laboratory. In the lab, we separated plasma from whole blood using centrifugation and froze samples at -80°C until analyzed in triplicate using a vapor pressure osmometer (± 6 mOsm/kg; model 5500xr; Wescor, Inc., Logan, UT) and procedures previously described (Davis and DeNardo, 2007). Second, we used portable ultrasonography (Concept/MLV; Dynamic Imaging, Ltd., Livingston, Scotland) to image the urinary bladder to determine when stored water was available to lizards, and we calculated the proportion of lizards that had water available in the bladder each month. We chose a binary scale (fluid detectable in the bladder or not) rather than a continuous scale (i.e., mL of bladder fluid) because we did not measure the bladder in three-dimensions and, thus, were unable to estimate bladder volume. Ultrasonography was also used to determine reproductive condition of female Gila Monsters and the presence of follicles (evident in three females

in May 2004) or eggs (enlarged and shelled in the same three females in June 2004, through oviposition in mid-July). Determination of reproductive state was important because it can affect body condition, activity levels, and temperature selection in lizards (Pianka and Vitt, 2003), all of which could confound results of this study.

We subjected body-condition data to tests of normality and equal variances prior to inference, and statistical analyses were completed using JMP IN (V. 5.1, SAS Institute, Inc., Cary, NC) and HLM (V. 6, SSI, Inc., Lincolnwood, IL). Values in figures are mean ± 1 SE and $\alpha = 0.05$ unless corrected as indicated for multiple comparisons. We used Student's *t*-test to compare initial SVL of female to male Gila Monsters. To avoid statistical biases associated with analyses of growth rate relative to initial body size (Packard and Boardman, 1999), we determined whether total growth differed between the sexes using analysis of covariance (ANCOVA) with initial SVL as the covariate, sex as the between subjects factor, and total growth (mm) during the study as the response variable.

Gila Monsters were inaccessible during some sampling periods; thus, we were unable to measure body mass 13 of 80 times in 2003 and body mass, tail volume, bladder content, and osmolality one of 64 times in 2004. To overcome missing data, we used the MIXED procedure to perform RMANOVA on body mass, tail volume, and plasma osmolality (Littell et al., 1996). We used sex as the between-subjects factor, date as the within-subjects factor, and body mass, tail volume, and plasma osmolality as the repeated measures. Mauchly's Criterion for Sphericity was violated for all analyses; therefore we applied Greenhouse-Geisser corrections prior to interpretation (Zar, 1999). Tukey-Kramer tests (adjusted for experiment-wise Type I error rate; $\alpha = 0.05/N$; $N =$ number of monthly comparisons; 2003 = 5 and 2004 = 4) were used post hoc to identify significant differences between sampling periods. We also compared stored water availability by calculating the proportion of Gila Monsters that had urine in the bladder each sampling period.

Body Temperatures and Surface-Activity Estimates.—During 2003, we recorded T_b and estimated surface-activity patterns of each Gila Monster using surgically implanted miniature temperature loggers. These temperature loggers are small (< 3 g), accurate ($\pm 0.5^{\circ}\text{C}$), and can store 2,048 temperature records at user-selected intervals (Angilletta and Krochmal, 2003). Moreover, these temperature loggers collect data at regular intervals, which reduces temporal, spatial, and financial constraints often associated with traditional T_b and activity data

assessments (Taylor et al., 2004). Prior to implantation, we programmed 10 temperature loggers to collect T_b hourly (1 April to 23 June), which enabled temperature data collection from some animals during the mating season (April to May). We programmed the remaining six temperature loggers to collect T_b every 2 h (23 April to 31 August) to obtain less frequent data from some animals through the dry summer (late May to July) and monsoon season (mid-July to mid-September). We surgically retrieved temperature loggers at the end of the study (31 August to 4 September 2004) and returned animals to their site of collection within 48 h.

We used temperature-based activity estimation (TBAE), which relies on a simple comparison of temporally synchronized T_{air} and T_b data, to estimate individual surface-activity and refuge-use patterns in 2003. TBAE correctly predicts Gila Monster location (surface active or in a refuge) >95% of the time (Davis et al., 2008). Using TBAE, we calculated the proportion of hours that individual lizards were surface active (number of hours on surface/total available hours) each week and determined the timing of activity (i.e., diurnal, crepuscular, nocturnal). Because T_b , and thus TBAE, was not collected from all individuals for the same duration of time, we used a series of separate RMANOVA models to analyze surface-activity patterns of males and females during three active-season sampling periods: (1) postemergence and early mating season, 1 April to 30 April, $N = 10$; (2) dry summer and late mating season, 1 May to 22 June, $N = 16$; and (3) dry summer to monsoon season, 23 June to 31 August, $N = 6$. For analyses, sex was the between-subjects factor, time was the within-subjects factor, and surface activity was the dependent variable. Mauchly's Criterion for Sphericity was violated for the 22 June to 31 August activity analysis; therefore we applied a Greenhouse-Geisser correction prior to interpretation (Zar, 1999). We used Tukey-Kramer tests (adjusted for experiment-wise Type I error rate; $\alpha = 0.05/N$; $N =$ number of statistical

comparisons) post hoc to identify significant differences in surface activity during each sampling period.

RESULTS

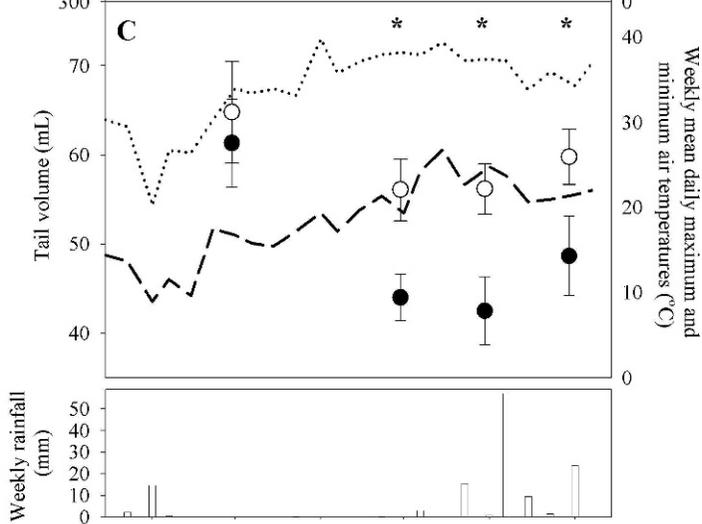
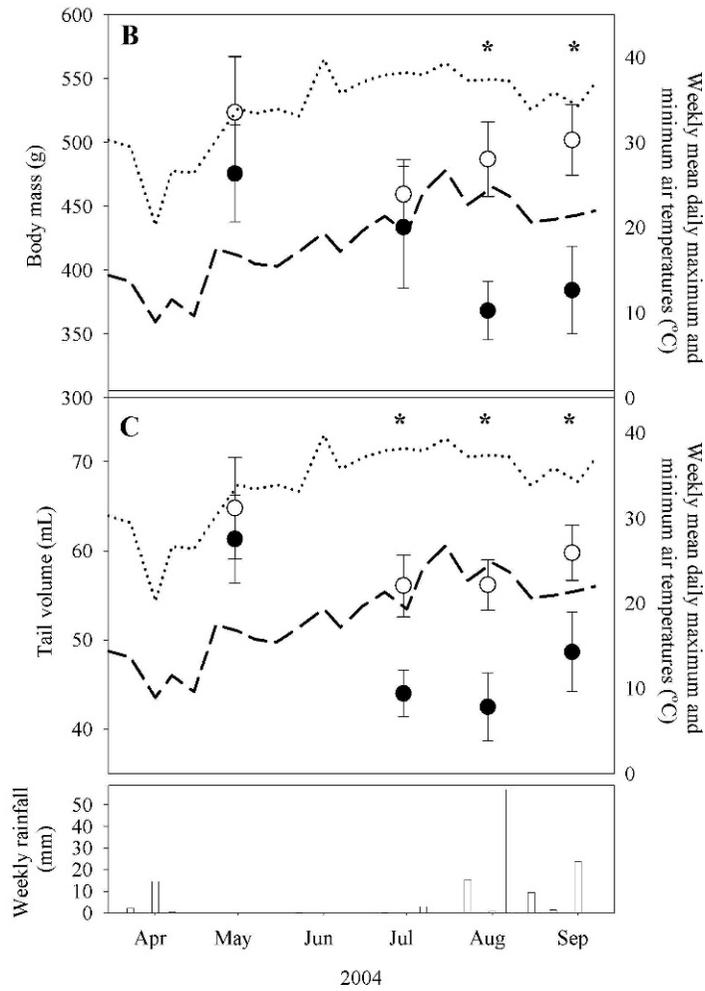
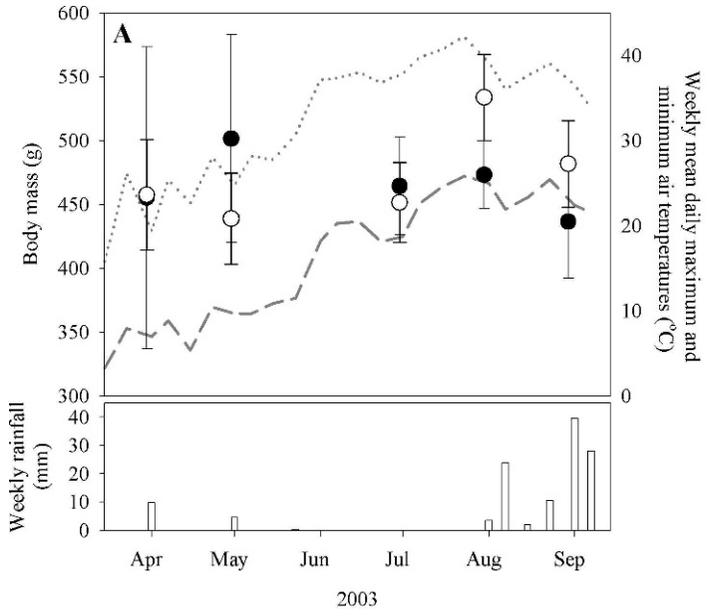
Weather Conditions.—Climate is dramatically seasonal during the Gila Monster active season, particularly with regard to rainfall. Air temperatures are relatively cool (weekly mean maximum and minimum $T_{air} = 15\text{--}30^\circ\text{C}$ and $5\text{--}18^\circ\text{C}$, respectively) in spring (15 March to 30 April) but then increase substantially (weekly mean maximum and minimum $T_{air} = 28\text{--}40^\circ\text{C}$ and $10\text{--}25^\circ\text{C}$, respectively) and remain stable and elevated throughout the bulk of the active season (01 June to 15 September) (Fig. 1). Both 2003 and 2004 produced substantially below average rainfall from April to September throughout this region of the state (255.1 mm; based on the 30-year rainfall average for April through September in Tucson, Arizona, 50 km south of our site; NOAA, 2009). Specifically, at our field site from April through September, precipitation was 123.8 mm and 129.2 mm for 2003 and 2004, respectively. Rainfall was also bimodally distributed. Light spring rains were followed by severe drought (number of weeks total rainfall <5 mm) that lasted 14 and 16 weeks (7 April to late-July) in 2003 and 2004, respectively. Drought was relieved by summer monsoon rains, which in 2003 and 2004, produced 87 and 84%, respectively, of the total active-season rainfall in just seven weeks (Fig. 1).

Growth Rate, Body Condition, and Hydration State.—Growth was significantly correlated with initial SVL ($R^2 = 0.81$; $F_{2,13} = 55.1$; $P < 0.0001$) (Fig. 2). Initial SVL did not differ between the sexes (301.5 ± 13.1 mm and 298.9 ± 5.7 mm for females and males, respectively, $t = -0.18$; $P = 0.86$) and neither did total growth ($F_{2,13} = 0.35$; $P < 0.56$).

Body mass of Gila Monsters remained relatively stable in 2003, that is, the RMANOVA model failed to detect a significant effect of sex or date or a sex by date interaction (Fig. 1A; all

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FIG. 1. Seasonal variation in body condition of female (●, $N = 6$) and male (○, $N = 10$) Gila Monsters (*Heloderma suspectum*) during two active-seasons at our Sonoran Desert site. In 2003 (A), body mass (g) of both sexes remained stable. In 2004, body mass (B) and tail volume (C) decreased during drought, but males maintained body mass ($P < 0.001$) and tail volume ($P = 0.047$) significantly better than females. Values shown are mean ± 1 SE, and * indicates significant differences ($P < 0.05/N$) between sexes at each time point. Weather conditions recorded at our Sonoran Desert field site during the 2003 (A) and 2004 (B, C) active seasons. Dotted lines denote weekly mean daily air temperature maxima ($^\circ\text{C}$), dashed lines indicate weekly mean daily air temperature minima ($^\circ\text{C}$), and vertical bars below primary figures indicate weekly rainfall (mm). We do not show individual data points for clarity. Note extensive drought (mid-May through mid-July) and subsequent monsoon rains (mid-July through September) each year. Weather data are also plotted in Figures 3 and 4 to illustrate the relationship between weather and hydration state and activity patterns.



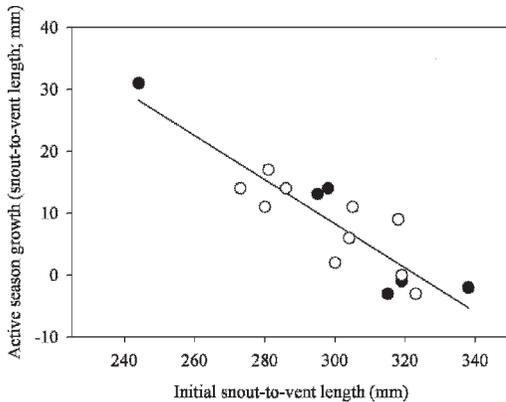


FIG. 2. Initial SVL was strongly correlated with total growth of female (●, $N = 6$) and male (○, $N = 10$) Gila Monsters (*Heloderma suspectum*).

$P > 0.60$). In 2004, female and male body mass generally decreased between May and July; then body mass diverged with females continuing to decline and males slightly increasing after the onset of the monsoon rains (Fig. 1B). Accordingly, the RMANOVA model detected significant effects of date ($F_{3,12} = 4.23$; $P = 0.03$) as well as a significant sex by date interaction ($F_{3,12} = 30.86$; $P < 0.001$), but sex did not have a significant effect ($F_{3,12} = 3.12$; $P = 0.098$). Females and males began with similar caudal energy stores, but tail volume decreased in both sexes by July (females significantly more than males) and remained stable thereafter (Fig. 1C). Tail volume changed over time ($F_{1,14} = 30.51$; $P < 0.001$) and was affected by sex ($F_{1,14} = 2.87$; $P = 0.047$); however the sex by date interaction was not significant ($F_{1,14} = 5.02$; $P = 0.17$) (Fig. 1C).

Hydration states of Gila Monsters were highly seasonal. Gila Monsters stored fluid in the urinary bladder following rain, yet no females and only one of 10 males retained fluid in the urinary bladder following the 16-week drought (Fig. 3A). Moreover, the RMANOVA model detected a significant effect of date ($F_{3,12} = 3.50$; $P = 0.048$), but not sex ($F_{3,12} = 0.47$; $P = 0.50$) or sex by date ($F_{3,12} = 2.45$; $P = 0.23$), on plasma osmolality, indicating that osmolality of females and males changed similarly over time (Fig. 3B).

Body Temperatures and Surface-Activity Estimates.—Temperature-based activity estimates suggest that Gila Monsters at our Sonoran Desert study site were surface active 17.1% of all hours between April and August with activity peaks occurring in association with rainy periods and lows coinciding with hot and dry months (Fig. 4). Separate RMANOVA models for each of the three sampling periods indicated no significant effects of sex or date and no sex by date interaction (all $P > 0.30$) during

sampling periods 1 (April) and 3 (June 23 to August). In contrast, during sampling period 2 (May to June 22), sex ($F_{1,13} = 11.10$; $P = 0.006$), date ($F_{1,13} = 4.60$; $P = 0.003$), and the sex by date interaction ($F_{1,13} = 167.60$; $P < 0.001$) were significant, indicating that activity levels changed differently for males and females over time between 15 May and 15 June (Fig. 4). Additionally, all Gila Monsters demonstrated a coordinated shift in the timing of surface activity. Activity was predominantly diurnal only during April, late-afternoon crepuscular in May (1600–2200 h), and nocturnal (2000–0600 h) for the duration of the hot active season (June to mid-September).

When compared across the entire active season, mean Gila Monster T_b was not affected by surface activity ($26.4 \pm 0.83^\circ\text{C}$) or shelter use ($26.1 \pm 0.66^\circ\text{C}$). Interestingly, comparison of weekly values produces similar results. However, comparison of daily values shows that shelter use substantially reduces variation in T_b compared to T_b variation when surface active, even when mean T_b s are equal.

DISCUSSION

Growth, Body Condition, and Hydration State.—Despite severe seasonal drought (Fig. 1) and presumably limited and highly seasonal resource availability, most Gila Monsters grew during the study (Fig. 2), indicating that lizards were able to capitalize on pulsatile energetic resources when available. Gila Monsters in this study were shorter (September 2004 mean SVL = 308 ± 3.9 mm) than lizards in Utah (Beck, 1990) and New Mexico (Beck, 2005) but longer than those in Nevada (C. Gienger, unpubl. data). Neither body size nor growth rate of Gila Monsters differed between sexes in this study, even though three females produced energetically expensive clutches in 2004. This similarity in body size and growth rate supports the previously posed hypothesis that male Gila Monsters divert substantial energy away from growth to other processes including mate-searching and intense male–male agonistic encounters (Beck, 1990; Beck et al., 1995). Gila Monsters mate in late spring (Beck, 2005), and males in our study were surface active significantly more than females (19.2% vs. 10.9%, respectively) during May and June 2004 (Fig. 4), which suggests that male and female Gila Monsters allocate similar energy to reproduction, albeit to entirely different activities (i.e., mate acquisition vs. egg production and possibly nesting). The comparative energetic demands of reproduction in male and female Gila Monsters and the temporal separation of the demands is deserving of further study.

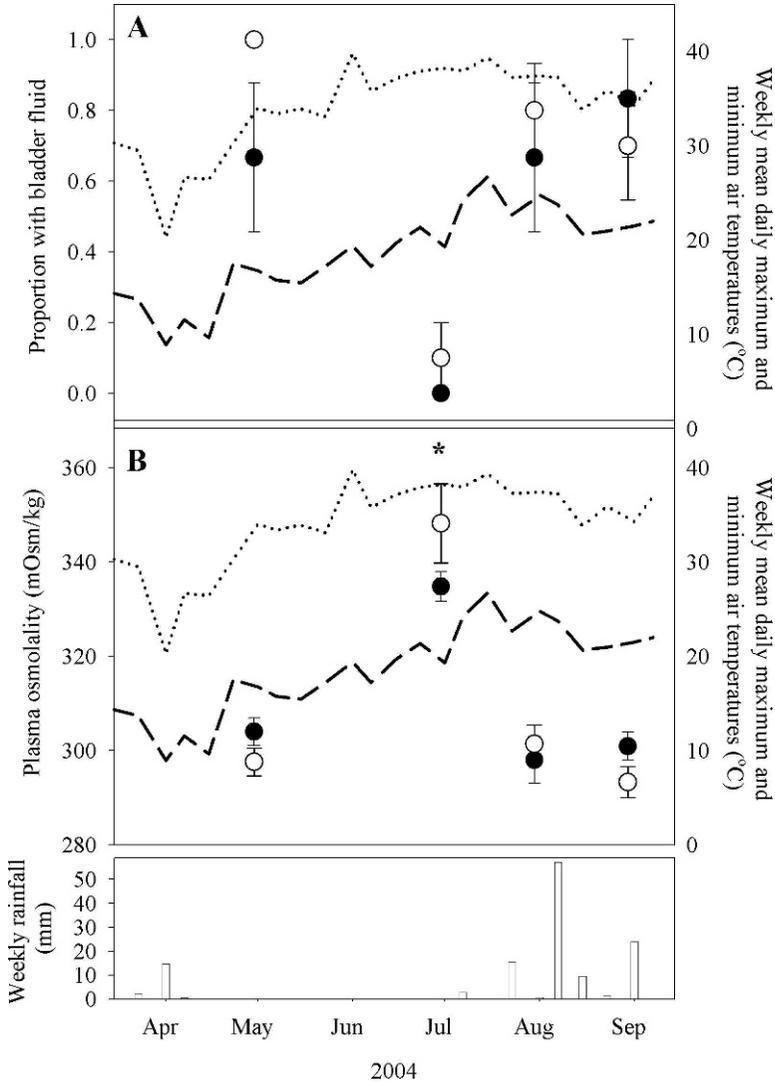


FIG. 3. Seasonal variation in hydric condition of female (●, $N = 6$) and male (○, $N = 10$) Gila Monsters (*Heloderma suspectum*) during the 2004 active-season at our Sonoran Desert site. Gila Monsters retained water in the urinary bladder (A) following spring rains but not after several weeks of drought. Plasma osmolality (B) of both sexes increased significantly ($P = 0.048$) during drought as bladder water was reabsorbed and prey consumption presumably decreased. Values shown are mean \pm 1 SE, and * indicates significant differences ($P < 0.05$ /sampling periods) between dates.

The body mass of Gila Monsters we studied ($N = 10M : 6F$; September 2004 mean = 458 ± 25.6 g) was similar to Gila Monsters in Utah ($N = 22$; mean = 479 ± 37.9 g) (Beck, 1990). During this study, Gila Monsters tolerated body mass fluctuations of $32 \pm 2.0\%$, yet with the exception of females in 2004, body mass was relatively stable during the active season (Fig. 1A, B). Several plausible explanations may explain this pattern. (1) Three females reproduced in 2004, and because oviposition in our population occurs in mid-July (unpubl. data), the signifi-

cant decrease in female body mass we observed after July (Fig. 1B) was likely attributable to clutch production (which is not a yearly event in female Gila Monsters). (2) In addition, Gila Monsters are widely foraging nest predators that will consume altricial young of mammals as well as bird, lizard, and tortoise eggs (Barrett and Humphrey, 1986; Stitt et al., 2003; Beck, 2005). Some of these resources, particularly tortoise eggs, can remain buried in the substrate for months and, thus, may have been consumed by Gila Monsters to maintain body mass

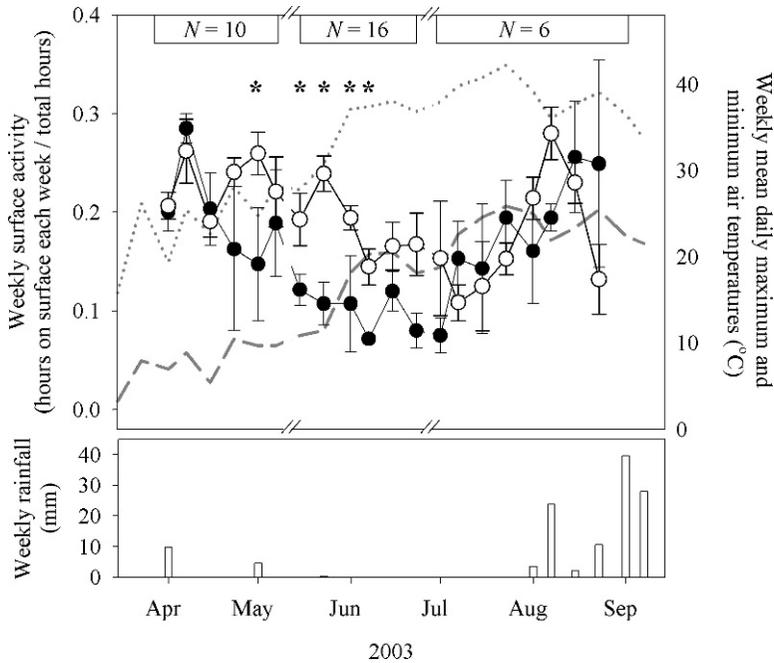


FIG. 4. Temperature-based activity estimates of weekly surface-activity for female (●) and male (○) Gila Monsters (*Heloderma suspectum*) during the 2003 active-season at our Sonoran Desert site. Surface-activity was assessed during three sampling periods (see Materials and Methods), distinguished by breaks in the figure, and sex differences only occurred during the mating season (May through mid-June) when males were significantly more active than females ($P = 0.006$). Surface activity followed a similar pattern as rainfall. Values shown are mean ± 1 SE, and * indicates significant differences ($P < 0.05$ /sampling periods) between dates. See Materials and Methods for details on changes in samples size during each sampling period.

independent of rain-dependent mammal and bird reproduction. (3) Moreover, Gila Monsters can ingest meals equivalent to 35% of their own body mass (Beck, 1990; JRD, pers. obs.), and mean mass of the population would have been inflated if data were collected following a recent meal from the majority of the population. Similarly, Gila Monsters can store a substantial volume of fluid in the urinary bladder ($\leq 20\%$ total body mass) (Davis and DeNardo, 2007), which would also inflate body mass values. Indeed, bladder water likely contributed to greater body mass measurements in 2004 because we determined that at least two-thirds of the population retained water in the bladder every month in 2004 except July (Fig. 3A).

To evaluate body condition of Gila Monsters using a more stable index, we measured tail volume as a more specific index of energy stores because the immediate effects of a meal (or drink or defecation) do not affect fat stores in the tail (Davis and DeNardo, 2007, unpubl. data). During 2004, tail volume decreased in males and females over time but, unlike body mass, did not begin to increase following the onset of the monsoon rains (Fig. 1C). This suggests that the rapid increase in body mass

associated with the start of the monsoon likely reflects consumption of water. Moreover, tail volume of females decreased more than males in 2004, possibly because of the substantial energetic demands associated with producing a clutch. Thus, tail volume is likely a good long-term indicator of energetic status in this species though further studies of energy expenditure in the field are needed to confirm this.

Like body mass and tail volume, the hydric condition of Gila Monsters declined during the spring and summer prior to the monsoon season. Nearly all lizards began 2004 with fluid in their urinary bladder, but after nearly four months of drought Gila Monsters had apparently reabsorbed all fluid from the bladder to aid osmoregulation (Fig. 3A). Despite beginning with an intrinsic water reservoir, plasma osmolality of both male and female Gila Monsters increased significantly by July (Fig. 3B). The mean plasma osmolality increase observed in all Gila Monsters we studied ($298\text{--}343$ mOsm/kg $^{-1}$) is substantial compared to other Sonoran Desert lizards, including the Desert Iguana (*Dipsosaurus dorsalis*) and Chuckwalla (*Sauromalus ater*), which experience little change in plasma solute concentration (Nagy, 1972; Min-

nich, 1976). Notably, these species are herbivores and possess nasal salt glands, which affect osmoregulation in other ways. However, the changes observed in Gila Monsters are not as drastic as in some other desert species that also use the urinary bladder as a water reservoir, including the Desert Tortoise (290 to >400 mol/kg⁻¹) and Couch's Spadefoot Toad (*Scaphiopus couchii*) (250 to >600 mOsm/kg⁻¹) (McClanahan, 1967; Nagy and Medica, 1986; Peterson, 1996a). Still, our results indicate the ecological relevance of the Gila Monster urinary bladder as a physiological reservoir, because plasma osmolality of Gila Monsters in this study did not peak until July, after 14 weeks of drought. Under simulated drought conditions in the laboratory, we previously demonstrated that bladder fluid was absorbed to prevent such an increase in plasma osmolality for nearly 11 weeks compared to less than five weeks when facing simulated drought with an empty bladder (Davis and DeNardo, 2007). Moreover, after one drinking bout, plasma osmolality can return to baseline levels (i.e., 290 mOsm kg⁻¹), and the urinary bladder reservoir can be replenished (Davis and DeNardo, 2007). In this study, plasma osmolality returned to May levels, and most lizards had fluid in the urinary bladder by August (Fig. 3).

Body Temperatures and Surface-Activity Estimates.—The mean activity temperature of Gila Monsters we studied ($26.4 \pm 0.83^\circ\text{C}$) is lower than mean activity temperatures reported for Gila Monsters in other studies ($29.0\text{--}31.0^\circ\text{C}$) (Beck, 2005). This difference is likely attributable to 24 h/day sampling in our study, which revealed substantial nocturnal activity in our population, compared to primarily diurnal sampling in other studies (Beck, 2005). Notably, when in shelters, T_b of lizards in this study ($26.1 \pm 0.66^\circ\text{C}$) was within the range reported for Gila Monsters from April to September in New Mexico ($23.5\text{--}28.5^\circ\text{C}$) (Beck, 2005). On average, Gila Monsters we studied in the Sonoran Desert were surface active between 8% (115 min/day) and 23% (331 min/day) of the hours each week (Fig. 4), although individuals would commonly be inactive for a week or more. These activity levels exceed other estimates for Gila Monsters living in the Chihuahuan Desert (Red Rock, New Mexico) and Mojave Desert (St. George, Utah) (3–5%) (Beck, 1990, 2005); however it is important to note differences in data collection techniques (hourly estimates based on T_b vs. opportunistic direct observation). Compared to their close relatives, the diurnally active varanid lizards, Gila Monsters are often thought of as more secretive. However, the activity of our Gila Monsters (115–331 min/day) was comparable to levels reported for *Varanus rosenbergi*

(mean = 47.6 min/day) and *Varanus panoptes* (mean = 228 min/day) (Christian and Weavers, 1994).

Although our temperature-based activity estimates are substantially greater than those previously published for the species, they are likely accurate for this population for several reasons. Notably, nocturnal activity, which is often underestimated when using direct observation, accounted for the vast majority of activity in our population during most of the active season (June to September). Additionally, compared to other North American deserts, the Arizona-Upland subdivision of the Sonoran Desert where we conducted this study has a much more reliable monsoon rainy season, and the monsoon rains strongly influence wildlife (Orland and Kelt, 2007; Small et al., 2007) as evidenced by the progressively increasing activity of our Gila Monsters during July and August compared to May and June.

Surface-activity estimates for Gila Monsters in our study demonstrate that reproduction and rainfall are primary factors influencing activity patterns. During the mating season (mid-April to June), males spend significantly more time on the surface than females, and notably, males also have larger home ranges than females during this time (Gallardo, 2003). Activity patterns also appeared to be correlated with rainfall patterns (Fig. 4), although data collection methods limited our ability to assess the entire active season statistically. The possible link between water availability and activity patterns is deserving of further study because activity patterns of other reptiles are influenced by intrinsic (Nagy and Medica, 1986; Crowley, 1987; Ladyman and Bradshaw, 2003) and environmental (Peterson, 1996b; Daltry et al., 1998; Lorenzon et al., 1999) hydric conditions. For example, in many regions of the Mojave Desert, rain falls only in the winter and spring, if at all. Under these conditions assuming equal bladder reservoir capabilities, populations of Gila Monsters likely demonstrate activity periods constrained to the spring months (March through May) and perhaps tightly linked to specific rainfall events outside of the typical rainy season (i.e., late summer rains may stimulate bursts of activity). Studies in these regions and manipulative field studies that alter resource availability are needed to elucidate causal relationships between seasonal patterns of hydric condition, activity, and body condition in the Gila Monster.

Conclusions.—Data on individual physiological and behavioral parameters exist for many species, including Gila Monsters (DeNardo et al., 2004; Beck, 2005; Davis and DeNardo, 2008), yet the integration of these processes, especially in nature, is rarely studied. Survival of animals,

particularly in highly seasonal deserts, requires integration of morphological and physiological responses (Degen, 1997; Walsberg 2000; Williams and Tieleman, 2002) with complementary behavioral responses (i.e., refuge selection, timing of activity) (Lustick and Aspey, 1983; Bradshaw, 1997; Bulova, 2002; Tracy and Walsberg, 2002). Our results indicate that Gila Monsters' survival strategy during seasonal drought combines flexible behavioral patterns (i.e., the timing and duration of activity), resource storage and economical use, and tolerance of significant physiological disturbance. These data provide an important baseline of integrated physiological and behavioral parameters for a species that is not well understood in nature. Given the relatively limited geographic distribution of Gila Monsters (Beck, 2005), the rapid urbanization occurring within the species' distribution in cities like Las Vegas, Phoenix, Tucson, and St. George (U.S. Census Bureau, 2008), and the ineffectiveness of translocation as a conservation tool (Sullivan et al., 2004), the data presented here become increasingly important in a conservation context. Such data are lacking, especially for reptiles and amphibians (Gardner et al., 2007) yet are essential for predicting animal responses to changes in local resource availability caused by urbanization or even climate change (Tracy et al., 2006; Wikelski and Cooke, 2006).

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