Water Supplementation Affects the Behavioral and Physiological Ecology of Gila Monsters (*Heloderma suspectum*) in the Sonoran Desert

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ABSTRACT

In desert species, seasonal peaks in animal activity often correspond with times of higher rainfall. However, the underlying reason for such seasonality can be hard to discern because the rainy season is often associated with shifts in temperature as well as water and food availability. We used a combination of the natural climate pattern of the Sonoran Desert and periodic water supplementation to determine the extent to which water intake influenced both the behavioral ecology and the physiological ecology of a long-lived desert lizard, the Gila monster (*Heloderma suspectum*) (Cope 1869). Water-supplemented lizards had lower plasma osmolality (i.e., were more hydrated) and maintained urinary bladder water reserves better during seasonal drought than did control lizards. During seasonal drought, water-supplemented lizards were surface active a significantly greater proportion of time than were controls. This increased surface activity can lead to greater food acquisition for supplemental Gila monsters because tail volume (an index of caudal lipid stores) was significantly greater in supplemented lizards compared with controls in one of the two study years.

Introduction

Rainfall is the dominant factor influencing biological productivity in hot arid environments (Noy-Meir 1973). Rainfall affects many crucial processes in animals, including activity patterns (McClanahan 1967; Bigler 1974; Peterson 1996*b*; Duda et al. 1999) and reproduction (Sullivan and Fernandez 1999;

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Grant et al. 2000; Chesson et al. 2004; Small et al. 2007; Shine and Brown 2008). Rainfall also influences long-term processes, including population and community structures of animals, by improving resource availability and body condition before mating and during mating and juvenile development, which can increase recruitment long after specific rainfall events (Chesson et al. 2004; Langlands et al. 2006; Madsen et al. 2006; Chamaille-Jammes et al. 2007). Because rainfall affects environmental conditions in many ways, it may be difficult to discern whether behavioral and physiological responses to rainfall observed in nature are attributable to water intake or to indirect effects, including, but not limited to, greater food availability.

Supplemental feeding studies have clarified mechanisms underlying the physiology and ecology of invertebrates (Kreiter and Wise 2001; Pelletier and McNeill 2003), birds (Boutin 1990; Schoech and Hahn 2007; Schoech et al. 2008), mammals (Banks and Dickman 2000; Meserve 2003; Orland and Kelt 2007), and reptiles (Dunham 1978; Eifler 1996; Blouin-Demers and Weatherhead 2001; Taylor et al. 2005). Despite recent evidence that hydric conditions influence body temperature (T_b) and activity patterns of reptiles (Daltry et al. 1998; Lorenzon et al. 1999; Ladyman and Bradshaw 2003), few empirical studies have tested mechanisms by which limited water intake, independent of food availability, affects activity patterns, body condition, and reproduction. Notably, water supplementation of the temperate-zone sagebrush lizard (*Sceloporus graciosus*) in the laboratory had no effect on growth rate (Sears and Angilletta 2003); yet, laboratory and field-water supplementation studies of the tropical lizard *Anolis aeneus* increased growth rate (Stamps and Tanaka 1981). These conflicting results may be attributed to differences in study design because *Sceloporus* were held at a constant temperature and *Anolis* were allowed to thermoregulate in the laboratory and were also studied in the field, which likely enabled lizards to maintain higher temperatures and grow faster (Sears and Angilletta 2003). Water supplementation also benefitted desert tortoise (*Gopherus agassizii*) conservation efforts (Field et al. 2007), increased clutch size in wild sparrows (Coe and Rotenberry 2003), and increased growth rate in crickets (McCluney and Date 2008). Clearly, field studies that combine water supplementation of individuals in nature with integrative assessments of body condition and activity patterns are needed to clarify direct effects of water intake.

The Gila monster (*Heloderma suspectum*) is a large (adult body mass = 350–700 g and snout-to-vent length = 260–360 mm), long-lived (>20 yr), and venomous lizard (Beck 2005) especially suitable for water supplementation and integrative

behavioral and physiological studies for several reasons. 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 extending slightly into adjacent deserts (Beck 2005). In nature, Gila monsters use shelters extensively (Lowe et al. 1986; Beck 1990; Beck and Jennings 2003), store energy caudally (Bogert and Martín del Campo 1956; Beck 2005), have an unusually low resting metabolic rate (Beck and Lowe 1994), and store water in the urinary bladder (Davis and DeNardo 2007, 2008). Nevertheless, seasonal drought conditions are associated with decreased surface activity and significant decreases in body water (i.e., decreased hydration and stored water) and body conditions (i.e., body mass and tail volume); the latter may reduce reproductive output in the capital breeding Gila monster (Davis and DeNardo 2010). Notably, Gila monsters respond strongly to rainfall during the active season by increasing activity and drinking copious amounts of water from puddles. Gila monsters can consume 9%–22% (36–75 mL) of their body mass in a single drinking bout (Davis and DeNardo 2007, 2008), and much of this water (up to 60 mL; J. R. Davis and D. F. DeNardo, unpublished data) can be stored in the urinary bladder. However, it is unknown whether water intake is a proximate mechanism that directly influences surface activity patterns and thus body condition of Gila monster lizards in nature. We examined the effects of water intake, independent of food availability, on surface activity patterns and body condition by providing supplemental water monthly to free-ranging Gila monsters in the Sonoran Desert. We predicted that, compared with control lizards, lizards receiving supplemental water would maintain better hydric conditions and be surface active a greater proportion of time, especially during periods of drought. Because Gila monsters are active foragers, we also predicted that increased surface activity would result in better body condition.

Material and Methods

Study Site and Weather Conditions

The study was conducted during two Gila monster activity seasons (April–September 2005 and 2006) at a previously described (Davis and DeNardo 2010) undeveloped 3-km^2 area located in the Arizona Upland subdivision of the Sonoran Desert in Pinal County, Arizona (32°36′N, 111°07′W, 800–1,100 m elevation). A heterogeneous matrix of Sonoran Desert plants covers the sandy plain, which is intersected by intermittent washes. Numerous mammal burrows that provide important subterranean refugia for Gila monsters (Beck 1990; Beck and Jennings 2003; Gallardo 2003) are distributed across the study site.

We recorded rainfall (≥2 mm), using an automated rainfall gauge (model RG3-M, Onset Computer, Bourne, MA) left continuously in the field, and air temperature (T_{air}; ±0.2°C) hourly, using an automated temperature logger (StowAway Tidbit, Onset Computer) placed at a central location at the site. We reduced direct solar irradiation of the temperature logger by shad-

ing the logger in an uncapped PVC tube suspended vertically from a tree branch 1 m above the ground. We were unable to collect rainfall data at the field site during 2005 because of problems with the rainfall gauge; thus, we obtained rainfall data from the nearest National Climate Data Center's (NCDC) Picacho, Arizona, climate station (32°39′N, 111°24′W, 557 m; COOP 026513) located 25 km west of the field site. The NCDC Picacho rainfall data from 2005 are likely a reasonable representation of rainfall at our field site because 2006 weekly rainfall amounts we recorded at our field site are similar to the 2006 NCDC Picacho data.

We calculated weekly precipitation, total active season precipitation (mid-March through September), 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 daily maximum and minimum T_{air}.

Samples Sizes and Radiotelemetry

This research was conducted in accordance with the Arizona State University (ASU) Institutional Animal Care and Use Committee policies (IACUC protocol 01-671R) under Arizona Game and Fish Department scientific collection permits SP683420 and SP739769. We used 23 (11M : 12F) adult Gila monsters collected from the field site and implanted with radiotransmitters (13 g model SI-2, Holohil Systems, Carp, Ontario) at various times of capture for this and previous studies (Davis and DeNardo 2010). Radiotransmitters were replaced as needed based on battery life (24 mo) at either the beginning or the end of the active seasons. In late March 2005, all Gila monsters were collected and transported to the laboratory at ASU, where a miniature temperature logger (Thermochron iButton, model DS1922L, Maxim, Dallas) was surgically implanted into the intracoelomic cavity of each lizard using methods similar to those used previously for rattlesnakes (Taylor et al. 2004). After surgery, but before 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 studied 21 of the same lizards in 2006, and because two lizards were lost during 2005 because of premature radiotransmitter failure, we also added three new lizards in 2006 (12M : 12F).

We located Gila monsters approximately weekly during both active seasons (April 1–September 1). To increase the likelihood of locating all individuals on the surface for water supplementation and body condition measurements (see below), we substantially increased radiotelemetry efforts during the first week each month and focused efforts on diel Gila monster activity periods determined previously (Davis and DeNardo 2010).

Water Supplementation and Hydric Condition

We separately assigned males and females to either a water-supplemented (WTR) or control (CON) treatment group using a random-number generator. In 2005, six males and six females

were designated as WTR, and five males and six females were used in the CON group. In 2006, seven males and six females were designated as WTR, and five males and six females were CON. To supplement hydric conditions of WTR lizards, we exploited two key aspects of the Gila monsters' physiology: (1) water introduced into the stomach of Gila monsters by way of an intragastric tube is rapidly absorbed into circulation (Davis and DeNardo 2007) and (2) Gila monsters use their bladder as a water reservoir and thus can store significant quantities of water (Davis and DeNardo 2007). In both years, we administered experimental treatments to each lizard once during an approximately 7-d processing period at the beginning of each month from May to August. We used a 60-mL syringe and an intragastric tube to introduce 50 mL (approximately 10%–15% of body mass) of tap water (28 mOsm/kg) into the stomach of WTR lizards and to provide a sham treatment (intubation without water) to CON lizards. Although we could not control the access of animals to natural water resources, such resources are very rare during the seasonal drought. Thus, our treatment likely increased the water intake of WTR lizards compared with CON lizards, especially during periods when water was naturally constrained.

We assessed two aspects of the lizards' hydric condition during processing periods at the beginning of each month (April–September) in 2005 and 2006. All measurements were made before water supplementation to avoid confounding effects on bladder condition, plasma osmolality, and body mass (see below). First, we used portable ultrasonography (Concept/MLV, Dynamic Imaging, Livingston, Scotland) to determine when water was stored in the urinary bladder and available to lizards and then calculated the proportion of lizards that had bladder water each month. Second, we used plasma osmolality (mOsm/kg) as an indicator of hydration state to determine whether water supplementation reduced or eliminated dehydration in WTR lizards compared with CON lizards. To measure osmolality, we collected 0.2 mL of blood from the caudal vein of each lizard using a heparinized 1-mL syringe. We stored samples in 1-mL screw-top vials in a cooler until transported back to the laboratory. There, 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, Logan, UT) and previously described calibration and analytical procedures (Davis and DeNardo 2007).

Surface Activity Estimates

During 2005 and 2006, we used the hourly data from the surgically implanted temperature loggers to estimate surface activity patterns of each Gila monster. These temperature loggers are small (6 mm thick and 17.4 mm in diameter), lightweight (3.1 g), precise ($\pm 0.5°C$), and they can record temperatures at user-selected intervals (Angilletta and Krochmal 2003). Moreover, these temperature loggers collect up to 8,192 data points semicontinuously (i.e., at regular intervals), which eliminates observer biases associated with traditional T_b and activity data

assessments (Taylor et al. 2004). Before implantation in 2005, we programmed temperature loggers to record T_b hourly between April 1 and September 1, 2005. At the end of the 2005 active season, we collected lizards from the field, transported them to the laboratory at ASU, exchanged temperature loggers with others programmed to record T_b hourly between October 1, 2005, and September 1, 2006, and returned lizards to their site of collection within 48 h. This enabled us to assess lizard T_b and activity during both active seasons and the 2005–2006 overwinter (November to early March) period (J. R. Davis and D. F. DeNardo, unpublished manuscript).

We used temperature-based activity estimation (TBAE), which relies on a simple comparison of synchronized T_{air} and T_b data, to estimate surface activity and refuge use patterns of WTR and CON lizards. TBAE correctly predicts Gila monsters' locations (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).

Body Condition

We collected these data primarily in the field during the monthly processing periods when we used radiotelemetry to locate Gila monsters on the surface. However, we collected data from lizards three times in the laboratory when lizards were brought to ASU for radiotransmitter and temperature logger implantation (late March 2005) and temperature logger exchange (September 2005 and 2006). We measured body mass (± 0.1 g) in the laboratory with an electronic scale (Acculab GS-2001, Edgewood, NY) while lizards were anesthetized to improve measurement accuracy. We measured body mass (± 10 g) in the field using a 1,000-g-capacity spring scale (Pesola, Switzerland). Because body mass can vary drastically (15%–35%) between serial samples in Gila monsters as a result of feeding (Beck 1990), drinking (Davis and DeNardo 2007, 2008), reproduction (Beck 2005), or defecation, we also measured tail volume (± 1 mL) using water displacement. We submerged each lizard's entire tail up to the vent in a 100-mL graduated cylinder filled with water and then measured the volume of water displaced by using another graduated cylinder to refill the cylinder. Tail volume provides an effective index of stored energy because Gila monsters store energy reserves caudally (Bogert and Martín del Campo 1956; Beck 2005) and tail volume is not influenced by fecal elimination or water intake (Davis and DeNardo 2007).

Statistical Analyses

We determined whether data met assumptions of parametric tests before statistical inference and $\log_{10}$-transformed data when necessary before analyses using JMP IN (ver. 5.1, SAS Institute, Cary, NC) and SAS (ver. 8.1, SAS Institute). Values in figures are back transformed and means ± 1 SE are plotted; $\alpha = 0.05$ unless corrected as indicated for multiple compari-

sons. We used Student's t-tests to determine whether random assignment of WTR and CON treatment groups resulted in initial differences in plasma osmolality, body mass, or tail volume in 2005 and 2006.

Gila monsters are secretive lizards and spend up to 95% of the time in shelters (Beck 1990; Davis and DeNardo 2010), so we were unable to locate some lizards during some sampling periods (2005 = 3 of 138; 2006 = 15 of 144). To compensate for missing data, we thus used the MIXED procedure in SAS (Littell et al. 1996) to perform repeated-measures ANOVA (RMANOVA). We assessed the effectiveness of water supplementation in reducing seasonal dehydration each year using RMANOVA with treatment as the between-subjects factor, time as the within-subjects factor, and plasma osmolality as the dependent variable. We also analyzed surface activity using RMANOVA with sex and treatment as between-subjects factors, time as the within-subjects factor, and surface activity as the dependent variable. Sex was included in the model because males and females differ in surface activity during portions of the active season (Davis and DeNardo 2010). We analyzed body mass and tail volume using RMANOVA with treatment as between-subjects factors, time as the within-subjects factor, and body mass and tail volume as the dependent variables. For all analyses, Mauchly's criterion for sphericity was violated, so we applied a Greenhouse-Geisser correction before interpretation (Zar 1999). We used Tukey-Kramer tests (adjusted for experiment-wise Type I error rate; $\alpha = 0.05/N$) post hoc to identify significant differences in plasma osmolality, surface activity, body mass, and tail volume between treatments during each sampling period.

Results

Weather Conditions

Rainfall was variable, seasonal, and relatively low during the Gila monster active seasons. In 2005, total active season rainfall was only 160.8 mm; however, the seasonal drought (i.e., the number of consecutive weeks that total rainfall <5 mm) was not extensive because of unusual late May and June rainfall. Drought was limited to 5–6 wk before the reliable summer monsoon produced 77% of the total rainfall in just 7 wk (Fig. 1A). In 2006, total active season rainfall was much greater (226 mm) than that in 2005, with 87% of the total occurring at the end of June, the beginning of July, and during the monsoon. However, the seasonal drought was prolonged to 12 wk because no spring rains occurred (Fig. 1B). In both years, spring (mid-March to mid-May) air temperatures were relatively cool (weekly mean minimum and maximum $T_{air} = 6°–16°C$ and $20°–30°C$, respectively) but then increased substantially (weekly mean minimum and maximum $T_{air} = 15°–26°C$ and $31°–42°C$, respectively) and remained stable and elevated throughout the active season (late May to mid-September; Fig. 1).
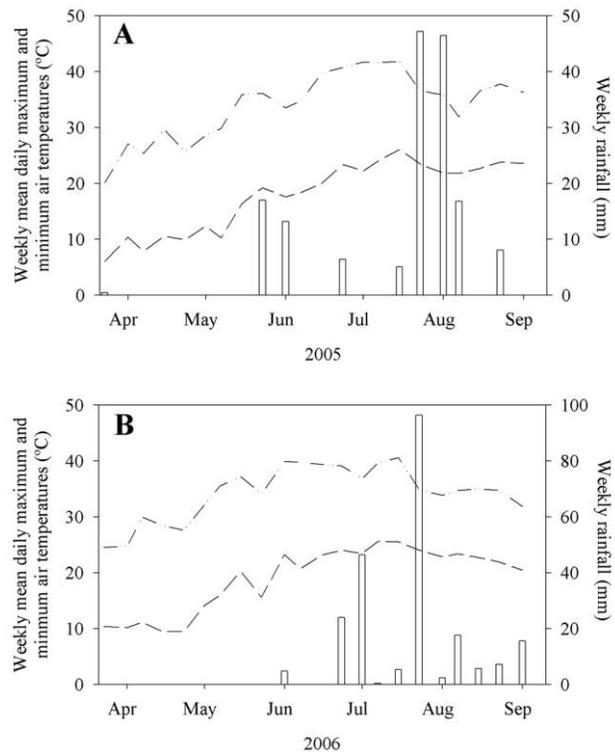

Figure 1. Weather conditions recorded at the Sonoran Desert field site during the 2005 (A) and 2006 (B) active seasons. Dashed lines denote weekly mean daily air temperature maxima (°C) and weekly mean daily air temperature minima (°C), and vertical bars denote weekly rainfall (mm). Weather conditions are plotted in Figures 2–5 for reference. Note that rainfall is highly seasonal, with dramatic increases in rainfall in midsummer despite little to no change in temperature.

Water Supplementation and Hydric Condition

WTR and CON lizards began each active season with plasma osmolalities that were similar (2005: WTR = 300.5 ± 2.76 mOsm/kg vs. CON = 294.3 ± 3.96 mOsm/kg; $t = -1.10$, $P = 0.29$; 2006: WTR = 279.1 ± 3.02 mOsm/kg vs. CON = 281.2 ± 4.77 mOsm/kg; $t = 1.70$, $P = 0.11$) and comparable to hydrated values (280–300 mOsm/kg) for many amphibians and reptiles (Minnich 1976; Shoemaker and Nagy 1977), including hydrated Gila monsters (Davis and DeNardo 2007). Water supplementation improved the hydric condition of Gila monsters during both years. The proportion of WTR lizards that had fluid in the urinary bladder was greater than that of CON lizards in every month except April 2005 and April, August, and September 2006 (Fig. 2A, 2C). Notably, WTR lizards always had fluid in the urinary bladder. WTR lizards remained hydrated; that is, they maintained plasma osmolality near the April value, throughout both active seasons, whereas CON lizards became significantly dehydrated during July and September 2005 and June and July 2006 (Fig. 2B, 2D). In 2005, the RMANOVA model detected significant time ($F_{3,16} = 4.1$, $P = 0.025$) and treatment ($F_{1,16} = 10.4$, $P = 0.005$) effects, but sex and the sex-by-treatment interaction were not significant ($P > 0.24$; Fig. 2B). Similarly, in 2006, the time ($F_{3,7} = 6.9$,
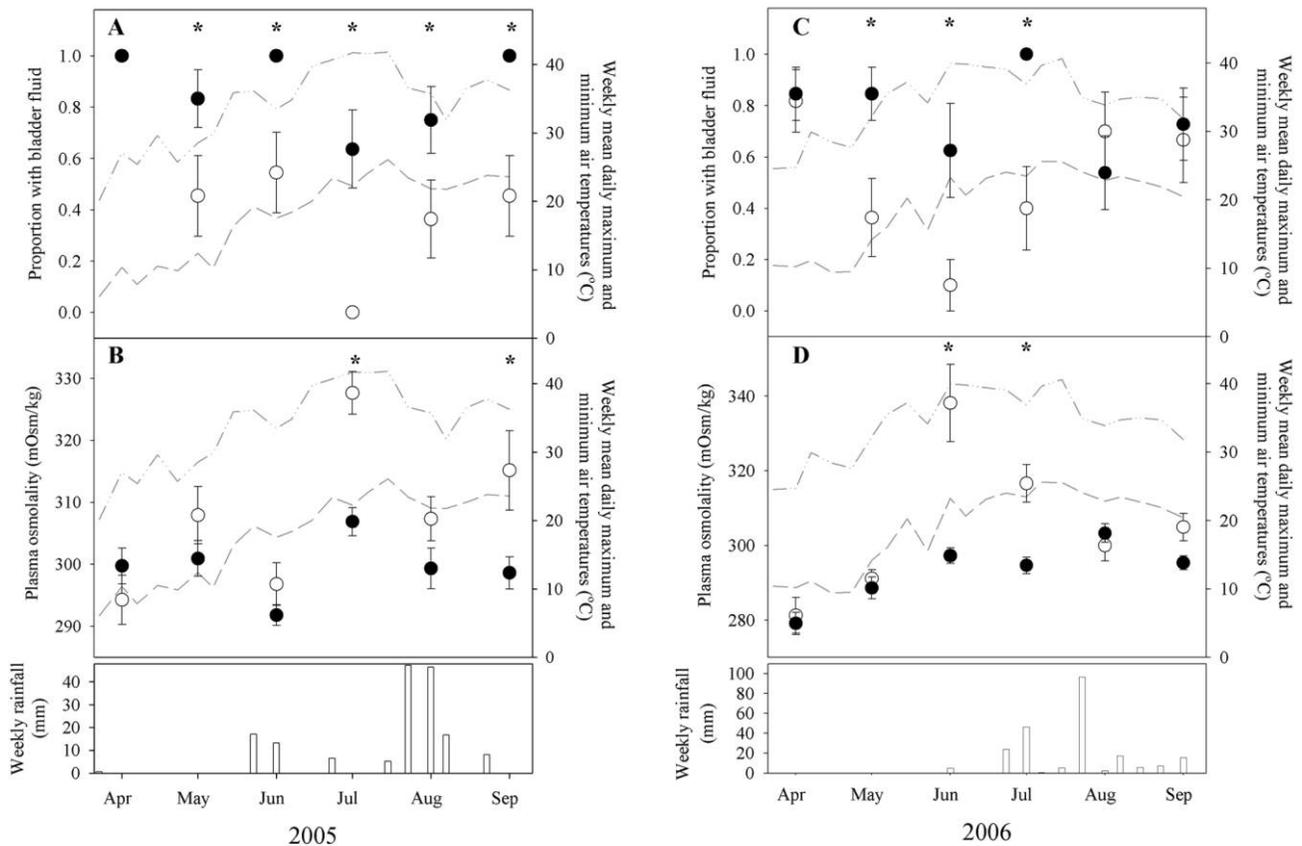
Figure 2. Seasonal variation in hydric condition of water-supplemented (WTR; *filled circles*) and control (CON; *open circles*) Gila monsters (*Heloderma suspectum*) during the 2005 (WTR : CON = 12 : 11) and 2006 (13 : 11) active seasons in the Sonoran Desert. A greater proportion of WTR lizards retained fluid in the urinary bladder (*A, C*) compared with CON lizards. Note that all WTR and CON lizards had bladder fluid in April 2005 (thus, CON symbol is not visible), and there are no error bars when all or none of the lizards retained fluid in the bladder. Plasma osmolality (mOsm/kg; *B, D*) of WTR lizards remained stable across both active seasons and increased significantly in CON lizards following drought and as bladder water was absorbed. Values shown are means $\pm$ 1 SE, and an asterisk indicates significant differences ($P <$ 0.05/N) between treatments.

$P = 0.017$) and treatment ($F_{1,7} = 19.3$, $P = 0.003$) effects were significant, and sex and the treatment-by-sex interaction were not ($P > 0.5$; Fig. 2D). Post hoc analyses indicated that plasma osmolality of WTR lizards was significantly lower compared with that of CON lizards in July 2005 and June and July 2006 (Fig. 2B, 2D).

Surface Activity

Gila monsters were surface active in this study a total of 14.2% of all hours during the active season in 2005 and 13.0% in 2006. In 2005, Gila monsters were surface active most in April (17.9% of all hours in the month) and August (21.7%), with the low occurring in June (7.3%; Fig. 3A). In 2006, surface activity peaked in July (15.6%) and August (23.5%), with lows in May and June (8.0% and 7.4%, respectively). During both active seasons, WTR lizards were surface active at least 20% more of the time than CON lizards (2005: WTR = 15.5% $\pm$ 1.1% vs. CON = 12.9% $\pm$ 0.9%; $F_{1,18} = 6.4$, $P = 0.021$; 2006: WTR = 14.4% $\pm$ 1.7% vs. CON = 11.5% $\pm$ 0.8%; $F_{2,19} =$

3.9, $P = 0.005$), and males were active more than females (2005: $F_{1,18} = 43.4$, $P < 0.0001$; 2006: $F_{2,19} = 3.6$, $P = 0.0008$; Fig. 3). Post hoc tests revealed that males were active significantly more than females only during portions of the mating season (May to mid-June), and WTR lizards were more active than CON lizards when seasonal activity was lowest (Fig. 3). All Gila monsters demonstrated a seasonal shift in the timing of surface activity from diurnal in April to late-afternoon crepuscular (1600–2200 hours) in early May to predominantly nocturnal (2000–0600 hours) for the duration of the hot active season (June to mid-September).

Body Condition

Both treatment groups began each year with similar body mass in 2005 (WTR = 450.3 $\pm$ 26.3 g vs. CON = 420.4 $\pm$ 24.0 g; $t = -0.84$, $P = 0.41$) and 2006 (WTR = 434.9 $\pm$ 23.4 g vs. CON = 436.5 $\pm$ 29.3 g; $t = -2.03$, $P = 0.15$). Initial tail volume was also similar between treatments in 2005 (WTR = 52.0 $\pm$ 3.3 mL vs. CON = 47.5 $\pm$ 2.8 mL; $t = -1.75$, $P =$
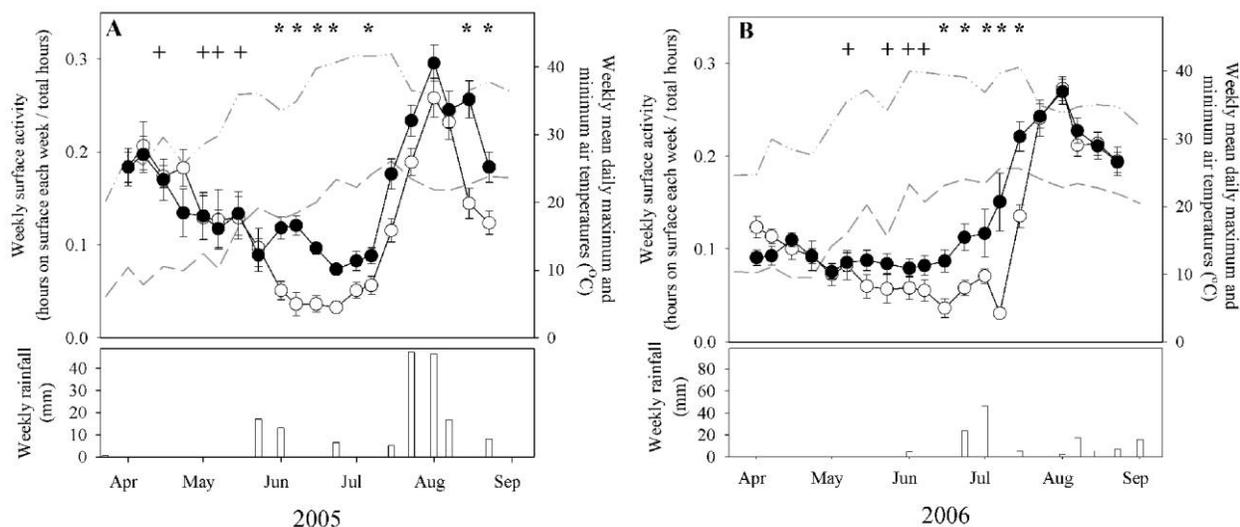
Figure 3. Temperature-based activity estimates of the proportion of hours each week that water-supplemented (WTR; *filled circles*) and control (CON; *open circles*) Gila monsters (*Heloderma suspectum*) were surface active during the 2005 (*A*; WTR : CON = 12 : 11) and 2006 (*B*; 13 : 11) active seasons in the Sonoran Desert. In general, surface activity followed a seasonal pattern similar to that of rainfall. However, WTR lizards were significantly more active than CON lizards during the periods of lowest activity when plasma osmolality was lower in WTR compared with CON animals. Values shown are weekly means ± 1 SE, an asterisk indicates significant differences between treatments, and a plus sign indicates sampling periods when there were significant differences between sexes (sex differences not depicted in the figure; $P < 0.05/N$).

0.10) and 2006 (WTR = 50.0 ± 2.8 mL vs. CON = 49.5 ± 5.0 mL; $t = -1.85$, $P = 0.08$). In 2005 and 2006, there were no significant effects of time, treatment, or any interactions on body mass (all $P > 0.06$), indicating that body mass remained relatively stable across the active seasons (Fig. 4). Similarly, in 2005, there were no significant effects of time, treatment, or any interaction terms on tail volume (all $P > 0.20$; Fig. 5*A*). In 2006, there was also no time effect on tail volume ($P = 0.15$), but the treatment ($F_{1,11} = 4.08$, $P < 0.035$) and treatment-by-time interaction ($F_{1,11} = 3.66$, $P = 0.028$) terms were significant. Despite similar initial tail volumes, post hoc analyses identified differences between treatment groups in tail volume by June because WTR lizards maintained tail volume during the active season while CON lizard tail volume decreased significantly (Fig. 5*B*).

Discussion

Providing supplemental water to individual lizards demonstrated that water intake can directly influence behavior and, in turn, body condition of free-living animals. Specifically, WTR Gila monsters maintained lower plasma osmolality and consistently had fluid reserves in the urinary bladder compared with CON lizards, which had increased osmolality and typically no bladder fluid during the hottest and driest times of the year (Fig. 2). Indeed, plasma osmolality and bladder condition of CON lizards in this study were similar to those of Gila monsters studied at the same field site during a more severe seasonal drought in 2004 (Davis and DeNardo 2010). Hydric condition influenced the proportion of time that lizards were surface active because the more hydrated WTR lizards were surface

active significantly more of the time than dehydrated CON lizards at times when plasma osmolality differed significantly (Fig. 3). Finally, although body mass did not differ, the more active WTR lizards were able to maintain tail volume (caudal energy stores) throughout the active season. In contrast, less active CON lizards endured significant decreases in tail volume (Fig. 5). Thus, Gila monsters in this study responded to seasonal dehydration by decreasing surface activity, which in turn limited foraging opportunities at a short-term cost to energy stores. Similar patterns of behavioral adjustments and endurance of significant perturbations in physiological conditions have been described for archetypical desert species, including the desert tortoise (*Gopherus agassizii*; Peterson 1996*b*; Henen et al. 1998) and Couch's spadefoot toad *Scaphiopus couchii* (McClanahan 1967); however, such long-term responses to water intake have not been previously documented in lizards to our knowledge.

Surface activity of Gila monsters at our study site is clearly influenced by both the reproductive season and water intake. Throughout their distribution, male Gila monsters search great distances to locate potential mates (Beck 2005), and activity peaked during the reproduction season between late April and mid-June in a New Mexico population (Beck and Jennings 2003). Our data are in agreement with this finding and indicate that males, regardless of treatment group, were more active than females during this time (Fig. 3). Our results indicate that rainfall has a more pronounced effect across the population because surface activity of males and females peaks during the rainy monsoon season (Fig. 3; Davis and DeNardo 2010). Moreover, Gila monsters emerge from shelters immediately in response to monsoon rainfall and, as documented in *G. agassizii*
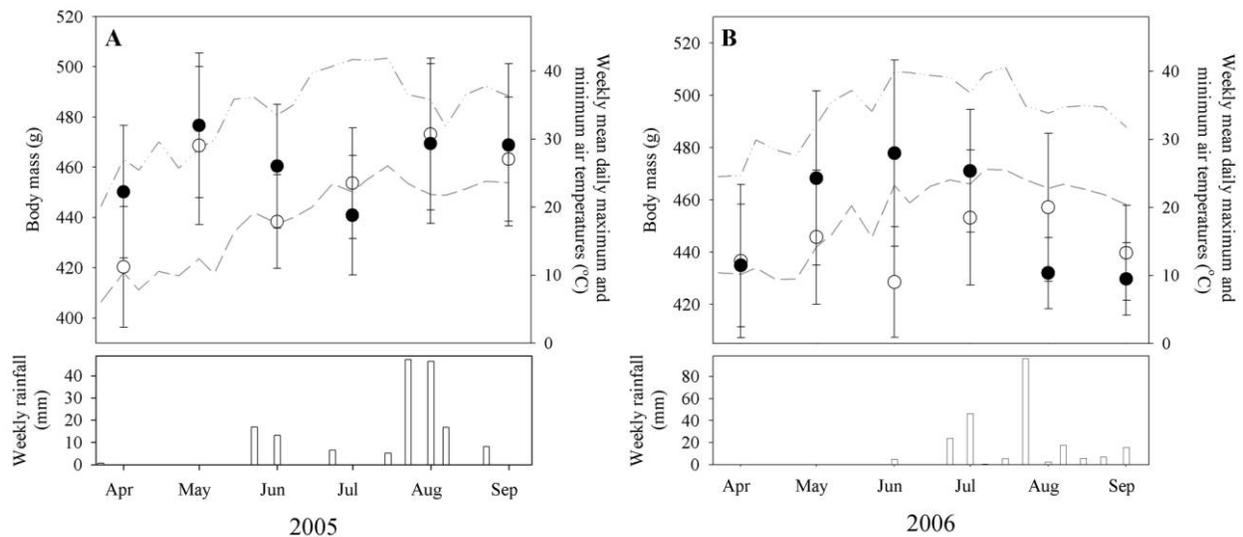
Figure 4. Seasonal variation in body mass of water-supplemented (WTR; *filled circles*) and control (CON; *open circles*) Gila monsters (*Heloderma suspectum*) during the 2005 (WTR : CON = 12 : 11) and 2006 (13 : 11) active seasons in the Sonoran Desert. In 2005 (*A*) and 2006 (*B*), there were no significant differences in body mass of WTR and CON lizards, and neither treatment changed significantly over time. Values shown are means ±1 SE.

(Nagy and Medica 1986; Peterson 1996*a*, 1996*b*), will drink copiously from pools that form (J. Davis, personal observation). Gila monsters can rapidly rehydrate following one drink (Davis and DeNardo 2007), and this behavior provides a clear osmoregulatory benefit in nature as evidenced by the decrease in plasma osmolality and replenishment of urinary bladder fluid following rains (Fig. 2; Davis and DeNardo 2010).

The specific hydric benefits that CON lizards received because of reduced surface activity are less clear and were not measured in this study. Decreased activity levels have been correlated with hydric constraints in other reptiles (Sexton and Heatwole 1968; Dmi'el 1972; Stamps and Tanaka 1981; Henen et al. 1998), as well as mammals (Reichman and Van de Graaf 1973; Waser 1975; Degen 1997) and invertebrates (Polis 1990; Ward and Slowtow 1991; Eisen et al. 2002). This relationship is often explained as a water conservation strategy because evaporative water loss (EWL) increases with increased T_b, metabolism, respiration, and locomotion (Minnich 1976; Mautz 1982; Banta 2003). Gila monsters likely benefit hydrically from reduced activity because they can select hydrically and thermally favorable shelters (Beck and Jennings 2003), which allows them to avoid T_b's > 35°C, which significantly increase EWL (DeNardo et al. 2004). Moreover, shelter use also reduces energy expenditure and reduces predation risk. Notably, activity estimates for WTR (15%) and CON (12%) lizards in this study were comparable to previous estimates for the population (17%; Davis and DeNardo 2010) but were considerably greater than estimates (3%–5%) for conspecifics in the Chihuahuan and Mojave Deserts (Beck 1990, 2005). The differences may be explained by several factors, including differences in data collection techniques, extensive nocturnal activity in our study

population, and the influence of the monsoon rains (Fig. 3; Davis and DeNardo 2010).

Our data provide partial support for the hypothesis that water intake can directly influence surface activity patterns, and thus body condition, in nature. We predicted that more active lizards (WTR) would benefit from more foraging opportunities and thus would remain in better body condition than less active lizards (CON). Body mass of WTR and CON Gila monsters did not differ significantly during the study, perhaps because body mass can vary significantly (15%–35%) in this species following a meal (Beck 1990), drink (Davis and DeNardo 2007), reproduction (Beck 2005), or defecation. Indeed, the body mass of individual Gila monsters in this study changed 25.4% ± 1.9% (range = 10%–41%) in 2005 and 20.6% ± 2.5% (range = 1%–46%) in 2006, which may be explained by observed variation in urinary bladder fluid (Fig. 2*A*, 2*D*). Tail volume provides a less variable index of body condition because these lizards are known to store fat, but not water, in their tail (Bogert and Martin del Campo 1956; Davis and DeNardo 2007). Tail volume did not differ between WTR and CON lizards in 2005. However, tail volume of WTR lizards was significantly greater than that of CON lizards from June to August 2006, which suggests that increased activity allowed WTR lizards to locate more prey than CON lizards, thereby benefitting body condition of WTR lizards.

Field and laboratory studies examining the effects of variation in water availability or direct water supplementation on the body condition of other species have yielded mixed results as well. For example, growth rates of two tropical *Anolis* lizards in the field are higher in the wet season than in the dry season, even when food and thermal conditions are similar (Stamps
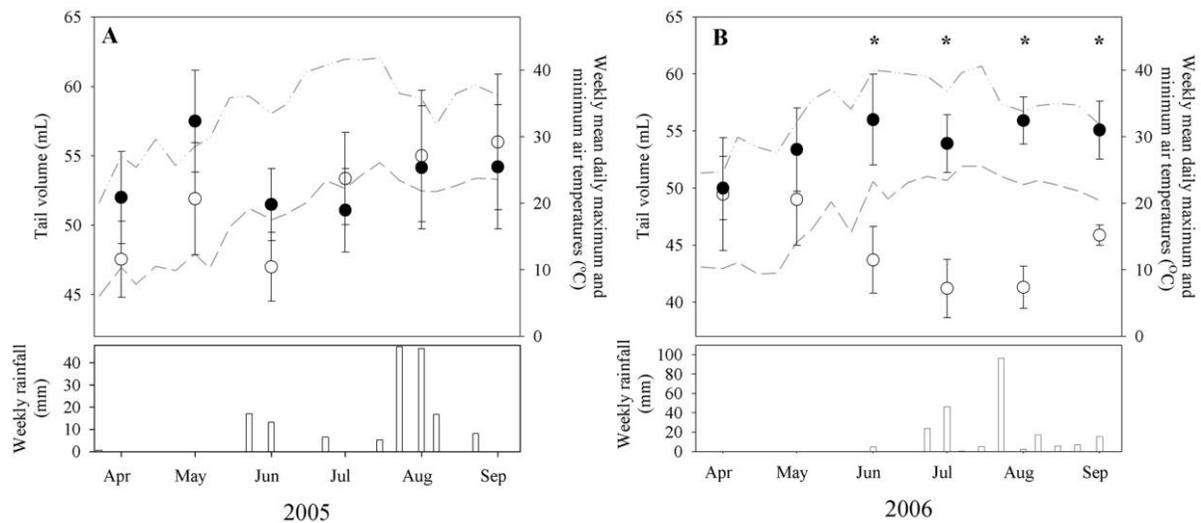
Figure 5. Seasonal variation in tail volume (mL) of water-supplemented (WTR; *filled circles*) and control (CON; *open circles*) Gila monsters (*Heloderma suspectum*) during the 2005 (WTR : CON = 12 : 1) and 2006 (13 : 11) active seasons in the Sonoran Desert. In 2005 (*A*), there were no significant differences in tail volume between WTR and CON lizards, and neither treatment changed significantly over time. WTR lizards maintained significantly greater tail volume than CON lizards in 2006 (*B*). Values shown are means ± 1 SE, and an asterisk indicates significant differences ($P < 0.05/N$) between treatments.

and Tanaka 1981; Jennsen and Andrews 1984). However, supplemental water produced no changes in growth of *Sceloporus undulatus* in the field, even though activity was increased (Jones et al. 1987). Laboratory experiments have shown that lizards with unrestricted water grow faster than those with limited access to water (Stamps and Tanaka 1981; Lorenzon et al. 1999), yet others have failed to demonstrate a significant difference in growth between water-supplemented and water-restricted lizards (Sears and Angilletta 2003). Similarly, supplemental water positively affects body mass or fat stores of other vertebrates (Kam and Degen 1994; El-Bakry et al. 1999) and invertebrates (Ward and Slowtow 1991; Floater 1997; McCluney and Date 2008) yet may have no effect on body mass in others (Ghosh 1975; Yahr and Kessler 1975).

Conclusions and Prospectus for Future Research Directions

Understanding how climatic variation affects the physiology, behavior, and, ultimately, population structure of animals is critical when considered in light of the substantial effects that climate change and urbanization are having on resource availability worldwide. Our data contribute to this understanding by identifying mechanistic relationships between water intake, hydric condition, behavior, and body condition in a long-lived desert lizard. As we continue to recognize patterns and mechanisms of change associated with these global phenomena (Shochat et al. 2006), the integrative hypothesis-driven approach of conservation physiology (Tracy et al. 2006; Wikelski and Cooke 2006) will be useful in clarifying the physiological mechanisms underlying conservation issues.

Literature Cited

Angilletta M.J. and A.R. Krochmal. 2003. The thermochron: a truly miniature and inexpensive temperature-logger. Herpetol Rev 34:31–32.

Banks P.B. and C.R. Dickman. 2000. Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. Can J Zool 78: 1775–1783.

Banta M.R. 2003. Merriam's kangaroo rats (*Dipodomys merriami*) voluntarily select temperatures that conserve energy rather than water. Physiol Biochem Zool 76:522–532.

Beck D.D. 1990. Ecology and behavior of the Gila monster in southwestern Utah. J Herpetol 24:54–68.

———. 2005. The Biology of Gila Monsters and Beaded Lizards. University of California Press, Berkeley.

Beck D.D. and R.D. Jennings. 2003. Habitat use by Gila monsters: the importance of shelters. Herpetol Monogr 17:111–129.

Beck D.D. and C.H. Lowe. 1994. Resting metabolism of helodermatid lizards: allometric and ecological relationships. J Comp Physiol B 164:124–129.

Bigler W.J. 1974. Seasonal movements and activity patterns of the collared peccary. J Mammal 55:851–855.

Blouin-Demers G. and P.J. Weatherhead. 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. J Anim Ecol 70:1006–1013.

Bogert C.M. and R. Martín del Campo. 1956. The Gila monster and its allies: the relationships, habits, and behavior of the lizards of the family Helodermatidae. Bull Am Mus Nat Hist 109:1–238.

Boutin S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can J Zool 68:203–220.

Chamaille-Jammes S., H. Fritz, M. Valeix, F. Murinadagomo, and J. Clobert. 2007. Resource variability, aggregation and direct density dependence in an open context: the local regulation of an African elephant population. J Anim Ecol 77: 135–144.

Chesson P., R.L.E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M.S.K. Ernest, A. Sher, A. Novoplansky, and J.F. Weltzin. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

Coe S.J. and J.T. Rotenberry. 2003. Water availability affects clutch size in a desert sparrow. Ecology 84:3240–3249.

Daltry J.C., T. Ross, R.S. Thorpe, and W. Wuster. 1998. Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. Ecography 21:25–34.

Davis J.R. and D.F. DeNardo. 2007. The urinary bladder as a physiological reservoir that moderates dehydration in a large desert lizard, the Gila monster *Heloderma suspectum*. J Exp Biol 210:1472–1480.

———. 2008. Water storage compromises endurance in an active forager: evidence of a trade-off between osmoregulation and locomotor performance. J Comp Physiol A 194: 713–718.

———. 2010. Seasonal patterns of body condition, hydration state, and activity of Gila monsters (*Heloderma suspectum*) at a Sonoran Desert site. J Herpetol (forthcoming).

Davis J.R., E.N. Taylor, and D.F. DeNardo. 2008. An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. J Arid Environ 72:1414–1422.

Degen A.A. 1997. Ecophysiology of Small Desert Mammals. 1st ed. Springer, Berlin.

DeNardo D.F., T.E. Zubal, and T.C.M. Hoffman. 2004. Cloacal evaporative cooling: a previously undescribed means of increasing evaporative water loss at higher temperatures in a desert ectotherm, the Gila monster, *Heloderma suspectum*. J Exp Biol 207:945–953.

Dmi'el R. 1972. Effect of activity and temperature on metabolism and water loss in snakes. Am J Physiol 223:510–516.

Duda J.J., A.J. Krzysik, and J.E. Freillich. 1999. Effects of drought on desert tortoise movement and activity. J Wildl Manage 63:1181–1192.

Dunham A.E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloperus merriami*. Ecology 59:770–778.

Eifler D.A. 1996. Experimental manipulation of spacing patterns in the widely foraging lizard *Cnemidophorus uniparens*. Herpetologica 52:477–486.

Eisen L., R.J. Eisen, and R.S. Lane. 2002. Seasonal activity patterns of *Ixodes pacificus* nymphs in relation to climate variation. Med Vet Entomol 16:235–244.

El-Bakry H.A., W.M. Zahran, and T.J. Bartness. 1999. Control of reproductive and energetic status by environmental cues in a desert rodent, Shaw's jird. Physiol Behav 66:657–666.

Field K.J., C.R. Tracy, P.A. Medica, R.W. Marlow, and P.S. Corn. 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biol Conserv 136:232–245.

Floater G.J. 1997. Rainfall, nitrogen, and host plant condition: consequences for the processionary caterpillar, *Ochrogaster lunifer*. Ecol Entomol 22:247–255.

Gallardo L.I. 2003. The Role of Thermal Biology on Home Range Ecology and Refuge Use in Gila Monsters. MS thesis. Arizona State University, Tempe.

Ghosh P.K. 1975. Thermoregulation and water economy in Indian desert rodents. Pp. 397–412 in I. Prakash and P.K. Ghosh, eds. Rodents in Desert Environments. Springer, The Hague.

Grant P.R., R. Grant, L.F. Keller, and K. Petren. 2000. Effects of El Nino events on Darwin's finch productivity. Ecology 81:2442–2457.

Henen B.T., C.C. Peterson, I.R. Wallis, K.H. Berry, and K.A. Nagy. 1998. Effects of climate variation on field metabolism and water relations of desert tortoises. Oecologia 117:365–373.

Jennsen T.A. and R.M. Andrews. 1984. Seasonal growth rates of the Jamaican lizard, *Anolis opalinus*. J Herpetol 18:338–341.

Jones S.M., S.R. Waldschmidt, and M.A. Potvin. 1987. An experimental manipulation of food and water: growth and time-space utilization of hatchling lizards. Oecologia 73:53–59.

Kam M. and A.A. Degen. 1994. Body-mass at birth and growth-rate of fat sand rat (*Psammomys obesus*) pups: effect of litter size and water-content of *Atriplex halimus* consumed by pregnant and lactating females. Funct Ecol 8:351–357.

Kreiter N.A. and D.H. Wise. 2001. Prey availability limits fecundity and influences the movement pattern of female fishing spiders. Oecologia 127:417–424.

Ladyman M. and D. Bradshaw. 2003. The influence of dehydration on thermal preferences of the Western tiger snake, *Notechis scutatus*. J Comp Physiol B 173:239–246.

Langlands P.R., K.E.C. Brennan, and D.J. Pearson. 2006. Spiders, spinifex, rainfall, and fire: long-term changes in an arid spider assemblage. J Arid Environ 67:36–59.

Littell R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for Mixed Models. SAS Institute, Cary, NC.

Lorenzon P., J. Colbert, A. Oppliger, and H. John-Alder. 1999. Effect of water constraint on growth rate, activity, and body temperature of yearling common lizard (*Lacerta vivpara*). Oecologia 118:423–430.

Lowe C.H., C.R. Schwalbe, and T.B. Johnson. 1986. The venomous lizards. Pp. 7–19 in The Venomous Reptiles of Arizona. Arizona Game and Fish Department, Phoenix.

Madsen T., B. Ujvari, R. Shine, and M. Olsson. 2006. Rain, rats, and pythons: climate-driven population dynamics of predators and prey in tropical Australia. Aust Ecol 31:30–37.

Mautz W.J. 1982. Patterns of evaporative water loss. Pp. 443–481 in C. Gans, ed. Biology of the Reptilia. Vol. 12. Academic Press, New York.

McClanahan L.L. 1967. Adaptations of the spadefoot toad, *Scaphiopus couchi*, to desert environments. Comp Biochem Physiol 20:73–99.

McCluney K.E. and R.C. Date. 2008. The effects of hydration on growth of the house cricket, *Acheta domesticus*. J Insect Sci 8:1–9.

Meserve P.L., D.A. Kelt, W.B. Milstead, and J.R. Gutierrez. 2003. Thirteen years of shifting top-down and bottom-up control. Bioscience 53:633–646.

Minnich J.E. 1976. Water procurement and conservation by desert reptiles in their natural environment. Isr J Med Sci 12:740–758.

Nagy K.A. and P.A. Medica. 1986. Physiological ecology of desert tortoises in southern Nevada. Herpetologica 42:73–92.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annu Rev Ecol Syst 5:195–214.

Orland M.C. and D.A. Kelt. 2007. Responses of a heteromyid rodent community to large- and small-scale resource pulses: diversity, abundance, and home-range dynamics. J Mammal 88:1280–1287.

Pelletier L. and J.N. McNeil. 2003. The effect of food supplementation on reproductive success in bumblebee colonies. Oikos 103:688–694.

Peterson C.C. 1996a. Anhomeostasis: seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. Physiol Zool 69:1324–1358.

———. 1996b. Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. Ecology 77:1831–1844.

Polis G.A., ed. 1990. The Biology of Scorpions. Stanford University Press, Stanford, CA.

Reichman O.J. and K.M. Van de Graaf. 1973. Seasonal activity and reproductive patterns of five species of Sonoran Desert rodents. Am Midl Nat 90:118–126.

Schoech S.J., E.S. Bridge, R.K. Boughton, S.J. Reynolds, J.W. Atwell, and R. Bowman. 2008. Food supplementation: a tool to increase reproductive output? a case study in the threatened Florida scrub-jay. Biol Conserv 141:162–173.

Schoech S.J. and T.P. Hahn. 2007. Food supplementation and timing of reproduction: does the responsiveness to supplementary information vary with latitude? J Ornithol 148:625–632.

Sears M.W. and M.J. Angilletta. 2003. Life-history variation in the sagebrush lizard: phenotypic plasticity or local adaptation? Ecology 84:1624–1634.

Sexton O.J. and H. Heatwole. 1968. An experimental investigation of habitat selection and water loss in some anoline lizards. Ecology 49:762–767.

Shine R. and G.P. Brown. 2008. Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry Tropics. Philos Trans R Soc B 363:363–373.

Shochat E., P.S. Warren, S.H. Faeth, N.E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic ecology. Trends Ecol Ecol 21:186–191.

Shoemaker V.H. and K.A. Nagy. 1977. Osmoregulation in amphibians and reptiles. Pp. 449–471 in E. Knobil, ed. Annual Review of Physiology. Vol. 39. Annual Reviews, Palo Alto, CA.

Small T.W., P.J. Sharp, and P. Deviche. 2007. Environmental regulation of the reproductive system in a flexibly breeding Sonoran Desert bird, the rufous-winged sparrow, *Aimophila carpalis*. Horm Behav 51:483–495.

Stamps J. and S. Tanaka. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). Ecology 62:33–40.

Sullivan B.K. and P.J. Fernandez. 1999. Breeding activity, estimated age structure, and growth in Sonoran Desert anurans. Herpetologica 55:334–343.

Taylor E.N., D.F. DeNardo, and M.A. Malawy. 2004. A comparison between point- and semi-continuous sampling for assessing body temperature in a free-ranging ectotherm. J Therm Biol 29:91–96.

Taylor E.N., M.A. Malawy, D.M. Browning, S.V. Lamar, and D.F. DeNardo. 2005. Effects of food supplementation on the physiological ecology of female Western diamond-backed rattlesnakes (*Crotalus atrox*). Oecologia 144:206–213.

Tracy C.R., K.E. Nussear, T.C. Esque, K. Dean-Bradley, C.R. Tracy, L.A. DeFalco, K.T. Castle, L.C. Zimmerman, R.E. Espinoza, and A.M. Barber. 2006. The importance of physiological ecology in conservation biology. Integr Comp Biol 46:1191–1205.

Ward D. and R. Slotow. 1991. The effects of water availability on the life history of the desert snail, *Trochoidea seetzeni*. Oecologia 90:572–580.

Waser P. 1975. Monthly variations in feeding and activity patterns of the mangabey, *Cercocebus albigena* (Lydekker). Afr J Ecol 13:249–263.

Wikelski M. and S.J. Cooke. 2006. Conservation physiology. Trends Ecol Evol 21:38–46.

Yahr P. and S. Kessler. 1975. Suppression of reproduction in water-deprived Mongolian gerbils. Biol Reprod 12:249–254.

Zar J.H. 1999. Biostatistical Analysis. 4th ed. Prentice Hall, Upper Saddle River, NJ.