

Water storage compromises walking endurance in an active forager: evidence of a trade-off between osmoregulation and locomotor performance

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Abstract Trade-offs between locomotor performance and load-carrying in animals are well-established and often result from requisite life processes including reproduction and feeding. Osmoregulation, another necessary process, may involve storage of fluid in the urinary bladder of some species. The purpose of this study was to determine whether storage of urine in the urinary bladder reduces walking endurance in an actively foraging lizard. The results of our paired-design study indicate that the volume of fluid stored in the urinary bladder (36.5 ± 1.6 ml) contributed a significant load (9.2% of body mass) to the lizards. This load resulted in a disproportionate $24.5 \pm 2.8\%$ decrement in walking endurance. Specifically, *Gila* monsters walked at a fixed pace for a significantly shorter duration when the urinary bladder contained fluid (26 ± 2.0 min) compared to when the bladder was empty (34.3 ± 2.3 min). Since fluid stored in the bladder contributes to osmoregulation in this species, our results indicate the presence of a trade-off between osmoregulation and endurance in *Gila* monsters. Bearing other loads (e.g., a clutch or meal) influences the evolution of life-history traits and foraging strategy; thus the negative effect of fluid storage on endurance may also have evolutionary implications.

Keywords Foraging · *Heloderma* · Physiological reservoir · Water balance

Abbreviations

E	Empty urinary bladder condition
F	Fluid in urinary bladder condition
RBM	Relative bladder mass
RCM	Relative clutch mass
RMM	Relative meal mass
SEM	Standard error of the mean

Introduction

Nearly all solutions to biological problems have secondary consequences reflecting character interactions between processes. The interactions between load carrying and locomotor performance provide a familiar model of such trade-offs, which benefit one process at the expense of the other. The additional load associated with pregnancy or gravidity can impair a variety of locomotor performance measures including acceleration, sprint speed, endurance, flight, and swimming, resulting in a significant “cost of reproduction” (Shine 1980; Bauwens and Theon 1981; Seigel et al. 1987; Lee et al. 1996; Plaut 2002; Shine 2003b; Aubret et al. 2005). The severity of the cost varies, but can include reduced foraging ability and increased predation risk for females (Shine 1980; Berglund and Rosenqvist 1986; Magnhagen 1991; Lee et al. 1996; Reguera and Gomendio 1999). Similarly, consumption of a large meal (25–100% of predator body mass) can produce significant decrements in locomotor performance in both sexes, also resulting in reduced foraging ability or increased predation risk or both (Garland and Arnold 1983; Huey et al. 1984; Mehta 2006). The bulk of research has examined these

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trade-offs in squamate reptiles (i.e., snakes and lizards) (Shine 1980, Shine 2003a, b; Bauwens and Theon 1981; Huey et al. 1984; Seigel et al. 1987; Aubret et al. 2005), yet they occur commonly in a variety of invertebrates (Winfield and Townsend 1983; Berglund and Rosenqvist 1986; Gu et al. 2006; Lorenz 2007) as well as fish (James and Johnston 1998; Plaut 2002), birds (Lee et al. 1996; Veasey et al. 2001), and mammals (Trillmich et al. 2003; Hoogland et al. 2006).

Osmoregulation, like reproduction and feeding, is a requisite life process that may also have deleterious effects on locomotor performance. This trade-off is most likely to occur in species that possess a physiological reservoir—defined here as an anatomical location where water can be sequestered from, and later returned to, general circulation. Scientists have described and empirically studied the osmoregulatory role of the bladder in amphibians and chelonians for centuries (Townson 1799; Darwin 1839; Minnich 1976; Shoemaker and Nagy 1977; Jorgensen 1998) and we now know that many anuran amphibians and chelonians rely on this osmoregulatory mechanism to survive when water is unavailable (Ruibal 1962; McClanahan 1967; Minnich 1976; Shoemaker and Nagy 1977). Recently, we demonstrated that a desert lizard, the Gila monster (*Heloderma suspectum*) (Cope 1869), also uses its urinary bladder as a physiological reservoir (Davis and DeNardo 2007), but it is not likely the only lizard to do so considering that many other species possess a urinary bladder (Beuchat 1986). The amount of fluid stored is species-dependent, but may approach or exceed the mass of a meal or litter. Desiccation-resistant species such as the desert tortoise (*Gopherus agassizii*) and Gila monsters and obligatory aquatic species like *Xenopus* frogs typically store volumes of fluid equivalent to 1–30% of their body mass (Bentley 1979; Nagy and Medica 1986; Peterson 1996; Davis and DeNardo 2007). Species highly susceptible to desiccation, including the desert anurans *Bufo cognatus* and *Scaphiopus couchii*, may store fluid in amounts equivalent to 50–100% of body mass (Ruibal 1962; McClanahan 1967; Shoemaker et al. 1969). The fluid reservoir provides a critical osmoregulatory benefit for these animals, but the resultant load is considerable and may affect locomotor performance. However, to date, any effects of bladder fluid storage on locomotion are unexplored.

We used a paired-comparison design to test the hypothesis that carrying fluid in the urinary bladder reduces locomotor performance. We measured the walking endurance of adult Gila monsters when each lizard's urinary bladder contained an ecologically relevant amount of fluid and after the bladder was experimentally emptied. Endurance is a functionally significant measure for this species because Gila monsters are active-foraging lizards that use a slow methodical gait to locate widely dispersed vertebrate nests

(Bogert and Martin del Campo 1956; Lowe et al. 1986; Beck 1990). Foraging bouts typically last hours with Gila monsters searching at average speeds ranging from 0.3 to 0.6 km/h (Beck 2005; Davis and DeNardo unpublished; Geinger personal communication). Moreover, Gila monsters can sequester, in their bladder, urine equivalent to 20% or more of body mass from which water can later be absorbed to significantly delay dehydration during drought (Davis and DeNardo 2007). For these reasons and because Gila monsters are amenable to treadmill studies (John-Alder et al. 1983; Beck et al. 1995) and urinary bladder manipulations (Davis and DeNardo 2007), these lizards provide an ideal model with which to examine the potential trade-off between osmoregulation and locomotion.

Methods

Study species and care

The Gila monster is a large (adult body mass 350–600 g and snout-vent length 300–360 mm), long-lived (~20 years), and venomous lizard that predominantly inhabits the Sonoran Desert of Arizona and Mexico (Bogert and Martin del Campo 1956; Beck 2005). These oviparous lizards produce heavy clutches (approximately 25–40% of body mass) every 2–3 years and are infrequent binge feeders that may consume prey equivalent to 35% of body mass (Lowe et al. 1986; Beck 2005). We obtained animals used in this study from the Arizona Game and Fish Department under permit # SP627813. We housed six adult lizards (2F:4 M) individually in plastic cages (36 × 24 × 12 cm, Freedom Breeder, Turlock, CA, USA) with subsurface heating available constantly at one end to allow thermoregulation. We maintained the cages in a temperature-controlled room with a 0700–1900 h photophase and 25°C air temperature. Prior to the study, we fed lizards one adult mouse (25 g) every 7–10 days and provided water ad libitum. To eliminate confounding variables associated with feeding and reproduction, we withheld food from lizards for 10 days prior to the study and used ultrasonography (Concept/MLV; Dynamic Imaging, Ltd, Livingston, Scotland, UK) to confirm that lizards were non-reproductive.

Urinary bladder condition

The volume of fluid stored in the urinary bladder is variable and not requisite, particularly in captivity, thus we randomly selected six Gila monsters for this study from our laboratory colony by using ultrasonography to visualize the urinary bladder in the sagittal plane and including the first six lizards whose urinary bladder dimensions were greater than $L = 30.0 \times D = 10.0$ mm. We chose these dimensions

because we have shown that a urinary bladder of this size provides a significant long-term osmoregulatory benefit to *Gila* monsters (Davis and DeNardo 2007) and is within the range of sizes we have measured for this species in the field (Davis and DeNardo unpublished). We measured each lizard's body mass (± 0.1 g) and urinary bladder height and length (± 0.1 mm) and then recorded walking endurance twice (see below) when the urinary bladder contained fluid (F).

We then removed the fluid from each lizard's urinary bladder following Davis and DeNardo (2007) to create an empty bladder condition (E). Briefly, we intubated and then anesthetized each lizard with isoflurane, transurethral catheterized the urinary bladder using a # 8 Foley catheter, used ultrasonography to verify proper catheter positioning, removed all bladder contents using a 60 ml syringe, and used ultrasonography to verify that the urinary bladder was empty. We recorded the volume of fluid removed from the bladder (± 1.0 ml) and the lizard's E body mass. To verify that mass could be used for analyses throughout, we compared the volume of urine removed to the difference between F and E body mass to verify that 1 ml of fluid weighed approximately 1 g; volume and mass were always within 1.0. We allowed lizards to recover for 72 h and then measured endurance twice under this condition (E).

Endurance trials

The order of trials could not be randomized as attempts to transurethral fill the bladder resulted in urination shortly after removal of the catheter. We conducted two endurance trials under each condition separated by 48 h on a 9 day schedule (Fluid = days 1 and 3; drain bladder and recover = days 4–6; empty = days 7 and 9) to minimize potential effects of fasting and water restriction on muscle performance and hydration state. To confirm that trial order does not effect endurance (i.e., the first trial does not provide learning or enhanced stamina so that endurance changes in a second trial), we ran two empty bladder condition trials on six *Gila* monsters not used in the previous study. In this control study, we emptied the bladder of fluid from anesthetized animals, conducted a first trial 2–4 days post-anesthesia, and a second trial 7–8 days after the first.

We used a custom built motorized treadmill consisting of a rubberized tread (100 cm \times 13.5 cm; functional length 49 cm), enclosed in a rectangular Plexiglas box (L: 50 cm \times W: 14 cm \times H: 14 cm) with a removable lid. We controlled treadmill speed using a Treadmill Simplex Controller (Columbus Instruments, Columbus, OH, USA) which we calibrated prior to use and periodically between trials to verify proper speed. We conducted all endurance trials in a temperature-controlled chamber set at 30°C because this temperature approximates both the preferred

body temperature (29.0°C) of *Gila* monsters measured in a thermal gradient (Bogert and Martin del Campo 1956) and the mean activity temperatures (28.5–29.5°C) of free-ranging *Gila* monsters from several localities (Beck 2005). Therefore, locomotor performance is likely maximized at this temperature. We moved lizards from their home cage into individual plastic containers (15 \times 20 \times 36 cm) and placed the containers in the 30°C chamber 4 h prior to trials to allow lizards to adjust to the trial temperature. We exercised lizards at 0.8 km/h because this pace is sub-maximal (Beck et al. 1995), but above this species' maximum aerobic speed (0.7 km/h) (John-Alder et al. 1983) and thus not sustainable. Moreover, 0.8 km/h has been used previously to examine temperature effects on locomotion and thus is suited for comparisons with published data (Beck et al. 1995). We placed the lizard on the tread, turned on the motor, and increased the speed slowly to 0.8 km/h, which initiated walking in most cases. Once started, lizards typically sustained a steady pace until exhaustion. We stimulated reluctant lizards to initiate or continue walking by lightly touching the tail and hind limbs with a small (3 cm wide) wire brush. We concluded each trial when the lizard stopped walking and failed to respond to three successive stimulations. We used a stopwatch to measure each lizard's endurance to the nearest second. In our experiment comparing fluid-filled and empty bladders, we measured endurance of each lizard four times, twice under each urinary bladder condition (F and E), allowing lizards 48 h to recover between trials, and used each lizard's maximum performance under each condition for analyses.

Data analysis

We tested data for violations of statistical assumptions prior to inference and completed statistical analyses using JMP IN (Version 5.1, SAS Institute, Inc., Cary, NC, USA). We used paired *t* tests to compare: (1) F and E body mass to determine whether the bladder volume contributed a significant load, (2) Trials 1 and 2 endurance values for F and E to determine whether performance varied between trials within bladder condition, and (3) maximum value of F and E walking endurance of *Gila* monsters to determine whether endurance differs between bladder conditions. We calculated the relative bladder mass (RBM; ratio of bladder fluid mass to E body mass), as a measure of the physical burden imposed on lizards in this study, which is analogous to the relative clutch mass (RCM; ratio of clutch or brood mass/body mass), commonly used in cost-of-reproduction studies to describe a female's burden (Shine 1980; Seigel et al. 1987). We used correlation to evaluate the relationship between RBM and change in endurance (E minus F endurance). Alpha-level was 0.05 for all analyses and values reported are mean \pm 1 SEM.

Results

The results from the control study indicate that endurance does not change between trials ($N=6$; paired t test— $P=0.90$; Trial 1 mean = 34.2 ± 1.5 min; Trial 2 mean = 34.3 ± 2.0 min). Moreover, these results also suggest that the 72 h post-anesthesia recovery time was sufficient to remove any effect that anesthesia might have on endurance.

Gila monsters were significantly heavier when the urinary bladder contained fluid (433.3 ± 44.6 g) compared to when the urinary bladder was empty (396.8 ± 44.7 g; $t=22.1$, $df=5$, $P<0.0001$) indicating that the volume of fluid stored in the urinary bladder (36.5 ± 1.6 ml) contributed a significant load. The RBM of 0.093 ± 0.006 showed that bladder fluid contributed 9.2% additional mass or roughly half of the maximum reported bladder contribution for this species (Davis and DeNardo 2007). This relatively modest additional load resulted in a disproportionate $24.5 \pm 2.8\%$ decrement in walking endurance. Endurance did not differ between trials within either bladder condition; F ($t=-0.15$, $df=5$, $P=0.56$) and E ($t=0.52$, $df=5$, $P=0.31$), so maximum endurance was used for comparisons between F and E bladder conditions. Endurance of Gila monsters was significantly greater when the urinary bladder was empty (34.3 ± 2.3 min) compared to when the bladder contained fluid (26.0 ± 2.0 min) (Fig. 1; $t=8.73$, $df=5$, $P=0.0002$). However, the performance decrement did not occur simply because of increased mass, since the correlation between RBM and endurance decrement was not significant ($r=0.22$, $N=6$, $P=0.66$).

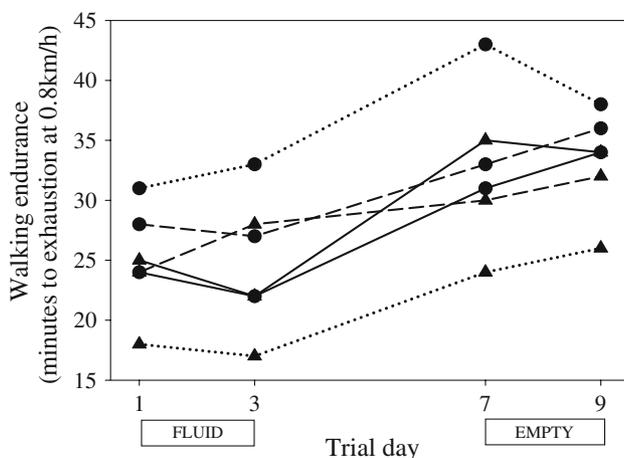


Fig. 1 The maximum walking endurance of *Heloderma suspectum* is significantly greater when the urinary bladder contains fluid compared to when the bladder is empty ($t=8.73$, $df=5$, $P<0.001$). Note that different line and symbol combinations represent individual lizards ($N=6$). Bladder condition during each trial is identified by the boxes below the x-axis

Discussion

Performance implications

Fluid reserved in the urinary bladder of Gila monsters provides these lizards a critical osmoregulatory resource (Davis and DeNardo 2007) at the cost of reduced endurance (Fig. 1). Lizards in this study retained 36.5 ± 1.6 ml of fluid, which is enough volume to either significantly delay dehydration or rapidly rehydrate these lizards (Davis and DeNardo 2007); however, endurance decreased significantly from 34.3 ± 2.3 min (E) to 26 ± 2.0 min (F) under this load (Fig. 1). Notably, these endurance values are consistent with those reported by Beck et al. (1995) for adult (30.0 ± 1.2 min) and all (28.5 ± 3.5 min) Gila monsters exercised at 0.8 km/h, though bladder condition was unknown. The mean $24.5 \pm 2.8\%$ performance decrement reported in this study nearly matches the mean decrement (24.6%) reported in 16 published studies of reproductive female lizards (reviewed in Shine 2003a, b) and is similar to post-feeding decrements reported for squamates (19–60%) (Garland and Arnold 1983; Huey et al. 1984; Seigel et al. 1987; Shine 2003a, b). It is unknown, however, whether the endurance decrement reported herein also results in reduced foraging ability or elevated predation risk or both as described in other species. Moreover, these consequences can directly influence the behavior of some animals (Bauwens and Theon 1981; Cooper et al. 1990; Schwarzkopf and Shine 1992), but whether a similar behavioral effect occurs as a result of the trade-off between osmoregulation and endurance is unknown. Furthermore, the extent to which the trade-off exists at other speeds or on other locomotor performance measures (e.g., maximum speed, maximum aerobic speed, cost of locomotion) requires additional study.

Fluid stored in the urinary bladder of Gila monsters in this study contributed a modest 9.2% additional load (RBM = 0.093 ± 0.006), but we have previously reported a 20% load (RBM = 0.20) for this species (Davis and DeNardo 2007), suggesting the potential for a much greater impact of bladder fluid on endurance than that reported here. Regardless, the load was substantial enough to reduce locomotor performance significantly (Fig. 1). The performance decrement was not solely related to the mass of the load, indicating that other characteristics associated with bladder fluid storage negatively affect endurance. For example, we have observed that a full Gila monster urinary bladder (80×30 mm; >60 ml) fills the majority of the intracoelomic cavity and may obstruct lung function causing reduced aerobic capacity. Additionally, changes in body shape, physiology, and load position associated with reproduction or feeding can directly influence locomotor performance and should be considered (McLean and

Speakman 2000; Olsson et al. 2000; Shine 2003a, b). The RBM of Gila monsters is within the ranges of RCM reported for lizards [0.04–0.50 and 0.04–0.32 by Vitt and Price (1982) and Shine (1992), respectively], and also relative meal mass (RMM) reported for lizards (0.05–0.70) (Pianka and Vitt 2003). Since RCM and RMM influence the evolution of life-history traits and foraging strategy (Shine 1980; Huey and Pianka 1981; Vitt 1981; Shine 1992), the negative trade-off between fluid storage for osmoregulation and endurance may also have evolutionary implications.

Ecological implications

Recently, Shine (2003a) emphasized the importance of evaluating the effects of body state (e.g., reproductive status, gut contents) on locomotion in an appropriate ecological context. This is an important, yet challenging, undertaking because locomotor performance of animals is influenced by a variety of dynamic biological conditions that vary in intensity, and thus consequence, over time (Garland and Arnold 1983; Cooper et al. 1990; Shine 2003b; Trillmich et al. 2003; Mehta 2006). Consider lizards, a diverse group in which locomotor performance typically decreases with increasing load and notably, some load is nearly always carried. Lizards' stomachs contain food 35–100% of the time (Huey et al. 2001), nearly half of lizard species possess a urinary bladder of variable volume (Beuchat 1986; Davis and DeNardo 2007), and females may produce clutches 1–3 times annually or once every 1–4 years depending on species and resource availability (Pianka and Vitt 2003). Thus, the combination of these conditions may cause these animals to carry a substantial load the majority of time, effectively establishing sub-maximal locomotor performance as the normal functional state. Gila monsters likely experience this performance decrement since these lizards consume large meals (RMM = 0.35–0.50), use the bladder as a physiological reservoir (RBM \leq 0.25), and produce relatively large clutches (RCM = 0.35) every 1–3 years (Lowe et al. 1986; Beck 2005; Davis and DeNardo 2007). Moreover, Beck et al. (1995) emphasized the potential negative effect that endurance decrements may have on key high-intensity physical activities including male–male agonistic interactions. Long-term field studies are clearly needed to elucidate the relationships between these dynamics and any associated consequences in free-ranging animals.

Evolutionary implications

The broader implications of the osmoregulation–locomotion trade-off are unknown. Not all vertebrates have a urinary bladder, but the organ is present in all mammals,

chelonians, amphibians, and tuatara and roughly half of the lizards and fish (Shoemaker and Nagy 1977; Bentley 1979; Beuchat 1986). The capacity (i.e., volume) and specific functions of the bladder vary by species from osmoregulation (anurans, chelonians, *H. suspectum*) to social signaling (canids and felids). Regardless, bladder contents contribute a load and thus likely compromise locomotor performance and influence the biology of a variety of species. Evidence supporting the notion that the osmoregulation–locomotion trade-off has significant evolutionary implications can be found in species with contrasting urinary bladder use strategies. For example, many species known to store fluid in the bladder, like the desert tortoise (*G. agassizi*), Colorado River toad (*Bufo alvarius*), and Gila monster, do not rely on locomotion to avoid predation; rather each primarily depends on relatively large body size and armor, toxins, or venom, respectively. Thus, one potential cost of fluid storage, increased predation risk due to decreased locomotor ability, may be moderated using compensatory defense mechanisms thereby reducing selection against fluid storage. Further evidence suggesting evolutionary implications can be found in birds. The need to reduce load in order to improve flight capacity has likely favored selection against fluid storage, ultimately eliminating copious fluid storage from the biology of most birds. Interestingly, and in support of the proposed conflict between flight and fluid storage, large flightless ratites, including ostriches (Duke et al. 1995), store fluid in a modified out-pocketing of the proctodeum. Furthermore, many birds conspicuously eliminate short-term stored digestive and nitrogenous wastes when they initiate flight or running. Together, these examples support the notion that the osmoregulation–locomotion trade-off has a variety of significant evolutionary implications deserving of further study.

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