Heads or tails? Sexual dimorphism in helodermatid lizards

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Abstract: We tested the hypothesis that helodermatid lizards (Gila monsters, *Heloderma suspectum* Cope, 1869, and beaded lizards, *H. horridum* (Wiegmann, 1829)) show sexual dimorphism in morphological traits related to male–male agonistic behaviors. Male–male combat in helodermatid lizards involves repeated sequences of ritualized grappling. Male Gila monsters use their heads in attempts to gain or maintain a superior position during repeated combat bouts that may last for hours. Pairs of fighting male beaded lizards form spectacular body arches, with abdomens adpressed and snouts, forelimbs, and tail tips contacting the ground. We measured body size, head size, and tail length in 208 preserved *H. suspectum*, and body size and tail length (but not head size) in 79 live *H. horridum*, then tested for sexual dimorphism using analysis of covariance. Male Gila monsters had proportionately larger heads than females but did not differ in tail length or body size. Male beaded lizards had proportionately longer tails than females and were larger in body size only when the largest individuals were included in the analysis. Differences in head dimensions (in *H. suspectum*) and tail length (in *H. horridum*) are likely the result of sexual selection acting through male–male agonistic behaviors in this unique lizard taxon.

Résumé : Nous avons évalué l'hypothèse selon laquelle les lézards hélodermatidés (les monstres de Gila, *Heloderma suspectum* Cope, 1869 et les lézards perlés, *H. horridum* (Wiegmann, 1829)) possèdent un dimorphisme sexuel des caractéristiques morphologiques reliées aux comportements agonistes mâle–mâle. Les combats entre mâles chez les lézards hélodermatidés impliquent des séquences répétées de prises de corps ritualisées. Les monstres de Gila utilisent leur tête lors de tentatives pour atteindre ou maintenir une position de supériorité durant des épisodes répétés de combat qui peuvent se poursuivre pendant des heures. Durant leurs combats, les paires de lézards perlés mâles forment des arcs spectaculaires avec leurs corps, leurs abdomens accolés et leurs museaux, pattes antérieures et bouts de la queue en contact avec le sol. Nous avons mesuré la taille corporelle, la taille de la tête et la longueur de la queue chez 208 spécimens de musée d'*H. suspectum*, ainsi que la taille du corps et la longueur de la queue (mais non la taille de la tête) chez 79 spécimens vivants d'*H. horridum*; nous avons ensuite vérifié le dimorphisme sexuel à l'aide de l'analyse de covariance. Les monstres de Gila mâles ont la tête proportionnellement plus grande que les femelles, mais ne diffèrent pas en ce qui a trait à la longueur de la queue ou de la taille du corps. Les lézards perlés mâles ont une queue proportionnellement plus longue que celle des femelles et n'ont une taille corporelle supérieure que lorsque les individus les plus grands sont inclus dans l'analyse. Ces différences de taille de la tête (chez *H. suspectum*) et de longueur de la queue (chez *H. horridum*) sont vraisemblablement le résultat de la sélection sexuelle qui agit à travers les comportements agonistes entre mâles chez ce taxon tout à fait particulier de lézards.

[Traduit par la Rédaction]

Introduction

Sexual size dimorphism occurs in many animals and has been attributed to several evolutionary and ecological factors, such as intersexual differences in niches and growth rates and male–male agonistic behaviors (Shine 1978; Berry and Shine 1980; Stamps 1983; Carothers 1984; Shine 1989, 1994; Herrel et al. 1999; Blanckenhorn 2005; Pomfret and Knell 2006). Sexual dimorphism may be expressed as intersexual differences in many other traits besides body size, such as the size of appendages (i.e., heads, tails, and limbs) or ornamentation, scalation, and coloration. The specific traits influenced by sexual selection may vary with the type of mating system (Stamps 1983; Andersson 1994; Arnold and Duvall 1994).

In species where males compete strongly for mates, sexual selection may act on body size or morphology. Larger individuals, or those with larger heads, may have an advantage in physical tests of dominance (Shine 1978; Gvozdík and Van Damme 2003; Pomfret and Knell 2006). The winner of male–male agonistic interactions may gain better access to females and thereby show increased reproductive success (Bull and Pamula 1996; Wikelski et al. 1996; Gvozdík and Van Damme 2003). If male reproductive success is directly influenced by either larger body size or larger head size, relative to conspecific males, then selection might favor those traits in males alone.

In the helodermatid lizards (Gila monsters, *Heloderma suspectum* Cope, 1869, and beaded lizards, *H. horridum* (Wiegmann, 1829)), male–male combat involves repeated sequences of strenuous, ritualized grappling postures (Gates 1956; Demeter 1986; Ramírez-Velázquez and Guichard-Romero 1989; Beck 1990; Beck and Ramírez-Bautista 1991). During these encounters, individuals use their heads

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Fig. 1. (*a*) Two male Gila monsters (*Heloderma suspectum*) engaged in combat behavior. Individuals use their heads and torsos to subdue each other, and the winner of the encounter is typically the one who can repeatedly force his opponent down into an inferior position during a series of bouts. (*b*) Body arch formed by male beaded lizards (*H. horridum*) during combat; the individual with the longer tail can form a higher arch and maintain a dominant position.
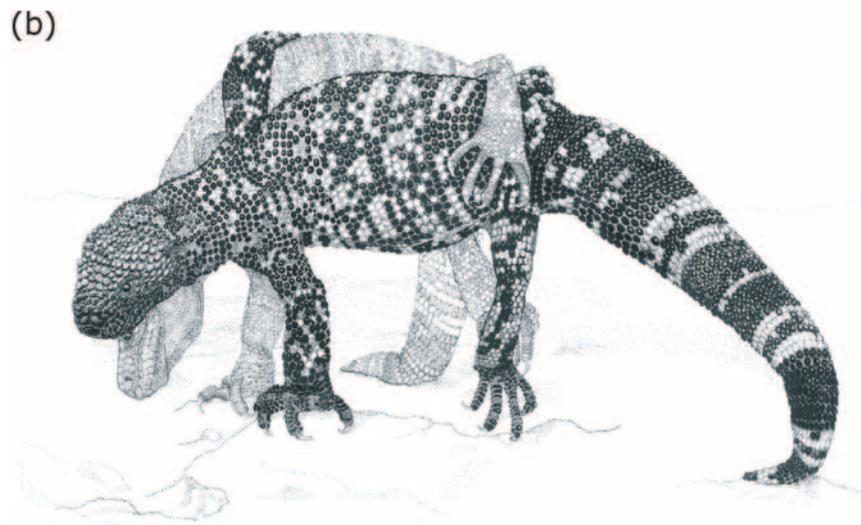
and torsos in attempts to subdue each other (Fig. 1). The winner is typically the one who can repeatedly force his opponent into an inferior position during a series of bouts (Beck 1990; Beck and Ramírez-Bautista 1991). In both species, combat may range from one or two bouts lasting only a few minutes to a series of bouts extending several hours (Ramírez-Velázquez and Guichard-Romero 1989; Beck 1990; Beck and Ramírez-Bautista 1991; authors' personal observations). Participants occasionally bite and sustain superficial lacerations.

Pairs of agonistic male *H. horridum* form a spectacular body arch, with their venters adpressed and snouts, fore-limbs, and tail tips forming contact points on the ground (Fig. 1; Ramírez-Velázquez and Guichard-Romero 1989; Beck and Ramírez-Bautista 1991). The combatants remain in the body arch until pressure from the individuals pushing laterally against one another eventually collapses it, with the dominant lizard typically ending up on top (Beck and Ramírez-Bautista 1991). Tail strength and possibly tail length appear to be important factors in the ability to form a higher arch and emerge on top when the arch collapses (Beck and Ramírez-Bautista 1991).

In *H. suspectum*, the body arch is replaced by a body twist, which begins as one male climbs on top of the other,

clasping his forelimbs around his opponent in a dorsal straddle. The bottom lizard responds by raising his head and twisting his head and body against his opponent in an attempt to gain the superior position (see Fig. 10 in Beck 1990). The superiorly positioned lizard responds by arching his back and pointing his snout upward. This action results in a body twist with each lizard hissing and rocking in an apparent effort to either gain or maintain a superior position. The head is frequently used in attempts to press the opponent to the ground or gain the superior position (Fig. 1).

Male–male combat in helodermatid lizards likely functions in dominance and social hierarchies, as it does in other squamate reptiles (Carpenter 1967; Carpenter and Ferguson 1977). Combat occurs seasonally when individuals are reproductively active (Goldberg and Lowe 1997; Goldberg and Beck 2001; Beck 2005). In *H. suspectum*, males fight during the spring (when both sexes commonly pair within shelters); *H. horridum* combat takes place during the fall (Beck 1990; Beck and Ramírez-Bautista 1991; Beck and Jennings 2003; Gienger 2003). In nature, Gila monster combat has been observed almost exclusively when a female inhabits a shelter near the fighting males (Beck 1990, 2005; Gienger 2003).

In this study we test the hypothesis that helodermatid lizards show sexual dimorphism, and we identify specific characters upon which sexual selection may have acted. Helodermatid lizards exhibit some traits that suggest sexual selection may be acting on their physiology and morphology. Males appear to have higher aerobic capacities than females (Beck et al. 1995), and subtle differences have been anecdotally observed in head size, body proportions, and tail length (Bogert and Martín del Campo 1956; Alvarez del Toro 1982; Seward 2002).

Given the specific combat behaviors of male helodermatid lizards, we consider body size, head morphology, and tail length as morphological characters that are important in combat and likely influenced by sexual selection. We predict that if sexual selection has acted on these traits, male helodermatids will (*i*) achieve larger body size than females and (*ii*) have larger heads than females and (*iii*) male *H. horridum* will have proportionately longer tails than females.

Methods

We measured 208 preserved *H. suspectum* and 79 live *H. horridum*. The preserved specimens were housed in the herpetological collections of the University of Arizona (Tucson, Arizona) and the Natural History Museum of Los Angeles County (Los Angeles, California). For all lizards, we measured snout-to-vent length (SVL) and tail length (TL; distance from vent to tip of tail) to the nearest 1.0 mm with a straight rule. For each *H. suspectum*, we used dial calipers to measure maximum head width (HW) and head length (HL; distance from the rostral scale to the intersection with a perpendicular line across the back of the head connecting the superior apices of the tympanic openings) (Figs. 2 and 3). We considered adults to be individuals with a minimum SVL of 239 mm (the minimum size at which *H. suspectum* reach sexual maturity, based on histological examination by Goldberg and Lowe 1997). We included only individuals whose sex could be verified via dissection to reveal testes, ovaries, follicles, or eggs

(preserved *H. suspectum*) or by extrusion of hemipenes, egg laying, and ultrasound imaging (live *H. horridum*; Morris and Alberts 1996; Morris and Henderson 1998).

Because we could not obtain an adequate sample of preserved *H. horridum*, and because of problems with pooling data from preserved and living specimens, we analyzed measurements of SVL and tail length only from live *H. horridum* in the field, zoos, museums, and private collections. Due to these limitations, we were unable to obtain accurate measurements of head size in living *H. horridum*.

Data analyses

Differences in SVL between sexes were initially assessed using *t* tests. Because body size (SVL) is an important determinate of appendage size (TL, HW, and HL), we used an analysis of covariance (ANCOVA, with SVL as a covariate) to control for the possible influence of SVL on the other measured variables. To determine whether male helodermatids have longer tails than females (relative to body size), we used type III sums of squares analysis of covariance (ANCOVA; Sokal and Rohlf 1995) with SVL as the covariate. Similarly, we used ANCOVA to determine whether head width and head length differed between male and female *H. suspectum*, but we were unable to test this hypothesis in *H. horridum*.

Data were checked for adherence to the assumptions of ANCOVA (normally distributed errors and homogeneous within-group regression slopes; Quinn and Keough 2002). Because helodermatids exhibit asymptotic growth curves (Beck 2005), data were log transformed prior to analysis to account for the possibility that different parts of the body grow at different rates. When group regression slopes were heterogeneous and traditional ANCOVA could not be used, we instead used a separate slopes ANCOVA model (Huitema 1980).

For *H. suspectum*, sample sizes permitted us to analyze juveniles and adults separately to examine ontogenetic effects. Because sexually dimorphic traits may not diverge until after sexual maturity, we chose to first analyze all individuals together and then analyze by age group (either adult or juvenile) as well as by sex.

Lastly, we conducted a restricted set of analyses for each species. In the restricted analyses, we used only the measurements from the 10 largest individuals of each sex. We again conducted ANCOVA with SVL as the covariate to test differences in TL, HW, and HL. Analyzing the largest individuals allows for control of possible bias due to age structure of the sampled individuals (Case 1976) as well as bias in sampling of individuals in the field, such as temporal variation in sexual size dimorphism (Andrews and Stamps 1994) or preferential sampling of females for studies of reproduction (Crowley 2000).

Results

Our analyses suggest that helodermatid lizards show sexual dimorphism in head size (for *H. suspectum*) and tail length (for *H. horridum*) but not SVL (Table 1; Figs. 2–4). Snout-to-vent length did not differ significantly between males and females in either *H. horridum* or *H. suspectum* (t_{77} = –0.77, P = 0.44; t_{206} = –0.83, P = 0.41, respectively).

Table 1. Sex-specific body measurements (mm) for *Heloderma suspectum* and *H. horridum* used in this study.

Species	Sex	Snout-to-vent length	Tail length	Head width	Head length
H. suspectum	Male	249.9±5.1 (111)	117.4±2.4 (110)	41.9±0.9 (111)	49.0±0.9 (111)
	Female	244.4±6.2 (97)	113.0±3.0 (96)	37.6±0.9 (96)	45.9±1.0 (96)
H. horridum	Male	394.7±10.8 (40)	303.9±9.8 (40)		
	Female	381.9±8.4 (39)	270.6±7.3 (39)		

Note: Data are means ± SE with sample sizes in parentheses.

Fig. 2. Relationship between head width and snout-to-vent length in *Heloderma suspectum*. Males have significantly wider heads than females. Data were log transformed prior to analysis; details appear in Table 3.
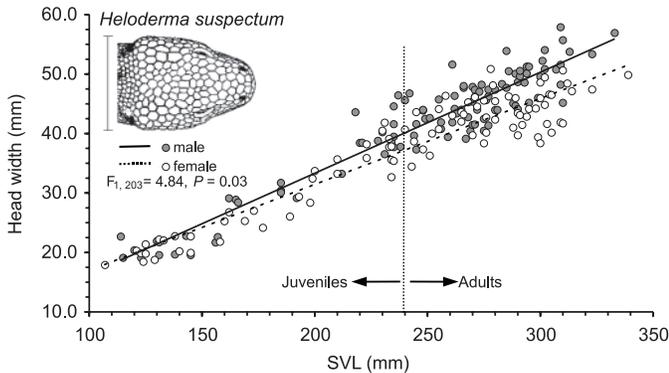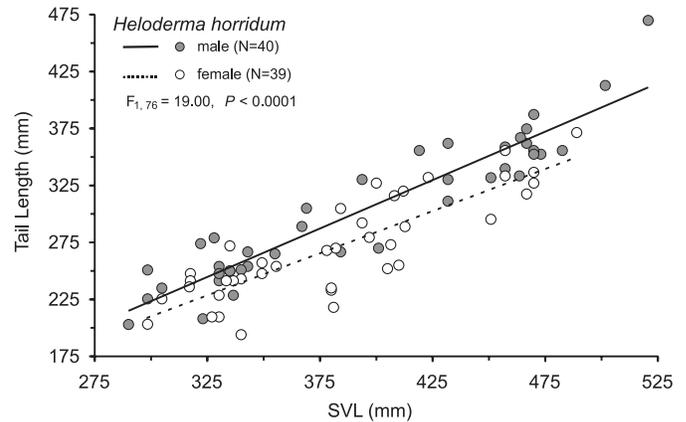

Fig. 3. Relationship between head length and snout-to-vent length in *Heloderma suspectum*. Males have significantly longer heads than females. Data were log transformed prior to analysis; details appear in Table 3.

Fig. 4. Relationship between tail length and snout-to-vent length in *Heloderma horridum*. Males had significantly longer tails than females. Data were log transformed prior to analysis; details appear in Table 2.
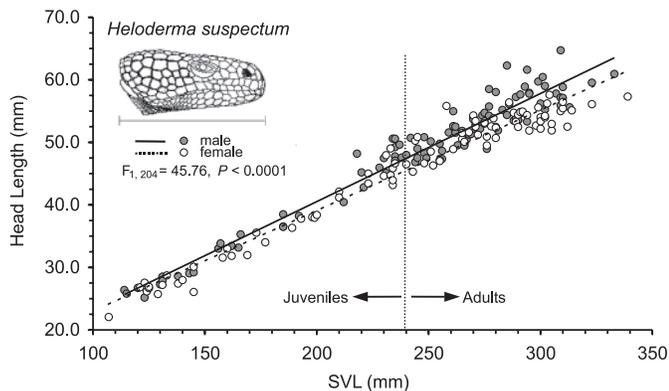
Tail length did not differ significantly between male and female *H. suspectum* (homogeneous slopes ANCOVA, $F_{[1,202]} = 2.90$, $P = 0.09$). However, male *H. horridum* had significantly longer tails than females (homogeneous slopes ANCOVA, $F_{[1,76]} = 19.00$, $P < 0.0001$). Male *H. suspectum* had significantly wider (separate slopes ANCOVA, $F_{[1,203]} = 4.84$, $P = 0.03$) and longer heads (homogeneous slopes ANCOVA, $F_{[1,204]} = 45.76$, $P < 0.0001$) than females. For *H. horridum*, our sample size was too small to test whether head size (HW or HL) differed between the sexes.

Analyses of *H. suspectum* by age class (either adult or juvenile) indicate that there was no significant difference in SVL or TL between the sexes for either juveniles or adults (Table 2). Male *H. suspectum* had larger HW and HL, regardless of age class (Table 3). The results for the restricted

analyses (10 largest of each sex for each species) are nearly identical to those for the full analyses (all individuals included), except that SVL of male *H. horridum* (mean = 478.5 mm) was significantly larger than SVL of female *H. horridum* (mean = 450.8 mm; $t_{18} = -4.73$, $P = 0.001$, Table 4).

Discussion

In many vertebrates that exhibit male–male combat, males have larger (typically wider) heads than females (Shine 1978; Vitt 1983; Vitt and Cooper 1985; Cooper and Vitt 1989; Kratochvíl and Frynta 2002; Bonduriansky and Rowe 2003; Okada and Miyatake 2004). Larger heads have been considered weapons in aggressive encounters (Kratochvíl and Frynta 2002) and may relate to reproductive success. For example, reproductive success in the sleepy lizard, *Tiliqua rugosa* (Gray, 1825), is related to sexual selection for head size through competition among males for mates. Young *T. rugosa* with larger heads typically achieve higher lifetime reproductive success by obtaining their first reproduction at an earlier age (Bull and Pamula 1996).

Our results suggest that helodermatid lizards show SVL-adjusted sexual dimorphism in head size (HW and HL for *H. suspectum*) and tail length (for *H. horridum*). Larger head size in male *H. suspectum* is likely the result of sexual selection acting through male–male agonistic behaviors. Many of the postures demonstrated during combat in the helodermatids involve use of the head to bite, push, twist, and otherwise subdue the opponent (Fig. 1; see also Ramírez-Velázquez and Guichard-Romero 1989; Beck 1990; Beck and Ramírez-Bautista 1991 for descriptions of specific postures). A larger head would be specifically advantageous

Table 2. Comparisons of snout-to-vent length (SVL) (*t* test) and tail length (TL) (homogeneous slopes ANCOVA) for *Heloderma* spp.

Species	Comparison	Group	Statistic	df	*P*
H. suspectum	SVL	All males vs. all females	$t = -0.83$	206	0.41
		Juvenile males vs. juvenile females	$t = -0.55$	70	0.58
		Adult males vs. adult females	$t = 1.19$	134	0.24
	TL	All males vs. all females	$F = 2.89$	202	0.09
		Juvenile males vs. juvenile females	$F = 3.64$	69	0.06
		Adult males vs. adult females	$F = 0.12$	130	0.73
H. horridum	SVL	Adult males vs. adult females	$t = -0.77$	77	0.44
	TL	Adult males vs. adult females	$F = 19.00$	76	<0.0001

Note: SVL was used as a covariate and all variables were log transformed prior to analyses. Sample sizes were not sufficient to make comparisons for juveniles of *H. horridum*.

Table 3. Analysis of covariance comparing head width and head length between age groups and sexes of *Heloderma suspectum*.

Comparison	Group	*F*	df	*P*
Head width	All males vs. all females	4.84[†]	203	0.03
	Juvenile males vs. juvenile females	5.80*	69	0.02
	Adult males vs. adult females	7.26[†]	131	0.008
Head length	All males vs. all females	45.76*	204	<0.0001
	Juvenile males vs. juvenile females	14.53*	69	0.0003
	Adult males vs. adult females	9.12[†]	131	0.003

Note: SVL was used as a covariate and all variables were log transformed prior to analyses.
*Homogeneous slopes ANCOVA.
[†]Separate slopes ANCOVA.

Table 4. Restricted analyses (10 largest of each species) for *Heloderma* spp.

Species	Comparison	Male mean	Female mean	Statistic	df	*P*
H. suspectum	SVL	316.6	318.4	$t = 0.37$	18	0.72
	TL	146.4	142.2	$F = 1.10$*	17	0.31
	HW	53.8	46.3	$F = 27.14$*	17	<0.0001
	HL	58.8	55.0	$F = 15.48$*	17	0.001
H. horridum	SVL	478.5	450.8	$t = -4.73$	18	0.001
	TL	379.0	327.8	$F = 5.02$[†]	16	0.04

Note: SVL was used as a covariate and all variables were log transformed prior to analyses. Because of small sample size, HW and HL of *H. horridum* were not analyzed. Data are in millimetres.
*Homogeneous slopes ANCOVA.
[†]Separate slopes ANCOVA.

during head shove and body twist sequences of *H. suspectum*, since the individual with the larger head and jaw adductor muscles may be better able to exert control over his opponent and maintain a dominant position.

In *H. horridum*, a longer tail may allow an individual to form a higher body arch, lean on his opponent with more force, and increase the chances of emerging on top as the arch collapses and the combat sequence ends. In contrast to *H. horridum*, *H. suspectum* does not form the body arch during male–male agonistic interactions; therefore, a longer tail would presumably confer little benefit to males, which is supported by our results.

It is unknown how larger HW, HL, and TL directly relate to fitness in *Heloderma*. Presumably, males having larger combat weaponry (heads or tails) would benefit in agonistic encounters, allowing them to win more combat bouts, mate more frequently, and achieve higher reproductive success relative to conspecific males. Although this scenario is quite

likely in *Heloderma*, it has yet to be tested. In other lizards, performance of combat weaponry (e.g., bite force), and to a lesser extent weapon size (HW), is most important in determining dominance, mating success, and potential reproductive output (Lappin and Husak 2005; Husak et al. 2006; Lailvaux and Irschick 2006). For example, bite force in the collared lizard (*Crotaphytus collaris* (Say in James, 1823)) influences reproductive success and is correlated with head width (Lappin and Husak 2005; Husak et al. 2006). Male helodermatid lizards occasionally bite each other during combat, but biting seems to be a lesser feature of agonistic encounters than of ritualized grappling postures (Beck 2005). In *Heloderma*, bite force may be more important in delivering an incapacitating venomous bite to a potential predator than in conferring an advantage to males during combat sequences. Future studies might investigate whether *Heloderma* spp. show sexual dimporphism in bite force. Moreover, future studies should explore the link between re-

Fig. 5. General differences in body form between a female (top) and a male (bottom) Gila monster (*Heloderma suspectum*). Although these two individuals are of approximately equal body size, note that the head of the male is markedly larger than that of the female.
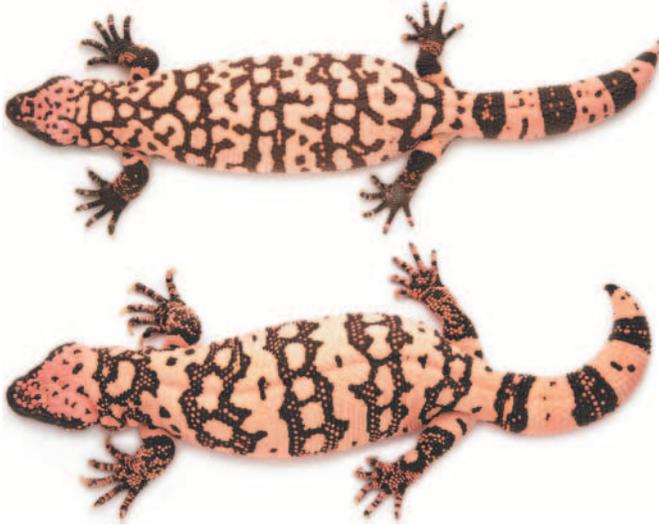
productive success and sexually dimorphic morphologies related to combat (HW, HL, or TL) in helodermatid lizards.

With the exception of the 10 largest *H. horridum* in our sample, we found no difference between males and females in body size (SVL) in either species of *Heloderma*. Larger body size imparts an obvious benefit in physical tests of dominance, and in many reptile species showing strong male combat, males are larger than females (Stamps 1983; Andersson 1994; Kratochvíl and Frynta 2002). The presence of sexual dimorphism in other traits related to combat (i.e., head size in *H. suspectum*, tail length in *H. horridum*) begs the question: why are male helodermatid lizards (particularly *H. suspectum*) not larger than females?

Just as sexual selection may be acting on male traits, other evolutionary factors may act on females to confer benefits to larger body size or differences in body shape (Olsson et al. 2002; Cox et al. 2003; Blanckenhorn 2005). Sexual dimorphism in body shape without sexual size dimorphism is relatively common in lizards (Braña 1996; Schwarzkopf 2005). In females, longer trunk length (the distance between front and hind legs) may allow more space for eggs and thereby increase fecundity. Fecundity selection and sexual selection may thus act together to produce sexual dimorphism in shape without sexual dimorphism in body size (Olsson et al. 2002; Schwarzkopf 2005). Unfortunately we did not measure trunk length in our sample of female helodermatids. However, subtle intersexual differences in trunk length seem to exist in some populations (D.D. Beck, personal observation). A glance at Fig. 5 illustrates that a test of whether fecundity selection may be acting on trunk length in female helodermatids would be an important direction for future studies of sexual dimorphism in the Helodermatidae.

Acknowledgements

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