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Combat Behavior of the Beaded Lizard, *Heloderma h. horridum*, in Jalisco, México

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Male-male agonistic behaviors have been described for many squamate families (see Carpenter and Ferguson, 1977; Gillingham, 1987; Auffenberg, 1988 for reviews). In helodermatid lizards, male-male combat

involves strenuous grappling postures performed during a series of bouts that may last for several hours (Demeter, 1986; Lowe et al., 1986; Ramírez-Velázquez and Guichard-Romero, 1989; Beck, 1990). Combat sequences have been described for *H. horridum* in captivity (McCrystal and Lawler, 1989; Ramírez-Velázquez and Guichard-Romero, 1989), but no published accounts of combat behavior exist for Mexican beaded lizards in the wild. In this paper we describe fighting behavior in free-ranging *H. horridum* in coastal Jalisco, México.

On 20 September 1984 a fight between two *H. horridum* was observed from 1715 to 1830 h on a small entrance road (130 m elevation) to the Estación de Biología Chamela of the Universidad Nacional Autónoma de México (UNAM). This reserve, covering 16 km² of lowland tropical deciduous forest, has been the site of other studies of *H. horridum* (see Beck and Lowe, 1991). Ambient temperature during the fight was 29 C, the sky was overcast, and rain had just stopped. Six repeated sequences of behavioral acts (bouts) of approximately 8-10 min occurred during 70 min of observations. One lizard, the darker animal in Figs. 1 and 2, appeared larger (body size was not measured) and was apparently dominant, emerging on top after each bout sequence.

Each bout began with the dominant lizard straddled atop the subordinate (Fig. 1A). The subordinate then flexed its torso laterally and placed a forelimb and hindlimb above the pectoral and pelvic areas of the superiorly-positioned lizard (Fig. 1B). The lizards then pressed laterally against each other, turning their heads and tails away from each other and pressing their snouts to the ground to begin forming an arch (Fig. 1C). Further pressure exerted by the lizards resulted in a high arch posture, with venters adpressed and snouts, forelimbs, and tail tips as contact points on the ground (Figs. 1D and 2). Additional pressure eventually collapsed the arch, with the dominant lizard ending up on top (Fig. 1E, F).

The combatants never separated fully between bouts. After the first bout, each arch sequence was initiated by the subordinate lizard. The dominant lizard responded by lifting its body, pushing snout and tail against the ground, into the arched posture. The lizards gradually arched higher, pressing their ventral surfaces against each other, repeating the sequence. The dominant lizard often bit the subordinate on the lower jaw after the arch collapsed (Fig. 1F).

After the sixth bout the lizards had moved about 10 m in a semicircular path across the road from where they began. The subordinate lizard broke loose and moved quickly toward a small arroyo off the roadside. The dominant lizard pursued until the subordinate dropped into the canyon; the dominant lizard then turned in the opposite direction, crossed the road, and crawled into the forest.

The objective during each bout was apparently to force the opponent onto its back, collapsing the arch. Attempts were made by the dominant lizard to keep the subordinate on its back by biting and pressing the venter against the subordinate (Fig. 1F). In all cases except the last bout, the subordinate was able to twist onto its side and initiate another arch. Both lizards had engaged in considerable physical effort after 60 min, and were bleeding along their jaws where

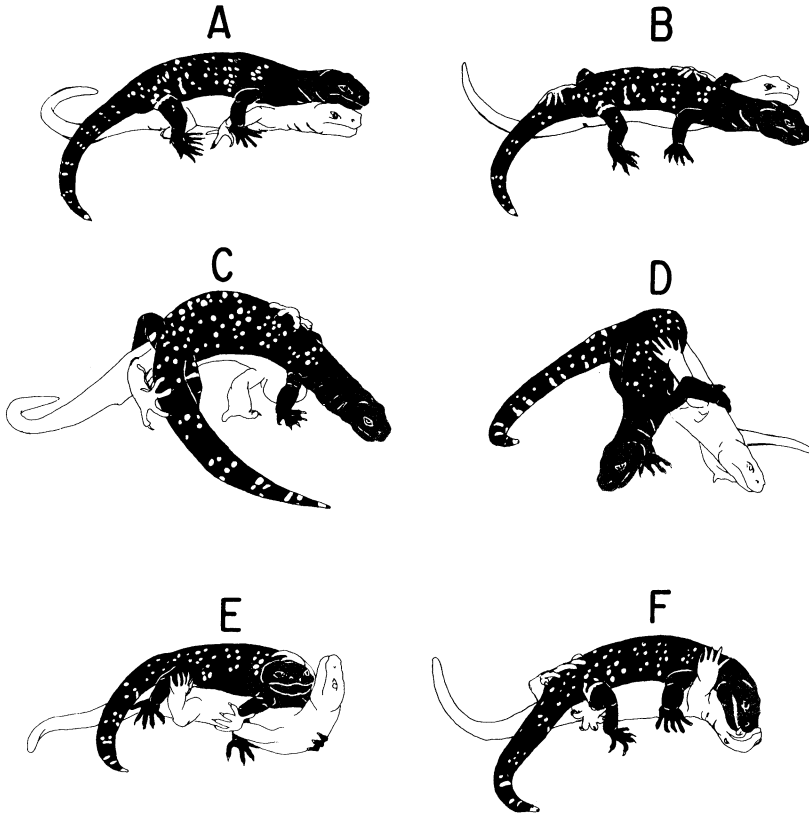


FIG. 1. Combat sequences of *Heloderma horridum horridum* as described in text: drawn from photographs. Dominant lizard dark, subordinate light. (A) Dorsal Straddle; (B) Lizards begin arch sequence by placing a forelimb and hindlimb on dorsum of opponent, turning heads and tails away from opponent, and exerting force laterally against each other; (C) Lateral force lifts lizards into a Body Arch; (D) Full Body Arch posture; (E) Collapsed arch with dominant lizard on top; and (F) Dominant lizard bites subordinate.

they had bitten each other. The larger lizard was consistently able to arch higher, shifting its center of mass above the opponent and exert greater force. Tail strength appeared to be an important factor in the ability to form a high arch.

Álvarez del Toro (1982) noted that during September to November males of *H. h. alvarezii* near Tuxtla Gutiérrez, Chiapas "fight ferociously and bite each other tenaciously." Ramírez-Velázquez and Guichard-Romero (1989) give an excellent description of combat in captive *H. h. alvarezii* from Tuxtla Gutiérrez that is very similar to the fight we report in the free-living *H. h. horridum* from Jalisco. Combat in their captive animals differed primarily in that the combatants circled and attempted to bite each other before assuming the straddling posture. In captivity, fights may last 15–16 h, although such an extreme duration may be a result of confinement (Ramírez-Velázquez and Guichard-Romero, 1989). The fight we report was already underway when it was discovered, thus 70 min is a minimum estimate of its duration. An agonistic encounter between two captive male *H. horridum* described by McCrystal and Lawler (1989) included biting by one lizard while the other responded by spinning 360° along its longitudinal body axis,

away from its opponent. This behavior was repeated several times over 20 min until the biting lizard retreated from the enclosure.

Male-male combat in *H. horridum* appears to be a test of dominance through a display of superior physical strength and endurance. The "winner" may increase his access to females and probability of mating. Fighting in captive males of *H. horridum* in Chiapas takes place in September and October and coincides with courtship and mating (Álvarez del Toro, 1982; Ramírez-Velázquez and Guichard-Romero, 1989). Although we did not observe courtship or mating, combat during September in free-ranging *H. horridum* may coincide with peak sperm production in Jalisco and Sonora, Mexico (Beck and Lowe, unpubl. data). In *H. suspectum*, combat occurs from late April into June and also coincides with courtship and mating (Lowe et al., 1986; Beck, 1990).

There are similarities as well as striking differences between the combat sequences displayed by *H. horridum* and *H. suspectum*. Male fighting in Gila monsters (*H. suspectum*) involves repeated bouts of head raising, dorsal straddling, twisting of bodies, and occasional biting. The head nudge and neck arch, common postures performed during combat in *H. suspectum* (De-

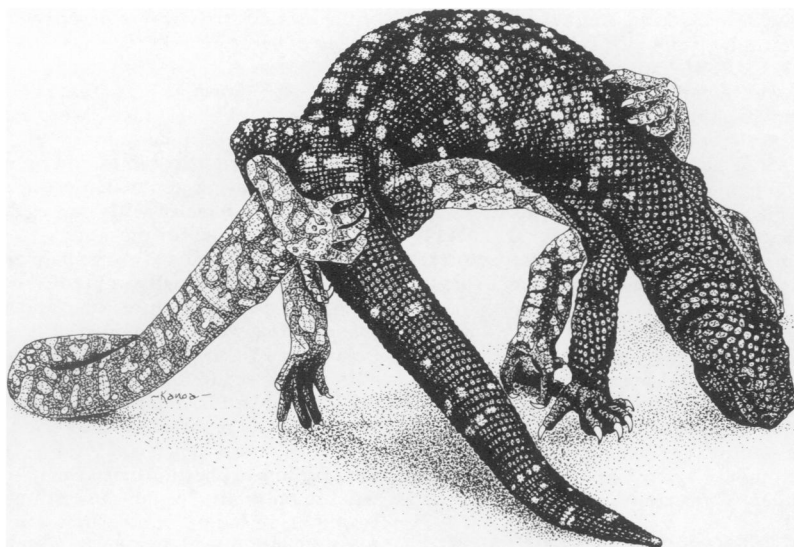


FIG. 2. Detail of Body Arch posture. Dominant lizard in foreground (darker) is able to form a higher arch, exert more force, and remain on top after the arch collapses.

meter, 1986; Beck, 1990), are also displayed by *H. horridum* while in dorsal straddle position. The major difference is the formation of the body arch in *H. horridum*. *Heloderma suspectum* typically proceeds into a body twist from the dorsal straddle position (Beck, 1990), but formation of the body arch has not been reported in this species.

Combat in *H. horridum* more closely resembles fighting in monitor lizards, *Varanus*, than in *H. suspectum*. The arching postures of *H. horridum* are strikingly similar to those of *Varanus gilleni* (Murphy and Mitchell, 1974; Carpenter et al., 1976) and *V. bengalensis* (Auffenberg, 1981). *Heloderma* belongs to the Varanoidea, which includes *Varanus* and *Lanthanotus* as the only other living taxa (Pregill et al., 1986). Although *Varanus* and *Heloderma* have in common many morphological characters, they differ greatly in several behavioral and ecological traits such as their thermal ecology, levels of activity, and foraging ecology. The strongly similar combat postures of *Varanus* and *H. horridum* suggest that such behavior has been highly conserved in the Varanoidea over its 70 myr evolutionary history, and likely represent homologous behaviors that occur as a synapomorphy in these taxa. In agonistic behaviors of anguillid lizards, the sister-group of the varanoids, a body arch, circling, and biting have been described (Carpenter and Ferguson, 1977; Bowker, 1988; Formanowicz et al., 1990), but stereotyped grappling postures are not a major feature. In the Varanoidea, ritualized grappling postures are more pervasive in agonistic interactions than are the visual displays of posturing, threat, and head bobs exhibited by most other lizard families. Interestingly, combat in monitor and beaded lizards more closely resembles the entwining and grappling postures exhibited by snakes.

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Nesting Behavior of the Lizard *Anolis carolinensis*

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Maternal behaviors displayed by oviparous lizard species range from oviposition without any perioviposition behaviors to nest-building and/or egg-guarding (see Duvall et al., 1979; Tokarz and Jones, 1979; Vitt and Cooper, 1989). Egg-directed or maternal behaviors of *Anolis* are limited to digging a nest in soil or humus, ovipositing a single egg in the nest, and burying the egg under dirt (Carr, 1940; Greenberg and Noble, 1944; Gordon and Tinkle, 1960; Rand, 1967; Stamps, 1976). Anoline lizards are also known to deposit eggs in bare crevices in, for example, wood and rock piles (Rand, 1967).

Although general aspects of oviposition and nesting behavior in *Anolis carolinensis* have been reported previously (Greenberg and Noble, 1944; Tokarz and Jones, 1979), the details of the complete nesting sequence have not been fully described. The purpose

of the present study was to describe and quantify all aspects of behavior associated with nesting by female *A. carolinensis*.

Between 8 June and 11 August 1989, female *A. carolinensis* were obtained once a week from Buck's Live Animals, La Place, Louisiana. Within 1 h of arrival, all females were palpated to determine if they contained a single egg in one oviduct or an egg in each oviduct. Only females with two eggs (one in each oviduct) were used for the study.

In week 1, immediately after palpation, 16 females were placed individually in plastic boxes (16 × 31 × 8 cm) and provided with water and mealworms *ad libitum*. Boxes were maintained during the 10 h scotophase at 25 C in Percival incubators. The temperature was raised to 32 C during the 14 h photophase (0600 to 2000 h). To determine the effects of injection for a study not reported here, on the day after arrival to the laboratory, all females (N = 16) received an intraperitoneal injection of 0.05 ml saline at 0800. This was the only time during the study that females received an injection. Immediately after injection, all females were placed together in a single 75 L terrarium (31 × 61 × 42 cm) containing 5 cm of moist potting soil consisting of a mixture of peat moss and vermiculite. Females were provided with artificial plants for perches, mealworms and water *ad libitum*, two males, and a 40 watt bulb as a heat source. The light was placed at one side of the cage to provide the lizards with a heat gradient. Humidity was measured with a humidistat and varied between 50 and 70%. On this day, females were observed continuously from the time of injection until 1600 h. During the following two days, females were observed from 0730-1600 h. Of the 16 females observed (see below), 4 exhibited complete nesting sequences.

Each week following week 1, 15-20 females were placed in a large observation terrarium (61 × 121 × 42 cm) overnight. These females did not receive an injection. Conditions in the terrarium were identical to those described for the 75 L terrarium used in week 1, except that a 90 watt bulb was used to provide heat and light. For three days after their arrival, all animals were observed from 0730-1600 h. Complete sequences were observed for 6 animals.

In both sets of studies (during week 1 and following week 1), an observer used a tape recorder and verbally noted the time at the beginning and end of each behavioral stage of the nesting sequence (defined in Table 1). From these voice recordings, the durations of each behavioral stage and of the entire nesting sequence were obtained. No significant differences were detected (at $\alpha = 0.05$ level) in the duration of any behavioral stage, or in the total time spent in the entire nesting sequence between the saline-injected animals from week 1 (N = 4) and non-injected females from subsequent weeks (N = 6; Students t tests; Stage 1, $t = 1.0787$, $P = 0.312$; Stage 2, $t = 0.1577$, $P = 0.879$; Stage 3, $t = 0.0346$, $P = 0.973$; Stage 4, $t = 2.2379$, $P = 0.06$; Stage 5, $t = 1.9649$, $P = 0.085$; Total time nesting, $t = 0.1453$, $P = 0.888$). All data were tested and found to be valid for the assumptions of parametric tests (normality and equal variance). Because there were no differences between these two groups, their results were pooled. Therefore, complete sequences for 10 nesting females were recorded.

In the large terrarium, all females dug nests in the