

AN ABSTRACT OF THE THESIS OF

Sara K. Tallarovic for the degree of Doctor of Philosophy in Zoology presented on February 18, 2000. Title: Reproductive and Aggressive Behaviors in the Giant Hairy Desert Scorpion.

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Abstract approved: _____

Philip H. Brownell

The giant hairy desert scorpion, *Hadrurus arizonensis*, is a long-lived species of North American scorpion that is presented here as an important model for research in mating systems evolution and sexual selection. Many behaviors found in this species were undocumented and are described here for the first time. This thesis includes studies of the following aspects of *H. arizonensis* behavior: 1) a description of courtship and mating behavior, 2) an empirical study of variance in courtship success among males and females as an indicator of mate choice in both sexes, 3) a descriptive and empirical study of aggression and agonistic behaviors in non-reproductive inter- and intrasexual interactions, and 4) an observational study of intrasexual competition over mates in both males and females. Experiments were performed in the laboratory and behaviors observed were videotaped for data collection and analysis. All subjects used in this study were field-captured prior to use in behavioral experiments. This species exhibits both reproductive and aggressive behaviors that are stereotyped and can be quantified, either by ranking their intensity, or measuring in terms of time. *H. arizonensis* is a polygamous species with external sperm transfer (via a spermatophore). Both males and females

appear to exhibit mate choice. Large females elicit more intense courtship behavior from males, and males may preferentially court larger females to increase their own reproductive success. Furthermore, both males and females interfere in the courtship of conspecific pairs, indicating that both sexes potentially compete intrasexually for mates. Such findings may be attributable to the substantial contributions each sex makes in reproduction. This species also exhibits complex aggressive behaviors during agonistic interactions that may function in both species recognition and competition.

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Reproductive and Aggressive Behaviors in the Giant Hairy Desert Scorpion

by

Sara K. Tallarovic

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Sara K. Tallarovic, Author

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CONTRIBUTION OF AUTHORS

John Melville assisted in data collection for two of the studies. The experiments were performed in the laboratory of Dr. Philip Brownell who assisted in the interpretation of data.

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DEDICATION

I dedicate this thesis to my maternal grandmother, Belle Kinney Ball, who has always wanted to be a biologist but grew up during an era when such dreams were difficult to realize. She is an avid amateur naturalist and has fostered my interests in science and nature throughout my life. She has been a remarkable inspiration to me in my professional career and my personal life, and therefore this work is for her.

Reproductive and Aggressive Behaviors in the Giant Hairy Desert Scorpion

Introduction

Studies of animal behavior allow for a better understanding of how organisms relate to each other and to their environment. By examining evolutionary and life histories in conjunction with behavioral patterns, we learn how organisms might have evolved under varying environmental conditions or evolutionary constraints. Reproductive behaviors are important activities for sexually reproducing organisms. They are unique in that they are not essential to the immediate survival of an individual organism, but they are necessary for perpetuation of a species. Like other behaviors, they often reflect the ecological and/or physiological parameters under which an organism evolved. Mating systems research involves the study of behavioral, physiological, ecological and morphological parameters involved with the union of gametes and the production of offspring. Studies of mating systems often integrate behavioral studies with a perspective of what factors shape those behaviors presently and evolutionarily. Furthermore, comparisons of behavioral patterns across related taxa allow speculation about the evolutionary history behind a particular mating system.

Since Darwin's discussion of sexual selection (Darwin 1859, 1871) as a reason for variation in reproductive success in animals, the topic has been the focus of intense study (reviews in Anderssen 1994; Gould and Gould 1997). Sexual

selection as Darwin viewed it primarily occurs by two basic mechanisms: male-male competition and female choice. Females generally contribute more energy into reproduction in the form of a nutrient rich egg and are often reproductively limited by gestation or care of offspring, while males produce a large number of energetically cheaper sperm and rarely are required to nurture offspring. Trivers (1972) examined this concept of differential parental investment as a primary influence in sexual selection. The number of reproductively active males to females, commonly known as the “operational sex ratio” (OSR) was proposed by Emlen and Oring (1977) as a major driving force in sexual selection. The OSR is closely related to the potential reproductive rate of males and females, which has been proposed as an alternative to Trivers hypothesis of parental investment (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). Other proposed measures that reflect the potential for sexual selection include time spent searching for mates (Sutherland 1985), intrasexual variance in breeding success (Payne 1979), intersexual breeding success (Ralls 1977; Payne 1979), variance in mating rate (McCauley 1983), and the ratio between relative variance in numbers of mates and relative variance in total breeding success (Wade and Arnold 1980; Arnold and Wade 1984a). By examining and measuring these parameters, researchers try to determine what factors most influence the intensity of sexual selection.

To determine whether sexual selection may be operating in a species, it is first necessary to determine whether there is differential reproductive success among individuals. An individual’s reproductive success is most accurately measured as the

total number of offspring that reach reproductive age. For species that have a relatively short generation time, and for which parentage can be traced, this is a plausible measure. For long-lived species, and for species in which parentage is difficult to trace, it is often necessary to measure other factors to determine whether the potential for sexual selection exists.

Much of the mating systems research in non-vertebrates has focused on insects (reviews in Thornhill and Alcock 1983; Alexander et al. 1997; Brown et al. 1997). Other taxa, particularly those that use more “primitive” methods of sperm transfer (discussed below), have been largely neglected. Among arthropods, arachnids as a group include a spectrum of different mating patterns, many of which have been described but not further studied (Weygoldt 1969; Schaller 1971). Scorpions represent a group that has received only minimal attention in mating systems research. As evidenced by the fossil record, they are a relatively ancient arthropod group, appearing during the Silurian period (450 mya), and changing very little in morphology over evolutionary history. They would seem an outstanding research model for those interested in the evolution of mating systems, as they potentially represent an archaic group. Curiously, they have been overlooked. Closer examination of this group is important to better understand mating systems evolution and patterns of reproductive behavior in relation to sexual selection.

Mating systems evolution in arachnids and scorpions as a model system

Arthropods exhibit a wide range of complexity and organization in their mating behaviors with some of the most primitive being represented by arachnid groups (Weygoldt 1969; Schaller 1971). Scorpions provide a valuable model for studying mating systems and behavior because, in comparison to other arthropods, they utilize a primitive method of sperm transfer, using an external spermatophore instead of a specialized intromittent organ. Scorpion spermatophores are encased in sclerotized cuticle (similar substance to that which creates their exoskeleton). They are elaborate and divergent enough in structure to aid in taxonomic classification (Francke 1979a, Eberhard 1985). Sperm transfer by spermatophore that involves courtship requiring that both sexes are present is considered a derived characteristic (Weygoldt 1969; Schaller 1971; Eberhard 1997). Some pseudoscorpions and mites transfer sperm indirectly without even forming mating pairs. Males leave spermatophores for females to find (Weygoldt 1969; Schaller 1971; Thomas and Zeh 1984). Other arachnid groups such as most solfugids (or “solpugids”), spiders and some mites use direct sperm transfer in which they ejaculate sperm and then transfer it to the female with tarsal appendages, chelicerae or, in the case of harvestmen, a penis (Cloudsey-Thompson 1961; Amitai, Levy and Shulov 1962; Muma 1966; Schaller 1971; Robinson 1982; Thomas and Zeh 1984). Male scorpions do not directly place sperm on or inside the female’s gonopore. Instead males guide females close to the spermatophore and must ultimately rely either on the female’s cooperation or her actions to discharge the sperm into her reproductive tract. Other arachnids including some of the uropygids, holopeltids, amblypygids, and some

pseudoscorpions use this indirect transfer of sperm, often prefaced by a courtship display (Weygoldt 1969; Schaller 1971; Thomas and Zeh 1984; but see Weygoldt 1970). Scorpions provide a potential intermediate among arachnid mating systems. Furthermore, their unusual life-history traits make scorpions a particularly intriguing model for study.

The giant hairy desert scorpion, *Hadrurus arizonensis*

The model chosen for this body of work was the giant hairy desert scorpion, *Hadrurus arizonensis*. Common to the Sonoran and Mojave Deserts, it is the largest species of scorpion in North America. *H. arizonensis*, in spite of its conspicuous presence in desert ecosystems (not to mention its rather flamboyant common name), has been studied very little. Like other scorpions they tend to be long lived, although their 25+-year life span exceeds that of many other scorpion species (Stahnke 1966). They are viviparous, with females providing limited maternal care of offspring until their first molting cycle. Although parturition had been documented in the laboratory (Williams 1969), no other aspects of their reproductive or agonistic behaviors have been previously studied.

H. arizonensis is an ideal model for behavioral research in the laboratory for a number of reasons. It is easily collected in reasonable numbers in the field using a portable black light (Stahnke 1972). It is large in size for a terrestrial arthropod, allowing for high resolution in the visualization of most behaviors. Furthermore, it is a dorso-ventrally flattened animal that is most active on a 2-dimensional surface. Its

behaviors in the laboratory under red light (to which scorpions appear blind, Machan 1968) are robust and do not seem to diminish over the course of an experiment if the animals are well fed and kept at summer-like temperatures in the laboratory (Brownell, unpublished data). Its size, shape, 2-dimensional activity and non-sensitivity to certain wavelengths of light make this animal easy to record with a low-light video camera in the laboratory. Furthermore, removing a human observer during the behavioral event and collecting all data on videotape for later analysis can minimize disturbance by air movement or vibration (to which scorpions are extremely sensitive, Brownell 1977; Brownell and Farley 1979).

Statement of purpose

The specific aim of this research project was to investigate both inter- and intrasexual behavioral interactions between adult *Hadrurus arizonensis* in reproductive and non-reproductive contexts, and (when possible) to relate those behaviors to the animal's life history, ecology, and evolution, with a specific focus on possible mechanisms of sexual selection. It was my intention to provide qualitative and quantitative descriptions and analyses of previously undocumented behaviors, and to establish *H. arizonensis* as a model system for further studies in mating systems research. The research project included studies of the following aspects of *Hadrurus arizonensis* behavior: 1) a description of courtship and mating behavior, 2) variance in courtship success among males and females as an indicator of mate choice in both sexes, 3) aggression and agonistic behaviors in non-

reproductive inter- and intrasexual interactions, and 4) intrasexual competition over mates in both males and females.

Chapter 2

Courtship and Mating in the Giant Hairy Desert Scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae)

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Abstract

Among arthropods, scorpions provide intriguing and useful models for studies of mating systems. Mating in these terrestrial arthropods involves complex behaviors apparently suited to their extreme environments and unusual life-history patterns. *Hadrurus arizonensis* is a long-lived (>25 years) species of desert scorpion with lengthy, stereotyped courtship behaviors that lead to sperm transfer via an external spermatophore. Mating behavior in *H. arizonensis* and other members of the Iuridae family has not been described. *H. arizonensis* have reproductive behaviors similar to those of other scorpions, including the *promenade a deux*, but with some unique components described here for the first time. Courtship and mating behaviors of *H. arizonensis* are presented in a flowchart to emphasize their stereotypical nature and suitability for experimental manipulation in field and laboratory studies.

Introduction

Behaviors related to mating and reproduction are often the most elaborate and specialized activities animals perform. The stereotyped patterns of reproductive behaviors associated with the diverse array of mating systems found among arthropods make them excellent models for the study of mating system evolution and ecology. Courtship and mating in scorpions involves a complex series of ritualized behaviors, many of which are conserved among taxa. In all described scorpion mating systems there is a courtship period of stereotyped behaviors followed by a

transfer of sperm to the female via a stationary spermatophore. Although most of the previous studies of reproductive behavior in scorpions have been mainly descriptive (this paper is no exception), scorpions may provide an advantageous model for examining questions involving mating system dynamics and evolution because of the ease with which courtship can be observed and manipulated in the laboratory. In this paper we describe the mating system of *Hadrurus arizonensis* and explore its utility and potential significance in future studies. Mating behaviors have been described for about 30 species (reviewed by Polis and Sissom 1990), representing six of 16 families (taxonomic revision by Fet et al. 1999) of Scorpionida, but have not been provided for the family Iuridae. This is a curious omission because one of the Iurids, *H. arizonensis*, is the largest species of scorpion in North America (adults average 7 grams) and their mating behavior is robust to disturbance and easily observed in the laboratory, making them an appealing subject of study. This family, comprised of only five genera, is distributed through southwestern Eurasia, western South America, and western North America. Iurids are represented in the western United States and Mexico by the genus *Hadrurus* (eight spp.).

As a group scorpions are unusual among terrestrial arthropods in their longevity (for some species) and length of time to reach maturity (Polis and Sissom 1990). *H. arizonensis* is somewhat exceptional among scorpions with a potential life span of 25 years or longer (Stahnke 1966). They exhibit other life-history characteristics typical of an equilibrium species having relatively small litter sizes (approximately 10 according to Williams 1969, however pregnant field caught

females have given birth to as many as 36 offspring in the laboratory, Tallarovic, unpubl. data), and maturing to adulthood over several years. They give birth to live young and exhibit limited parental care like other scorpions (Williams 1969).

Methods

Scorpions were located in the field at night by using a portable UV light because of the fluorescent quality of their cuticle (Pavan 1958; Stahnke 1972). Field studies of *H. arizonensis* using UV illumination are somewhat problematic because *H. arizonensis* are more negatively phototactic to UV light than other species of scorpion (e.g. *Paruroctonus mesaensis*, which shares the same habitat in the Mojave Desert). Some *H. arizonensis* move away from the light into a burrow or under vegetation soon after being located from as far as 10 meters away. Mating pairs often separate and retreat (sometimes together into a burrow) when approached with UV lights (pers. obs.). However *H. arizonensis* collected during reproductive season will usually exhibit courtship behaviors in the laboratory, especially under red light illumination, which scorpions cannot see (Machan 1968). Some animals will enter courtship under UV illumination in the laboratory but with less success at completing mating.

Study animals and field procedures

H. arizonensis used in this study were collected from sand dune habitats in the Mojave Desert near Baker and Indio, San Bernadino County, California using portable black lights (Stahnke 1972). Observations were made in the laboratory of

the Desert Studies Center at Zzyzx, CA (near Soda Lake) within days of collection and also in the laboratory at Oregon State University several weeks after collection. At the field station laboratory animals were kept individually in gallon-sized air permeable Ziploc bags with sand as a substrate. The bags were closed with air inside so as to provide walking space for the animals. In the laboratory in Oregon animals were housed individually in plastic cups (375 ml) with natural dune sand substrate collected with the animals. In order to extend mating behaviors in the laboratory into the fall (in Oregon) the animals were kept at late-summer temperatures characteristic of their natural dune environment (29-35° C) and fed frequently (three wax moth larvae, *Galleria mellonella*, weekly).

Observation procedures

This study was conducted in August and September of 1996 and September and October of 1997 (animals were collected prior to each study period). Interactions between males and females were visualized in two different ways: 1) animals were placed inside a glass chamber (25 cm x 17.5 cm x 5 cm) with mirrors that could be positioned such that top and bottom views could be obtained simultaneously with a side view, and behavior was recorded under UV light (15 Watt fluorescent tube) using an 8 mm Sony Handicam® video camera; 2) animals were placed inside a circular PVC arena (d= 21 cm, h= 15.5 cm) filled with approximately 500 cc of sand and filmed from above under red light (25 W bulb at a distance of approximately 50 cm) using a low-light Watec® WAT-902A video camera. The first method (glass box) was a slippery substrate for the animals to maneuver but yielded an excellent

visualization of spermatophore extrusion onto the glass. A stick was provided to animals filmed in the sand-filled arenas for spermatophore deposition. With the exception of the above-mentioned trial using the glass box, all data presented in this paper are from observations made using the second visualization method (sand-filled arena illuminated with red light).

A total of 14 interactions involving courtship were observed, 10 of which included deposition of a spermatophore by a male. Males and females of similar size and weight were haphazardly paired. If mating was initiated within one hour from their introduction into the arena, pairs were left together and filmed for 8 hours (T160 videotapes were used, allowing 8 hours of continuous recording). If mating was not initiated within an hour, one or both members of the pair were replaced. In one case in which a pair continued courtship beyond the 8 hour period, the videotape was replaced and recording continued. The air temperature ranged from 29°-35°C. In several of the trials the substrate was heated to 35°C using a heating pad beneath the sand-filled arena while the air temperature remained at 29-30°C. This latter regime mimics the natural dune environment as measured by thermal probes (Onset HOBO H8).

Results

Mating in *Hadrurus arizonensis* is composed of a stereotyped series of behaviors that we have separated into the following phases (after review in Polis 1990): 1) initiation, 2) *Promenade a deux*, 3) sperm transfer, and 4) termination.

Courtship is complex and comprised of several distinct sequences that often repeat or return to previous stages. A diagram (Fig. 2.1) of the mating behaviors described below shows their temporal organization and interrelationships. Values for times spent in a particular behavior (reported with the behavioral descriptions) represent ranges observed in this study. They are presented here as observational data only because of the relatively small sample size and varied environmental conditions during observations.

Initiation

Males initiate mating in *Hadrurus arizonensis*. When a male or female becomes aware of another animal nearby, walking stops and they adopt a stance characteristic of general conspecific interactions (Tallarovic et al. 1999). Either sex may rock (a slow lateral swaying motion of the abdomen over a fixed position of the tarsi) or judder (a high frequency swaying motion forward and back) in the presence of the other. Juddering is not sex-specific or restricted to reproductive behavior in *H. arizonensis* as observed in other species. Female *H. arizonensis* judder as robustly and as often as males in response to males or females (juddering, or “yuddering” has also been observed during mating in female *Leiurus quinquestriatus* by Shulov and Amitai 1958). Alternatively, walking may bring a male and female into contact without either showing awareness of the other’s presence before contact. In either case, they may or may not make physical contact before the male displays its first unequivocal orientation toward the female. This initial move involves an aggressive lunge toward the female in which he seizes her slightly to one side (Fig. 2.2). One of

his pedipalps grasps one of her pedipalps while the other grasps the side of her abdomen (usually near or on the last segment of the mesosoma, but occasionally grasping the metasoma or one of her legs instead). With this initial contact the female usually becomes immediately passive as indicated by withdrawal of the pedipalps to a contracted position close to her body. The male then moves his metasoma and sting to contact the female, probing areas of soft cuticle as in the “sexual sting” described in several species of Chactidae and Vaejovidae (Angermann 1955, 1957; Francke 1979b). The male may also use his metasoma to “club” the female as described in *Paruroctonus mesaensis* (Polis and Farley 1979). In this event, the sting is reflected backward as the male taps the intersegmental membrane exposed between his metasoma and telson on the female’s mesosoma (Fig. 2.2). This sting or “clubbing” behavior can last less than one minute to 15 minutes or longer (up to 35 minutes has been observed under laboratory conditions). Males may release the female, judder, and repeat these behaviors several times before continuing with the next phase of the mating sequence. Males were observed to sting the female from one to 14 times in a single mating interaction.

The male eventually manipulates his grip on the female and realigns himself until he is grasping both of her pedipalps in such a manner as to prevent her tibia and tarsus (chela) from opening. Usually the male begins the next phase of mating, the *promenade a deux* (Maccary 1810), immediately after he assumes the pedipalp grip. On several occasions males grasped a female’s metasoma instead of the pedipalps. In one instance, the male attempted to initiate the *promenade a deux*, leading her

around by the metasoma for almost 5 minutes before reverting briefly to the lunge/sting behavior and finally grasping her pedipalps to continue mating. This manipulation of grip to the pedipalps may take from one to 10 minutes. In one case the male sat still grasping the female by the pedipalps (but not beginning the next phase) for over 3 hours.

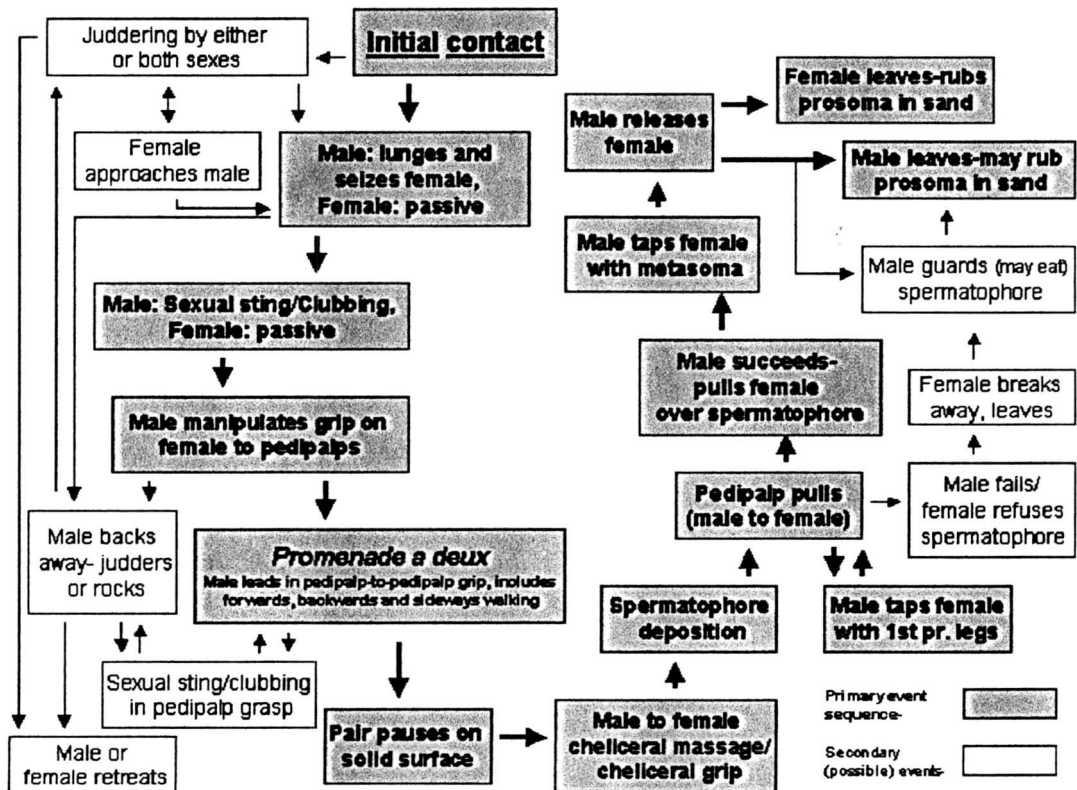


Fig. 2.1 Temporal organization of mating behaviors in *Hadrurus arizonensis*. The events in shaded boxes represent the primary sequence of events that occur in all successful matings (female appears to be inseminated). Events in white boxes occur in some matings but not all.

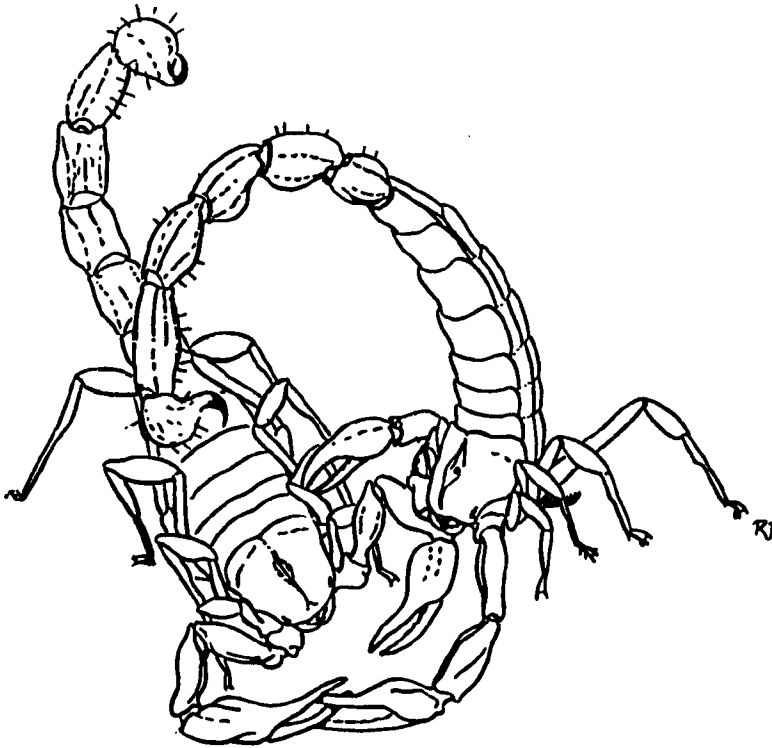


Fig. 2.2. Initiation of courtship in *Hadrurus arizonensis*: Male (right) lunges and seizes female with his pedipalps during the initial phase of mating. He may administer a “sexual sting” or tuck his sting under and “club” the female during this stage.

Occasionally females participate in the initiation of mating by approaching the male. A receptive female will approach a male with raised pedipalps and either bump or walk over the male until he responds with a lunge and grasps her in the manner described above. Some females display behaviors also seen in confrontations between females (Tallarovic et al. 1999). Females that continue these behaviors beyond the initial interaction with a male are presumably non-receptive.

Promenade a deux

The *promenade a deux* has been observed in all scorpion species for which mating behaviors have been described (reviewed in Polis and Sissom 1990). In

Hadrurus arizonensis the *promenade a deux* involves the pedipalp-to-pedipalp grip and includes both forward and backward walking. The male will also walk sideways to turn the pair. The male elevates his body above the ground, with metasoma raised, while the female's body remains flattened and close to the substrate with metasoma lowered and curled behind her (Fig. 2.3). The male leads the female in the *promenade* and locates a surface suitable for spermatophore deposition, usually a stick or a rock. The female usually walks with the male to where he guides her, providing only occasional resistance. If the pair is left on loose sand the *promenade* will continue indefinitely until either one of them becomes agitated and breaks away, or a suitable substrate is provided. Mating pairs in the laboratory have continued the *promenade* overnight and into the next day if kept in a dark room.

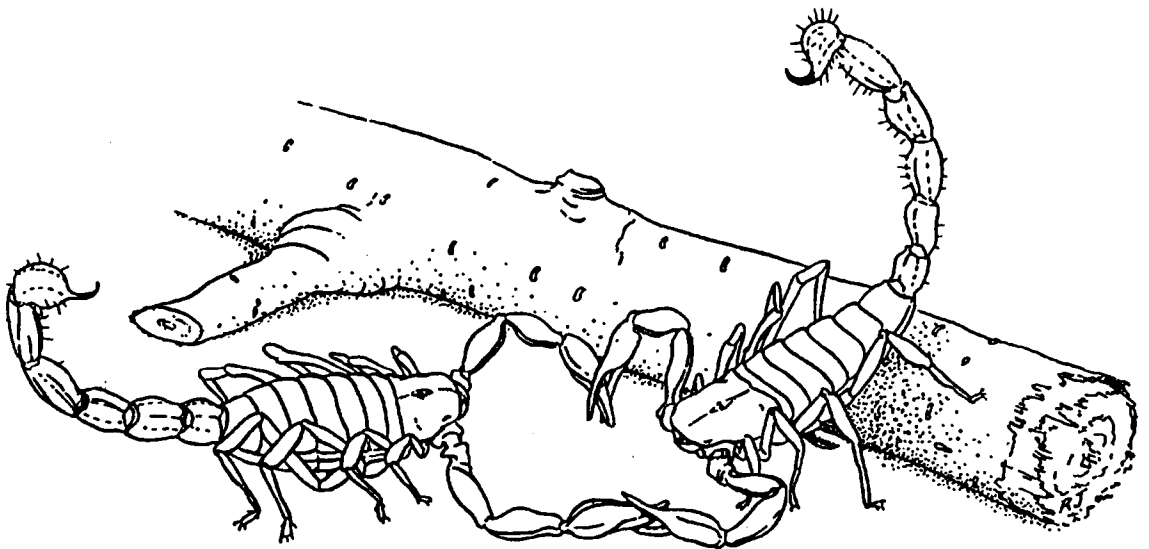


Fig. 2.3 Courtship behavior in *Hadrurus arizonensis*: During the *promenade a deux*, the male (right) leads the female (left) by the pedipalps forwards, backwards and sideways across the substrate until a stick or rock is located.

The male is the most active of the pair and guides the *promenade a deux*. His pectines and first pair of legs are very active during the *promenade*, especially when contacting the surface of an object. The movement of the first pair of walking legs is a rapid “tapping” that occurs occasionally during the *promenade* but also during sperm transfer (see below). This behavior may be analogous to the sand scraping described in several buthid species (Alexander 1959) but is different in that it involves only the first pair of legs and there is no displacement of substrate, as it almost always occurs on a hard surface.

In the field *H. arizonensis* have been observed engaging in the *promenade* in or near the entrances of burrows and up the trunks of trees and shrubs (pers. obs.). In some of the laboratory observations the male will try repeatedly to walk up the vertical face of the enclosure, or alternately to push the female up the side of the arena. They will settle for a horizontal surface, although there may be a preference for sloped or vertical ones. The *promenade* lasts from under one hour (~40 minutes) to over 12 hours (in the laboratory under dark conditions). Once they have located a surface, they may pass over it multiple times and in several different directions before the male finally stops to deposit the spermatophore. Often during the *promenade* the male will draw the female closer and reach for her chelicerae with his own and administer a cheliceral massage as observed in 26 species (reviewed in Polis and Sissom 1990). This is usually just before or during spermatophore deposition, and seems to be in response to an uncooperative female that refuses to walk with the male.

Sperm transfer

As in other scorpions, sperm transfer in *H. arizonensis* occurs via a spermatophore that is cemented to a solid surface such as a stick, or a rock. When a location for spermatophore deposition has been chosen, the male draws the female close and grasps her chelicerae with his own. The pair remain relatively still before (up to 2 minutes), during (6-16 seconds), and immediately after (up to almost 2 minutes) the extrusion of the spermatophore. One or both of the males rear legs twitch for several seconds during spermatophore deposition and serves as a convenient indication of that event when viewed from above. The males first pair of legs are sometimes active in the “tapping” described above. In a cheliceral grip the male’s first legs are under the female and seem to be in contact with her first pair of legs or possibly her prosoma. Likewise, the female’s first pair of legs is under the male. The spermatophore (described by Francke 1979a) has a cement-like substance at the base and quickly adheres to the surface when deposited. After deposition the male pulls the female to towards him and over the spermatophore by tugging on her pedipalps (Fig. 2.4). He often alternates pedipalp pulls with tapping his first pair of legs. It is possible that he uses this tapping behavior to judge the female’s location in relation to the spermatophore or in signaling the female, as it seems to stop once the female is positioned directly over the spermatophore. The last pull brings the female over the spermatophore so that the valves of the spermatophore contact her gonopore. He allows her to rest on top of the spermatophore (the weight of her body is presumably sufficient to discharge the sperm from the capsule) and the pair remain still for as long as 10 minutes. Females typically remain passive during this process

and a male may sometimes maneuver a female over the spermatophore in less than two minutes. Females do not always cooperate and may use their legs to anchor themselves. The male may struggle for 2 to almost 22 minutes after spermatophore deposition with an uncooperative female that resists being pulled forward and some females refuse the spermatophore completely.

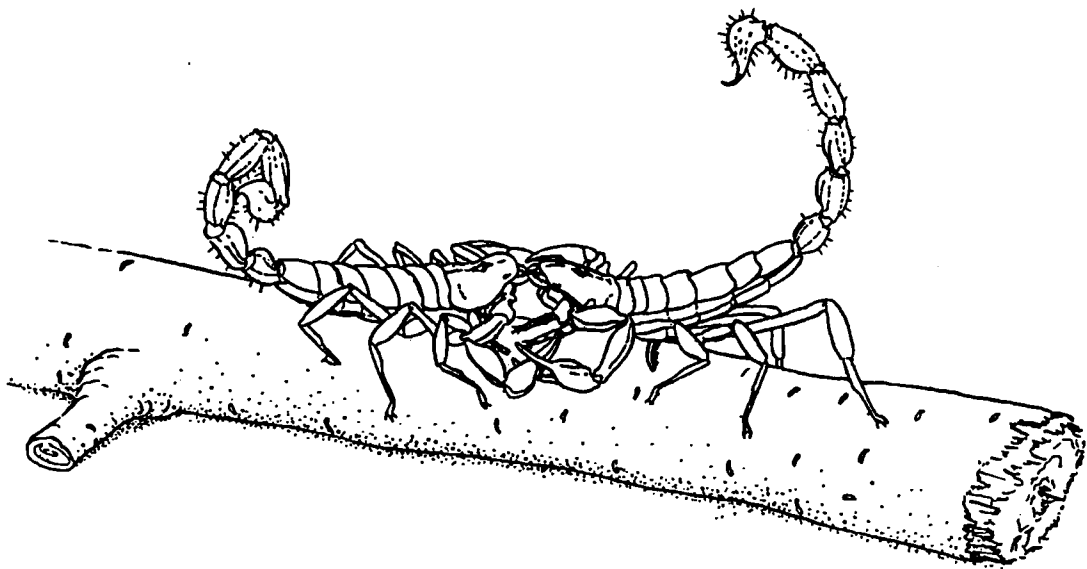


Fig. 2.4 Sperm transfer in *Hadrurus arizonensis*: During spermatophore deposition the male (right) holds the female (left) in a cheliceral grip while depositing a spermatophore on a solid substrate (in this case a stick). He then draws the female forward over the spermatophore so that she can discharge it.

Termination

Mating terminates when the female pulls gently away from the male. He responds by raising his metasoma and contacting her abdomen briefly in a manner reminiscent of the “clubbing” behavior seen in mating initiation, then dropping his metasoma back and simultaneously releasing her pedipalps and chelicerae. This release behavior is similar to that described in *Opisthophthalmus latimanus*

(Alexander 1956) in which the male taps the abdomen of the female with his metasoma but does not sting her. He may release her pedipalps first (45 seconds to 12.5 minutes after his last pull), and then repeat this metasoma contact, releasing her chelicerae after a second or third tap (7 seconds to 4 minutes after pedipalp release). Occasionally a male will simply let go of the female (without the metasomal taps) after she initially pulls away, especially if she has refused the spermatophore. The female leaves the site of spermatophore deposition first, walking several centimeters away before stopping to rub the ventral surface of her prosoma in the sand as described by Alexander (1959) in some buthid scorpions. She may also alternate this behavior with brief periods in which she displaces the sand with her first and second pair of legs as if digging. The male remains in place near the spermatophore and will often vigorously guard the spermatophore against the female if she returns. Males eventually abandon the spermatophore after 5 to 10 minutes or may eat it. The male may also leave the spermatophore temporarily to rub his prosoma in the sand in the same manner as the female and then return to the spermatophore to guard it from the female. If the male and female remain together they appear to ignore each other during subsequent interactions, climbing over or around each other. Occasionally the male may initiate the lunge-sting phase of mating very briefly and then release the female and walk away. Subsequent matings between recently mated pairs were not observed in this study.

Additional observations

Multiple matings by females and males were not directly investigated in this study, but one male attempted to mate on three separate occasions. He successfully mated with the same female twice (on two occasions one month apart). He unsuccessfully courted another female and deposited a spermatophore. After she refused it and departed, he quickly consumed it.

Post-mating cannibalism in *H. arizonensis* was not observed in any of the 14 matings observed in the lab and was not seen in the three observations of courtship in the field. One fatal interaction between a male and female occurred when a researcher attempted to separate a pair that was in the “lunge-grip” stage of mating. The male became agitated and stung the female near the gonopore. She died the following day. That incident represents the only fatality observed between males and females in mating or non-mating interactions during the course of this study.

Many of the females that mated during this behavioral study underwent parturition in the laboratory during the summer of 1998 and delivered viable offspring (Tallarovic, unpubl. data).

Discussion

Arthropods exhibit a wide range of complexity and organization in their mating behaviors with some of the most primitive being represented by arachnid groups (Weygoldt 1969; Schaller 1971). Scorpions provide an often neglected model for studying mating systems and behavior because, in comparison to other

arthropods, they utilize a primitive method of sperm transfer, using an external spermatophore instead of a specialized intromittent organ. Scorpion spermatophores are rather elaborate in structure and divergent enough to aid in taxonomic classification (Francke 1979a, Eberhard 1985). Sperm transfer by spermatophore involving courtship requires that both sexes are present and this is considered a more derived characteristic (Weygoldt 1969; Schaller 1971; Eberhard 1997). Scorpions provide a potential intermediate among arachnid mating systems. Furthermore, their unusual life-history traits make scorpions a particularly intriguing model for study.

Most of the mating behavior of *H. arizonensis* is not remarkably different than that described in other scorpions but it includes novel components. Juddering by females during courtship has only been described in one other species (Shulov and Amitai 1958). Leg tapping by males has not been described in other taxa. The vigorous behaviors seen in this species in the laboratory makes it an ideal candidate for further studies regarding mating and non-mating interactions. Behavioral interactions in this species occur readily in the laboratory and are easily observed and recorded by videotape for closer analysis. Behavioral phases are stereotyped enough to be ranked as to intensity and/or timed. Many compelling questions may be addressed regarding the mating system dynamics and social interactions of this species and will be the subject of future research.

Mating systems that involve courtship behaviors, particularly courtship that may take long intervals of time, provide females (and males) with opportunities for selection of mates. This opportunity may be true of scorpions, although the

possibility has not been investigated in depth. Male size seems to influence mating success in *Euscorpius flavicaudus*, although it appears to do so by male-male competition and not female choice (Benton 1992). The lengthy courtship of *H. arizonensis* may imply that sexual selection operates by means of female choice in this system.

Female mate choice may also be implied by the occasional refusal of a female *H. arizonensis* to accept a spermatophore. The parameters by which a female chooses a male is not known but it can be hypothesized that male size or persistence in courtship may influence the female decision. Female refusal to discharge the spermatophore has also been observed in a buthid species, *Bothriurus flavidus* (Peretti 1996). In some species of pseudoscorpions it has been suggested that females select males on the basis of male size or on male pedipalp size (Zeh 1987; Zeh and Zeh 1992). There are no exaggerated sexually dimorphic characters in *H. arizonensis* that would suggest sexual selection based on a physical structure but a larger or more persistent male may be more successful in “persuading” a female to accept his spermatophore. Females may have a threshold of resistance that can be overcome by male strength or length of time that he pulls her towards the spermatophore. Such possibilities will be investigated in future studies.

The possibility exists that some of the lengthy courtship observed in this study might be an artifact of the laboratory. The courtship of sympatric species *P. mesaensis* takes only a fraction of the time in the field (5 to 35 minutes as described by Polis and Farley 1979) that *H. arizonensis* does in the laboratory, but differences

in size and predatory behavior may account for interspecific differences. As the largest arthropod in its ecosystem *H. arizonensis* may have less pressure to mate quickly and depart. Furthermore there does not appear to be any post-mating cannibalism in *H. arizonensis* such as there is in *P. mesaensis* (Polis and Farley 1979) and therefore males would not need to be in hurry to escape being eaten by an aggressive mate.

Males occasionally reject females early in the courtship (prior to the *promenade a deux*). Whether this is prompted by a factor such as female size or reproductive condition (possibly via a pheromonal cue) is not known. The sudden lunge of male toward female at the initiation of mating suggests the presence of a chemical cue, as it often occurs with no apparent physical contact between individuals and often with very little or no movement such as juddering. This behavior may be useful as a bioassay for other areas of study, including pheromone research and trailing behavior.

Males may be able to aid their recovery from mating (especially from a failed attempt) by eating what remains of the spermatophore. Producing a spermatophore seems to be energetically expensive as male *H. arizonensis* usually lose a significant portion of their body weight after depositing one and require a number of days between matings (Tallarovic, unpublished data). Eating the spermatophore may be an important method of recovering nutrients for the male, particularly if the female has refused to be inseminated. In some organisms males provide nutrients in the spermatophore to the female as a nuptial gift (crickets and katydids, Gwynne 1997).

In some scorpion species the female has been observed eating the spermatophore after mating (Angermann 1955, 1957). This does not seem to be the case in *H. arizonensis*, as females were not observed eating the spermatophore at any time in this study.

Multiple matings by both sexes were observed anecdotally in this study and should be investigated further under experimental conditions. If multiple matings by females occur regularly then it is also possible that lengthy courtship may be a form of pre-copulatory mate guarding in which the male engages the female in courtship in an attempt to keep her from mating with other males. Population densities for *H. arizonensis* are relatively low, and it would seem unlikely for females to encounter males on a regular basis, but this possibility exists and remains an interest for future study.

Continued studies into the behavior of *H. arizonensis* and other species of scorpions may prove useful in understanding the evolution of mating behaviors in arachnids and arthropods in general. The difficulty of observing *H. arizonensis* in the field remains a problem, but the ability to observe and experimentally manipulate mating pairs in the laboratory and culture this animal in captivity opens new areas of study that were not possible before. Not only can we study the possibility of mate choice in scorpions, but possible fitness consequences may become apparent by examining the size, number and viability of offspring produced by laboratory matings.

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Chapter 3

Evidence of Male and Female Mate Choice in a North American Desert

Scorpion, *Hadrurus arizonensis*

Sara K. Tallarovic and Philip H. Brownell

In preparation for submission to Ethology

Abstract

In theory, the selection of a mate should be exerted by the sex that has a higher energetic investment in reproduction. In most mating systems females appear to have a higher reproductive investment than males, but in animals like scorpions males transfer sperm indirectly via an external spermatophore that can be costly to produce. Mate choice was studied in a large North American desert scorpion, *Hadrurus arizonensis*. Larger females tend to have larger litters, thus it was predicted that size may be important in both male and female courtship success. Field-collected adults were randomly paired ten times each with the opposite sex over a period of 50 nights for videotaped interactions in the laboratory. Reproductive behavior for each interaction was scored separately for males and females in terms of courtship success, and time spent in specific behavioral phases was recorded. Size parameters for each individual were also recorded, including weight change during the experiment. Both males and females varied in courtship success, and variance was equal between the sexes. Female courtship success was positively correlated with female body size, but male courtship success was not. Males and females on the same feeding schedule exhibited different patterns of weight change over the course of the experiment. Females gained more weight and at a faster rate than males and this may reflect energetic costs incurred by males in spermatophore production. Males may preferentially court larger females to increase their reproductive success by maximizing the return on their energetic investment.

Introduction

Mate choice can be described as “any pattern of behavior, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others” (Halliday 1983). Mate choice by females as a mechanism of sexual selection has been the focus of intense study, and has been documented in a wide range of vertebrate and invertebrate mating systems (reviews Andersson 1994; Gould and Gould 1997). In most mating systems it is assumed that females have a higher reproductive investment than males, and thus are expected to be the sex that chooses a mate (Trivers 1972). Alternatively, in systems where male reproductive investment is high, males often show mating preferences (Gwynne 1981). Male reproductive investment can take the form of paternal care of offspring or nutritional benefits to the female (Trivers 1972) in the form of nuptial gifts (Thornhill 1981; review in Gwynne 1997). Alternately, the operational sex ratio (Emlen and Oring 1977) and the potential reproductive rates of males and females can predict the direction of sexual selection (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992).

Male investment in reproduction can also include simply the cost of gamete production and the mechanism of transfer to the female (Dewsbury 1982). In the latter case, the cost of these investments may still be high enough to influence mating decisions by males (Cook 1975; Manning 1975; Morris 1980). Males and females in these situations are likely to be more similar in their reproductive investment, and therefore we might predict that they would also be more similar in the degree of

mating preferences they display. Curiously mate choice in both sexes under these circumstances has been understudied.

In scorpion mating systems, males and females both make significant contributions in reproduction. Males transfer sperm to females during mating via a complex stationary spermatophore. Females give birth to live offspring and provide limited parental care of larvae for several weeks. Both sexes have potentially large investments, but scorpion have long been overlooked as a model in mating systems research. Reproductive behavior has been described for approximately 30 species of scorpions (reviewed in Polis and Sissom 1990; Tallarovic et al. submitted) in seven of 16 families (taxonomic revision by Fet et al. 1999), but few studies have examined the dynamics of reproductive interactions based on the evolutionary peculiarities and constraints of this unique and ancient group of arachnids.

Sperm transfer in scorpions is preceded by an elaborate and stereotyped series of courtship behaviors. Mating behavior in most scorpions can be separated into the following phases: 1) initiation, 2) *promenade a deux*, 3) sperm transfer, and 4) termination (as organized in Polis and Sissom 1990). Typically initiation occurs abruptly when the male seizes the female aggressively at which time the female becomes passive. The male then leads the female in the *promenade a deux* (Maccary 1810) which has often been described in function as a search for an appropriate substrate for spermatophore deposition (although further significance of this phase may be yet unrealized). Sperm transfer occurs when the male deposits the external spermatophore on a solid substrate and pulls the female over it so that she may

discharge it and become inseminated. Termination follows soon after when the male releases the female and both depart.

Only recently have studies begun to examine whether sexual selection may be operating in scorpions. Male-male competition has been suggested in *Euscorpis flavicaudus* (Benton 1992), and mate rejection by females (as an indicator of possible female choice) has been observed in both *Bothriurus flavidus* (Peretti 1996) and *Hadrurus arizonensis* (Tallarovic, et al., submitted). In *H. arizonensis*, females sometimes reject males during or after the *promenade a deux*, and will often refuse to walk over a spermatophore to become inseminated. Males sometimes reject females as well, although this occurs earlier in the courtship usually before the *promenade a deux* and after initiation (SKT, pers. obs.) These initial observations motivated the more intensive study of experimentally manipulated mating pairs of *Hadrurus arizonensis* that we present here.

The giant hairy desert scorpion, *Hadrurus arizonensis*, provides an ideal behavioral model for laboratory studies of reproductive behavior in scorpions because of the particularly robust and highly stereotyped behavior displayed by this species in captivity. Reproductively active adults collected from the field during the late summer mating season will display mating behaviors for approximately two months in the laboratory if maintained at late summer temperatures (Tallarovic, et al., submitted). Native to the Mojave Desert, *H. arizonensis* is the largest species of scorpion in North America, and is long lived (25+ years, Stahnke 1966). Like other scorpions, females give birth to live young and provide limited maternal care of

offspring during the first larval instar. Based on our earlier observations of reproductive behavior in this species, we hypothesized that mate choice by one or both sexes may occur in this species. Males and females are likely to have comparable investments in reproduction: males, in the form of a spermatophore that requires time and energy to produce, and females, in the form of viviparous offspring and some maternal care. It was further hypothesized that body size may be an influential factor in courtship success for both males and females based on the following observations: 1) preliminary data on field-caught gravid females suggests that larger females have more offspring per litter (data presented with this study); and 2) small males often appear to have difficulty courting large females and rarely seem to transfer sperm successfully even after depositing a spermatophore. Alternatively, we predicted that males that invest more time in courtship behaviors such as the initiation phase, or the *promenade a deux* may enjoy a higher courtship success. The aim of this study was to establish whether both males and females varied in courtship success over a randomized series of isolated encounters with the opposite sex, and to determine what factors may influence courtship success.

Methods

Litter size data

Thirteen adult female *H. arizonensis* were collected from sandy areas of the Mojave Desert near Baker, CA from May to June 1998. Twelve females were sacrificed within 5 days of collection (by chilling to -15°C) and dissected. The

ovariuterus was removed and placed into scorpion saline, and either late state follicles (early May animals) (M. Warburg, pers. comm.), or developing embryos were counted. One additional female was collected in October of 1997 and was kept in the laboratory over the winter. That female and one other from the early June 1998 collection were kept in the laboratory until parturition and their live broods were counted. These two females were kept on a laboratory temperature cycle that mimics the natural dune (Brownell, unpubl. data).

Courtship success experiment

Animals: Adult *H. arizonensis* were collected from sandy areas of the Mojave Desert near Baker, CA and Indio, CA in August of 1999 and shipped to Oregon State University in Corvallis, OR. Animals were sexed, assigned an identification number, weighed, and fed (5-week old crickets, *Archeta domesticus*) upon arrival in the laboratory. Scorpions were housed in individual plastic containers lined with a native sand substrate. Twenty males and twenty females were used in the experiment. Upon arrival in the laboratory animals were placed on a shifted light cycle (with nightfall occurring at 4:30 p.m. and lasting 10 hours) for one week prior to the beginning of the experimental trials. Furthermore, animals were subjected to a daily heat cycle of 28-35°C, mimicking conditions of the natural dune (Brownell, unpubl. data).

Experiment: Each male-female interaction occurred in a 35 cm (l) x 23 cm (w) x 30 cm (h) plastic observation container divided in half by a removable panel

and filled with filtered heat-treated (to 200°C in a drying oven for sterilization purposes) native sand as substrate. A heating pad was placed under each container to maintain the substrate at 34-35°C. A piece of ceramic brick was provided as a spermatophore deposition substrate in each container. Containers were rinsed and dried, and sand and bricks heat-treated (also to 200°C) between trials. Each animal was randomly paired with a member of the opposite sex 10 times over 50 nights in the following manner: Males ($n = 20$) were randomly assigned to one of 5 groups (4 males per group). Because males require 4-5 days to produce a new spermatophore, groups of males were rotated such that a group of four was used once every five nights (allowing each male 5 days between trials). Four interactions were staged concurrently at once on any given night. A five-night period represented one series of interactions in which each male was paired with one female. Females ($n = 20$) were randomly assigned to males for each series such that females interacted once every 4 to 7 nights and no pair interacted twice. There was one exception to the latter rule, in which a male and female were accidentally paired a second time. The results for both trials were identical, and the second result was removed from the data set. A make-up trial for each individual with a new randomly assigned mate was performed at the end of the entire experiment. One female died halfway through the experiment after participating in 5 interactions. Her average courtship success rating (over 5 interactions instead of 10) was included in the analysis.

Each night, four interactions were staged concurrently and were begun approximately 1.5 hours after artificial sunset inside a temperature- and light-

controlled behavioral chamber in a darkened room. Animals were placed on either side of a divider in the container and allowed 5 minutes to acclimate. The divider was then removed and the interaction recorded on videotape for 8 hours. Interactions were video taped using a low-light Watec® WAT-902a camera under red light (40 watt), which scorpions appear not to see (Machan 1968).

Videotaped interactions were viewed by a single researcher and ranked according to the intensity of reproductive behavior (“courtship success”) in each interaction. The following ranking system initially was used: 0 = no reproductive behaviors; 1 = male initiated mating only briefly and stopped; 2 = male initiated mating several times and stopped; 3 = male initiated mating and pair began *promenade a deux*, but stopped; 4 = male initiated mating and pair began *promenade a deux*, but male did not deposit spermatophore (*promenade* continued for hours); 5 = male deposited spermatophore but female did not walk over it (female not inseminated); 6 = male deposited spermatophore and female was inseminated (female showed mating plug). An additional ranking of 5.5 was added for interactions in which it was difficult to tell whether a female had been inseminated. It is possible for the mating plug to break away following insemination and its absence is therefore not a good indicator of mate rejection. This initial ranking system was used to assess female courtship success (a measure that is directly correlated with the amount of courtship behavior a female solicits from a male), and was used for both sexes to determine the variance in courtship success for comparison.

A second supplemental ranking system was devised to describe courtship success for males, as rejection of females by males occurs early in the courtship. Interactions in which males did not court females beyond the initiation phase were not ranked and were excluded from non-parametric analyses (since male rejection of a female should not be considered a lack of male courtship success). If a male courted a female beyond the initiation phase, these interactions were ranked using the following scale: 0 = male leads female in *promenade a deux*, but male did not deposit spermatophore, *or* male deposited spermatophore but female was not inseminated (in either case, this is a lack of success for the male); 1 = male deposited spermatophore and female *may* have been inseminated; and 2 = female definitely inseminated and showed mating plug the next day.

Animals were weighed and fed (one cricket each) the day following each trial in which they were used. Food intake was monitored (and with few exceptions all food provided was consumed). Females were examined the morning following each interaction for the presence of a mating plug. At the end of the 50-night experimental period, each animal was measured for body length (from front edge of carapace to posterior edge of telson) and other body size parameters (carapace length and width, chela length and width, and telson length).

Data Analysis: Courtship success among both males and females were analyzed using parametric and non-parametric methods. A one-way ANOVA of courtship success (using the 0-6 ranking scale for both sexes) was performed to obtain a measure of variance for each sex. Mean courtship success among females

(as quantified by the ranking system of 0–6) was compared using a Kruskal-Wallis test. Mean mating success among males was also compared (measured by the male ranking system of 0–2, and excluding interactions in which the male rejected the female) using a Kruskal-Wallis test. Multiple linear regression analysis was used to determine the relative effects of female identity, male identity, female body length, male body length, and interaction number on courtship success for both males and females (using the 0-6 and 0-2 scales respectively). A simple regression analysis was also used to determine whether reproductive behavior changed over the course of the experiment (a potential confounding factor). Statview® and JMP® (SAS Institute) software were used for analyses in this study.

Mass change over time: An extra sum of squares F-test (Ramsey and Schafer 1996) was used to test whether the regressions for male and female mass over time were statistically different.

Results

Litter size

A positive relationship exists between female size (body length) and the number of potential offspring ($R^2 = 0.695$, $P = 0.0004$) (Fig. 3.1).

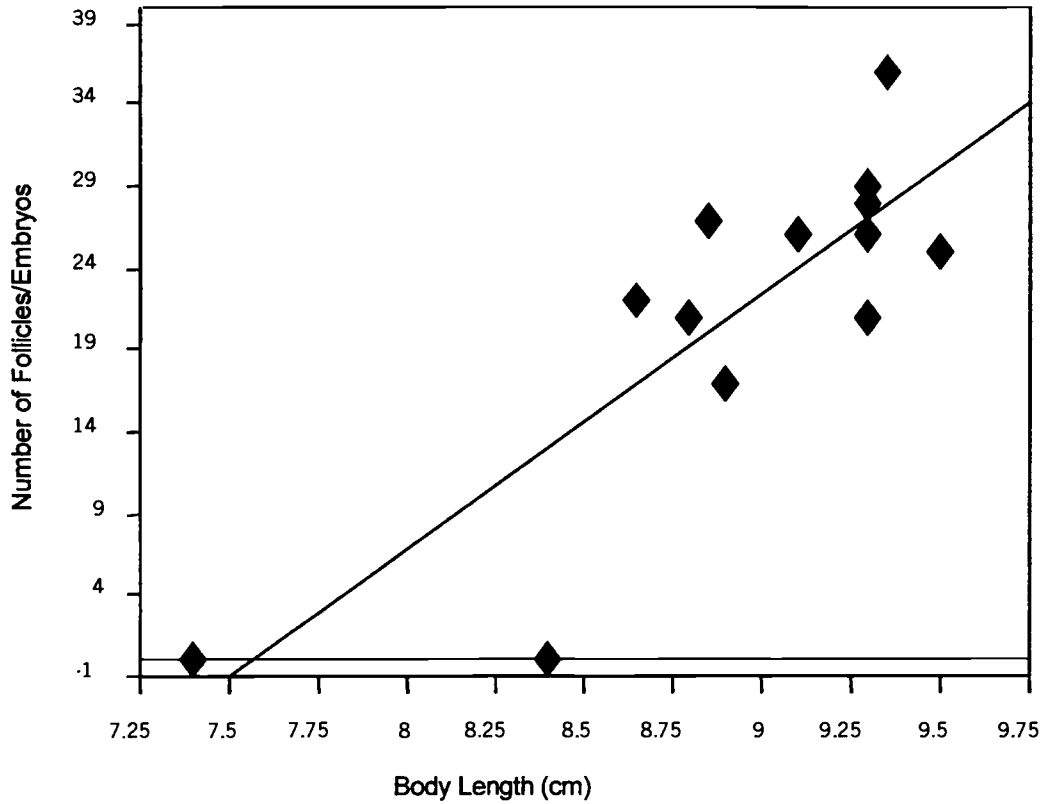


Fig. 3.1. Litter size is positively related to body size of gravid female *H. arizonensis* collected from the field (measured from rostral edge of carapace to distal edge of telson) ($R^2 = 0.695$, $P = 0.0004$, $Y = -118 + 15.63 * X$).

Courtship success

Of the 20 females in the study, 65% were potentially inseminated by at least one male, and 40% were potentially inseminated by more than one male. Three females (15%) were possibly inseminated by 6 different males each. Of the 20 males in the study, 85% potentially inseminated at least one female, and 55% potentially inseminated more than one female. One male potentially inseminated as many as 5 different females.

When males and females were ranked on the same scale (0-6) and analyzed using a one-way ANOVA, females varied significantly in courtship success but males did not (females: $F_{19} = 8.467$, $P < 0.0001$; males: $F_{19} = 1.252$, $P = 0.2213$). Variance among females was 4.269 (mean = 2.695, s.d. = 2.066) and among males was 4.291 (mean = 2.615, s.d. = 2.071).

Among females ($n = 20$) there was a significant difference in mean courtship success (Fig. 3.2) (Kruskal-Wallis test, $P < 0.0001$). Certain females elicited more reproductive behaviors from males than other females on average, and these females tended to be larger in size than others (see cumulative courtship success below). When male courtship success was ranked using the alternate scale (0-2), mean courtship success differed significantly between males (Fig. 3.3) (Kruskal-Wallis test, $P = 0.003$). Some males potentially inseminated more females than did other males.

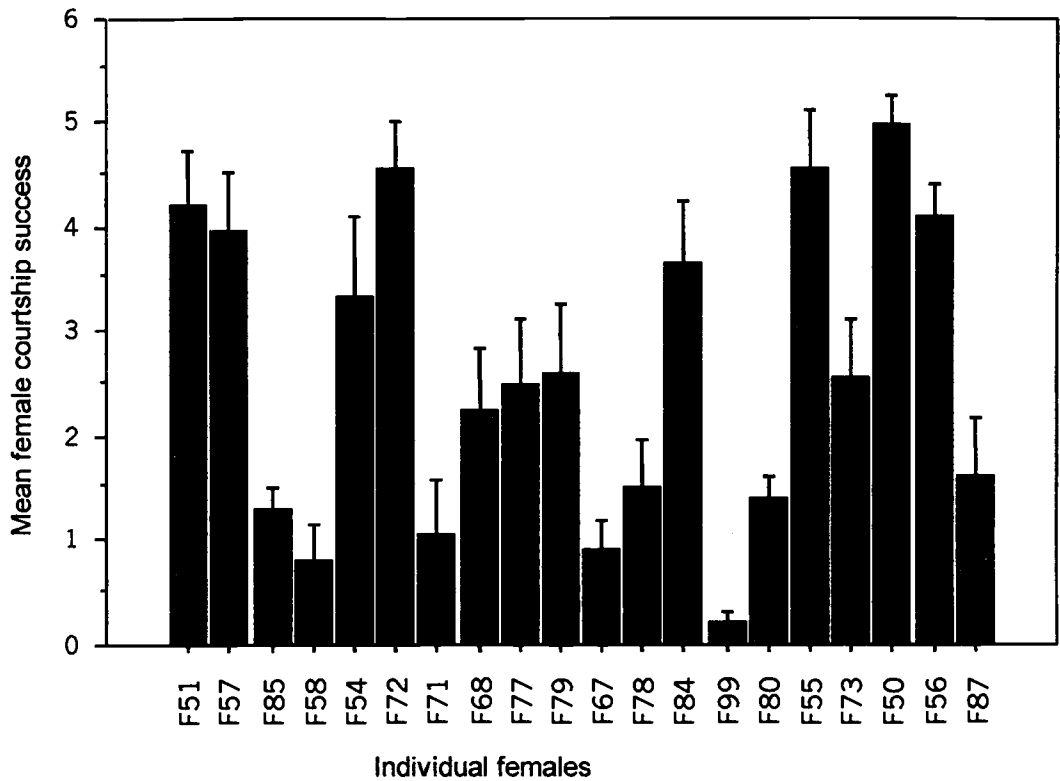


Fig. 3.2. Mean courtship success of 20 female *Hadrurus arizonensis* over a randomized series of 10 pairings with males. Each vertical bar represents an individual female (identified here by number). Courtship success for females in each interaction was ranked from 0-6. There was a statistically significant difference in mean mating success among females (Kruskal-Wallis test, $P < 0.0001$).

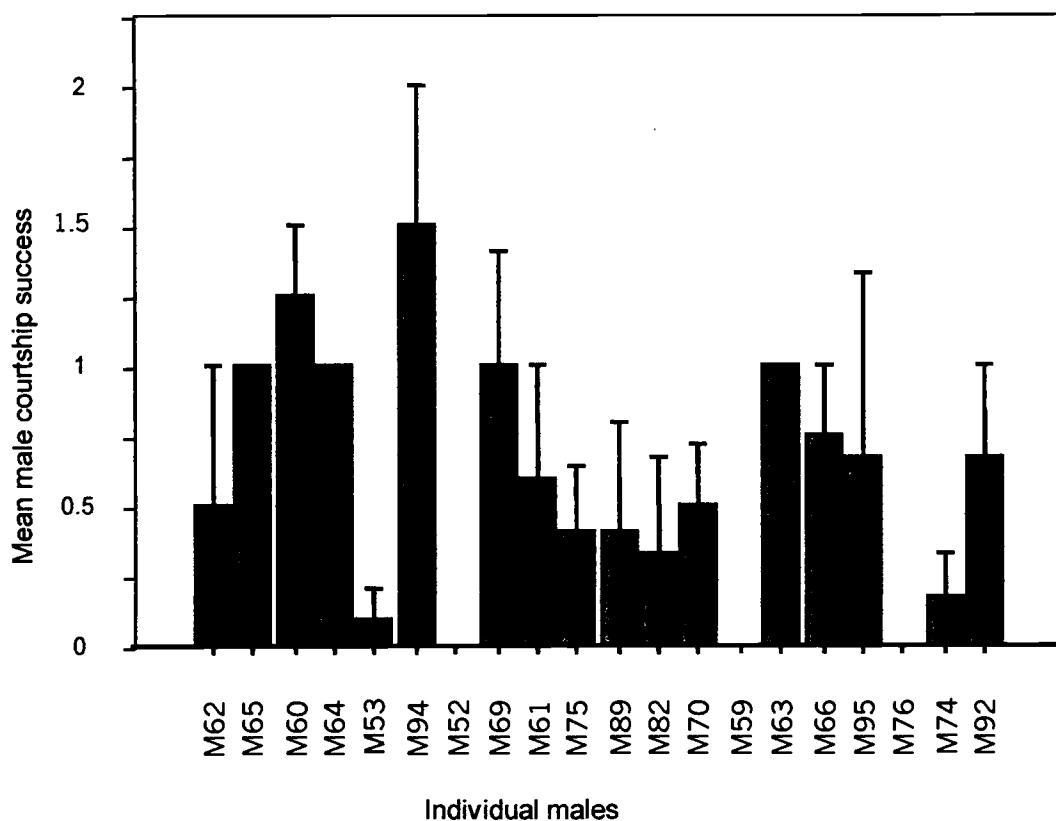


Fig. 3.3. Mean courtship success of 20 male *Hadrurus arizonensis* over a randomized series of 10 pairings with females. Each vertical bar represents an individual male (identified here by number). Courtship success for males in each interaction was ranked from 0 to 2. There is a statistically significant difference in mean mating success among males (Kruskal-Wallis test, $P = 0.003$).

The effects of identity, size and interaction on female and male success are presented in Tables 1 and 2, respectively. Female and male identity had the most significant effect on female success, while male identity alone had the most significant effect on male success.

Table 3.1 Analysis of variance in female courtship success.

Source	Degrees of Freedom	Sums of Squares	F-Ratio	P
Female length	1	0.05401	0.0237	0.8779
Male Length	1	0.00395	0.0017	0.9669
Female ID	18	225.47152	5.4949	<0.0001
Male ID	19	92.67886	2.1398	0.0063
Interaction	9	23.88764	1.1643	0.3224
Model	47	492.65049	4.5981	<0.0001
Error	142	323.70386		
Total	189	816.35395		

Table 3.2 Analysis of variance in courtship success for males using alternative ranking scheme (0-2).

Source	Degrees of Freedom	Sums of Squares	F-Ratio	P
Female length	1	0.123628	0.3636	0.5494
Male Length	1	0.146652	0.4313	0.5146
Female ID	16	4.244578	0.7802	0.6988
Male ID	19	15.389502	2.3820	0.0081
Interaction	9	4.430009	1.4476	0.1957
Model	45	25.244131	1.6498	0.0460
Error	47	15.981676		
Total	92	41.225806		

Courtship success rankings for each individual's 10 interactions were averaged over the 50 nights. A positive relationship exists between mean courtship success of each female ($n = 19$) and body length (Fig. 3.4) ($R^2 = 0.384$; $P = 0.0046$). Per interaction ($n = 200$) female courtship success was also positively correlated with the ratio of female to male body size ($R^2 = 0.118$, $P < 0.0001$) (Fig. 3.5). There was no significant relationship between average male courtship success and body length, or between male courtship success and the amount of time spent in courtship behaviors (initiation or *promenade a deux*). Overall courtship success among females and males did not change over the course of the experiment (females: $Y = 2.957 - 0.57 * X$, $R^2 = 0.006$, $P = 0.2680$; males: $Y = 3.028 - 0.075 * X$, $R^2 = 0.011$, $P = 0.1410$).

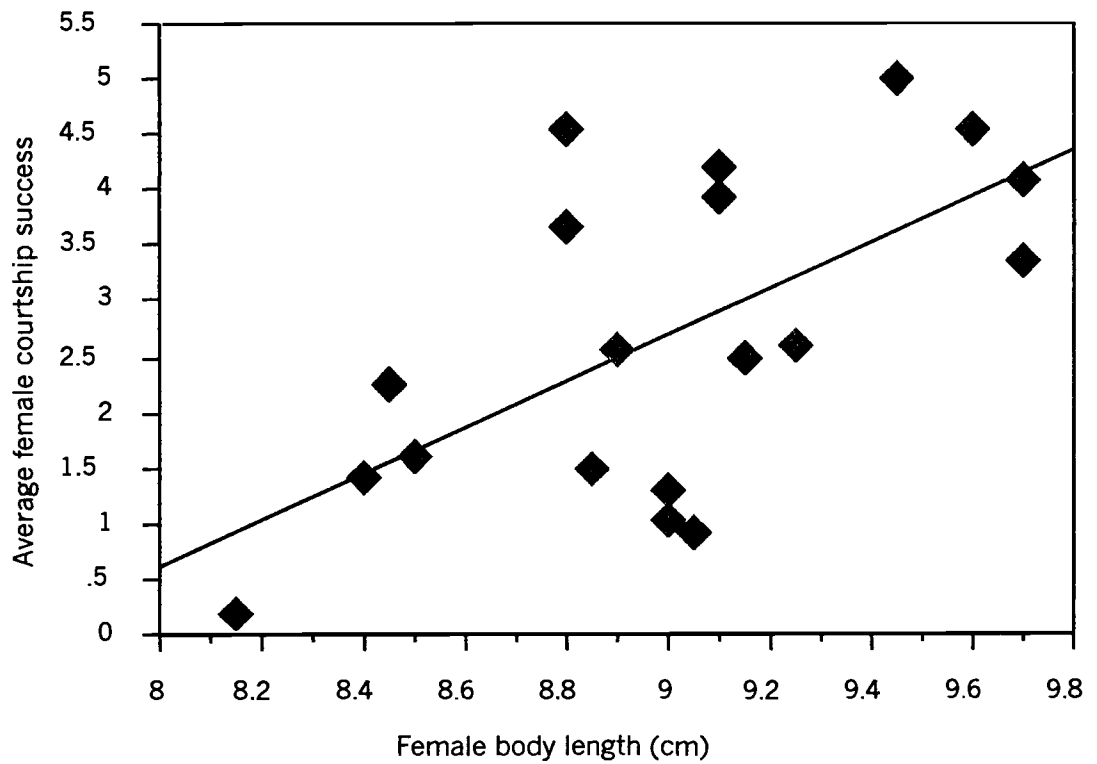


Fig. 3.4. The mean courtship success score for females (averaged over 10 interactions) is positively related to female body length ($R^2 = 0.384$; $P = 0.0046$). Larger females elicited more courtship behavior from males than small females. ($Y = -15.969 + 2.074 * X$)

Mass change over time: The regressions for male and female mass over time were significantly different ($F_{2,18} = 283.78$; $P < 0.0001$). Females increased in mass at a faster rate than males and gained more weight overall (Fig. 3.5).

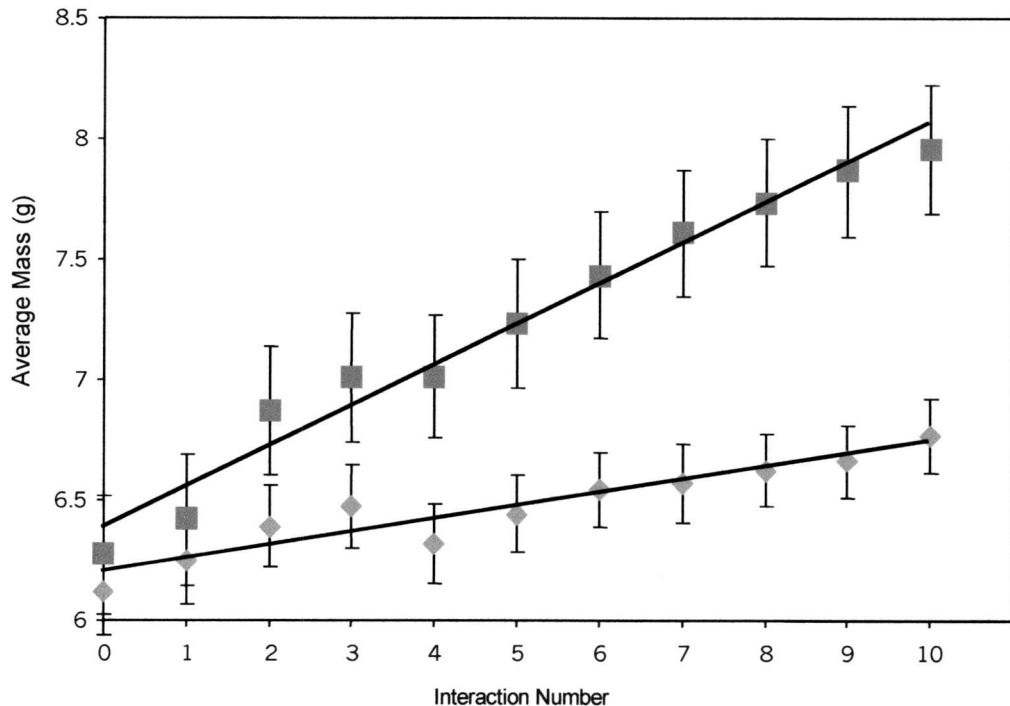


Fig. 3.5. The regression for female (squares) mass over time (plotted here against the interaction) is significantly higher than that for males (diamonds) when compared using an extra sum of squares F-test ($F_{2,18} = 283.78$; $P < 0.0001$). Over the course of the experiment (10 reproductive interactions over 50 days) females gained more weight than males and at a faster rate.

Discussion

For sexual selection to occur, there must be differential reproductive success among members of one or both sexes (Howard 1979). Sexual selection is usually more intense on the sex that has a relatively lower reproductive investment, often

because the sex with a higher reproductive investment exerts more control (in the form of mate choice) over the mating event (Trivers 1972). Although the most accurate measurement of reproductive success would be to quantify the number of offspring per individual that reach reproductive age throughout an individual's lifetime, courtship success can be used as an indicator of reproductive success. Variance in courtship success was found among female *H. arizonensis* using both parametric and non-parametric analyses in this experiment, and among males using non-parametric analysis. This finding supports the hypothesis that female mate choice and male mate choice exists in *H. arizonensis*. This result is based on laboratory studies of male-female courtship. Such studies allow mate choice and/or correlates of courtship success to be examined without the effects of intrasexual competition or environmental variation (Houck et al. 1985; Houck 1988; Poramarcom and Boake 1991; Balshine-Earn 1996; Phelan and Baker 1997; Vinnedge and Verrell 1998). Ideally, studies of lifetime reproductive success of animals in the field yield the most accurate measures of sexual selection (Fincke 1988; McVey 1988), but laboratory-based studies can help identify characteristics to focus on in the field.

Choosy females *and* males? Variances in courtship success in *H. arizonensis* in this study were roughly equal for males and females, which is a different result than has been seen in similar laboratory studies of mate choice (Houck et al, 1985). Typically the sex under more intense selection has higher variance in courtship or mating success and this is usually males. Mate choice by

females occurs in many mating systems. Females are expected to be the choosier sex based on their (usually) higher reproductive investment in the offspring, or alternately their lower reproductive rate. As female scorpions give birth to live young and provide some maternal care, it would not be unusual to see female choice in this system. Males are usually choosy only when their reproductive investment involves more than gametes, such as the courtship feeding and nuptial gifts of certain insects (Gwynne 1997), paternal care of offspring (Trivers 1972), or when they are the limited sex (Emlen and Oring 1977). Male *H. arizonensis* do not allow females to eat the remains of their spermatophore and often consume the remains themselves (Tallarovic et al. submitted) and are therefore not likely to be providing a food resource as an investment. Whether a benefit is derived from sperm or seminal fluids is unknown.

Male scorpions are temporally limited in their reproduction by the production of a spermatophore. Males require 4-5 days between spermatophores, and the spermatophore itself is a complex sclerotized structure that varies among species (often distinctive to individual taxa, Francke 1979). The difference in male and female weight gain over the course of the experiment suggests that courtship is energetically more costly for males than for females. In this experiment males lost a significant proportion of their body weight when they deposited a spermatophore, even though males and females were fed equally (and showed no difference in food consumed). These data may reflect a metabolic difference between males and females, as has been observed in spiders (Kotiahho 1998). Depositing a

spermatophore is likely to be both an energy- and time-consuming process, and a male's investment in one mating may limit future mating opportunities (Dewsbury 1982). This latency to produce a new spermatophore itself may arguably be the cause of choosy behavior in males by decreasing their potential rate of reproduction (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). This possibility should be investigated more closely in regard to actual reproductive rates in the field and in relation to experimentally manipulated food resources in the laboratory.

Relative body size and courtship success. Past observations of *H. arizonensis* (Tallarovic et al. submitted) have noted that pairs more closely matched in size are more likely to mate successfully. Larger *H. arizonensis* females tend to have larger litters, and males that preferentially court larger females may be able to maximize their reproductive investment in siring a larger litter. Courting too large a female, however, can result in failure. During the sperm transfer phase of mating the male must pull the female forward over the spermatophore where she then discharges it with the weight of her body. A smaller male might be less likely to succeed in pulling a larger female forward to inseminate her. The identity of individual males and females in the study were the most significant variables in predicting courtship success, and appeared to be independent of body size. Although we found a positive relationship between female body size and average female courtship success, courtship success of each sex may actually be the product of a number of interacting factors, including the behavioral interaction between the sexes during courtship, such as has been documented in plethodontid salamanders (Vinnedge

and Verrell 1998). We analyzed male and female courtship success separately. By intentionally excluding interactions in which males rejected females from analyses of male courtship success, we only rated males that attempted to court a female, and we consider this a more accurate reflection of male success. Although we found no correlation between male courtship success and male body size, or between courtship success and time spent in courtship, there may be other factors that correlate with male success that were not revealed by this study.

More recent definitions of sexual selection have been expanded to include topics such as competition between gametes (sperm competition, Parker 1970) and female manipulation of sperm or zygotes after insemination (cryptic female choice, Eberhard 1996). Such competition or choice can occur after multiple matings by females. Some female *H. arizonensis* potentially were inseminated by as many as 6 males, while others were only minimally courted by one or two males. Certainly sperm competition and/or cryptic female choice may be operating in this system and should be investigated further. Whether females may gain benefits from multiple matings remains another important question of interest. Recent advances in maintaining *H. arizonensis* in the laboratory may allow further elucidation of these questions and more.

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Chapter 4

Intraspecific Aggression and Agonistic Behaviors in the Giant Hairy Desert

Scorpion, *Hadrurus arizonensis* (Scorpionida, Iuridae)

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Abstract

Hadrurus arizonensis, the giant hairy desert scorpion, is a solitary species of scorpion native to North American deserts. Its diet is comprised of heterospecifics but not conspecifics. Adult *H. arizonensis* display behaviors unique to intraspecific interactions that are aggressive but do not result in injury or death. These behaviors can be separated into phases based on the level of physical interaction and usually terminate with a “winner” and “loser”. Pairwise interactions of *H. arizonensis* were observed by videotaping in the laboratory in male-male, female-female, and male-female combinations. Observations were also made of interactions of adult *H. arizonensis* with juvenile conspecifics and juvenile heterospecifics (*Paruroctonus mesaensis*). The agonistic behaviors are described and defined as the *alert*, *contact* and *contest* phases. Males and females both displayed these behaviors but intersexual and intrasexual interactions differed in the amount of time spent in each behavioral phase. Females spent the majority of interaction time in the *contact* phase, and males spent the majority of interaction time in the *alert* phase. Interactions between two females showed a positive relationship between body size and winning status, with winners being larger. Behaviors of adults toward juvenile conspecifics were similar to interactions between adults, whereas heterospecifics were often captured and eaten. The agonistic behaviors displayed by *H. arizonensis* appear to have communication value and each phase may have a specific function. It is proposed that the *alert* phase may function in species recognition, while the *contact* and *contest* phases may function in competition over potential resources.

Introduction

Aggressive behaviors are generally seen as having two primary functions: 1) a response to danger, and 2) competition over resources or status. Although these functions are usually distinct, they may occur concurrently in cannibalistic species. Many scorpion species are at least occasionally cannibalistic (Smith 1966; Probst 1972; Polis 1980), and interspecific (or “intraguild”) predation has been well documented in many North American species (Polis 1979, 1980; Polis, Sissom and McCormick 1981). It is often difficult to study behavioral interactions in some scorpion species unless conducting a study of predatory behavior. For such species, conspecifics may simultaneously represent potential competitors and either prey or predator.

The giant hairy desert scorpion, *Hadrurus arizonensis* (the largest species of scorpion in North America) does not appear to be highly cannibalistic. Instead, sympatric species such as the sand scorpion, *Paruroctonus mesaensis*, contribute significantly to its diet (Polis and McCormick 1986). *H. arizonensis* adults can be placed together for observation in the laboratory with little concern for a fatality, and pairs of animals can be housed together in the laboratory for months and even years (pers. obs.). Mating pairs will go through an elaborate courtship display (Tallarovic, Melville and Brownell, submitted) that almost never ends in cannibalism. Similarly, non-reproductive interactions between individuals in the laboratory (same-sex or non-mating pairs) involve a behavioral display that appears aggressive, yet rarely results in death or even injury. The behavioral display between non-reproductive

pairs or same-sex conspecifics is distinctly different from behaviors related to reproduction or predation.

Hadrurus arizonensis is a solitary species of scorpion common to the Mojave Desert. Like many desert animals they occupy a burrow by day and are active at night. *Hadrurus arizonensis* is an extremely long-lived species (25 years or more according to Stahnke 1966) and take several years to reach maturity. Females give birth to live young in the burrow and the first instar larvae stay on the mother's back until the first molt, at which time they disperse as second instars. Very little is known about the ecology or life history of *H. arizonensis*. We studied their non-reproductive behavioral interactions to investigate what parameters may influence intraspecific aggression in this solitary species, and whether these behaviors may function in species recognition. We hypothesized that females may be more aggressive than males and predicted that larger females may have an advantage over smaller females, and over males in general. These hypotheses were based on life history observations indicating that females may remain close to a burrow whereas males appear to wander in search of females during mating season (Polis 1990; Polis and Sissom 1990). Furthermore, daytime surface temperatures in the Mojave Desert can exceed 70°C (Brownell, unpubl. data) making a burrow an essential resource. This paper represents the first description of non-reproductive interactions in *H. arizonensis* and the first quantitative study regarding the factors that may influence these behaviors.

Methods

Animals: *H. arizonensis* used in this study were collected in May, July and September of 1997 from sandy areas in the Mojave Desert (Soda Springs near Baker, California and Indio, San Bernadino Co., California). Animals collected in May and July were used in laboratory experiments conducted at Oregon State University. Experiments involving intraspecific aggression between adults were conducted in July, August and September. Animals were housed individually in plastic cups with sand substrate. When experiments were conducted, animals were kept at 26° to 30° C and fed one wax moth larvae (*Galleria mellonella*) every 3 weeks. When experiments were not being performed animals were maintained at temperatures of 20° to 25° C and kept on the same feeding schedule. Animals were weighed in the laboratory at the beginning of the study.

Animals collected in September were used in experiments performed at a field station laboratory at the Desert Studies Center in Zzyzx, (San Bernadino Co.) California. Animals were weighed immediately after collection, and experiments began the day after collection. Animals were housed individually in 1-gallon plastic Ziploc® bags filled with air (refreshed twice a day) to which sand was added as a substrate (this allowed animals to move around and groom themselves). Temperatures ranged from 29° to 34°C.

Laboratory experiments involving adult females and juveniles were conducted in March 1998 after the adults had been housed for six months in large (19L) sand-filled containers. All animals had experienced a “winter” cycle during

the months of December and January, during which time the temperature was reduced to 15°C. Temperatures were gradually raised to 22-25°C over February and trials took place at approximately 25°C.

Agonistic behaviors between adults: Interactions took place in a circular PVC arena (d = 21 cm, h = 15.5 cm) filled with approximately 500 cc of native desert sand that was replaced before every trial. A pair of animals was placed into the arena on each side of a divider, and allowed to explore for 5 minutes, after which the divider was removed and the animals allowed to interact. The animals were filmed from above for 15 minutes or until the interaction ended (some interactions lasted up to 20 minutes) using a Watec® WAT-902A low light video camera. The arenas were illuminated with a 25 watt red bulb (both at a distance of approximately 50 cm). All trials were conducted inside a darkened room. Trials at Oregon State University were conducted after 9:00 p.m. Trials at the Zzyzx field laboratory took place beginning at 1:00 p.m. and continued until approximately 6:00 p.m. (allowing nighttime field collection of additional animals used in later experiments).

Encounters between animals were randomly assigned such that no two animals were paired twice and that no animal had more than a single encounter in one night. Animals were sexed, assigned an identification number, marked with that number (using a tape label attached to the mesosoma), weighed, and measured (from tip of pedipalp to end of telson) by one researcher who did not participate in viewing the interactions. Videotaped interactions were viewed by another researcher who was blind to both sex and measured size (mass, length) of the animals. Behavioral

actions during encounters were first analyzed for descriptive purposes. We describe three behavioral phases that characterized the encounters. From taped interactions the following data were recorded: 1) type of interaction (behavioral phase) when animals first meet; 2) time (in seconds) of each behavioral phase (defined in this paper); 3) “winner/loser.” An individual that remained in place after an interaction was considered the “winner” while an individual that retreated was considered the “loser.” A total of 57 encounters were recorded. Of these encounters, 30 were between male-female pairs (M-F), 16 were between two females (F-F), and 11 were between two males (M-M).

Encounters between juveniles and adults: The purpose of this observational experiment was to compare behaviors of adult *H. arizonensis* in response to a juvenile conspecific and in response to a juvenile heterospecific *Paruroctonus mesaensis*. Ten adult female *H. arizonensis* (mass ranging from 6.51-10.53 g) were used in this experiment. Either a small juvenile conspecific ($n = 4$; 2.00-2.36 g) or a heterospecific ($n = 6$; 0.67-1.69g) was randomly assigned and introduced into the home container of the adult *H. arizonensis*. Interactions were recorded for approximately 45 minutes after the introduction of the juvenile into the adult’s container.

Data analysis: Size (length and mass) comparisons of winners and losers were made with an unpaired one-tailed t-test. Comparisons of winner/loser size were made for each type of interaction (F-F, M-M and M-F). Times spent in each

behavioral phase were also compared for each type of interaction using a one-way ANOVA. Data were analyzed using Statview® (SAS® Institute) software.

Results

Description of behaviors

Behaviors associated with agonistic interactions between *H. arizonensis* can be separated into three phases based on the amount of physical contact involved. These phases do not always occur in a predictable order and often appear to result from the manner in which the animals first come into contact with one another. Some interactions do not involve all three phases and an individual may retreat during any behavioral stage (see below).

Alert phase: This behavioral phase begins when individuals become aware of the presence of another scorpion. They adopt a characteristic “alert” posture with the pedipalps raised and held slightly outward from the body and the metasoma raised just above the body (Fig. 4.1). This posture is not the same as the defensive posture displayed by very agitated individuals (Stahnke 1966). In the *alert* position they will both judder, a fast-paced series of rocking or shaking movements of the body (Polis and Sissom 1990) and also rock (a sideways swaying of the body, slower than juddering). There is no physical contact during this stage.

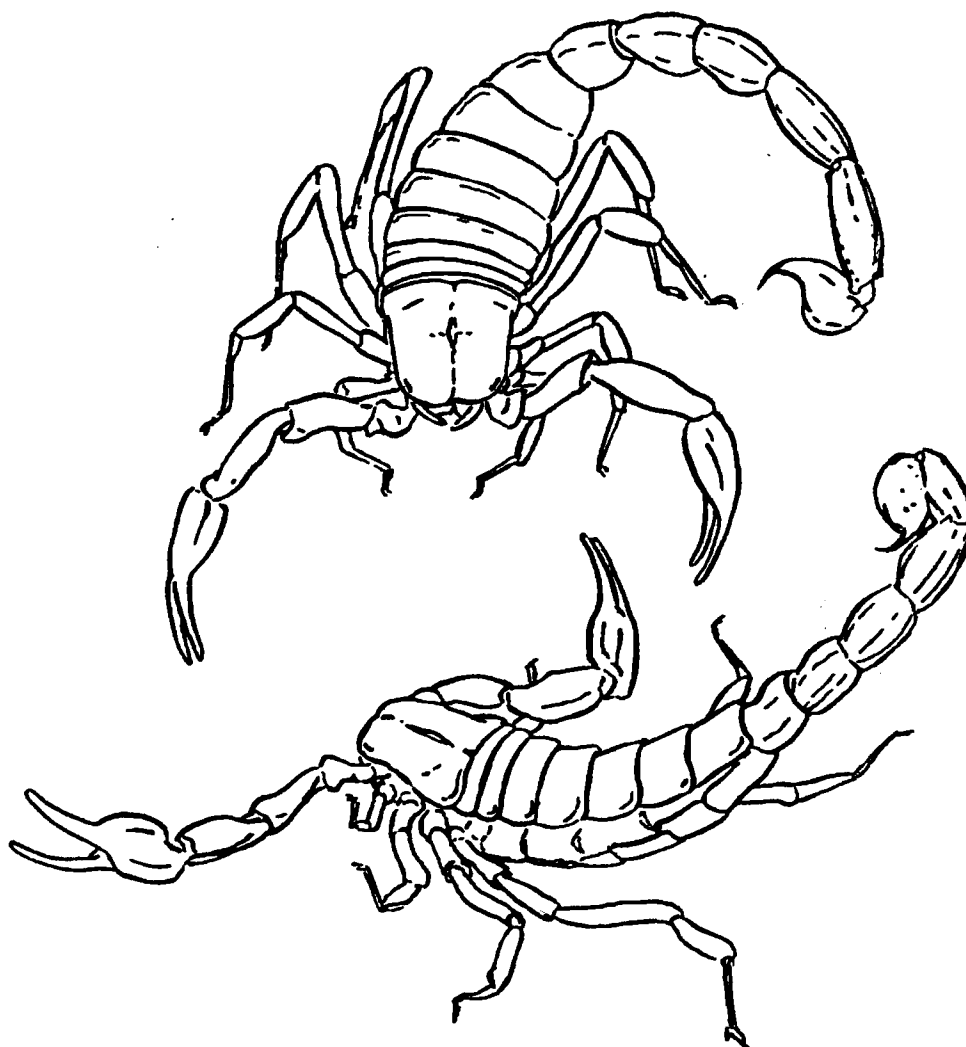
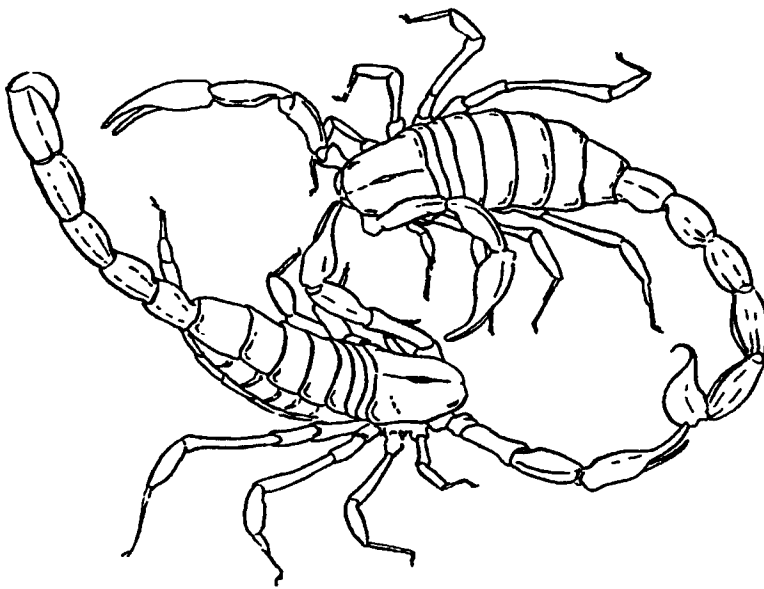


Fig. 4.1. *Alert* phase behaviors displayed in agonistic interactions between *Hadrurus arizonensis*. During this behavioral phase individuals stand facing each other but making no physical contact. Each individual judders or rocks during this phase with the metasoma raised and slightly to the side and the pedipalps held at body level. The lower scorpion in this illustration is displaying a typical *alert* posture while the upper scorpion in this figure is beginning to exhibit a *contact* posture.

Contact phase: This behavioral phase begins when one or both animals moves close enough to the other to make physical contact. Each individual lengthens the body sideways while facing the other (Figs. 4.2a and 4.2b) and pushes or jabs with the metasoma and/or pedipalps. The pair can either be head to head

(Fig. 4.2a) or head to tail (Fig. 4.2b). When head to head each scorpion pushes the last joint of its metasoma (with the stinger tucked under) into the sand or against the other's metasoma while occasionally jabbing with its pedipalps towards the other's chelicerae. When head to tail each scorpion continues to push with the metasoma but also grabs at the metasoma of the other with the pedipalps, occasionally gripping it for several seconds. If either individual does not let go of the other, or if the metasomas become entwined (in the head to head position), this behavior often leads into the third stage.



a)



b)

Fig. 4.2. *Contact phase behaviors displayed in agonistic interactions between *Hadrurus arizonensis**: a) When the scorpions are aligned head-to-head each individual lengthens their body and pushes the last joint of the metasoma into the sand or against the metasoma of the other while jabbing at the other with the pedipalps; b) When the scorpions are aligned head-to-tail each individual further lengthens the body and grabs at the other's metasoma with the pedipalps while pushing their own metasoma into the sand.

Contest phase: This stage involves the most physical contact between the pair. It begins when the scorpions entwine their metasomas and raise them while gripping the pedipalps of the other (Fig. 4.3). Each scorpion appears to push towards the other and occasionally one will flip the other over. Although this stage appears to be very aggressive and involves the use of the metasoma, neither participant stings the other.

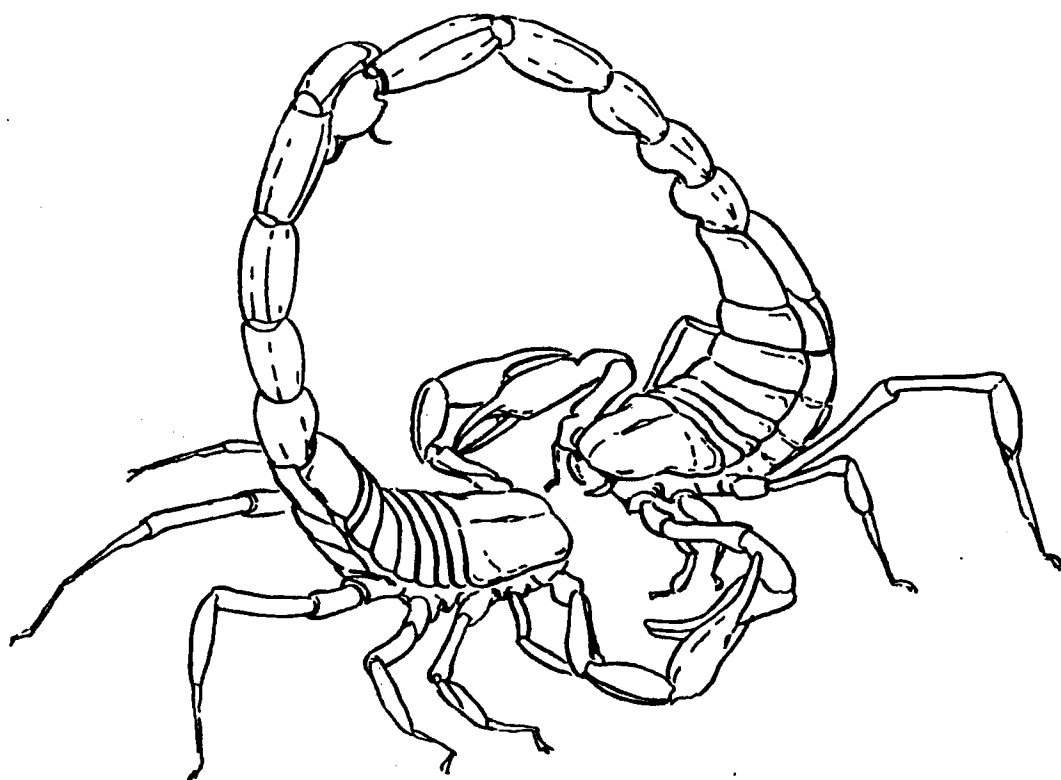


Fig. 4.3. *Contest* phase behaviors displayed in agonistic interactions between *Hadrurus arizonensis*. The scorpions grasp each other's pedipalps and entwine their metasomas overhead while pushing forward against the other.

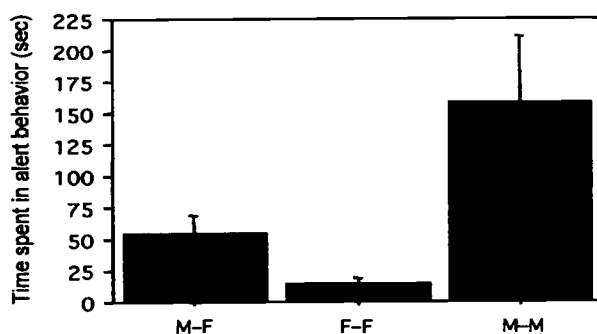
Remaining and retreating (“winning” and “losing”): Each interaction between two *H. arizonensis* ends with one of the scorpions remaining in place (often displaying *alert* behavior) while the other retreats rapidly. Retreat may occur during any of the three behavioral phases described above.

Analysis of behavior.

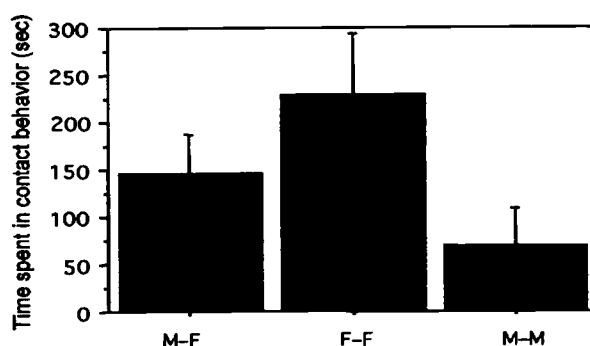
Winners vs. losers? Interactions between females usually resulted in the larger female remaining in place (“winning”) and the smaller female retreating (“losing”). Body length and mass were directly correlated, therefore we present statistical results for body length data only. On average female winners (mean = 14.085 cm, s.d. = 0.850) were larger than female losers (mean = 13.369 cm, s.d. = 1.132) in length (t-test, $p = 0.0405$). For male-male (M-M) interactions there was no significant difference between lengths of winners and losers ($p = 0.7514$; winners: mean = 14.264 cm, s.d. = 1.631; losers: mean = 14.618, s.d. = 0.483). For M-F interactions there was also no significant difference between lengths of winners and losers ($p = 0.2703$; winners: mean = 14.166 cm, s.d. = 1.072; losers: mean = 13.972 cm, s.d. = 1.306). There was also no relationship between sex and winning or losing in M-F interactions.

Comparisons of behaviors among types of interactions. The amount of time pairs spent in particular behavioral phases differed depending on the type of interaction (F-F, M-M or M-F). M-M interactions involved more time spent in the *alert* phase than either M-F interactions (ANOVA f-test, $p = 0.0036$) or F-F

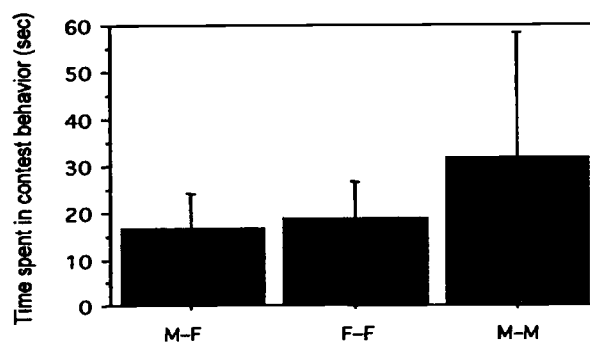
interactions ($p = 0.0003$) (Fig. 4.4a). F-F interactions involved more time spent in the *contact* phase than M-M interactions, although the difference was not statistically significant (ANOVA f-test, $p = 0.0731$) (Fig. 4.4b). There was no significant difference in time spent in the *contest* phase between F-F, M-F or M-M interactions (Fig. 4.4c).



a)



b)



c)

Fig. 4.4. Comparisons of behaviors among types of interactions: a) Interactions between males (M-M) involve more time spent in the *alert* phase than either intersexual (M-F) interactions (ANOVA f-test, $p = 0.0036$) or interactions between females (F-F) ($p = 0.0003$); b) F-F interactions involved more time spent in the *contact* phase M-M interactions, however not at a statistically significant level (ANOVA f-test, $p = 0.0731$); c) There was no significant difference in time spent in the *contest* phase between M-F, F-F and M-M interactions. Error bars indicate ± 1 standard error.

Behavioral responses to juvenile conspecifics vs. heterospecifics

Interactions between adult and juvenile *H. arizonensis* were similar to those between adults. Both participants displayed *alert*, *contact* and *contest* phases. None of the four interactions involving juveniles resulted in either participant being injured, although in two of the interactions the juvenile was grasped by the adult and then released. In contrast, interactions involving adult *H. arizonensis* and juvenile *P. mesaensis* resulted in predatory behavior in which the *P. mesaensis* was either killed and eaten (3 out of 6 trials), or escaped by running away. *Alert* phase behaviors were observed in 2 of the 6 interactions when the *H. arizonensis* first encountered the heterospecific.

Discussion

Hadrurus arizonensis, like most scorpions, is a solitary species. Although interspecific predation contributes significantly to their diet, *H. arizonensis* appear to discriminate between conspecifics and heterospecifics and avoid preying upon conspecifics. Furthermore, *H. arizonensis* display behaviors that are unique to intraspecific interactions. These behaviors may communicate information between individuals and may function in competition and/or species recognition. We propose that each behavioral phase may serve a particular function in this species.

The first phase that occurred in most interactions was the *alert* phase. This phase appears to be important for species recognition and may involve specialized communication. Juddering has been described in many species of scorpions and is

usually considered specific to males (although juddering or “yuddering” has been described in female *Leiurus quinquestriatus* during courtship by Shulov and Amitai 1958). Juddering is often observed with reproductive behavior. We know from this study that *H. arizonensis* females judder, and that both sexes judder outside of the context of reproductive behavior. Scorpions are extremely sensitive to substrate vibrations (Brownell 1977; Brownell and Farley 1979) and both juddering and rocking behaviors during this stage may function in vibrational communication through the substrate.

Little to nothing is known about parent-offspring interactions after the first larval instar or about dispersal of juveniles. Cannibalism among *H. arizonensis* seems to be extremely infrequent among adults, and even between adults and juveniles (pers. obs.), although *H. arizonensis* readily feed on smaller species (Polis 1981, Polis and McCormick 1986). Juvenile *H. arizonensis* display similar agonistic behaviors to adults when placed with conspecifics. Perhaps these agonistic interactions are a means of species identification that allow *H. arizonensis* to avoid feeding on conspecifics and potential relatives. The *alert* phase may be very important in species and/or sex recognition, as interactions between males differ from those between females in respect to time spent in this phase.

The *contact* phase appears to be an important behavioral stage, especially for females. The majority of time spent in interactions between two females and interactions between a male and a female was spent in this behavioral stage. The lengthening of the body (Fig. 2a and 2b) seen in this phase could provide a means of

assessing the size of the opponent. Since body size appears to have a strong influence on female interactions, we propose that this behavioral phase may allow a scorpion to compare its size with another before more aggressive interaction.

The *contest* phase is the most aggressive and energetically expensive behavioral stage. Locked in a pedipalp-to-pedipalp grip with metasomas entwined overhead (Fig. 3), pairs of scorpions in this phase resemble a tiny wrestling match. This stage is likely to function as a strength competition, especially since smaller scorpions occasionally are turned upside down by a larger opponent before being released. Although this phase appears to be highly aggressive, we never observed stinging or death. The *contest* phase may represent a ritualized combat in this species.

Aggression is recognized as a specialized form of resource competition (MacArthur 1972, Wilson 1975) and is likely to serve this function in scorpions. Burrows may represent a potential resource. Scorpions are generalist sit-and-wait predators (Polis 1979, McCormick and Polis 1990). Desert species are active at night and remain in underground burrows during the heat of the day. A *Hadrurus* burrow can be as deep as 2 meters (Stahnke 1966) and is often at the base of vegetation such as mesquite (pers. obs.). *Hadrurus* are often found in abandoned rodent and lizard burrows (Polis 1990). A burrow is an important refuge for any desert-dwelling animal, but for a female scorpion this refuge is also an essential resource for reproduction. A female undergoes parturition underground and broods the offspring on her back until the first larval molt. We postulate that competition

over burrow sites may exist and may be related to the intraspecific aggression observed in this species, particularly among females. Further studies of these behaviors should examine their relevance in the field and their role in communication between individuals.

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Chapter 5

Intrasexual Competition for Mates in Male and Female Scorpions

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In preparation for submission to *Ethology*

Abstract

Mate choice by males and female-female competition over mates are most often associated with sex-role reversed species, but these behaviors can also occur in mating systems that are not courtship role reversed. Both male and female mate choice has been suggested in *Hadrurus arizonensis*, a species of scorpion. In this study, groups of one male and two females, or one female and two males were observed in videotaped laboratory interactions. Mating interference by both sexes was observed, and in some cases, females displaced rivals and monopolized the courting male. These results imply that intrasexual competition occurs in this species by both sexes. Sex ratios were also determined in the field from two different populations. The ratio of adult males to females was slightly biased towards males at both sites. Coupled with the potential for mate choice by both sexes, the mating system of *H. arizonensis* does not fit either the traditional pattern of female choice and male-male competition, or the sex-role reversed pattern. Further studies are needed to determine the intensity at which sexual selection may operate, and which mechanisms may exert the most influence.

Introduction

Sexual selection according to Darwin (1859, 1871) generally occurs by two basic mechanisms: male-male competition and female choice. The proposed reasons underlying these behavioral patterns include the relative parental investment made by each sex (Trivers 1972) and the ratio of reproductively active females to males (Emlen and Oring 1977). Parental investment by females (in the form of nutrient

rich ova, gestation, maternal care of offspring, etc.) to be higher than that of males in most mating systems. Females are often the reproductively limited sex as a result of their energetic and time-consuming contributions to reproduction, therefore, we expect females to be choosy in their selection of a mate. Males are often thought to contribute little more than sperm to the reproductive effort, and subsequently are thought to be the sex more likely to compete with each other for mates and less likely to exhibit mate choice. Reversal of these behavioral patterns are associated with sex-role reversed (or “courtship-role reversed”, Gwynne 1991) systems in which females compete over males and males exhibit mate choice. In sex-role reversed systems male parental investment is substantial enough to limit their reproductive capacity compared with females (Gwynne 1981, 1997; Vincent et al. 1992).

Competition between females and mate choice by males are not confined to role-reversed systems, and not all species fit either the “traditional” pattern or the sex-role reversed pattern. Females may benefit from competing over males when males represent or provide a scarce resource that contributes to their reproductive success (Petrie 1983), and competition between females over mates occurs in systems without sex role reversal (Johnson 1982; Petrie 1989; Dale et al. 1992; Ahnesjö et al. 1993). Intrasexual competition over mates may also occur in both sexes when there is either high variability in mate quality, or if the sex ratio is skewed (Gwynne 1991). Male mate choice occurs in a variety of species that are not sex-role reversed (Manning 1975; Downhower and Brown 1981; Berven 1981),

One such species is the giant hairy desert scorpion, *Hadrurus arizonensis*. Like other scorpions, sperm is transferred externally from male to female *H. arizonensis* via a large, complex (and temporally limited) spermatophore (Francke 1979). Females give birth to live young and provide some maternal care after parturition (Stankhe 1966). Variation in both male and female courtship success has been observed under laboratory conditions in this species (Tallarovic and Brownell, in preparation), indicating that mate choice by both sexes may be operating. Furthermore, larger females elicit more intense courtship from males, indicating that males may preferentially court larger females (Tallarovic and Brownell, in preparation). *H. arizonensis* also exhibits agonistic and aggressive behaviors that may function in competition, especially between females (Tallarovic et al. submitted).

Because mate choice by both males and females may occur in *H. arizonensis* (Tallarovic and Brownell, in preparation), we also expected that intrasexual competition over mates may also occur in both sexes. We examined behavioral interactions between experimentally manipulated groups of reproductively active animals, rather than isolated pairs as previously studied (Tallarovic and Brownell, in preparation). We expected competitive interactions over mates to occur within both sexes, and that these interactions may play a part in mate choice by the deciding sex. Because sex ratios are important in the consideration and interpretation of our behavioral data (Emlen and Oring 1977), we obtained samples from two different wild populations to determine the sex ratio of adults in the field.

Methods

Observations were made at the Desert Studies Center (DSC), Zzyzx, San Bernadino Co., CA during the late summer of 1999. The following two experimental designs were used: 1) one male and two females ($n = 6$), referred to as experiment 1; 2) one female and two males ($n = 6$), referred to as experiment 2. Additional replicates of experiment 1 (one male and two females) were also made at Oregon State University in the fall of 1999 ($n = 8$), and data from those observations were added to the sample from the DSC. For observations made at the DSC, adult *H. arizonensis* were collected from sandy areas near Baker, San Bernadino Co., CA (from areas within the Rasor Off-road Vehicle Recreation Area) and from sandy areas near Indio, San Bernadino Co., CA in August 1999. For observations made at Oregon State University, animals were collected from sandy areas near Indio, CA in the early Fall of 1999.

Experimental groups of adult *H. arizonensis* were randomly created (by drawing numbers), and included one reproductively active male and two attractive females (females are screened upon arrival in the laboratory by placing them with a male for 15 minutes- if the female elicits courtship behavior from the male, she is considered “attractive”) for experiment 1, and one attractive female and two reproductively active males for experiment 2. The male was placed into the observation container (19L square plastic container) and allowed to roam freely for a five minute acclimation period. After the acclimation period, a plastic barrier was added at opposite ends of the container, confining the male to the center. A female

was added to each end behind the barrier and permitted to roam behind the barrier for five minutes. The barriers were then removed and the interactions recorded by video camera with red light illumination. Interactions were recorded for 3-4 hours. Groups were surveyed at 3 hours- if a courtship behavior was being displayed (eg. *promenade a deux*, Maccary 1810; Tallarovic et al., submitted) the interaction continued to be recorded until it was finished.

Sex ratios were determined by counting numbers of males and females collected haphazardly with portable UV lights (Stahnke 1972) from both of the above mentioned sites (near Baker, CA and Indio, CA). Samples were obtained from the Baker sites in August of 1999, and samples from Indio were obtained twice: once in late August and again in mid-September 1999. Animals over 5 g in weight were considered adults and were screened for reproductive behavior in the laboratory (Tallarovic, unpubl. data). Data from the Indio samples were combined.

Results

Experiment 1: One male x two females

Of the 14 trials recorded, five included no reproductive behaviors. Of the nine trials that did include reproductive behavior, three included a complete mating event between the male and one of the females (i.e., spermatophore deposition and possible insemination). In two of those trials, the male mated with the larger female, and in the other with the smaller. Seven of the trials included behaviors by uncourted females that interfered with the courtship of the other female. In two trials

an uncourted female successfully intercepted the male from the other female during the *promenade a deux* phase (the male-led courtship walk). The male in one case attempted to engage both females in the *promenade a deux* phase and actively led both of them for approximately 12 minutes before he finally released the smaller female and courted the larger. In the other case, each female repeatedly took over the male from the other back and forth a total of six times. A flowchart was constructed to illustrate the variety of situations that occurred and the proportion of trials in which they took place (Fig. 5.1).

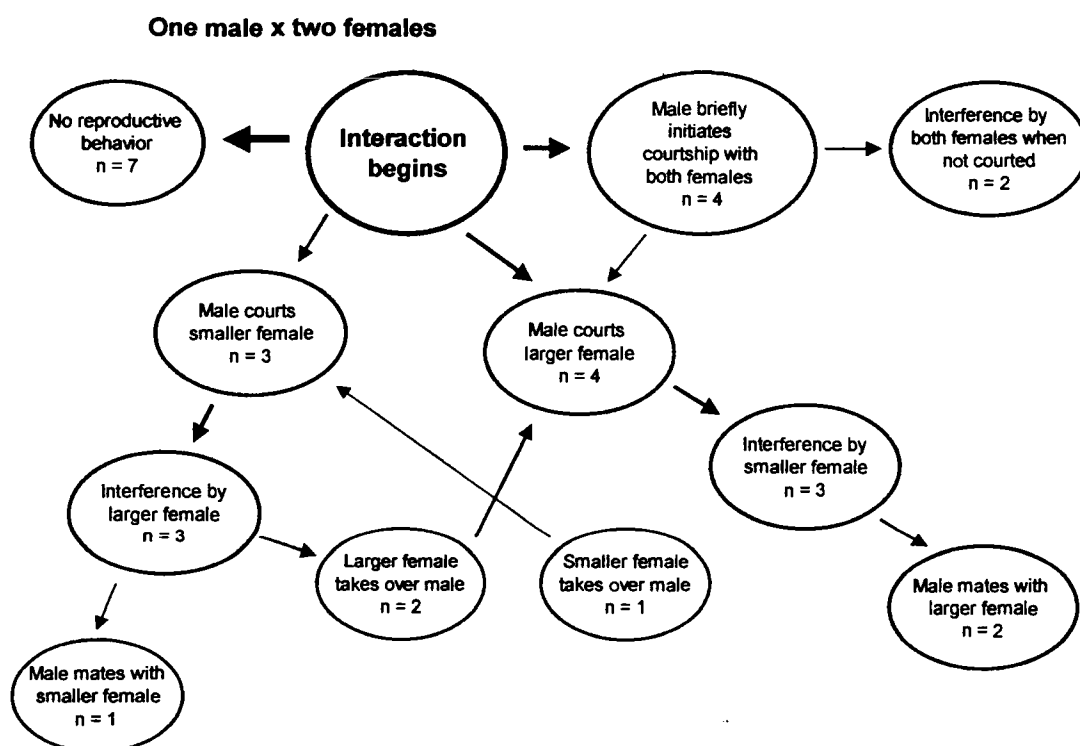


Fig. 5.1. Flowchart of behaviors observed in videotaped laboratory interactions involving one male and two female *Hadrurus arizonensis*. Numerical values in each circle represent the number of trials in which a particular behavior was observed. (Total number of trials, $n = 14$).

Experiment 2: One female x two males

Of the six trials recorded, one involved no reproductive behavior. The other five trials included courtship behavior, although none resulted in spermatophore deposition. In four trials, courtship was initiated first by the smaller of the two males and in the remaining trial the larger male initiated courtship but abandoned the female (she was then courted by the smaller male). In four cases where the smaller male courted the female, the larger male interfered with the courting pair. In three of those trials the larger male attacked and stung the smaller male, driving him away in two cases. In one case the small male continued to court the female despite repeated aggressive interference by the larger male. Interference occurred during both the initiation phase of courtship (when the courting male was grasping the female and stinging her), and the *promenade a deux*, when the courting male was leading the female in the active walking phase. In a single case both males alternately initiated courtship with the female but it was very brief and neither continued it beyond the initiation phase (no interference was observed in this case). A flowchart illustrates the variety of situations that occurred among the trials (Fig. 5.2) and their respective proportions.

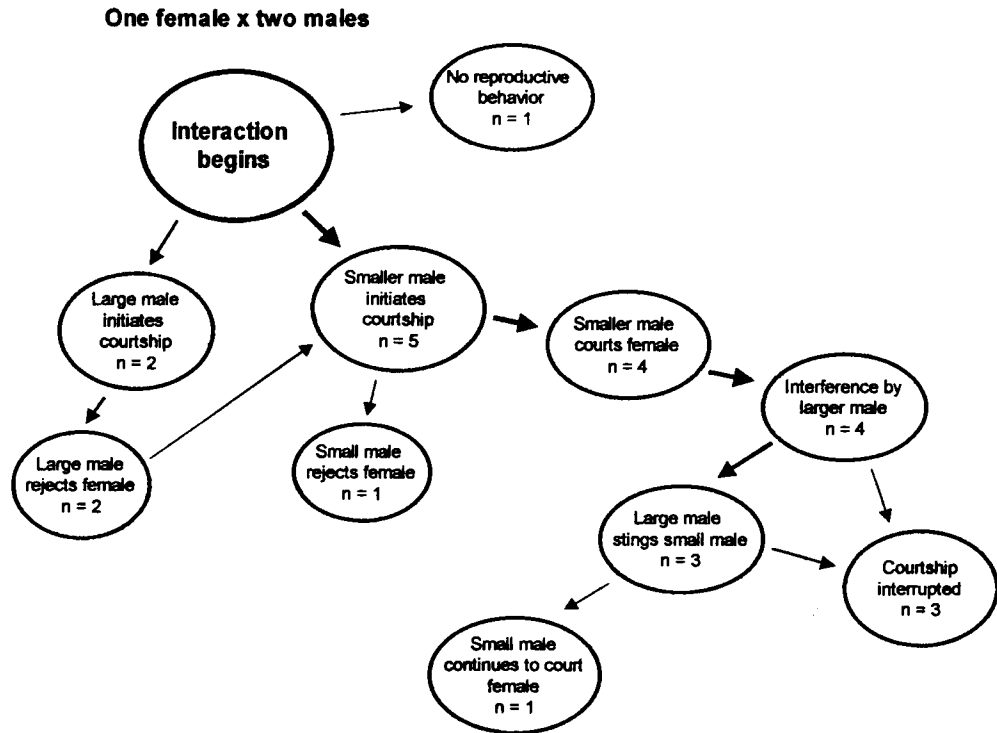


Fig. 5.2. Flowchart of behaviors observed in videotaped laboratory interactions involving one female and two male *Hadrurus arizonensis*. Numerical values in each circle represent the number of trials in which a particular behavior was observed. (Total number of trials, $n = 6$).

Sex ratio

The ratio of adult males to females was 1.14 (32:28) for the Baker, CA site and 0.92 (24:26) for the Indio, CA site. The ratio of total numbers of males to females (juveniles included) was 1.33 (48:36) for the Baker, CA site and 1.0 (41:41) for the Indio, CA site. Animals considered to be of adult size (over 5 g in mass) all displayed reproductive activities in the laboratory in the form of courtship initiation (in the case of males) or receptive behavior when courted (in the case of females).

Discussion

Both males and females actively interfered in courtship events involving conspecifics in *H. arizonensis*. Although the sample sizes in this laboratory study are relatively small, the behaviors observed certainly indicate that intrasexual competition occurs among males and females. Aggression between males in this experiment was more intense in comparison to previously documented male-male interactions (Tallarovic, et al., submitted). Males in this study stung the rival male in the presence of the female in half of the trials involving two males and one female. The presence of the female may elevate male aggression and instigate male-male competition. Females also interfered with mating pairs in this study. Furthermore, some females were observed actively taking over mates from other females. Interference by females with mating pairs has been documented in some insects (Johnson 1982; Choe 1994a,b) and birds (Foster 1983; Petrie 1992). Displacement of rivals and takeover of mates by females occurs in some sex-role reversed katydids (Simmons and Bailey 1990). It is interesting to note that although interference in

courtship was exhibited by both male and female *H. arizonensis*, only females took over mates from their rivals. Further study of this phenomenon is needed, particularly in the field. It is difficult to determine at this time the frequency at which a single male or female scorpion may encounter a courting pair in the field.

The sex ratio of males to females at both sites was near 1.0. Although it appears that males and females are in roughly equal abundance, the temporal limitation of the spermatophore should be considered. If males are only able to produce a spermatophore once every 4-5 days, this limitation may be significant enough to skew the operational sex ratio towards females. If so, this might account for the observation of competition among females for mates. If males are functionally limited, females may compete over them.

Sexual selection in scorpions has received minimal attention by researchers, and comparatively little is known about them when one considers the plethora of studies that focus on insects and vertebrate systems. Male-male competition over access to females has been documented in *Euscorpius flavicaudus* (Benton 1992), and mate rejection as an indicator of possible female choice has been suggested in *Bothriurus flavidus* (Peretti 1996) and *Hadrurus arizonensis* (Tallarovic et al. submitted). Under further examination, mate choice probably occurs by **both** sexes in *H. arizonensis* (Tallarovic and Brownell, in preparation. Furthermore, it seems likely from this experiment that intrasexual competition occurs in both sexes as well. Both males and females of this species are likely to have a considerable investment in offspring: females give birth to live young and provide limited maternal care (like

other scorpions), and males produce a spermatophore that appears to be energetically costly (Tallarovic and Brownell, in preparation). The results of this study raise more questions than can be answered (given its relatively small sample size), specifically, how strong might sexual selection in this species be, which sex experiences more intense sexual selection, and which mechanism most influences it? These questions should be further examined within this mating system using empirical studies.

Observations of female sexual behavior, especially in non sex-role reversed species, has been largely neglected in favor of male behaviors, which are often more overt and easily observed. However, researchers have begun to recognize the importance of females in influencing mating patterns, beyond the role of female choice (Rosenqvist and Berglund 1992; Ahnesjö, et al. 1993; Jennions and Petrie 1997). Further studies of species that do not fit the traditional or reversed pattern of courtship roles, like *H. arizonensis*, may reveal the occurrence and relative importance of multiple mechanisms that may interact to influence sexual selection.

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Conclusion

Summary

These studies have revealed many behavioral patterns that have not previously been documented in *H. arizonensis*. Some have never been documented in any scorpion species. The behaviors documented here include: 1) multiple mating by both sexes, allowing the potential for sperm competition or cryptic female choice; 2) possible mate choice by both sexes; 3) intrasexual competition for mates within both sexes, 4) agonistic behaviors that may function in species recognition and/or competition. Each finding and its implications are discussed below.

Both male and female *H. arizonensis* mate in the laboratory with multiple partners. Males, although temporally limited in spermatophore production, mate with multiple females. Females have no measurable decrease in receptivity after mating and will accept sperm from multiple males. Fertilization is internal in scorpions. This raises the question of whether there is sperm competition between males within a female reproductive tract, and/or whether females may exert cryptic female choice and manipulate male ejaculates after insemination. This situation also prevents any easy measure of offspring that can be linked to a particular sire. Any female that mates in the laboratory with more than one male presumably carries sperm from each. A further confounding factor is that any field collected female potentially carries sperm already in her reproductive tract. Until molecular genetic

techniques can be applied to this system to determine parentage, it is impossible to estimate the mating success of any male.

Because of the difficulty of measuring mating success in this species, courtship success was measured in the laboratory for males and females over a series of randomized encounters with the opposite sex. Both males and females exhibited variation in courtship success, suggesting that mate choice may occur in both sexes. Among females, courtship success was positively related to body size, implying that males may favor larger females. Because larger females appear to have larger litters in this species, males may increase their reproductive success by courting larger females (although this remains an untested hypothesis). Whether mate choice by either sex influences sexual selection in this species is yet unknown.

Both male and female *H. arizonensis* sexes display behaviors that interfere or disrupt courtship of conspecifics, indicating that both sexes might compete amongst each other for mates. The presence of mate choice in both sexes and intrasexual competition in both sexes makes *H. arizonensis* an intriguing and potentially valuable behavioral model. The more traditional mating pattern observed in nature is that of female-choice and male-male competition. In these systems, males usually contribute little more than sperm, and females are the more reproductively limited sex, investing comparatively more time and/or energy into the offspring. Species that exhibit male mate choice and female-female competition are usually considered to be sex-role reversed in that males often take on roles in caring for offspring and/or provide some essential resource to females that limits their own reproductive

capacity. In the case of *H. arizonensis*, males provide no paternal care of offspring, and contribute only gametes packaged in a spermatophore. However, the spermatophore itself is temporally limited and appears to be a potentially expensive energetic investment. Males probably have the ability to mate several times within a reproductive season, but not as often as females. The sex ratio of *H. arizonensis* in the field is roughly 50:50, but the temporal limitation of spermatophores may skew the operational sex ratio towards a females. This female bias may be enough to create competition among females for available males. Additionally, the spermatophore could have a hidden nutritional value to females in the form of seminal fluid, and if so, this resource may promote competition between females for access to males, and explain multiple mating by females in this species.

Furthermore, the relationship between female body size and litter size may correspond to differences in female quality, with larger females providing better quality mates that may produce more offspring. This variation in quality may be enough to cause competition for mates among males. This hypothesis is also supported by the behavioral relationship between female size and the intensity of courtship behavior she elicits from a male. If males prefer larger females, they may also compete for them.

In addition to intrasexual competition during mating events, *H. arizonensis* also display complex agonistic and aggressive behaviors that appear to function in intraspecific communication in both intra- and intersexual interactions outside of the reproductive season. Males and females undergo similar agonistic displays that

include many of the same behavioral elements, but differ in the amount of time devoted to those behaviors. They also differ in the pattern of resolution. In female-female interactions, the larger female usually remains in place (wins) while the smaller female retreats (loses). In male-male and male-female interactions, there is no apparent pattern to which animals wins or loses. Based on their life history traits and ecology, it is reasonable to suspect that females may compete over resources in the field, such as burrows. As discussed above, there is also reason to suspect that they at least compete over mates. Although interactions between males did not reveal a relationship between size and winning status, males too may compete in the field during reproductive season over females. Male-male interactions included more aggression (in the form of stinging) when a female was present than in the observations made without a female present. Although the sample size was small in the interactions involving two males and one female, it was the larger male that attacked and stung the smaller male, usually driving him away.

The agonistic behaviors displayed by *H. arizonensis* may function in communication and species recognition in addition to competition. Adults appear to discriminate between larval conspecifics and heterospecifics and avoid feeding on conspecifics. Unlike sympatric species, such as *Paruruoctonus mesaensis*, *H. arizonensis* are only rarely cannibalistic. I have never observed cannibalism in *H. arizonensis* in the field, and only several cannibalism events have occurred in the laboratory, and in each case was likely to be a result of overcrowding. *H. arizonensis* can be kept together in the laboratory if each animal is provided with a

separate shelter. Although this animal is considered solitary, it exhibits behaviors that might be considered almost subsocial. Nothing is known about the possible social structure of this animal in nature, or whether dominance hierarchies are established between individuals. Further laboratory and field studies may answer these questions and reveal additional importance of its agonistic displays.

These behavioral studies represent an early and essential process in the study of any organism as a model system. *H. arizonensis* was an enigmatic research animal prior to this project, known in the literature only in scant references to birthing (Williams 1969), phylogenetic relationships (Stahnke 1945; Williams 1970), spermatophore structure (Francke 1979), predatory influence in ecosystems (Polis et al. 1981; Polis and McCormick 1986), and anecdotes regarding its defensive behaviors, burrowing habits, and resistance to starvation in the laboratory (Stahnke 1966). This body of work provides both descriptive and quantitative data that provide a foundation for future laboratory and field studies of the reproductive and agonistic behaviors of *H. arizonensis* and how those behaviors function in sexual selection and social structure of communities.

Recommendations for future research

Now that it has been established that both mate choice and intrasexual competition occur in male and female *H. arizonensis*, their possible influence on sexual selection should be determined. Future studies should focus on the extent to which either or both of those phenomenon affect sexual selection. Before this will

be possible, however, paternity analysis must be possible in this system. Molecular genetics in scorpions have been used to determine phylogenetic relationships (Yamashita and Fet, in press), and it is possible that paternity analysis techniques using microsatellite DNA markers could be developed in future studies for use in *H. arizonensis* or other scorpion species. Such techniques would provide powerful tools, not only in determining male mating success (and ultimately the strength of sexual selection), but and also in studies of sperm competition and cryptic female choice. Furthermore, if culturing of this organism in the laboratory can be perfected, it may be possible to maintain lineages in the laboratory for long term studies.

In addition to further studying sexual selection in *H. arizonensis*, the agonistic behaviors displayed by this species should be studied to better determine their relevance. We hypothesize that they function in intraspecific communication and competition, but these hypotheses need to be tested in the field. Additionally, further studies in the laboratory may determine whether *H. arizonensis* can discriminate between individual conspecifics and whether they retain a memory of such individuals, as has been demonstrated in other invertebrate systems (Karavanich and Atema 1998). Aggression in both males and females should also be studied as a potential factor in courtship success and fitness as has been found in some flies (Boake 1989; Poramarcom and Boake 1991)

H. arizonensis is a species that warrants further attention both in the laboratory and the field. I express a word of caution, however, regarding the potentially destructive collection of this species from wild populations. *H.*

arizonensis is an extremely long-lived scorpion, living up to and beyond 25 years (Stahnke 1966). Little is known about how quickly this species matures and begins to reproduce. Although relatively large numbers of adults can be found in some areas, they should not be over-collected. Some mature adults should always be left in situ. Laboratory culturing may alleviate some of these concerns, but it remains an issue of consideration.

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