

BEHAVIOR AND ECOLOGY OF MATING IN THE
CANNIBALISTIC SCORPION, *PARUROCTONUS MESAENSIS*
STAHNKE (SCORPIONIDA: VAEJOVIDAE)

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ABSTRACT

During the seasonal mating period, mature males undergo alteration in behavior and ecology; they are more vagrant and feed less than all other components of the population.

Cannibalism of mature males by mature females combined with other factors related to mating contribute to a higher death rate of adult males as compared to adult females.

Reproductive behavior consists of mating rituals which minimize predatory behavior and elicit the cooperation necessary for indirect sperm transfer. These rituals include the *promenade à deux*, cheliceral massage, post-mating escape and heretofore undescribed behavior which precedes the actual mating dance.

INTRODUCTION

Mating behavior is often complicated by conflicting stimuli which simultaneously produce the incompatible tendencies to flee, attack and mate (Tinbergen 1953, Morris 1956). Agonistic and escape behaviors must be inhibited so partners can obtain sufficient proximity for transfer of sperm. This is often accomplished during courtship where a stereotyped series of cues allows recognition of potential mates and produces a non-aggressive interaction with sufficient coordination and cooperation for successful fertilization (Bastock 1967, Morris 1970). To understand how the behavioral requisites for mating are achieved, courtship can be analyzed through an ethogram of its component behaviors. Such analysis may also reveal species-specific mechanisms which inhibit genetic introgression by closely related species (Mayr 1963).

Scorpions have many characteristics which suit them well for this type of behavioral analysis: since they fluoresce under ultraviolet light (Stahnke 1972) they are easily detected and observed in the field at night; they are faunistically diverse and abundant in desert habitats (Polis and Farley, in press); they are often cannibalistic (see Table 1); and they have an elaborate courtship (Alexander 1956, 1957, 1959).

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Scorpion courtship and mating have been described for many species (Tables 1 and 2; Garnier and Stockman 1972). However, it is not clear in those accounts how recognition of sexual partners occurs or how aggressive and escape behaviors are sufficiently inhibited so mating can be completed.

The purpose of the present study is to analyze the relationship between mating behavior and cannibalism of mature males by mature females. Our data show that adult females normally feed upon adult males even in the breeding season. Courtship consists of a sequence of behaviors which apparently function to decrease predation and elicit the cooperation and coordination necessary for indirect sperm transfer. The breeding season is characterized by marked changes in the behavior and ecology of mature males which decrease male survivorship and increase the probability that these males will be cannibalized. This is the first account of courtship for a member of the family Vaejovidae. All data in this paper are from the field.

METHODS

This study was conducted at a sand dune adjacent to state Highway 111 about 9 km northwest of Palm Springs in Riverside County, California. It is at 33° 54' N, 166° 37' W, at an elevation of 320 m. Located at the foot of Mount San Jacinto (elevation 3,300 m), the dune is in the northwest extreme of the Colorado Desert. This area is subject to seasonally high diurnal temperatures, low relative humidity, and low annual precipitation (average = 13.30 cm) (Edney 1974, U.S. Environmental Data Service 1975). In suitable habitats, this species occurs at very high densities. In the study area, maximum density of scorpions active on the surface was over 1500/hectare while maximum total densities estimated from marked animals exceeded 3000/hectare (Polis in prep).

The entire study area was about 75 hectares. Within this area a grid 28 by 50 m was constructed by placing marker stakes 2 m apart in 15 longitudinal rows. Each row was separated by 2 m. Portable lights (Coleman Charger 3000 and Burgess safari-light) with ultraviolet bulbs (Sylvania F8T5) were used to locate scorpions. All data were gathered from May 1973 through September 1977 during 900 field hours on over 225 different nights. In the four years of this study, over 850 scorpions observed in the grid were individually color coded. Unique markings were achieved by using fluorescent paints of different colors in various dot combinations. Individual burrows were marked with coded stakes. Individual activity, forage range from burrow, and the distance scorpions moved between successive sightings were tabulated from repetitive surveys of the grid area. Grid surveys were conducted on the average of once per week for the entire research period. Data from the first sighting of scorpions after marking were never used as the markings may have disturbed the animals enough to cause changes in behavior or ecology. However, such changes were rarely observed.

Data obtained by surveying the entire study area include sex and age structure, mating observations, feedings, cannibalism and percent of individuals moving when first observed. Data on diet and cannibalism were readily obtained since scorpions digest their prey externally in a process which often lasts several hours.

Field data were recorded on a pocket tape recorder and were transcribed later. By using the tape recorder, data were usually gathered without using white light. Photographic records were obtained using an electronic strobe and macro lens. Distances were usually measured, but to avoid disturbance during matings, distances were estimated to

the nearest 5 cm (if greater than 15 cm) or to the nearest 2 cm (if less than 15 cm). All scorpion lengths were standardized according to Stahnke (1970) and were measured from anterior edge of prosoma to the end of the last metasomal segment.

RESULTS

Cannibalism as a Mortality Factor.—The scorpion, *Paruroctonus mesaensis* Stahnke, is a facultative raptorial predator which primarily uses substrate vibrations to locate prey (Brownell 1977a and 1977b). The direction of objects moving on or just beneath the substrate can be determined at distances up to 50 cm. The scorpion turns abruptly towards the source of the substrate disturbance, advances and seizes the object with its pedipalps. Any moving object in the proper size range is attacked without apparent discrimination.

This foraging behavior explains the high rate of cannibalism exhibited by this species. Conspecific individuals constitute 9.10 percent of the diet ($n=792$). This was the fourth most commonly observed prey item. Further, 17.1 percent of all cannibalisms consisted of mature females preying on mature males during the breeding season.

Cannibalism of mature males apparently has a significant effect on demography and age distribution (Polis, in preparation). Males generally do not live past their first breeding season. The average survivorship of mature males from one breeding season to the following is significantly lower than for mature females. Of 145 mature males marked during the summers of 1973, 1974, and 1975, only 5.8 percent were observed to be present the next spring. By contrast, the survivorship of marked mature females ($n=169$) was 18.9 percent.

Annually, most males are newly matured virgins. At the start of the breeding season in late spring 1975 and 1976, only 18.2 percent of the mature males ($n=121$ scored) were mature the previous year. At this time, overwintering mature animals of both sexes are readily distinguished from newly matured virgins by differences in length and weight. By the end of the breeding season, individuals that reached maturity that season constituted the great majority of mature males. By comparison, 62.7 percent of the mature females ($n=186$ scored) were mature the previous season. The oldest marked male observed was only 37 months, while the oldest marked female was at least 58 months.

In *P. mesaensis*, the behavior associated with cannibalism is stereotyped and has some components not present during attack on insect prey. In the six instances in which we observed the onset of a cannibalistic attack, the attacked individual was moving. On being seized, the attacked scorpion flicks its metasoma at its attacker in an attempt to sting. Almost immediately, each scorpion grabs the other scorpion's metasoma with one chela. The other chela is used to grasp another part of the adversary's body. No individual was observed to attack a larger moving scorpion.

Behavior During the Mating Season.—Matings were observed in the field as early as 26 May (1976 and 1977) and as late as 2 October (1975), but 80 percent of the observed matings occurred in August and September (distribution of matings by month in percent: May—10; June—5; July—0; August—50; September—30; October—5). Of all matings recorded, 95 percent occurred on nights of new moon or when the moon was not present.

During the mating season, the behavior of adult males is substantially altered. They become skittish and strike with the slightest provocation, and they appear to feed less than mature females. In 1974, 1975, and 1976, males represented 35.5 percent of the total

adult population (n=1197 scored). However, adult males feeding at the time of observation constituted only 32.1 percent of the total number of adults (n=209) observed feedings.

Adult males also become vagrant (Fig. 1) during the mating season and abandon their burrows nightly. The average distance between successive sightings (on different nights) of marked mature male scorpions was 34.7 m (Table 3). Some marked individuals were observed to travel more than 100 m in a night and over 23 m in one-half hour. Further, 48.3 percent of all mature males were moving at the moment of first sighting.

This is in marked contrast to the rest of the population. Normally, mature females, immature scorpions of both sexes and adult males not in the breeding season forage a short distance from their burrows. Marked mature females (n=168) were observed (mean \pm S.D.) 0.9 ± 1.1 m from their marked burrows. The average distance between successive sightings (on different nights) of marked mature female scorpions was 4.0 m. This value is significantly different from the of mature males. Mature females, immature animals and mature males out of the breeding season are normally sedentary. Only 1.8 percent of females and immatures were moving at the moment of observation. Only 5.2

Table 2.—Scorpion species for which courtship have been studied. Roman numbers and letters correspond to families and species respectively in Table 1.

TAXON	REFERENCE
I—Bothriuridae	
a) <i>Bothriurus bonariensis</i> (Koch)	de Zolessi 1956, Varela 1961
b) <i>B. asper araguayae</i> (Pocock)	Matthiesen 1968
c) <i>Urophonius brachycentrus</i> (Thorell)	Maury 1968
II—Buthidae	
d) <i>Buthus occitanus</i> Amoreux	Fabre 1923, Auber 1963
e) <i>Tityus trivittatus</i> Lutz and Mello	Bücherl 1956
<i>Tityus bahiensis</i> (Perty)	Bücherl 1956
f) <i>Leiurus quinquestriatus</i> (H. et E.)	Thorton 1956, Shulov and Amitai 1958, Abushama 1968
g) <i>Buthotus judaicus</i> Simon	Shulov and Amitai 1958
h) <i>Parabuthus planicauda</i> (Pocock)	Alexander 1959
<i>Tityus trinitatis</i> (Pocock)	Alexander 1959
i) <i>Centruroides insulanus</i> (Thorell)	Baerg 1961
j) <i>Centruroides vittatus</i> (Say)	McAlister 1965
k) <i>Isometrus maculatus</i> (De Geer)	Probst 1972
l) <i>Androctonus australis</i> (L.)	Auber-Thomay 1974
III—Chactidae	
m) <i>Euscorpium italicus</i> Herbst	Angermann 1955, 1957
<i>Euscorpium flavicaudis</i> De Geer	Angermann 1955, 1957
<i>Euscorpium carpathicus</i> (L.)	Angermann 1955, 1957
IV—Diplocentridae	
n) <i>Nebo hierichonticus</i> (Simon)	Shulov and Amitai 1958, Rosin and Shulov 1963
V—Scorpionidae	
o) <i>Urodacus abruptus</i> Pocock	Southcott 1955, Smith 1966
p) <i>Opisthophthalmus latimanus</i> (Koch)	Alexander 1956, 1957, 1959
q) <i>Heterometrus scaber</i> Koch	Mathew 1957
r) <i>Pandinus imperator</i> Koch	Garnier and Stockman 1972
VI—Vaejovidae	
s) <i>Paruroctonus mesaensis</i> Stahnke	Present study
t) <i>Paruroctonus borregoensis</i> Williams	Present study

percent of mature males out of the breeding season were observed moving. These values are significantly different from the percentages obtained for males in the breeding season.

In the study area, males of four sympatric scorpions (*Paruroctonus borregoensis* Williams, *Hadrurus arizonensis* Ewing, *Vaejovis confusus* Stahnke and *V. puritanus* Gertsch), were also observed to be vagrant during spring and summer. A large percentage of males of these species were moving when first observed while females and immature animals were generally stationary.

Courtship and Mating.—*Promenade à deux* and spermatophore deposition were observed in the field on twenty occasions. Pre-promenade behavior was observed on three occasions. In all cases notes were taken. Photographic records were obtained from four matings.

The mating described below and depicted in Fig. 2 occurred 11 August 1975 between a male, 1.72 g and 70 mm long and a female, 2.71 g and 74 mm long. Parenthetical Roman numerals correlate the text with Fig. 2. The moving male was first observed about 7 m from the stationary female. Its movement took it to within 30 cm of the female. The male exhibited no apparent awareness of the female and began to move away. Quite rapidly, however, the female moved to the male, grasped and released the male's body with her chelae, clubbed or attempted to sting him with her metasoma, and then retreated (Fig. 2, I). We call this the female's "mating attack behavior". Clubbing is defined as hitting with the metasoma while the sting is tucked away (McAlister 1966). The male then began to "strut defensively" (Stahnke 1966). During this behavior, the male stilt on his legs, his metasoma is raised perpendicular to the ground, and he remains still or moves intermittently while his pectines slowly sweep the substrate. This behavior is common after disturbance or attack.

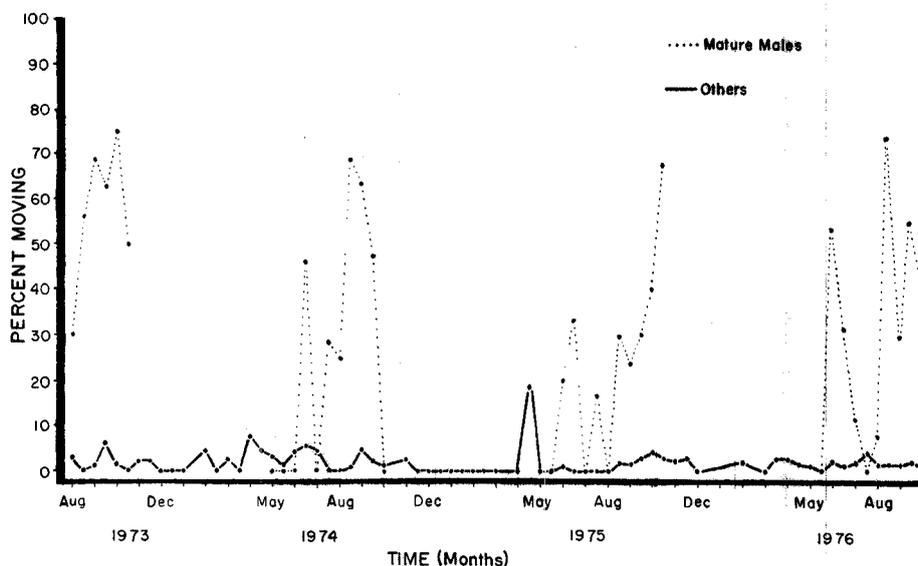


Fig. 1.—Percent animals moving at moment of first sighting. Mature males were not present on the surface during the winter months. Data taken from observation of 334 mature males and 4,348 mature females and immature animals.

After several minutes, the male ceased to strut and began to move normally. The female repeated her attack behavior (II). The male responded as before. After strutting a short time, the male "juddered" (Alexander 1957). Juddering consists of rapid rocking or shaking of the body back and forth on immobile legs. The pectines are spread out during this behavior. The male then began to move haltingly. The female advanced and grasped the male with her chelae but did not club or attempt to sting (III). The male turned, raised his metasoma, but he also did not club or attempt to sting. The male then strutted and juddered but the strutting time was relatively short and neither the body nor the metasoma were raised as highly as previously. The female again advanced to the male as in the third encounter (IV), but this time the male did not strut. He juddered twice. In the fifth encounter (V), the female gently touched the male on his chelae before she retreated a short distance. The male turned lightly and appeared to search for the female. His pectines were spread and occasionally swept the substrate.

Whereas prior to this time the female had made advances and the male responded, now the male seemed to take the initiative. He advanced and contacted the intermittently-moving female (VI). He touched the female for about 30 seconds by simultaneously grasping the base of the female's metasoma and the base of her right pedipalp. He released the female, retreated a short distance and juddered (VII). The female then moved to the male and grasped his left chelae with her right chelae. She soon released him and retreated 2 cm. The male juddered again before contacting the female. They remained motionless for 15 seconds before beginning the *promenade à deux* (VIII). The promenade (Fabre 1923) is the "mating dance" during which the male grasps the female's chelae with his own; the male then leads the female as the pair moves together. The promenade began 22 minutes after the initial contact. They moved together about 25 cm before the male released his grasp of the female for a short period. The male juddered before reinitiating the promenade.

During the promenade, several behaviors occurred. The male's pectines were widely spread and sporadically swept the substrate. The male generally traveled directly backwards. Commonly, the male alternately pulled more strongly on one than the other of the female's pedipalps as they traveled. On four occasions, the female actively resisted movement. The female was generally dragged forward at these times although once she moved backwards and pulled the male forward a short distance. Each time the female resisted,

Table 3.—Vagility of mature males during the breeding season compared to other components of the population. On the average, mature males move further between successive sightings on different nights as compared to mature females. Mature males during the breeding season are more frequently observed to be moving at the time of first observation than all other components of the population. Distance moved represents mean and standard deviation. The Z statistic to test differences in means and differences in proportions was used to establish significance. (n=sample size; p=probability).

	Distance from last sighting (m)	n	Z	p
Marked mature males during breeding season	34.7±24.9	44		
Marked mature females during breeding season	4.0± 8.7	177	3.0	.001
	Percent moving	n	Z	p
Mature males during the breeding season	48.3	315		
Mature males out of the breeding season	5.2	19	3.6	.0001
Mature females and all immature scorpions	1.8	4,348	36.5	<.0001

the male initiated "cheliceral massage" ("kissing", Southcott 1955). During this behavior, the male grasps and kneads with his chelicerae the female's chelicerae, prosomal edge, and/or the articulation of the pedipalps.

The promenade lasted 9.25 minutes before the initiation of spermatophore deposition. The pair traveled approximately 8 m during this time. The male encountered a twig 6 mm in diameter and 15 cm long (IX). The body axis of the male was perpendicular to the long axis of the stick. He backed up until his genital segment was directly over the stick. He showed several behaviors during this time and before deposition of the spermatophore: cheliceral massage was almost continual; he juddered on two occasions; his metasoma was curled so far forward that it touched the base of the female's pedipalp; his pectines were actively sweeping; and his second and third pair of legs moved sporadically in the sand, actually producing grooves ("sand scraping", Alexander 1959). The male's genital aperture was adressed against the stick while the spermatophore was extruded and secured to the stick (IX).

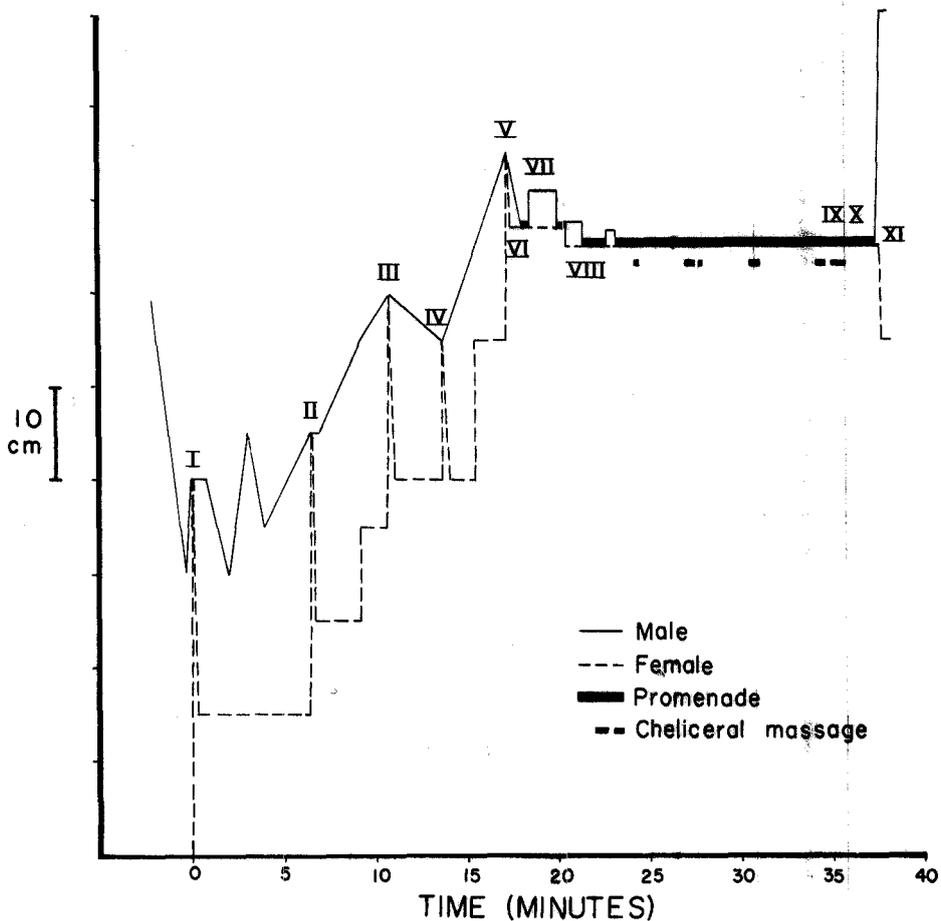


Fig. 2.—Interaction and spatial relationship of male and female during courtship and mating behavior. The ordinate indicates movement of either male or female relative to each other but not movement of the pair together during the promenade. Roman numerals correlate with descriptions of behavior in text.

The male then pulled the female over the spermatophore. They moved back and forth over the stick three times before the female exhibited "head-stand behavior." During this behavior, the female stilted her mesosoma while she pressed her genital region close to the stick. The spermatophore remained on the stick while the sperm was presumably transferred. Both scorpions remained motionless for a short time before the male exhibited "escape behavior." He quickly and repeatedly probed the female's mesosoma with his sting while concurrently disengaging his grasp. We could not determine if the male stung the female. He then ran off about 25 cm (XI). The female slowly moved a short distance before stopping. She then began "swaying" for about 45 seconds. During swaying the female raised her body above the ground while moving side to side on her immobile legs. Finally, the female began to move away. The male remained motionless. From the first encounter to the end of the swaying, the entire mating lasted 38.5 minutes.

Slight variations of these basic mating behaviors were observed in other matings. In the other two observations of pre-promenade behavior, the initial forays by the female during mating attack behavior were at distances of 20 and 25 cm. One of the mating attack behaviors by the female consisted of a series of three encounters while the other was of four encounters.

During the promenade, the male occasionally leads the female by only one chela. This is most common when the pair must execute a sharp turn to avoid an obstacle. Once during a promenade, the male released the female. Then, perpendicular to the long axis of the female's body, the male seized the base of her pedipalp and her metasoma. This lasted about 30 seconds before the promenade was resumed.

During headstand behavior, we observed that the female's genital operculum opens during her headstand and makes contact with the apex of the spermatophore. This contact, resulting in insemination, lasts only 3 to 5 seconds.

Variations also were observed in escape behavior. The male either probes the female with his sting (five to fifteen times) or bats the female with his metasoma (two to five times). This disengagement process is usually rapid, lasting only 3 to 10 seconds. On three occasions, the female chased the male for a short distance; in most cases the female remained motionless or moved slowly.

Courtship from first observation of promenade through end of swaying was observed to last between 5 and 35 minutes. The distances traveled ranged from under 3 m to over 25 m. In 18 of 20 matings, spermatophores were deposited on sticks from 5 to 8 mm in diameter. Spermatophores were once deposited on a piece of sheet metal and once on the sand. The spermatophores remained fixed to all substrates except the sand. After deposition on the sand, the entire spermatophore was later found between the female's genital plates.

One mating of the congeneric species, *P. borregoensis*, was also observed in the field. This occurred on 2 October 1975 between a male (31 mm long, 0.37 g) and a female (35 mm long, 0.50 g). Most components of mating behavior were quite similar to those of *P. mesaensis*. The promenade was in progress when the pair was discovered. The following behaviors were observed: *promenade à deux* with chelae grasp; cheliceral massage following female resistance; the male's pectines actively sweeping the substrate; male juddering, sand scrapping, and cheliceral massage during spermatophore deposition; female headstand at the time of sperm transfer; male escape behavior, and female swaying. The male was unable to free himself from the female for a few seconds after he initiated escape behavior. Further, the female chased the male for a distance of about 15

cm before the male escaped. The promenade and mating lasted about 5 minutes. They traveled 0.8 m. The spermatophore was deposited on a stick 7 mm in diameter and 10 cm long.

DISCUSSION

The data show that cannibalism of mature males by mature females during the breeding season contributes to a higher death rate of adult males as contrasted to adult females. For mating to occur, there must be a reduction of these predatory tendencies and this appears to be accomplished in the courtship ritual by a series of brief but aggressive contacts which gradually increase in duration but decrease in violence.

Table 1 summarizes the mating behavior reported for scorpions. Mate cannibalism is common among scorpions and occurs within almost all other orders of archnids (Cloudsley-Thompson 1968). In spiders, as in scorpions, mate cannibalism occurs frequently and males often do not live more than one mating season (Bristowe 1941, 1958).

Intraspecific predation on mature male scorpions by mature females occur both during or directly after mating and during activity not associated with mating. There are several reasons why mature males are so vulnerable to cannibalism. On the average, mature males are significantly smaller than mature females (Polis and Farley 1979) and are within the normal size range of prey eaten by mature females (Polis in prep.). This dimorphism is important since, in all cases of cannibalism observed in the field ($n=76$), the prey was smaller than the predator. In 68.4 percent of 19 matings for which the participants were measured, the male was smaller than the female.

Further, when mature males move during the breeding season they produce substrate vibrations which are sensed by non-receptive (gravid or previously inseminated) females which appear to interpret moving males as potential prey. Finally, we observed cannibalism after mating on two occasions. In both cases the spermatophore was present on a stick and the female was eating the male.

Cannibalism is only partially responsible for the marked differential mortality of mature males compared with mature females. Other factors, related to breeding, may also contribute to male mortality: greater risk of predation during nightly movement; possibility of migration out of the habitat to less optimal areas; increased risk of heat death in shallow burrows which must be constructed nightly; greater energetic costs produced by movement and nightly burrowing; decreased foraging time and food intake as activity is devoted to reproduction rather than hunting; and increased probability of overwintering mortality due to inadequate food reserves. We have evidence from the field that moving males were attacked and eaten by vertebrate predators (Grasshopper mouse, *Onychomys torridus* (Wied-Neuwied) and owls). Male scorpions were observed while moving in adjacent habitats which do not support populations of *P. mesaensis*. In summer at dawn we have witnessed several males rapidly digging in freshly excavated shallow burrows.

It is probable that mature males of all vaejovoid species become vagrant during the mating season. Males of the scorpions *Hadrurus* sp. (Williams 1970), *Anuroctonus phaiodactylus* (Wood) (Williams 1966), and *Paruroctonus boreus* (Girard) (Tourtlotte 1974) are nomadic during the breeding months. Analyses of can trap data (Gertsch and Allred 1965, Hibner 1971) almost always indicate a severe trap bias for mature vaejovoid

males. This bias is probably a result of male movement during the breeding season (Allred 1973). Mature males of the scorpion *Urodacus abruptus* Pocock, in the family Scorpioniade, are more mobile than mature females (Smith 1966). Male vagrancy at this time may well be the main cause of gene flow among populations.

Female initiation of courtship has been reported in other scorpion species (Table I). Although he did not describe the mating, Bacon (1972) stated that females of the vaejovid scorpion, *Uroctonus mordax* Thorell initiate courtship. However, female mating attack has not previously been described. In female *P. mesaensis* this behavior is different from cannibalistic attack behavior; this suggests that she is in a receptive state prior to mating attack or the adult male triggers a less violent attack. During mating attack, the female does not secure a hold on the male's body. She retreats after each contact with the male, and she continues her forays to the male.

Substrate vibrations may be employed to identify potential mates and reduce violent interaction. Although mate recognition by information received through vibrations has not been reported in scorpions, it does occur in other organisms: many spider families (Bristowe 1941, 1958), fiddler crabs (Salmon 1965), Orthoptera (Frings and Frings 1958), and mosquitoes (Frings and Frings 1958). Intraspecific communication via substrate vibrations is also reported for eight orders of insects (Frings and Frings 1958; Autrum 1963; Dumortier 1963; and Alexander 1967) and for many species of mammals (Tembrock 1963).

In spiders, the primary sense used for prey detection is often also used for mate recognition (Bristowe 1941, 1958). In spiders that utilize vibration to detect prey, the female recognizes the male via male-specific vibrations.

The promenade provides the male and female scorpion with the mobility and coordination necessary to find a suitable substrate on which to deposit the spermatophore. Duration of the courtship seems to be primarily determined by the length of time it takes to find a solid surface for the spermatophore (Alexander 1957, 1959; Shulov and Amitai 1958; Rosin and Shulov 1963). The male's pectines sweep the surface during the entire promenade and become very active upon encounter with the proper substrate. Our observations support Carthy's (1966, 1968) contention that the pectines are used in discriminating surface texture. The dimorphic use of the pectines by the male during mating implies that the pectines may be an important structure in courtship and sperm transfer. Using morphometric analysis of growth, we have shown (Polis and Farley 1979) that the pectines are sexually dimorphic and exhibit growth characteristics of a masculine secondary sexual characteristic.

Cheliceral massage was only observed during the promenade when the female ceased moving and during spermatophore deposit and uptake. In both cases, the female appeared to become more docile and cooperative, suggesting that this behavior may function to suppress female predatory tendencies during the mating process.

Headstand and swaying behaviors probably serve mechanical functions. Headstand behavior is displayed only when the female is over the spermatophore. As the female's genital aperture dilates at this time, headstand behavior is associated with sperm uptake. Swaying may cause the sperm to travel further into the female's reproductive tract. Both of these previously unnamed behaviors have analogies in other families of scorpions (Table 1).

Male post-nuptial behavior reduces the probability of cannibalism by the female. After insemination, the female's reproductive tendencies may decrease while her cannibalistic

tendencies increase. Alexander (1959) reported that the female is always more aggressive after mating and must be avoided by the male. Escape behavior decreases the incidence of cannibalism by removing the male from the immediate proximity of the larger female. Both male escape behavior and mate cannibalism are widespread among scorpions (Table 1).

Table 1 allows a comparison of mating behaviors between vaejovids and other scorpion families. Only two behaviors, promenade with chelae grip and male pectine movement, have been observed in the five other families reported in the literature. Behaviors exhibited by *P. mesaensis* and reported in at least three of the other five families include juddering, cheliceral massage, sand scraping, and mate cannibalism by the female. Behaviors which are shared with only one or two of the other five families include male movement, female initiation, clubbing, headstand and swaying. Accidental and male initiation, promenade with cheliceral grip, female post-mating escape, and consumption of the spermatophore are behaviors exhibited by members of other families but which are not observed in the present study.

Female mating attack and subsequent male response have not been reported previously. As our work was conducted exclusively in the field, it is possible that these behaviors (and male movement) are merely heretofore undescribed. It is our experience that scorpions are much less active and aggressive in the laboratory than in the field. These pre-promenade behaviors may be suppressed in the laboratory and the numerous reports of matings initiated by males (Table 1) may be a laboratory artifact.

SUMMARY

During the breeding season, adult males are eaten by adult females during or after mating and by simple predation. Approximately 10 percent of the diet is individuals of the same species. Cannibalism of mature males combined with other factors related to breeding contribute to a higher death rate of adult males than of adult females.

Mating is seasonal. During the breeding season, mature males undergo alteration in behavior and ecology; they roam more and feed less than all other components of the population. This increased vagility of the male increases the chances they will be cannibalized, since these scorpions use substrate vibrations to locate prey.

Courtship is discussed in terms of mating behaviors which reduce predatory tendencies and elicit the pair coordination necessary for indirect sperm transfer. The behaviors include the *promenade à deux*, cheliceral massage, post-mating escape by the male and heretofore undescribed behavior which precedes the actual mating dance. Brief but aggressive contacts gradually increase in duration but decrease in violence before the mating dance begins. Indirect sperm transfer is also described.

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