

BIOLOGY OF THE DIURNAL *METASOLPUGA PICTA* (KRAEPELIN) (SOLIFUGAE, SOLPUGIDAE) COMPARED WITH THAT OF NOCTURNAL SPECIES¹

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ABSTRACT

Metasolpuga picta (Kraepelin) is a diurnal solifuge restricted to the Namib Desert of SWA/Namibia. Burrowing, mating, oviposition, and feeding behaviors are described and compared with other solifuge species. Thermoregulatory behavior, previously undocumented for solifuges, is associated with diurnal habits. Populations were bivoltine in 1979, whereas all solifuges previously studied have been univoltine. The biology of *M. picta* is otherwise similar to that of nocturnal species from North African, South-west Asian, and North American deserts.

INTRODUCTION

Despite extensive work on some North American species (Muma 1966a-e, 1967), solifuges are relatively poorly studied (Cloudsley-Thompson 1977, Savory 1977). Since the publication of Cloudsley-Thompson's (1977) review, Muma (1974a,b, 1975a,b, 1979, 1980a,b), Gore and Cushing (1980), Thaler (1982), and Aliev and Gadzhiev (1983) have published additional biological information; and Aruchami and Sundara Rajulu (1978), Alberti (1979, 1980), Haupt (1982), and Bauchhenss (1983) have contributed morphological studies. Nevertheless, detailed biological data have been published for only four of the approximately 1000 described species of solifuge arachnids (Heymons 1902, Cloudsley-Thompson 1961a,b, Junqua 1966, and Muma 1966c). Published biological data on Solifugae are restricted primarily to members of the families Galeodidae, Eremobatidae, and Ammotrechidae. Little or nothing is known about the other nine solifuge families.

Cloudsley-Thompson (1977) stated that solifuges are nocturnal, with only "a few small colourful species" exhibiting diurnal habits. Previous biological studies have dealt almost exclusively with these nocturnal species. However, there are

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several large, diurnal solifuge species in the arid regions of southern Africa (Lawrence 1963, Wharton 1981).

Based on trap catches of 14 individuals, Holm and Scholtz (1980) determined that *Metasolpuga picta* (Kraepelin) was diurnal, and restricted to the interdune valley habitat of the Namib Desert dune ecosystem at Gobabeb (South West Africa/Namibia). Its biology is detailed here for comparison with its better known nocturnal relatives. Prior to Holm's studies of dune arthropods (Holm and Edney 1973, Holm and Scholtz 1980), only five specimens of *M. picta* had ever been collected (Kraepelin 1899, Purcell 1899, Lawrence 1963, 1965, 1967). The following account represents the first detailed biological study of a member of the family Solpugidae.

MATERIALS AND METHODS

Solifuge behavior was observed between November, 1978 and February, 1980 within a 5 km radius of Gobabeb (23°24'S, 15°03'E), in the Namib Desert of South West Africa/Namibia. This region consists of a southern dune habitat and a northern gravel plain bisected by the sporadically flowing Kuiseb River. Holm and Edney (1973), Holm and Scholtz (1980), Robinson and Seely (1980), Seely and Louw (1980), and Wharton and Seely (1982) have described and figured the dune and gravel plains habitats in this region. Nearly all observations were made directly in the field, on both sides of the Kuiseb River. Eleven individuals were also maintained for varying periods in laboratory cages to supplement field data on oviposition, feeding, response to temperature, and intraspecific aggression.

Although most solifuges, including those from the Namib Desert, readily climb out of pitfall traps, *M. picta* was unsuccessful in doing so unless the sides of the traps were exceptionally rough. As a consequence, populations could be readily sampled throughout the year using smooth-sided, metal, bowl-shaped traps (20 cm diameter x 12 cm deep). These traps could be quickly set in the sand and easily removed at the end of a trapping period with little disturbance to the habitat. Traps were placed in an interdune valley (1 km wide x 5 km long) on 10 different occasions throughout 1979 to record phenology and obtain estimates of population age structure. A minimum of 57 traps was used during each trapping period. Traps were monitored at least twice daily until a total of 24 *M. picta* had been captured. During June and July, decreased solifuge activity precluded capture of 24 solifuges within a 2 week period, and trapping was therefore terminated before the desired quantity was obtained. Trapped solifuges were taken to the laboratory, where they were measured and, if adult, sexed. Adult males were readily recognized by the presence of a flagellum, females by differences in development of the genital operculum. All identifications were done by the author. Solifuges were either maintained in the laboratory until the end of the current trapping period, or immediately marked and released (none of the 75 marked individuals was ever recovered). Cheliceral length was measured to ± 0.1 mm using vernier calipers. Measurements of other body parts proved considerably less reliable, based on repeated measurements of the same individual: the opisthosoma was capable of considerable stretching; endpoints of legs and palps were difficult to pinpoint; and the prosoma was flexible and subject to some distortion depending on position of chelicerae. While there was some evidence of wear on the cheliceral tips of a few of the larger adults, this

was not observed in immatures. Results of trap catches were plotted as size-frequency distributions, using 0.5 mm size classes. The 0.5 mm size class was based on a 0.4 mm range in measurements of 2nd instars.

Meteorological data for the study period (including ground surface temperatures) were obtained from the First Order Weather Station, Gobabeb. Additional temperature records were made using a YSI® rapid-response telethermometer, calibrated to correspond with Gobabeb Weather Station measurements. A Mettler® balance was used for weights recorded in the text. Where not otherwise stated, averages reported in the text are means (\bar{m}) \pm standard deviations. The term "pebble" is used repeatedly in the text, and refers to small pieces of quartz and CaCO_3 weighing 5 gm or less.

RESULTS AND DISCUSSIONS

Phenology and Diel Periodicity.—*Metasolpuga picta* was observed in the field between 0915 and 1845. Trap catches indicated that they were only active during the daylight hours, confirming the data presented by Holm and Scholtz (1980). Of 65 solifuges encountered in the field, only two were observed after 1745, and seven before 1200. This activity was confirmed during pitfall trap censuses (Fig. 1), where 79% of the individuals were trapped in the afternoon.

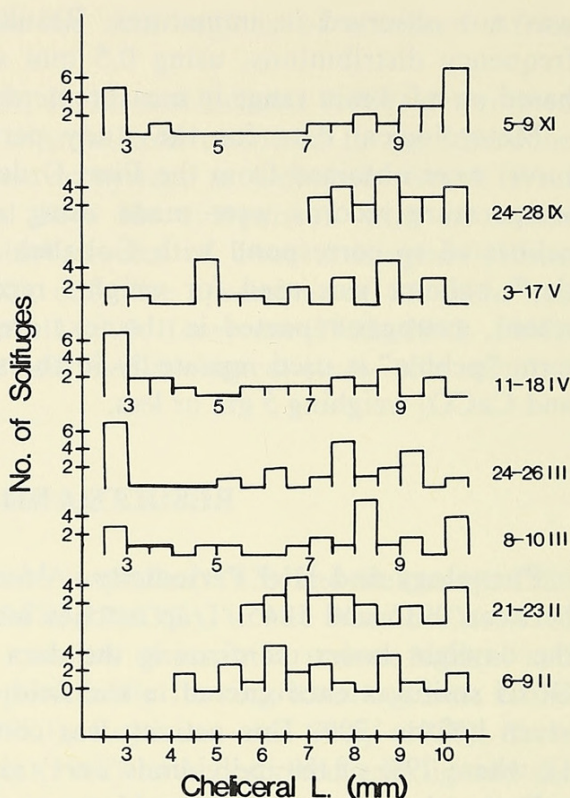
Both adult and immature *M. picta* were observed in the field during every month except June and July. No individuals were trapped during a 2-wk interdune valley pitfall trap census in June; and only one immature *M. picta* during a 9-day census in July. A pitfall trap census was not conducted in August. Results of remaining censuses are shown in Fig. 1.

Solifuges were active in the field at ground surface temperatures between 40 and 61°C. Nevertheless, caged individuals maintained at lower ambient temperatures of 25–30°C still actively burrowed, and quickly responded to stimulation of leg IV setae. Two individuals placed at $20 \pm 1^\circ\text{C}$, however, became lethargic and responded only weakly to the same stimuli. At 5–10°C, *M. picta* became completely torpid. Of approximately 190 individuals subjected to refrigeration at 5–10°C for up to 30 min during census periods (to facilitate cheliceral measurement), all recovered completely, usually within 10 min. There was no noticeable difference in response to refrigeration among the various instars.

Reduced *M. picta* activity during June and July was correlated with low temperatures (a relationship first noted by Heymons (1902) for solifuges). In 1979, June, July, and August (austral winter) were the only months in which mean monthly ground surface temperatures at 1400 were 40°C or less (Table 1). Assuming an activity threshold between 20 and 25°C, however, temperatures in overnight burrows (see burrowing section below) are more likely to be a limiting factor for activity than are surface temperatures. During June and July, monthly means at 1400, 10 cm below the surface, were 23.5 ± 1.8 and $22.0 \pm 1.9^\circ\text{C}$ (more than 10°C lower than the means for January and February). It is thus possible that *M. picta* remained lethargic in burrows during cool days or weeks, but emerged on warm days throughout the mild Namib Desert winter.

Based on trap catches (Fig. 1) and field observations, the interdune valley population was essentially bivoltine in 1979. Eggs were deposited primarily in the

Fig. 1.—Size-frequency distributions representing 8 pitfall trap samples of *Metasolpuga picta* (Kraepelin) taken from an interdune valley population in 1979; 24 solifuges per trapping period. Adults > 10.5 mm combined with the 10.0-10.5 mm class.



spring (September-October) and again in late summer (February-early April). Data presented by Heymons (1902), Cloudsley-Thompson (1961b), Muma (1963, 1974a), and Junqua (1966) on 11 other solifuge species suggest that they are all univoltine.

Figure 1 shows the appearance of the first motile instar (=2nd instar), with cheliceral length 2.5-3.0 mm, beginning in November and March of 1979. Cloudsley-Thompson (1977) has stated that in the Sudan and western North America, production of young solifuges occurs in the summer, during the time of annual desert rains. Andrewartha and Birch (1954) and Nichols et al. (1976) have discussed similar correlations between precipitation and natality in desert invertebrates and vertebrates. Rainfall in the Namib is sporadic (Schulze 1969, Robinson and Seely 1980), and production of young *M. picta* was not correlated with it. In 1979, for example, total monthly rainfall was >10 mm only in June. In 1978, such rains occurred in February, March, and April. In 1980, they did not occur. Similarly, production of young *Eremobates durangonus* Roewer (Muma 1966e) occurs even when it doesn't rain (Muma, personal communication).

Cheliceral length of adult males from the interdune valley ranged from 7.2-11.0 mm ($\bar{m} = 8.7 \pm 0.9$; $N = 42$), and adult females from 7.2-12.3 mm ($\bar{m} = 10.4 \pm 1.1$; $N = 28$). However, about half the individuals in Fig. 1 with cheliceral length ≥ 7.5 mm were still immature. Adults from the gravel plain were larger, with female cheliceral length 8.0-16.2 mm ($\bar{m} = 12.7 \pm 2.8$; $N = 12$). Only one male, with cheliceral length of 13.0 mm, was available for measurement from the gravel plain. These findings support those of Junqua (1966) that adult size is not fixed.

Cheliceral lengths of all individuals measured from the interdune valley population (trap catches plus hand-collected specimens) are shown in Fig. 2. The peak at 2.8 mm represents the first active or motile instar (= second instar). The

Table 1.—Mean (\bar{m}) monthly ground surface temperatures at 1400, during 1979 pitfall trap censuses. No trapping conducted in August and October. No *Metasolpuga picta* trapped during 2-week census in June; only one *M. picta* trapped during 9-day census in July.

Month	(\bar{m})	# days to trap 24 <i>M. picta</i>	# traps
Feb.	57.9	3	57
		3	63
Mar.	55.1	3	63
		3	65
Apr.	49.1	8	61
May	42.7	14	60
June	36.0	-	60
July	40.2	-	52
Aug.	40.4	-	-
Sept.	47.1	5	59
Oct.	50.9	-	-
Nov.	55.6	5	60

first instar is inactive and passed within the oviposition chamber in the Solpugidae; and the existence of a post-embryo was not determined during this study. These data suggest that there are at least four active instars before adulthood. The peak between 7.5 and 8.0 mm consists of nearly an equal number of immatures and adult males (only one female). Since smaller adults are almost entirely males, either females have one more instar than males, or male and female chelicerae grow at different rates.

These data on chelicerel lengths serve only as a rough estimate for number of instars; and Francke and Sissom (1984) have recently discussed the limitations of such indirect methods. Such estimates are of value as a basis for future work, however, especially in light of the difficulty of rearing solifuges in captivity. Similar estimates are available for only two other species. Muma (1966c) estimated 8-10 instars for *E. durangonus*; and Junqua (1962, 1966) estimated six instars for *Othoes saharae* Panouse. Junqua (1962, 1966) also stated that, because of considerable observed variation in size, some individuals probably achieved adulthood at the 4th instar, and others at the 9th or 10th instar.

Only five males were trapped in censuses from February through May (Fig. 1). Although males dominated trap catches in late September (15 of 23 adults), they had largely disappeared by early November (3 of 24 individuals, 3 of 15 adults). This change in dominance from slightly more males than females in September to many more females than males in November was corroborated by field observations. Muma (1963, 1966e, 1974a) discussed an apparently similar seasonal appearance of males before females in some North American species. The appearance of males before females supports the hypothesis that males may have one less instar than females. These data further suggest that adult male *M. picta* are short-lived; and die after a relatively brief mating period. This can be attributed to the high energy demands and low food intake observed during mate location (discussed below). Females may be longer-lived because of the time required for egg development and oviposition following mating. Supporting data for *M. picta*, however, is meager. A single field-collected female oviposited after one week in the laboratory, and died 2 weeks following oviposition.

Cloudsley-Thompson (1961b), Junqua (1962, 1966), and Muma (1963, 1966c) have also presented evidence suggesting adults are short-lived; and that solifuges

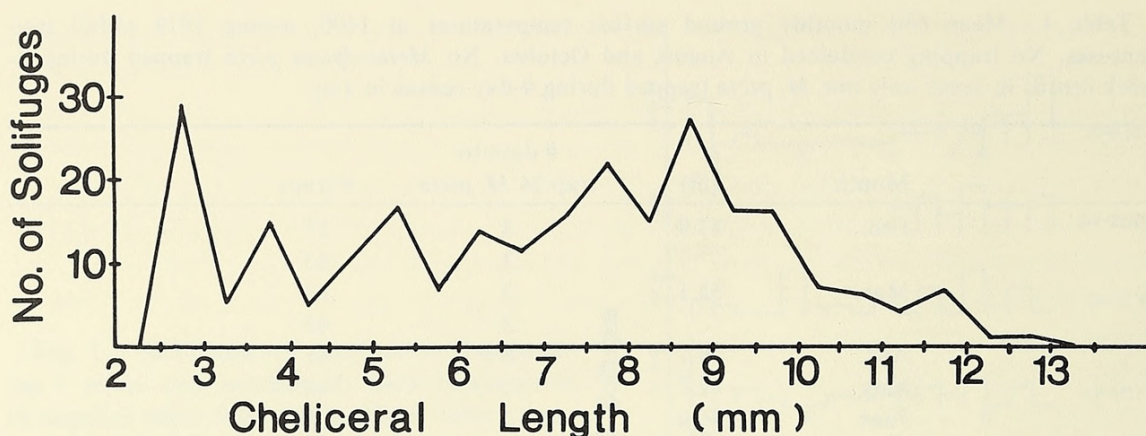


Fig. 2.—Size-frequency distribution for *Metasolpuga picta* (Kraepelin) chelicerae measured on solifuges collected from interdune valley habitat, 1/1979-1/1980 ($N = 257$). Includes solifuges from pitfall traps plus those collected by hand. Peaks at 2.8, 3.8, 5.3, and 6.3 mm suggest the presence of at least four nymphal instars between the first (immobile and spent in oviposition chamber) and the adults (starting at 7.2 mm). Peaks beyond 6.3 mm difficult to interpret because they represent mixtures of immatures and adults.

do not live more than one year. Junqua (1966) showed that male *O. saharae* lived for only about one week, but Muma (1966c) kept male *E. durangonus* alive for up to one month.

Burrowing.—Solifuge burrowing behavior has been described by several workers (Hutton 1843, Turner 1916, Hingston 1925, Junqua 1966, Muma 1966d, Cloudsley-Thompson 1977). Burrows are constructed for digestion, oviposition, ecdysis, hibernation, and retreats during inactive periods (Muma 1966d, Cloudsley-Thompson 1977). Solifuges also burrow as a displacement activity following disturbance (Cloudsley-Thompson 1961b).

Although solifuges studied elsewhere use rocks, logs, or other surface debris as shelters, or to conceal burrows, these were generally not present on the sandier substrates preferred by *M. picta*. The few large rocks available were not utilized by this species. Thus the generalization by Newlands (1978) that in southern Africa only hexisopodids occurred in sandy areas, and that members of other solifuge families sheltered under stones, does not hold for at least some Namib species. Otherwise, burrowing by *M. picta* was generally similar to that reported for other solifuge species.

Metasolpuga picta either excavated a new burrow or occupied an abandoned one at the end of each activity period. Although chelicerae are used extensively in burrowing by other solifuge species (as detailed in reviews by Muma 1966d and Cloudsley-Thompson 1977), they were utilized less readily by *M. picta*. Instead, the sandy soil was rapidly excavated primarily with the second pair of walking legs. As in other solifuges (Muma 1966d: 254), *M. picta* tossed soil out beneath the opisthosoma (in canine fashion) while excavating (Fig. 3). Chelicerae and the first pair of walking legs were used only rarely to loosen more compact soil particles. Chelicerae were also used to carry out larger pebbles during excavations. One adult male and two large immatures were each observed transporting pebbles weighing 0.6-0.7 gm. The pebbles weighed 2-5 times that of the solifuges (wet weight).

Position reversal within the tunnel during burrowing was accomplished with a simple turn rather than the more complicated operation described by Muma



Fig. 3.—*Metasolpuga picta* (Kraepelin) in the act of burrowing. From original kindly furnished by M. Seely.

(1966d) for several North American species. Plowing was accomplished by lowering the chelicerae onto the base of the accumulated refuse, and pushing the soil out of the hole. The palps and first pair of legs were held on either side of the pile. Burrow construction (total or partial) was observed in the field for 7 males, 9 females, and 4 immatures; and all excavated in this fashion. Burrow length ranged from 50-300 mm ($N = 13$), and angle of penetration about 30-70° from horizontal.

Solifuges plugged the entrance of overnight burrows with excavated sand 72.2% of the time ($N = 18$). All newly excavated burrows were plugged, but 62.5% of the solifuges occupying old, abandoned burrows ($N = 8$) left the entrance completely open. Both Turner (1916) and Cloudsley-Thompson (1961a) noted irregular plugging of burrows. Junqua (1966) and Muma (1966d), however, reported that burrows were regularly plugged.

Excavation of oviposition chambers by females differed from excavation of burrows used as overnight shelters. Of four females observed preparing oviposition chambers in the field, one completed the task in 25 min, but the others took at least 60 min. Muma (1966d) reported a similar range of burrowing times for both males and females of 4 North American species. Mean excavation time of *M. picta* overnight burrows, however, was only 7 min ($N = 5$).

Oviposition burrows were plugged much more thoroughly than overnight shelters, and it was difficult to trace them for measurements of burrow depth. Only three of the presumed oviposition burrows were successfully excavated, and these were 70, 120, and 170 mm deep. Mean vertical depth of overnight burrows was 54 mm ($N = 8$).

The dimensions of *M. picta* burrows compare favorably with those reported for most other solifuge species. Berland (1932) reported burrows of *Galeodes* up to 240 mm deep. Cloudsley-Thompson (1961a) described variation in burrow length of 100-200 mm. Muma (1966d) recorded burrow lengths of 6-54 mm for immatures and males, and 38-229 mm for females of 6 different species. Muma (1966d) also noted variation in length and depth of burrows used for egg deposition. Junqua (1966), however, reported a "remarkably constant" burrow configuration for *O. saharae* and a burrow length of about 80-90 mm.

Excavation of overnight shelters, as well as digging during prey and mate location (discussed below), was generally rapid. Thus the general conclusion by

Muma (1966d: 251) that solifuge "burrowing, although conducted with extreme vigor and activity, seems to be accomplished inefficiently and laboriously" is not appropriate for this species. In *M. picta*, there are six spatulate setae posteriorly on the second pair of walking legs. Most other members of the family Solpugidae have five apically pointed setae in this position. The spatulate setae are clearly adaptations to facilitate digging in sandy substrates.

Gore and Cushing (1980) concluded on the basis of four observations that males of a North American species normally returned to the same sheltered depressions for at least three consecutive nights to conserve energy. Unfortunately, the authors did not indicate whether the solifuges were marked to allow individual recognition or whether they were all given the same mark. Also, data on two of the four observed males (Gore and Cushing 1980: Table 1) may have been misinterpreted. In one case, only the depression was marked, rather than the solifuge, and the solifuge which occupied the depression on a subsequent day may not have been the same. In a second case, apparently two different individuals occupied a single depression on successive nights. In the case of *M. picta*, it is unnecessary to invoke homing as a means of conserving energy, since burrows abandoned by other arthropods and small vertebrates are plentiful, and readily occupied by this species.

Foraging.—Solifuges are extremely active, with most of their above-ground activity spent foraging or (in adult males) locating mates. Although Muma (1967) has interpreted much of their activity as simply "investigating their surroundings," I interpret such activity as typical foraging behavior in a cursorial predator.

Few field observations on solifuge foraging behavior have been made because species previously studied were nocturnal, and were difficult to follow in the dark. Diurnal solifuges in the Namib Desert were also difficult to observe because they were easily disurbed, extremely fast, and surprisingly cryptic.

Sixty-five *M. picta* were observed foraging in the field. Fifteen of these were followed continuously for at least 15 min each. Females and immatures searched the habitat by thoroughly covering the area in a rapid, zig-zag pattern. They probed all burrows, pebbles, and small pieces of detritus. Dead grass clumps and the few larger stones present in the study area were also thoroughly searched when encountered. However, nearly all of the foraging observed during this study occurred in the open. Actual distances covered by females and immatures during foraging generally could not be determined because of their rapid, zig-zag motion. However, seven individuals followed for periods ranging from 5-87 min traveled a mean straight-line distance of only 106.8 m/h. The single individual running more or less in a straight line traveled 978.9 m/h. This latter figure is comparable to velocities achieved by males.

Searching behavior of adult males differed from that of females and all immatures. Adult males traveled at nearly the same speed as females and immature, but rarely exhibited the intense, zig-zag searching behavior of the latter. They thus covered much greater straight-line distances (1062.1 ± 593.1 m/h; $N = 9$, range of observations, 5-100 min). When extensive searching of a limited area by males was observed, males searched in a more deliberate, circling pattern. Only two of 18 males found searching in the field searched in a zig-zag pattern for more than 10% of the observation time.

One immature with a body length of 13 mm was observed for 1.5 h on the gravel plain. It foraged mostly in the open, pawing at pebbles about a third its

body length or less. It used primarily the second pair of walking legs for digging, and the palps and the first pair of walking legs for perception. Although there were several dead grass clumps in the area being searched, the solifuge only foraged through one of these. The solifuge dug one burrow, but it collapsed shortly after the start of excavation. The solifuge also cleared the entrance to an abandoned burrow, and stayed within the tunnel for 4 min before resuming foraging. On four occasions, the solifuge stopped for 3 sec, then resumed foraging. The only other breaks in the foraging pattern occurred when four small invertebrates of undetermined identity were dug up from around four different pebbles and immediately fed upon. The solifuge covered an area of roughly 40 m² in 1.5 h. This foraging pattern was typical of all females and immatures observed, with variation limited to number of holes dug or occupied, number of feeding bouts or pauses unrelated to feeding, and amount of time spent around grass clumps.

Females and immatures fed, or attempted to feed, on every invertebrate encountered in the field. Males were observed feeding only twice, even though total observation time for males (5.5 h) was slightly more than that for females and immatures. Moreover, males on seven different occasions ran into potential prey (species eaten by similarly sized females or immatures) without attempting to feed on them.

Prey items were located primarily by direct contact (as detailed by Bolwig (1952)) during running, or while pawing around pebbles. Because of the frequency with which *M. picta* entered holes for short periods during foraging, it is possible that prey were also trapped and eaten in these holes. Field-captured prey of females and immatures were rarely identified because of their small size and the speed with which they were captured and ground up in the chelicerae. The single item positively identified was the tettigoniid *Comicus* sp.

Two of the nocturnal *Comicus* were excavated by a single solifuge. In each case, the solifuge dug three small holes 30 mm apart, with each hole about 30 mm from the cricket. The resulting pattern formed a square, with the cricket at one corner and excavations at the other three corners. The solifuge quickly alternated from one hole to the next, spending about 5 sec at each hole. At the first excavation site, the cricket emerged from its burrow 4 min after the solifuge began excavating, and jumped away. The solifuge pursued, but was unable to follow after two jumps of the tettigoniid. In the second excavation, the solifuge dug for 3 min, then ran immediately to the buried cricket and pulled it out of the sand with chelicerae and palps. The solifuge macerated the cricket for 15 sec, then carried it into a hole. The solifuge remained in the hole for 5 min before resuming foraging.

In both cases, there was no visible evidence of the cricket or its burrow on the surface of the soil. Thus, *M. picta* is capable of detecting prey other than visually or by direct contact. Muma (1966b) has discussed the interactions of sight, touch, and vibration in prey location by solifuges. Prey location is even more complex than this, however. Detection by means of a kairomone is possible, since the malleoli are chemoreceptors (Brownell and Farley 1974); and they touch the ground while the solifuge forages (Cloudsley-Thompson 1961a). Moreover, detection of sound waves through sandy soils has been shown to be an important method of prey detection in scorpions (Brownell 1977, Brownell and Farley 1979), and this method may be used by solifuges as well.

Caged *M. picta* ate all soft-bodied prey offered. These included termites (*Hodotermes mosambicus* (Hagen) and *Psammotermes allocerus* (Silvestri), mealworms (*Tenebrio molitor* L.), moths, roaches, and silverfish. Larger Coleoptera larvae were chewed apart at intersegmental membranes. Tips of the chelicerae were then used to scoop out soft parts from the otherwise intact exoskeleton. Numerous zophosine and two adesmiine Tenebrionidae were also fed upon in this fashion after head and prothorax had been severed from the rest of the body. In the field, only two encounters between adult beetles and *M. picta* were observed. In the first encounter, the solifuge picked up the beetle, but dropped it after one sec. In the second encounter, the solifuge touched the beetle with its palps, then ignored it. The hard exoskeleton of beetles and the normally rapid inspection of potential prey items by the solifuge would seem to preclude adult Coleoptera from being an important component of *M. picta*'s diet, even though this species is clearly capable of eating them.

Although Newlands (1978) stated that solifuges relied solely on the chelicerae to capture prey, *M. picta* occasionally brought prey to the chelicerae with the palps. Muma (1966b) has provided a good discussion of variation in the use of chelicerae and palps in prey capture.

The cheliceral teeth of male solifuges are often smaller, blunter, and/or less numerous than those of females and immatures of the same species. This is also true of *M. picta*. Reduced cheliceral teeth are correlated with reduced feeding by the males, and are also of benefit to the male during courtship (described below), since larger, sharper teeth might puncture the female opisthosoma during the massaging phase. The reduced cheliceral teeth and marginal interest in feeding support the hypothesis derived from phenological data that males are very short-lived.

Junqua (1966) accurately noted that potential prey of desert solifuges are often scarce, in part because solifuges feed largely on relatively soft-bodied invertebrates. Solifuges are also voracious predators (e. g. Hutton 1843, Bernard 1897, Heymons 1902, Turner 1916, Lawrence 1949, Cloudsley-Thompson 1958); and Muma (1966b) and Cloudsley-Thompson (1977) have reviewed their feeding habits. Extreme activity, voracious appetites, and widely dispersed prey (at least for desert species) are interrelated: to locate a sufficient quantity of food in a desert, solifuges must forage over large areas (or be highly specific such as some of the termitophilous species). By increasing foraging speed, they cover more territory per unit time, and therefore increase the probability of encountering prey. But increased foraging speed results in increased water loss, and is energy expensive. Therefore, to replenish energy stores used in foraging, solifuges must eat large quantities.

Opisthosomal Elevation.—Of the 15 solifuges observed foraging on the surface for more than 15 min, five frequently elevated the opisthosoma in scorpion-like fashion (Fig. 4), and one did so only rarely (3X in 1.7 h). The five which regularly exhibited this behavior were observed when ground surface temperatures were 55-60°C. Only three other *M. picta* were observed for more than 15 min at these temperatures. Although none raised the opisthosoma, two regularly stopped in the shade of grass clumps for 0.5-3.0 min periods.

Berland (1932), following Walter (1889), interpreted opisthosomal elevation as a defense reaction in the Galeodidae. Cloudsley-Thompson (1949) hypothesized that this behavior mimics scorpions, especially in some of the Rhagodidae.

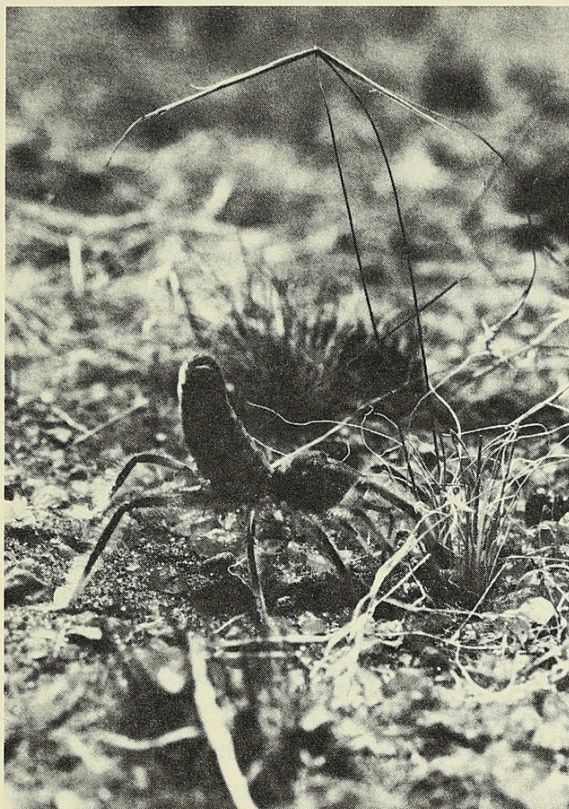


Fig. 4.—Elevation of opisthosoma by *Metasolpuga picta* (Kraepelin) as an apparent thermoregulatory response. From original kindly furnished by C. K. Brain.

However, since the opisthosoma is the softest part of the body (easily punctured, for example, by insect mandibles), elevation may be as important in protection (Pocock 1898) as in mimicry.

In *M. picta*, opisthosomal elevation was observed only during activity at high ground surface temperatures, and never during flight or defense behavior (see description of predator avoidance below). I therefore interpret opisthosomal elevation as a thermoregulatory response. The scorpion *Opisthophthalmus latimanus* (Koch) also elevates the opisthosoma as an adaptation to heat stress (Alexander and Ewer 1958). Krakauer (1972) and Robinson and Robinson (1974) have also discussed this behavior in detail for the spider *Nephila clavipes* (Linnaeus). The predictions of Robinson and Robinson (1974) regarding complex thermoregulatory behavior for cryptic species at low latitudes fit well for *M. picta*.

Predator Avoidance and Predators.—*Metasolpuga picta* responded to vibrations and tactile stimuli, and was also visually oriented. Flight response consisted of traveling several meters at greatly increased speed, with chelicerae and prosoma usually angled toward the source of the disturbance. This was followed either by resumption of normal foraging behavior and speed or a sudden stop, depending on strength of stimulus. When motionless, *M. picta* was not readily detected in the field by the human eye from a distance ≥ 2 m. The orange propeltidium and chelicerae resembled the many orange pebbles in the interdune valley and gravel plain. The yellow and black pattern on the rest of the body broke up the outline, and thus contributed to the crypsis. Solifuges in the field exhibited flight responses to a hovering sarcophagid fly, a hunting wasp (bembicine Sphecidae), and to other solifuges as well as the author. However, flight response and crypsis are more logically adaptations to visually oriented predators, such as vertebrates, than to these other disturbances.

Gore and Cushing (1980) concluded that there was little evidence of natural predators of solifuges. However, a number of mammals (Bothma 1966, 1971, Smithers 1971, Viljoen and Davis 1973, Roer 1975, Bigalke 1978, Nel 1978), reptiles (Louw and Holm 1972, Haacke 1976, Robinson and Cunningham 1978, Holm and Scholtz 1980), and birds (Distant 1892, Willoughby 1971, Brain 1974, Brain and Brain 1977, Dixon 1981, Clark et al. 1983) are known to eat solifuges in southern Africa, and there is one report of a hymenopteran predator (Bristowe 1973). During the present study, one large sparassid (Araneae) was observed capturing and eating a male *M. picta*; and *M. picta* chelicerae were found in one Ludwig's bustard (*Otis ludwigii* Ruppell) dropping and several raptor pellets (= regurgitations).

Of 80 pellets collected from beneath one roost on the gravel plain (occupied primarily by a greater kestrel, *Falco rupicoloides* A. Smith), 43 contained *M. picta* chelicerae, or moveable cheliceral fingers probably belonging to *M. picta*. There was an average of 1.2 complete sets (one set per solifuge) per pellet. Four other raptor pellets, two from an interdune valley and two from the gravel plain, were collected during the study period. All four contained *M. picta* chelicerae, and averaged 5.2 cheliceral sets per pellet. Chelicerae of *M. picta* were not found in several cape fox (*Vulpes chama* (A. Smith)), black-backed jackal (*Canis mesomelas* Schreber), or lizard (*Meroles cuneirostris* (Strauch), *Aporosaura anchietae* (Bocage), and *Mabuya occidentalis* (Peters)) droppings collected during this study. Thus, raptors may be the most important predators of larger solifuges active on the surface. This would help explain their visual sensitivity to objects moving overhead (such as the fly and wasp noted above). Predation of lethargic solifuges in subterranean burrows may also be important, but would be extremely difficult to document.

Ruggiero et al. (1979) studied the effects of certain prey characteristics on kestrel predatory behavior in a North American species. They found that the highest rates of attack were elicited by moving, familiar prey. Aberrant movement enhanced acceptability of familiar prey. They hypothesized that operation of these two factors should lead to selection for a uniform, immobile response in species which are heavily preyed upon. The quick flight and sudden stop of *M. picta* fits this model. Pianka and Pianka (1970) and Pianka (1971) have described similar escape responses for agamid lizards in sparsely vegetated habitats in Australia.

Mate Location.—Mate location may be summarized as follows: 1) male searches in a straight-line pattern; 2) female in burrow emits chemical or auditory cues; 3) male encounters cues, and switches from straight-line pattern to more intensive circular or criss-cross pattern; or, 3a) male directly encounters female on surface; 4) from step 3, male locates area directly above buried female and initiates digging; 5) female responds by coming to soil surface; 6) from steps 3a and 5, male touches female and jumps back; 7) male grabs female opisthosoma in his chelicerae.

Males of *M. picta* located conspecific females either by direct contact or by indirect detection through the soil surface. Five males were observed to detect females beneath the soil surface. In two of the encounters, different males successfully mated with the same female. In each case, the female was excavated at a spot showing no visible evidence of a burrow. The burrow opening which the female entered after the first mating was several centimeters away from the point of excavation by the second male. In the third encounter observed, a male

started excavating in an area where the soil was uneven (indicating recent burrowing), but with no visible burrow entrance. In all three cases, females came to the surface in response to the males' digging. Thus male digging may serve as a stimulus to the female rather than as an attempt to actually excavate her. In the fourth and fifth observations, males discovered open burrows occupied by females, and waited at the entrance until the females appeared.

Another five males detected females by direct encounter, while females were either excavating at the entrances of burrows or foraging. Only one of the encounters resulted in mating. This mating occurred after a male ran into a foraging female, then ran into her again a few minutes later as she was starting to dig a burrow. One additional mating was observed in the field, but the initial encounter was not witnessed.

The intense, zig-zag searching behavior of females is replaced in males by a pattern of long, straight-line runs. These long-distance runs (one male traveled 2 km in 1.7 h) were interrupted at intervals by intensive searching of restricted areas. Such searches were characterized by slow circling or pacing back and forth, rather than the high intensity zig-zagging of females and immatures. With one exception, these more restricted searches led to eventual discovery of females in burrows. The three females in closed-off burrows were located more quickly than those actively excavating.

Unreceptive females (including four of the five encountered while burrowing) exhibited three different responses. They often ignored males, continuing their foraging or burrowing without interruption. Alternatively, some exhibited a weak aggressive response towards the males. This consisted of raising the prosoma, extending the palps, and opening the chelicerae slightly. More rarely, burrowing females took one step towards the males before running back down the burrow for another load of soil.

Males which encountered unresponsive females in the act of burrowing remained at the burrow until the female closed off the entrance. Three such males remained for 47, 101, and 123 min before excavating their own overnight shelters. During these vigils, males usually stood near the entrance, with their palps overhanging the hole.

As in detection of concealed prey (described above), observations on mate location may be interpreted as evidence for either chemical or auditory cues (or both). If the malleoli are truly chemoreceptors (Brownell and Farley 1974), then their role in detection of a female pheromone is strongly suggested by their greater size in males. A single observation favors auditory over chemical cues: a searching male stopped in an area lacking a visible burrow or surface anomaly, and detected a large sparassid concealed within a trap-door covered tunnel. The solifuge exhibited none of the typical flight responses of disturbed *M. picta* when the spider sprang from its tunnel. Instead, the solifuge approached the spider with palps extended until direct contact was made. At this point, the sparassid pounced on the solifuge, killed it, and pulled it into its burrow. The sparassid was roughly the same size and shape as an adult *M. picta*, and the male solifuge exhibited the same behavior towards the sparassid as did other males encountering female *M. picta*. In this instance, the ability of the sparassid to mimic auditory stimuli of female *M. picta* can be explained by the similar size of these two burrowing arachnids. However, mimicry of chemical cues by the sparassid is also possible, and cannot be completely ruled out without further testing.

Males were unable to successfully pursue unresponsive females encountered on the soil surface, and lost them within seconds after the first encounter. Two males ran within 5 and 10 cm respectively of females burrowing and foraging on the surface without contacting them, and apparently without detecting them. One of these males, as well as a third one, ran by other females at least once before direct contact was made minutes later. These observations suggest that males of *M. picta* are unable readily to detect or follow females on the surface when passing within short distances of them, unless physical contact is actually made. Moreover, the sense used to locate mates (or prey) buried beneath the surface is apparently insufficient or at best inefficient for locating individuals on the surface in this species. These observations do not necessarily contradict the hypothesized role of vision in predator detection since the eyes are dorsally placed in solifuges, and much better adapted to detect motion from above, than laterally.

Mating.—Males initiated courtship by grabbing the posterior end of the female opisthosoma with their chelicerae, while touching the female prosoma and chelicerae with their palps. Females folded their legs up against their bodies, and their palps against their chelicerae, when grabbed in this fashion. Receptive females remained quiescent as the male thoroughly massaged the opisthosoma with his chelicerae. Males gradually worked forward onto the prosoma and female chelicerae. Unreceptive females began struggling as males moved anteriorly. In both observations on unreceptive females, females broke away, and males were unable to capture them. In the four successful matings observed, males massaged females in this fashion for 2.5 min. At the completion of the massaging phase, males were standing directly over females, both facing the same direction. Males held the females' legs and palps against their bodies (as described by Heymons (1902) and Junqua (1966)). Males then released a single spermatophore from the genital pouch at the base of the opisthosoma. Males next moved quickly backwards, used their chelicerae to pick up the spermatophore lying on the female's dorsum, lifted the female opisthosoma to a vertical position, and inserted the cheliceral tips and spermatophore directly into the female's genital opening. The flagellum was also inserted into the genital opening at this time. Although the flagellum in the family Solpugidae has an immovable base, the shaft is flexible. The shaft was held at a 45-90° angle from its resting position while inserted in the female's genital opening, but quickly returned to lie along the chelicerae after mating. Males held females in this position for 2.5-3.0 min. They used their palps (and to a lesser extent their first pair of legs) to hold the females; and constantly probed into the genital opening with the tips of the chelicerae. Females recovered from their torpor while in this position, and terminated mating by struggling free from the males. Total mating time was 5-6 min ($N = 3$). Two males ran off quickly after the female struggled free, but the other two remained in place. After mating, males wiped the tips of their chelicerae in the soil and flexed them for about 1 min before resuming a typical searching behavior. Two of the females re-entered burrows from which they emerged in response to males' digging stimuli, a third found and entered another burrow, and the fourth ran off.

Mating in solifuges has been described by Heymons (1902), Cloudsley-Thompson (1961b), Amitai et al. (1962), Junqua (1962, 1966), and Muma (1966c,e, 1967). All previous observations were limited to three genera in two families (Eremobatidae and Galeodidae). Detailed field observations were made only by Heymons (1902) and Junqua (1966).

Heymons (1902) and Junqua (1966) stressed the importance of the suddenness of the "attack" by the male in subduing the female (inducing torpor) and preventing her counter-attack. The reports by Amitai et al. (1962) and Muma (1966e, 1967) also suggest that the attack phase was critical. However, the females they studied were generally more passively subdued. In all species studied to date, including *M. picta*, both pedipalps and cheliceral massaging played a role in the initial phase of mating. Heymons (1902) and Junqua (1966) attempted to determine the relative importance of palps and chelicerae in mating, but were largely unsuccessful. Junqua (1966), however, was able to induce the catatonic state in receptive females with his fingertips, and Heymons (1902) by using forceps. Thus the submissive state in solifuges is produced mechanically, as a response to sudden attack. Heymons (1902) equated it to a similar phenomenon commonly seen in vertebrates. This state was also produced very briefly in two *M. picta* during initial rough handling when captured in the field.

Heymons (1902) stressed the importance of female receptivity on induction of torpor in *Galeodes*. Female receptivity was also important in *M. picta*, since males were unable to hold onto unreceptive females. A few observations (Junqua 1966, Wharton unpublished) suggest that torpor, once induced, was maintained even when the male was removed. Cloudsley-Thompson's observations on mating in *Galeodes granti* Pocock also suggest this. Thus, continued massaging during mating may not be necessary to maintain the torpid condition of the female.

In *M. picta* and the Galeodidae, chelicerae were used to massage the genital opening and to quickly transfer the spermatophore to the opening. Spermatophores were carried by only one chelicera in *Galeodes* (Amitai et al. 1962, Cloudsley-Thompson 1961b), and between both fixed cheliceral fingers in the galeodid *Othoes* (Junqua 1966). In the nocturnal or crepuscular galeodids, spermatophores were deposited, probably on the soil, while the female's abdomen was bent back over the prosoma. In *M. picta*, however, the spermatophore was deposited on the female's dorsum before her opisthosoma was pushed back over her head. This reflects either a basic difference between galeodids and solpugids, or a need to protect the spermatophore from the soil by the diurnal solpugid in response to high ground surface temperatures. In Eremobatidae, Muma (1966e) observed direct transfer of the spermatophore from the genital opening of the male to that of the female. Nevertheless, male eremobatids still massaged the area around the genital opening before and after transfer. This massaging may function in part in liberating the sperm from the spermatophore.

Mating was of approximately equal duration in all species studied thus far. Massaging of the female by the male chelicerae, especially after spermatophore transfer, was of longer duration in *M. picta* than in most other species. Recovery from torpor after spermatophore transfer was also longer in *M. picta* than in galeodids, but comparable to that in eremobatids. Heymons (1902), Amitai et al. (1962), Cloudsley-Thompson (1961b) and Junqua (1966) all reported at least some males picking up females with their chelicerae and carrying them about. This was not observed in *M. picta*.

Use of the flagellum has not been previously reported for any solifuge. Junqua (1966), in the most detailed study yet published on mating behavior, was unable to discern the function of this structure. Lamoral (1975) presented morphological evidence that the flagellum operates in storage and transmission of an exocrine secretion. Based on Lamoral's work, Cloudsley-Thompson (1977) suggested a role in "brief displays of territoriality among males during the mating season."

Male solifuges often have longer appendages than females of the same species. The longer legs and palps are correlated with the manipulation and containment of the female during mating, and also with the long-distance mate-searching behavior of the male.

Oviposition.—Actual oviposition by *M. picta* was observed only once. A female confined in a cage dug a deep burrow one week after capture. Construction of this burrow lasted several hours, and was similar to that described above for presumed oviposition burrows in the field. The female spent considerably more time packing soil to close off the burrow than she did during construction of overnight shelters. The female emerged from this oviposition chamber after 5 days, leaving 63 eggs behind. She then covered over her emergence hole. The female remained lethargic for nearly 2 weeks, did not feed, and did not return to the eggs. She then ate actively for one day before she died.

Oviposition in Solpugidae was previously observed by Lawrence (1947, 1949). He recorded the nocturnal *Zeria caffra* (Pocock) producing 192 eggs and *Z. hostilis* (White) 64 eggs. Muma (1966a) presented data for the Eremobatidae; and summarized findings for other Solifugae. He also noted that the number of eggs per mass was intraspecifically variable.

Confinement.—The effects of caging and temperature must be considered when interpreting solifuge behavior. This is particularly true for diurnal species such as *M. picta*. For caged *M. picta*, movement of the terrarium from a shaded laboratory into direct sunlight altered behavior. Solifuges which responded only weakly to tactile stimuli at 20–25°C in shaded cages usually responded quickly and aggressively to the same stimuli when cages were placed in the sun at 30–35°C.

Burrowing and feeding by *M. picta* was influenced by caged conditions. Unless the soil was of sufficient depth, quality, and compactness, burrows were not constructed efficiently, frequently collapsed, and often were not completed. Caged solifuges often huddled on the surface throughout the night instead of seeking shelter. Caged solifuges generally ate more than was available to them in the field per unit time. Moreover, heavily sclerotized invertebrates (such as many of the tenebrionids) were more readily eaten in cages than in the field. Ability or willingness to feed on adult beetles is directly related to continued contact in caged environments.

Mating behavior was also influenced by confinement, and especially by size of the arena. Field observations on *M. picta* suggest that males are generally able to flee from unreceptive females, or from females with which they had recently mated. When caged, however, fighting and resulting cannibalism are more common (e.g. Muma 1966b, Cloudsley-Thompson 1977). In confinement, males of *M. picta* were usually unable to approach females undetected, females generally exhibited more aggression towards males than in the field, and males were unable to flee from unresponsive females without constantly running into them again. Polis and Farley (1979) studied cannibalism-minimizing behavior during mating in the scorpion *Paruroctonus mesaensis* Stahnke. In the field, mating behavior in *M. picta* produces comparable results.

Construction of the oviposition chamber, incubation, and the maternal care observed by some workers (e.g. Hutton 1843, Lawrence 1949, Junqua 1966, Cloudsley-Thompson 1967) may be similarly affected by laboratory confinement. While maternal care in the Galeodidae is probable, it has not been observed in

Eremobatidae and Ammotrechidae (Turner 1916, Muma 1966a). Observations on *Z. caffra* (Lawrence 1949) and *M. picta* need to be supplemented to determine whether or not maternal care occurs in Solpugidae.

Muma (1966e, 1967) noted that caged individuals invariably reduced activity, became lethargic, and eventually died. He termed this behavior "taming"; and Cloudsley-Thompson (1977) has unfortunately followed this usage. This behavior would seem to be a natural result of confining any highly active animal. By greatly reducing the foraging area, and constantly offering food, the solifuge cannot balance energy expenditure with food intake. Moreover, contamination caused by increasing food and waste products in a confined area may also affect activity.

Since the great majority of published data on solifuge biology was obtained from caged individuals, behavioral comparisons must be made with caution. More field data are needed to verify and expand the limited biological information available from studies of caged individuals.

Distribution.—No attempts were made to determine the range of *M. picta*, but several predictions can be made, based on the above findings. Leg morphology (especially spatulate setae) and rapid burrowing behavior indicate that this species is limited to sandy substrates. The construction of discrete burrows, and *M. picta*'s inability to burrow in loose sand, further restrict this species' activities to more compact soils (and thus to inderdune valleys rather than the loose sands of the Namib dune slopes). Distribution north of the Kuiseb River and east of the dune ecosystem should be fairly limited due to the harder substrates. Suitable sandy conditions exist along the coast, but cooler temperatures brought about by the Benguela Current may preclude activity there.

SUMMARY

Metasolpuga picta is a diurnal, bivoltine species active throughout most of the year on compact, sandy soils in the Namib Desert. Thermoregulatory capabilities are vital to species such as this which are active at high temperatures in habitats largely devoid of vegetational and mineralogical shelters; and this topic merits further investigation. Activity at high daytime temperatures is counterbalanced by lethargy induced by the same cooler temperatures (20-25°C) at which many nocturnal species are active. Feeding, burrowing, and mating behaviors are similar to those reported for other solifuge species, but there are some differences. The voracious nature of solifuges was generally confirmed, with the exception of adult males. Both prey and mates concealed beneath the surface can be detected by *M. picta*, but the mechanism for such detection is unknown. Differences were observed in the types of burrows constructed or occupied, with overnight shelters being constructed much more rapidly than previously reported for solifuge burrows. Mating was similar to that reported for galeodids, but use of the flagellum during mating has not been previously recorded. Its function is still uncertain since possible uses (rupture of spermatophore, destruction of sperm or spermatophores from previous matings, transport of spermatophore up oviduct) do not explain species specificity in flagellum configuration. The absence of the flagellum in certain solifuge families leaves its function even more difficult to explain. The effect of vertebrate predators on solifuge behavior needs to be more

thoroughly explored, especially for nocturnal species. Vertebrates, especially small raptors, are important predators of *M. picta*.

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LITERATURE CITED

- Alberti, G. 1979. Licht- und elektronenmikroskopische Untersuchungen an Coxaldrüsen von Walzenspinnen (Arachnida: Solifugae). *Zool. Anz.*, 203:48-64.
- Alberti, G. 1980. Zur Feinstruktur des Hodenepithels und der Spermien von *Eusimonia mirabilis* Roewer 1934 (Solifugae, Arachnida). *Zool. Anz.*, 204:345-352.
- Alexander, A. J. and D. W. Ewer. 1958. Temperature adaptive behaviour in the scorpion, *Opisthophthalmus latimanus* Koch. *J. Expt. Biol.*, 35:349-359.
- Aliiev, Sh. I. and A. T. Gadzhiev. 1983. Solpugids (Arachnida, Solifugae) in the Azerbaijan SSR. *Izv. Akad. Nauk Azerbaijan SSR, Ser. Biol.*, 4:43-46.
- Amitai, P., G. Levy, and A. Shulov. 1962. Observations on mating in solifugid *Galeodes sulfuripes* Roewer. *Bull. Res. Council Israel (B) Zool.*, 11:156-159.
- Andrewartha, H. G. and L. C. Birch. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago. 782 pp.
- Aruchami, M. and G. Sundara Rajulu. 1978. An investigation on the poison glands and the nature of the venom of *Rhagodes nigrocinctus* (Solifugae: Arachnida). *Nat. Acad. Sci. Letters (India)*, 1:191-192.
- Bauchhenss, E. 1983. Morphology and ultrastructure of sensilla ampullacea in Solifugae (Chelicerata: Arachnida). *Int. J. Insect Morphol. Embryol.*, 12:129-138.
- Berland, L. 1932. Les Arachnides. *Encycl. Entomol.*, (A) 16:33-43.
- Bernard, H. M. 1897. 'Wind scorpions', a brief account. *Sci. Prog.*, 1:317-343.
- Bigalke, R. 1978. Mammals. Pp. 981-1048. *In* Biogeography and Ecology of Southern Africa. (M. J. A. Werger and A. C. Van Bruggen, eds.). Dr. W. Junk B. V., The Hague.
- Bolwig, N. 1952. Observations on the behavior and mode of orientation of hunting Solifugae. *J. Entomol. Soc. Southern Africa*, 15:239-240.
- Bothma, J. du P. 1966. Food of the silver fox *Vulpes chama*. *Zool. Africana*, 2:205-210.
- Bothma, J. du P. 1971. Reports from the mammal research unit: 2. Food habits of some Carnivora (Mammalia) from Southern Africa. *Ann. Transvaal Mus.*, 27:15-26.
- Brain, C. K. 1974. The use of microfaunal remains as habitat indicators in the Namib. *South African Archeol. Soc. (Goodwin Ser.)*, 2:55-60.
- Brain, C. K. and V. Brain. 1977. Microfaunal remains from Mirabib: some evidence of palaeo-ecological changes in the Namib. *Madoqua*, 10:285-293.

- Bristowe, W. S. 1973. A new lycosid spider in the Seychelles and an endemic eumenid wasp which stores spiders. *Entomologist*, 106:220-222.
- Brownell, P. 1977. Compression and surface waves in sand: used by desert scorpions to locate prey. *Science*, 197:479-481.
- Brownell, P. H. and R. C. Farley. 1974. The organization of the malleolar sensory system in the solpugid, *Chanbria* sp. *Tissue and Cell*, 6:471-485.
- Brownell, P. H. and R. D. Farley. 1979. Prey-localizing behavior of the nocturnal desert scorpion, *Paruroctonus mesaensis*: orientation to substrate vibrations. *Anim. Behav.*, 27:185-193.
- Clark, W. H., D. R. Frohlich, and P. L. Comanor. (1982) 1983. Shrike predation on the scorpion *Anuroctonus phaidactylus* (Wood) and on a solpugid (Scorpionida: Vaejovidae; Solpugida). *Pan-Pacific Entomol.*, 58:164.
- Cloudsley-Thompson, J. L. 1949. Notes on Arachnida, 9. Do Solifugae mimic scorpions? *Entomol. Monthly Mag.*, 85:47.
- Cloudsley-Thompson, J. L. 1958. Spiders, Scorpions, Centipedes, and Mites. Pp. 87-98 (revised ed., 1968, pp. 105-123). Pergamon, Oxford. 228 pp.
- Cloudsley-Thompson, J. L. 1961a. Some aspects of the physiology and behavior of *Galeodes arabs*. *Entomol. Exp. Appl.*, 4:257-263.
- Cloudsley-Thompson, J. L. 1961b. Observations on the natural history of the "camel-spider" *Galeodes arabs* C. L. Koch (Solifugae: Galeodidae) in the Sudan. *Entomol. Monthly Mag.*, 97:145-152.
- Cloudsley-Thompson, J. L. 1967. Reproduction in Solifugae. *Entomol. Monthly Mag.*, 103:144.
- Cloudsley-Thompson, J. L. 1977. Adaptational biology of the Solifugae (Solpugida). *Bull. British Arachnol. Soc.*, 4:61-71.
- Distant, W. L. 1892. Are the Solpugidae poisonous? *Nature*, 46:247.
- Dixon, J. E. W. 1981. Diet of the owl *Glaucidium perlatum* in the Etosha National Park. *Madoqua*, 12:267-268.
- Francke, O. F. and W. D. Sissom. 1984. Comparative review of the methods used to determine the number of molts to maturity in scorpions (Arachnida), with analysis of the post-birth development of *Vaejovis coahuilae* Williams (Vaejovidae). *J. Arachnol.*, 12:1-20.
- Gore, J. A. and B. S. Cushing. 1980. Observations on temporary foraging areas and burrows of the sun spider, *Ammotrechula penninsulana* (Banks) (Arachnida: Solpugida). *Southwest. Nat.*, 25:95-102.
- Haacke, W. 1976. The burrowing geckos of Southern Africa, 2 (Reptilia: Gekkonidae). *Ann. Transvaal Mus.*, 30:13-28.
- Haupt, J. 1982. Hair regeneration in a solfugid chemotactile sensillum during molting (Arachnida: Solifugae). *Wilhelm Roux's Arch. dev. Biol.*, 191:137-142.
- Heymons, R. 1902. Biologische Beobachtungen an asiatischen Solifugen. *Abh. Preussischen Akad. Wiss.*, 190:1-65.
- Hingston, R. W. 1925. *Nature at the Desert's Edge; Studies and Observations in the Bagdad Oasis*. Whitherby, London. 299 pp.
- Holm, E. and E. B. Edney. 1973. Daily activity of Namib Desert arthropods in relation to climate. *Ecology*, 54:45-56.
- Holm, E. and C. H. Scholtz. 1980. Structure and pattern of the Namib Desert dune ecosystem at Gobabeb. *Madoqua*, 12:5-39.
- Hutton, T. 1843. Observations on the habits of a large species of *Galeodes*. *Ann. Mag. Nat. Hist.*, 12:81-85.
- Junqua, C. 1962. Données sur la reproduction d'un solifuge: *Othoes saharae* Panouse. *C. R. Acad. Sci., Paris*, 225:2673-2675.
- Junqua, C. 1966. Recherches biologiques et histophysiologiques sur un solifuge Saharien *Othoes saharae* Panouse. *Mem. Mus. Natn. Hist. Nat., Paris (A)*, 43:1-124.
- Kraepelin, K. 1899. Zur Systematik der Solifugen. *Mitt. Naturh. Mus. Hamburg*, 16:187-259.
- Krakauer, T. 1972. Thermal responses of the orb-weaving spider *Nephila clavipes* (Araneae: Argiopidae). *Amer. Midland Nat.*, 88:245-250.
- Lamoral, B. H. 1975. The structure and possible function of the flagellum in four species of male solifuges of the family Solpugidae. *Proc. 6th Int. Congr. Arachnol.*, pp. 136-141.
- Lawrence, R. F. 1947. Some observations on the eggs and newly hatched embryos of *Solpuga hostilis* White (Arachnida). *Proc. Zool. Soc. London*, 117:429-434.
- Lawrence, R. F. 1949. Observations on the habits of a female solifuge, *Solpuga caffra* Pocock. *Ann. Transvaal Mus.*, 21:197-200.

- Lawrence, R. F. 1963. The Solifugae of South West Africa. *Cimbebasia*, 8:1-28.
- Lawrence, R. F. 1965. New and little known Arachnida from the Namib Desert, S. W. Africa. *Sci. Papers Namib Desert Res. Stn.*, 27:1-12.
- Lawrence, R. F. 1967. Additions to the fauna of South West Africa: solifuges, scorpions and Pedipalpi. *Sci. Papers Namib Desert Res. Stn.*, 34:1-19.
- Louw, G. N. and E. Holm. 1972. Physiological, morphological and behavioural adaptations of the ultrapsammophilous Namib Desert lizard, *Aporosaura anchietae* (Bocage). *Madoqua*, (II)1:67-85.
- Muma, M. H. 1963. Solpugida of the Nevada Test Site. *Sci. Bull. Brigham Young Univ. (Biol. Ser.)*, 3:1-13.
- Muma, M. H. 1966a. Egg deposition and incubation for *Eremobates durangonus* with notes on the eggs of other species of Eremobatidae (Arachnida: Solpugida). *Florida Entomol.*, 49:23-31.
- Muma, M. H. 1966b. Feeding behavior of North American Solpugida (Arachnida). *Florida Entomol.*, 49:199-216.
- Muma, M. H. 1966c. The life cycle of *Eremobates durangonus* (Arachnida: Solpugida). *Florida Entomol.*, 49:233-242.
- Muma, M. H. 1966d. Burrowing habits of North American Solpugida (Arachnida). *Psyche*, 73:251-260.
- Muma, M. H. 1966e. Mating behavior in the solpugid genus *Eremobates* Banks. *Anim. Behav.*, 14:346-350.
- Muma, M. H. 1967. Basic behavior of North American Solpugida. *Florida Entomol.*, 50:115-123.
- Muma, M. H. 1974a. Maturity and reproductive isolation of common solpugids in North American deserts. *J. Arachnol.*, 2:5-10.
- Muma, M. H. 1974b. Solpugid populations in southwestern New Mexico. *Florida Entomol.*, 57:385-392.
- Muma, M. H. 1975a. Two vernal ground-surface arachnid populations in Tularosa Basin, New Mexico. *Southwest. Nat.*, 20:55-67.
- Muma, M. H. 1975b. Long term can trapping for population analyses of ground-surface, arid-land arachnids. *Florida Entomol.*, 58:257-270.
- Muma, M. H. 1979. Arid-grassland solpugid population variations in southwestern New Mexico USA. *Florida Entomol.*, 62:320-328.
- Muma, M. H. 1980a. Comparison of three methods for estimating solpugid (Arachnida) populations. *J. Arachnol.*, 8:267-270.
- Muma, M. H. 1980b. Solpugid (Arachnida) populations in a creosotebush vs. a mixed plant association. *Southwest. Nat.*, 25:129-136.
- Nel, J. A. J. 1978. Notes on the food and foraging behavior of the bat-eared fox, *Otocyon megalotis*. *Bull. Carnegie Mus.*, 6:132-137.
- Newlands, J. 1978. Arachnida (except Acari). Pp. 685-702, *In* Biogeography and Ecology of Southern Africa. (M. J. A. Werger and A. C. Van Bruggen, eds.). Dr. W. Junk B. V., The Hague, 1439 pp.
- Nichols, J. D., W. Conley, B. Batt, and A. Tipton. 1976. Temporally dynamic reproductive strategies and the concept of r- and K- selection. *Amer. Nat.*, 110:995-1005.
- Pianka, E. R. 1971. Ecology of the agamid lizard *Amphibolurus isolepis* in Western Australia. *Copeia*, 1971:527-536.
- Pianka, E. R. and H. D. Pianka. 1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. *Copeia*, 1970:90-103.
- Pocock, R. I. 1898. On the nature and habits of Pliny's Solpuga. *Nature*, 57:618-620.
- Polis, G. A. and R. D. Farley. 1979. Behavior and ecology of mating in the cannibalistic scorpion, *Paruroctonus mesaensis* Stahnke (Scorpionida: Vaejovidae). *J. Arachnol.*, 7:33-46.
- Purcell, W. F. 1899. New and little known South African Solifugae in the collection of the South African Museum. *Ann. South African Mus.*, 1:381-432.
- Robinson, M. D. and A. B. Cunningham. 1978. Comparative diet of two Namib Desert sand lizards (Lacertidae). *Madoqua*, 11:41-53.
- Robinson, M. D. and M. K. Seely. 1980. Physical and biotic environments of the southern Namib dune ecosystem. *J. Arid Environ.*, 3:183-203.
- Robinson, M. H. and B. C. Robinson. 1974. Adaptive complexity: the thermoregulatory posture of the golden-web spider, *Nephila clavipes*, at low latitudes. *Amer. Midland Nat.*, 92:386-396.
- Roer, H. 1975. Zur Kenntnis der Chiropterenfauna Suedwestafrikas. *J. South West Africa Sci. Soc.*, 29:105-127.

- Ruggiero, L. F., C. D. Cheney, and F. F. Knowlton. 1979. Interacting prey characteristic effects on kestrel predatory behavior. *Amer. Nat.*, 113:749-757.
- Savory, T. 1977. *Arachnida* (2nd ed.). Academic Press, London, New York, San Francisco. 340 pp.
- Schulze, B. R. 1969. The climate of Gobabeb. *Sci. Papers Namib Desert Res. Stn.*, 37:5-12.
- Seely, M. K. and G. N. Louw. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *J. Arid Environ.*, 3:25-54.
- Smithers, R. H. N. 1971. The mammals of Botswana. *Mem. Mus. Nat. Hist. Rhodesia.*, 4:1-340.
- Thaler, K. 1982. Die Primaerlarve der Walzenspinne *Gylippus* cf. *cypriotica* Lawrence (Arachnida, Solifugae, Karschiidae). *Mitt. schweizerischen entomol. Ges.*, 55:93-95.
- Turner, C. H. 1916. Notes on the feeding behavior and oviposition of a captive American false spider. *J. Anim. Behav.*, 6:160-168.
- Viljoen, S. and D. H. S. Davis. 1973. Notes on stomach contents analyses of various carnivores in Southern Africa (Mammalia: Carnivora). *Ann. Transvaal Mus.*, 28:353-363.
- Walter, A. 1889. Transcaspische Galeodiden. *Zool. Jb. (Syst.)*, 4:1094-1109.
- Wharton, R. A. 1981. Namibian Solifugae (Arachnida). *Cimbebasia Mem.*, 5:1-87.
- Wharton, R. A. and M. Seely. 1982. Species composition and biological notes on Tenebrionidae of the lower Kuiseb River and adjacent gravel plain. *Madoqua*, 13:5-25.
- Willoughby, E. J. 1971. Biology of larks (Aves: Alaudidae) in the Central Namib Desert. *Zool. Africana*, 6:133-176.

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Wharton, Robert. 1986. "Biology of the Diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) Compared with That of Nocturnal Species." *The Journal of arachnology* 14(3), 363–383.

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