Natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae)

Fred Punzo
Dept. of Biology,
Box 5F, University of Tampa,
Tampa, FL 33606, USA

Summary

Studies were conducted on the natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart from the Trans Pecos region of western Texas (Chihuahuan Desert). The life cycle consists of an egg and post-embryo stage, followed by eight nymphal instars and the adult stage. Under controlled laboratory conditions (20°C, 70% RH, 12L:12D), embryonic development required 25–36 days; post-embryos required 4–7 days; and first-instar nymphs required 5–9 days. The mean life cycle required 226 days for males and 240 days for females. Clutch size ranged from 16–144 eggs/female. There was no significant difference between the sexes in the length of the body, palpi or chelicerae, or in the length or width of the propeltidium. However, there was a significant difference in the width of the chelicerae. There was a significant positive correlation between female body size (length and weight) and clutch size. In the field, adult males became active at the ground surface earlier in the season than females. Over 35% of males were collected during March and April as compared with only 5% of females. Gravid females were observed from the middle of June to the third week in July. Egg masses were found from the middle of June through August. Some females were still active at the surface in October; no males were observed after August. These solifuges are nocturnal, and no significant difference was found in the diel activity patterns between males and females. During the spring, peak activity occurred between 2200 and 2400 h Central Standard Time (CST). During the hotter summer months, peak activity periods shifted to a later time interval (2300 to 0100 h). These solifuges preferred sandy arroyos and adobe flats characterised by scattered clumps of vegetation. Adult females constructed more permanent and deeper tube-shaped burrows. Males are associated with shallow, bowl-shaped burrows or depressions found under rocks and decaying vegetation. Mating occurred most frequently in June (26%) and July (54%). The behavioural acts which comprise the overall mating sequence are discussed.

Introduction

Despite previous studies on the general taxonomy (Kraepelin, 1899; Muma, 1951), physiology (Cloudsley-Thompson, 1961a; Punzo, 1994a), ecology (Heymons, 1902; Junqua, 1966; Cloudsley-Thompson, 1977; Muma, 1980; Punzo, 1993, 1994a,b, 1997), reproduction (Lawrence, 1947; Junqua, 1962, 1966; Muma, 1966a,b; Wharton, 1987; Punzo, 1995a), and behaviour (Heymons, 1902; Bolwig, 1952; Muma, 1966c, 1967; Gore & Cushing, 1980; Wharton, 1987; Punzo, 1993, 1994a,c, 1995b, 1998a,b) of solifuges, few detailed studies exist concerning the life cycle or natural history of any particular species. Cloudsley-Thompson (1961b) studied reproduction, diel activity patterns, and habitat preferences in *Galeodes granti* from the Sudan. Muma (1966a,b) reported on the clutch size and developmental time of various life cycle stages of *Eremobates durangonus* (from Arizona and New Mexico), under controlled laboratory conditions. In one of the most detailed studies to date, Junqua (1966) examined various aspects of the physiology, ecology and behaviour of *Othoes saharae* from the Sahara Desert. Wharton (1987) described the growth, seasonal abundance, and various behaviours of a diurnal species, *Metasolpuga picta*, from southern Africa.

In the present study, I describe in detail the life cycle and natural history of the eremobatid solifuge *Eremobates marathoni* Muma & Brookhart, 1988, from Trans Pecos, Texas (Chihuahuan Desert). My study focuses on the following parameters: postembryonic growth and development, seasonal and diel patterns of activity, reproductive behaviour, and habitat preference.

Description of study site

The study area lies within a 7 km radius of Terlingua, Texas (Brewster Co., elevation 900–1025 m), located within the northern region of the Chihuahuan Desert. A detailed description of the geology and vegetational zones of Trans Pecos Texas is given by Tinkam (1948). The soils found in the study area are a mixture of sand, gravel, and adobe and they support a predominantly sotol-lechuguilla plant community. The Rio Grande River borders the western edge of the study area and provides a permanent source of water. A desert floodplain is found east of the river and merges into rolling foothills characterised by desert scrub in some areas and alluvial fans and gravel flats in others. The floodplain contains numerous arroyos and sandy washes at various locations. Bare (no vegetation) stretches of ground interrupt rocky and sandy vegetated areas. The dominant vegetation of the study area includes lechuguilla (*Agave lechuguilla*), sotol (*Dasylirion leiophyllum*), ocotillo (*Fouquieria splendens*), saltbush (*Atriplex cunescens*), tarbrush (*Flourensia cernua*), creosote (*Larrea divaricata*), mesquite (*Prosopis glandulosa*), cacti (*Opuntia imbricata*, *O. schotti*, *O. grahamii*, *O. rufida*, *O. engelmannii*, *O. macrocentra*, *Echinocereus enneacanthus*, *Echinocactus hamatacanthus*), and scattered clumps of chino grass (*Bouteloua breviseta*). Owing to wetter soil conditions, the river banks are characterised by a more dense and diverse stand of vegetation including button bush (*Cephalanthus occidentalis*), common reed (*Phragmites communis*), black willow (*Salix nigra*), and yew-leaf willow (*S. taxifolia*).

In this paper, I will refer to the following specific habitats: BAF (bare adobe flats lacking vegetation); VAF (vegetated adobe flats); ALF (alluvial fans); BSA (bare sandy arroyos); VSA (vegetated sandy arroyos); and BGF (bare gravel flats).

Material and methods

Solifuges (*E. marathoni*) were collected from January to December, 1995, through the use of pitfall traps as well as by hand using a headlamp as described previously by Punzo (1994b). For all habitats (BAF, VAF,

ALF, BSA, VSA, BGF), ten 0.30 ha square plots were chosen at random using a U.S. Geological Survey topographical map of the area. Within each plot, solifuges were sampled daily at 3 h intervals over a 24 h period using pitfall traps (2.0 l plastic cups). The sides of the plastic cups were treated weekly with Fluon in order to prevent the solifuges from escaping. At each plot I used five cross-shaped grids (10 × 10 m) as described by Bradley (1989). Each grid consisted of 21 traps with the centre trap shared between the lines. A distance of 0.5 m separated each trap within the grid. Information on total body length (TBL) (Muma, 1951), weight, width of propeltidium, length of chelicerae and palpi, sex, time and location of capture, was recorded for each animal. These data were used to describe adult morphometrics (n=100 males and females), assess the effect of body length and weight on clutch size, and describe seasonal and diel patterns of ground surface activity and mating behaviour. All body measurements were taken using calipers and a Unitron dissecting microscope fitted with an ocular micrometer (Punzo, 1995c). Body weight was recorded with a portable Metler electronic analytical balance.

Using the same sampling plots and procedure and the data on date of capture, I determined the seasonal ground surface activity for adult males (n=455) and females (n=748). I expressed the data as the number of males and females collected on a monthly basis for a 12-month period as described by Edney *et al.* (1974). I also used the data on time of capture to describe temporal (diel) patterns of activity as described by Punzo (1997). The time (CST) was recorded whenever a solifuge was observed at the surface or found in a trap. Results were expressed as the percentage of solifuges active at the surface at various times of the day. Data were tested for significance using the log frequency analysis procedure as reported by Sibley *et al.* (1990).

Data on location of capture were also used to identify microhabitat preferences in this species. Data were expressed as the percentage of solifuges found in the specific microhabitats described previously: BAF, VAF, ALF, BSA, VSA, and BGF.

The study area was inspected twice per week during daylight hours for solifuge burrows under rocks and decaying vegetation. Seventy-four burrows containing a solifuge were located under mesquite and creosote bushes and were excavated; additional burrows in the same area were inhabited primarily by rodents, toads, snakes, tantulas, scorpions, or millipedes. When a solifuge was found within a particular burrow, the depth and overall shape of the burrow were noted.

In order to study the phenology of mating behaviour in this species, I kept a record of the number of times a male and female were observed in courtship and mating activities in the field. The results were expressed as the percent mating activity for a given month out of the total number of courtship/mating bouts observed (n=100). Based on previous descriptions of solifuge mating behaviour (Muma, 1967; Wharton, 1987; Punzo, 1997), I used the presence of any one of the following behaviours as evidence for courtship or mating: (a) a male touching the body of a female with his palps or front legs; or (b) a male grasping a female with his chelicerae in the region of the propeltidium. I also recorded the specific behavioural acts which comprise the overall mating sequence in this species based on observations made under UV light in the field. Preliminary observations indicated that the use of UV light minimised the effect of any disturbance associated with movements of the observer on the behaviour of these solifuges.

In order to study growth rate and the duration of various life cycle stages, solifuges were transported back to the laboratory and housed individually in plastic containers (30 × 20 × 16 cm). They were fed on a mixed diet of crickets (*Gryllus* spp., *Acheta domestica*), larval mealworms (*Tenebrio molitor*), termites (*Neotermes castaneus*), cockroaches (*Periplaneta americana*), and grasshoppers (*Schistocerca* spp., *Neoconocephalus* sp.). Each container was provided with enough soil from the study area to allow burrowing. The soil was sterilised in an autoclave before being placed in the container. Solifuges were maintained at 20°C, 70% relative humidity (RH), and a photoperiod regime of 12L:12D as described by Punzo (1994a).

I also identified gravid females (Punzo, 1995a) and observed them on a daily basis until oviposition. Eggs from each clutch (22 clutches yielding a total of 1,581 eggs) were collected, placed in plastic containers and allowed to develop under environmental conditions identical to those described above. The mean duration (in days) required for the completion of embryonic development to the post-embryo stage was determined for each clutch. I also determined the amount of time required to complete the post-embryo stage and nymphal stages 1–8, as well as the longevity of adults. After reaching the second nymphal instar, solifuges were housed individually to prevent cannibalism. Whenever possible, specific life cycle stages were identified by the

Developmental stage	N	Mean width of propeltidium (mm)	Mean duration in days
Egg[1]	1581		31.4 (25–36)
Post-embryo	807		5.2 (4–7)
Nymph 1	654		6.3 (5–9)
Nymph 2	418		19.6 (15–31)
Nymph 3	204	0.7 [0.12]	31.4 (24–40)
Nymph 4	121	1.3 [0.04]	24.7 (18–27)
Nymph 5	72	1.7 [0.03]	18.3 (14–25)
Nymph 6	57	2.1 [0.24]	25.1 (21–34)
Nymph 7	41	2.9 [0.17]	14.5 (11–22)
Nymph 8	24	3.8 [0.19]	31.8 (23–51)
Adult males	455	4.4 [0.21]	17.7[2] (4–31)
Adult females	748	4.8 [0.24]	31.8[2] (22–63)

Table 1: Duration of various developmental stages (egg, post-embryo, nymphal stages 1–8, and adult) of *Eremobates marathoni*. Data for egg through nymph 8 stages were taken from individuals reared under laboratory conditions: 20°C, 70% RH, 12L:12D photoperiod regime. Data on adult sizes taken from individuals in the field. Values in parentheses represent the range; square brackets ± S.D. [1]Data from Punzo (1995a). [2]Values represent lifespan of adults reared in the laboratory: males (n=57); females (n=72).

	Mean length (mm)		Mean width (mm)	
	Males	Females	Males	Females
Body length	24.1 (3.1) [21–27]	25.3 (2.7) [19–29]		
Chelicerae	6.9 (1.1) [5.8–7.2]	7.4 (0.8) [6.8–7.6]	3.2 (0.5) [2.8–3.4]	4.6 (0.3) [4.1–4.8]
Propeltidium	2.5 (0.2) [2.3–2.6]	2.8 (0.3) [2.7–3.1]	4.4 (0.4) [3.8–4.6]	4.6 (0.3) [4.1–4.7]
Palpi	25.3 (3.1) [21–29]	22.1 (3.4) [18–25]		

Table 2: Adult morphometrics for *Eremobates mormonus* collected in the field. Values in parentheses represent ± S.D.; values in square brackets represent the range; $n=100$ males and females.

exuviae from each moult. I was not completely successful in this endeavour since nymphs were observed to feed on their shed exoskeletons on a number of occasions. Voucher specimens have been deposited in the Invertebrate Collection at Big Bend National Park (Big Bend, Texas).

During laboratory rearing of individuals from nymphal stages 2–8, each cage was provided with food (apterous fruit flies and small crickets) and water ad lib, and a scattering of small rocks and opaque jars under and into which solifuges could take refuge. These arachnids are extremely frenetic, do not adapt well to captivity, and will often run around cages continuously, sometimes to the point of exhaustion and death. As a result, solifuges have proved to be difficult to raise in captivity (Muma, 1966a). The nymphs of *E. marathoni* readily excavated small depressions under rocks and/or sought refuge in the opaque jars. The result was a marked decrease in their locomotor activity which resulted in 24 postembryos surviving to the adult stage out of an initial population of 807 postembryos (3%).

Results

The durations of various life cycle stages of *E. marathoni* are shown in Table 1. Previous studies showed that the average clutch size for laboratory-maintained *E. marathoni* (previously known as *E. mormonus*, and changed to *marathoni* in 1988 by Muma & Brookhart) from Lajitas, Texas was 53.2 eggs/female with a range of 41–69 (Punzo, 1995a). In the present study, data on embryonic development were recorded for a total of 1,581 eggs representing 22 clutches (mean 71.9, range 16–144). Under these laboratory conditions, embryonic development required an average of 31.4 ± 5.8 (S.D.) days. Post-embryos and first nymphal instars represent the shortest stages for this species. The entire life cycle (from oviposition to adult death) required means of 226 days for males and 240 days for females. Growth rate is reflected by changes in the width of the propeltidium (Table 1). The results also show that there are eight nymphal instars in this species.

The morphometric data for 100 field-collected adult males and females are shown in Table 2. There was no significant difference (t-test, $p>0.5$, Sokal & Rohlf, 1981) between the sexes in the length of the body, palpi, or

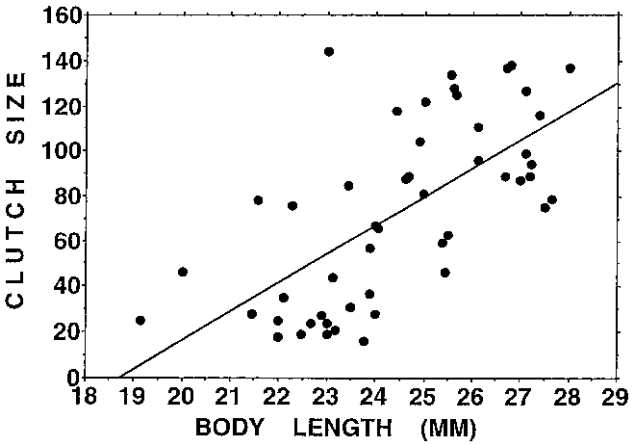

Fig. 1: Relationship between female body length (mm) and clutch size (number of eggs/female) in *Eremobates marathoni* ($n=50$).

chelicerae, or in the length or width of the propeltidium. However, there was a significant difference in the width of the chelicerae (t-test, $p<0.05$). The mean body length for all field-collected adult solifuges was 24.5 mm (± 2.1 S.D., range 19.1–29.0). The correlation between adult female body length and clutch size ($r=0.659$, $p<0.05$), as well as body weight and clutch size ($r=0.861$, $p<0.01$) was significant. Figure 1 shows the relationship between body length and clutch size (regression equation: $y=12.633x–235.986$, $r^2=0.434$). Figure 2 shows the relationship between body weight and clutch size (regression equation: $y=155.448x–245.889$, $r^2=0.741$).

The results also indicate that adult males became active at the surface earlier in the season than females (Fig. 3). Forty-seven (out of a total of 455) males were collected during March (10.3%); no females were collected during this time. Over 35% of males were collected during March and April as compared with only 5% of females ($G=14.9$, $p<0.01$; Sokal & Rohlf, 1981). Thirty-nine out of a total of 748 females (5.2%) were collected in April; this number increased significantly ($G=18.4$, $p<0.01$) to 256 (34.2%) in May. Four hundred and twenty-three females (56.6%) were collected during May and June; this dropped to 104 (13.9%) in July. Gravid

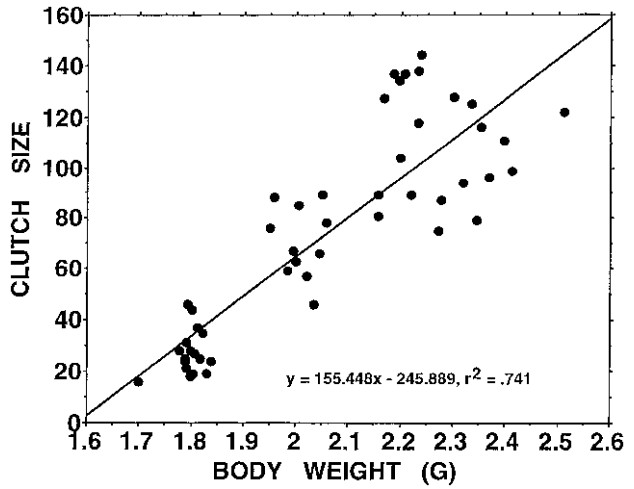

Fig. 2: Relationship between female body weight (g) and clutch size (number of eggs/female in *Eremobates marathoni* ($n=50$).

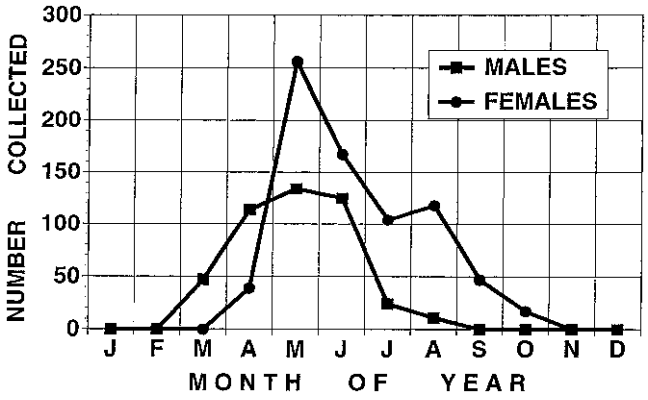

Fig. 3: Number of *Eremobates marathoni* adults collected on a monthly basis over a one-year period (January–December).

females were first observed during the middle of June; the last gravid female was collected on 24 July. Egg masses were found from mid-June through August. Females were found at the surface as late as the middle of October; no males were observed after August. The sudden reduction in male surface activity from mid-June to mid-July may reflect male mortality resulting from attempted mating. Late instar nymphs (5–7) were observed in June and July.

These solifuges were clearly nocturnal in their diel periodicity (Fig. 4). No significant difference was found in the diel activity patterns between males and females ($p>0.6$). During the spring (March–June), peak periods of activity were bimodal, occurring between 2200 and 2400 h, and 0300–0400 h (CST). During the hotter summer months, most activity shifted to a later time interval, from 2300 to 0100 h. Log frequency analysis (Sibley *et al.*, 1990) showed that activity patterns increased significantly during these time periods (spring: $F=13.6$, $p<0.01$; summer: $F=15.7$, $p<0.01$). No adults or nymphs were observed at the ground surface during daylight hours at this location.

Mating activities occurred most frequently in June (26%, Fig. 5) and July (54%), then decreased markedly during August (4%). The first observations of mating behaviour occurred during the last week in May (16%). The male initiated courtship by slowly approaching the female, either head-to-head (37%) or from a lateral direction (63%). The female usually responded to this approach by assuming an agonistic posture with the chelicerae open and the pedipalps elevated. The female frequently also exhibited a forward and backward rocking motion of the body. When the male moved within 2–5 cm of the female, he exhibited a rapid forward movement, grasping the female in the region of the propeltidium (77%) or posterior region of the opisthosoma (23%). The female responded by closing the chelicerae, lowering her head and relaxing her legs. Using his chelicerae, the male opened the genital orifice of the female and deposited seminal fluid. The transfer of sperm required 2.5–6.0 min. Once this was completed, the male released the female and moved rapidly away. Males usually succeeded in completing the mating sequence and escaping without being captured and killed by the female (81%).

At this study area, 28–40% of all solifuges were observed or collected in sandy arroyos characterised by relatively abundant, clumped vegetation (Fig. 6, VSA). The flora in these arroyos was dominated by lechuguilla, creosote, candelilla, catclaw, and several cacti (*O. imbricata*, *O. grahamii*). Grasses were noticeably absent from these arroyos. Between 24–32% of these arachnids were associated with vegetated adobe flats, also characterised by a clumped vegetation dispersion pattern and a more diverse flora. These adobe flats were dominated by ocotillo, creosote, lechuguilla, candelilla, tarbrush, black brush, false agave, different species of cacti (*E. enneacanthus*, *E. pectinatus*, *E. chloranthus*, *O. macrocentra*), and scattered clumps of chino grass. Fewer solifuges were collected from the bare adobe flats (9–13%), bare sandy arroyos (12–20%), and alluvial fans (9–11%). Very few solifuges were collected or observed on the bare gravel flats (0–2%).

Discussion

As mentioned previously, researchers have reported little success in rearing solifuges through one entire life cycle in the laboratory (Muma, 1966a; Cloudsley-Thompson, 1992). Thus, our knowledge concerning the growth and development of these arachnids is incomplete. Only a few authors have reported data on early instars (Hingston, 1925; Junqua, 1958, 1962; Wharton, 1987). Muma (1966a) studied the life cycle of *Eremobates durangonus* from Arizona under controlled laboratory conditions. In order to assess the effects of temperature on the rate of embryonic development, eggs were allowed to develop at 70% RH and temperatures ranging from 16–32°C. Most nymphs and adults were maintained at 27°C and 70% RH. A smaller group were exposed to temperatures ranging from 4–16°C and 70% RH. Few specimens of this species could be reared through more than three moults. Combining laboratory data with data extrapolated from field-collected specimens, Muma concluded that *E. durangonus* had nine nymphal instars and its entire life cycle (from egg through adult) ranged from 302–364 days.

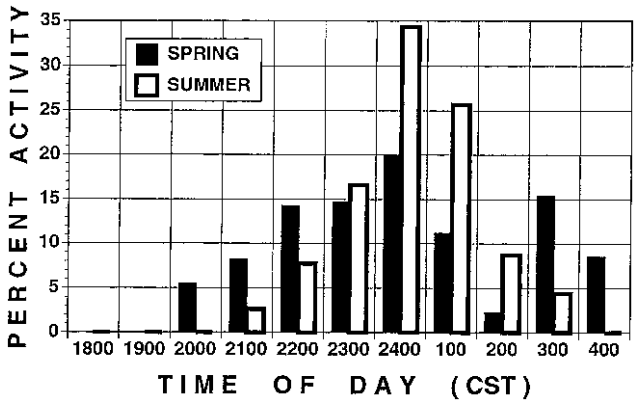

Fig. 4: Temporal (diel) patterns of activity for *Eremobates marathoni* during spring (March through June) and summer (July through September) months. Data expressed as the percentage of adult solifuges active at various time periods of the day (Central Standard Time, CST): 1800 represents the time period from 1800 to 1859, etc.

In comparison, the life cycle of *E. marathoni* consists of an egg and post-embryo stage, eight nymphal instars and the adult stage. Fertile eggs were white and subspherical in shape. A previous study reported eggs ranging in diameter from 1.55–1.59 mm, and weighing 0.39–0.42 mg (Punzo, 1995a). Approximately 12–15 days before hatching, the eggs exhibited invaginations at both ends, became darker in coloration, and the embryo exhibited well-defined eye spots as well as abdominal and peltidial setae. Only 51% of the eggs completed development to the post-embryo stage. Newly hatched post-embryos were translucent white, immobile, and had poorly developed chelicerae. I could not detect the presence of tarsal claws, malleoli, or racquet organs. Setae were present along the lateral margins of the abdominal segments and propeltidium. The movements of post-embryos lacked coordination; it took 8–24 min for them to move several mm away from the egg mass. Post-embryo development under these controlled laboratory conditions required 4–7 days.

First-instar nymphs were gregarious and did not feed. With the exception of the post-embryo stage, first-instar nymphs had the shortest duration of any life cycle stage. However, after moulting, second-instar nymphs were similar to adults with respect to feeding, burrowing, and agonistic behaviour patterns. In addition, under caged laboratory conditions where solifuges remain in close proximity with one another, second-instar nymphs began to cannibalise each other. Mortality from cannibalism may be reduced under field conditions which afford better opportunities for dispersal. Such dispersal may be rapid, as I encountered very few second-instar nymphs in the field. The entire life cycle of *E. marathoni* required 211–243 days.

Clutch size in solifuges seems to be related to female body mass; typically, larger females deposit more eggs (Muma, 1966b; Wharton, 1987; Punzo, 1995a, 1997). Many ecologists support the view that egg production is related to habitat in the sense that it represents an adaptation to counter harsh environmental conditions (Pianka, 1970). Solifuges are generally univoltine, and are characterised by relatively rapid developmental and population growth rates, and a short life span, traits generally considered to be r-selected (Pianka, 1972; Boyce, 1985). The extent to which solifuge population densities are above or below the carrying capacity of the environment is not known.

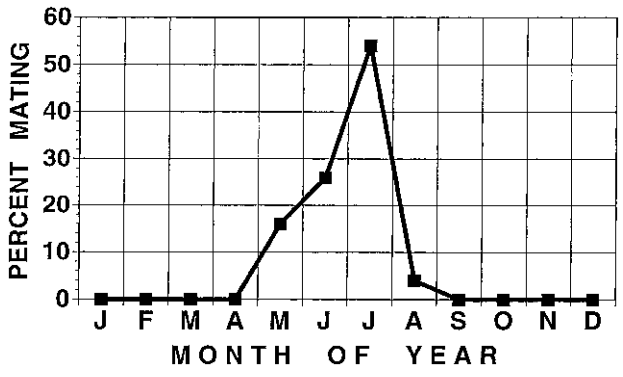

Fig. 5: Mating phenology for *Eremobates marathoni*. Data expressed as the percentage of mating bouts (n=100) occurring during various months of the year.

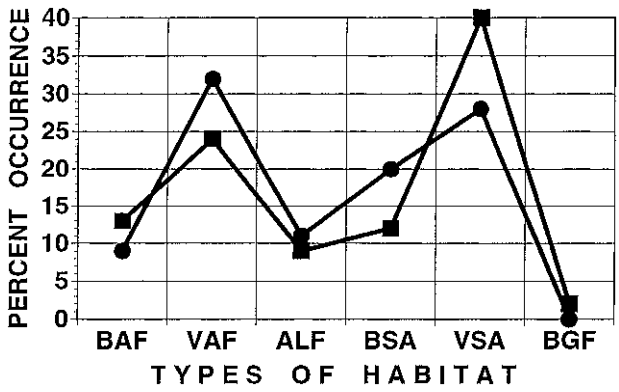

Fig. 6: Percentage of solifuges (*Eremobates marathoni*) occurring in various habitats (BAF=bare adobe flats; VAF=vegetated adobe flats; ALF=alluvial fans; BSA=bare sandy arroyos; VSA=vegetated sandy arroyos; BGF=bare gravel flats). Square symbols represent adult males; circles represent data for females.

Eremobates marathoni is a nocturnal species that was most active during April through June. Males were active earlier in the season as compared with females. This is in agreement with previous studies on seasonal activity patterns in other species of solifuges from New Mexico and Nevada (Muma, 1963, 1974). However, Punzo (1997) found that females of *E. palpisetulosus*, which occurred sympatrically with *E. marathoni* in Trans Pecos Texas, were active earlier in the season than males. Most of the mating activity of *E. marathoni* occurred in June and July and gravid females were first observed on 16 June. No gravid females were collected after 24 July. Thus, females were depositing eggs over a five-week period at this location. Nymphal instars were rarely encountered at the surface and may spend a great deal of time within burrows or under rocks (pers. obs.).

My numerous observations of adults at the surface indicated that males and females showed a high degree of locomotor activity in searching for prey. They exhibited rapid and apparently random running patterns with frequent changes in direction (Punzo, 1994b,c). This type of random cursorial searching behaviour has been reported for other solifuge species (Bolwig, 1952; Muma, 1967; Wharton, 1987; Punzo, 1995b, 1997), with the exception of termitophilous solifuges which tend to be more sedentary in nature (Cloudsley-Thompson, 1977).

The specific behavioural components (acts) of mating behaviour have been described for only a few species of solifuges (Junqua, 1966). Males of *Galeodes caspius* (Galeodidae) from Baku initiate courtship by using their palps to stroke the body of the female, which causes her to become lethargic (Heymons, 1902). Similar stroking behaviour has been described for *G. sulfuripes* (Amitai *et al.*, 1962) and *G. granti* (Cloudsley-Thompson, 1967), and appears to be characteristic of galeodids and solpugids (Heymons, 1902; Junqua, 1962, 1966). This initial stroking behaviour is not exhibited by males of eremobatid solifuges, including *Eremobates durangonus* and

E. nodularis (Muma, 1966d), *E. palpisetulosus* (Punzo, 1997), and *E. marathoni* (present study). There are three stages in the mating behaviour of eremobatid solifuges (Muma, 1966d). During the initial attack phase, both sexes assume agonistic postures (opening of the chelicerae, elevation of the palps and first pair of legs, and a rocking motion of the body). This is followed by a rapid forward movement of the male resulting in contact with the female. Upon contact with the male, the female usually acquiesces and assumes some type of submissive posture. *Eremobates marathoni* females relax their legs, lower their body to the ground, close the chelicerae and in some cases bend the peltidia backward over the abdomen. In some instances, instead of acquiescing, the female would attack the male. This can culminate in the death of the male. I have never observed female mortality resulting from a male attack. In fact, preliminary observations over several years suggest that females are more aggressive than males. I base this conclusion on several lines of evidence. Females exhibit agonistic displays toward conspecifics for longer periods of time, take longer to habituate to novel stimuli in the laboratory, exhibit longer bouts of locomotor and exploratory activity, and demonstrate a higher degree of cannibalism than do males. In addition, males generally have shorter lifespans and do not feed as much as females (Cloudsley-Thompson, 1961b; Junqua, 1958; Muma, 1974). This sexual dimorphism in agonistic behaviour warrants further investigation and quantification.

The attack phase is followed by a contact phase (Muma, 1966d) in which the male grasps the female using his chelicerae. The chelicerae are gradually moved towards the genital abdominal segment of the female. The female is then lifted by the male and placed on her back. At this point, the male will sometimes stroke the peltidia of the female using his palps and first pair of legs. Such stroking behaviour has been reported for *E. nodularis* (Muma, 1966d), but was not observed for *E. marathoni* in the present study. A droplet of seminal fluid is deposited from the male genital opening directly on to the genital opening of the female. Using his chelicerae, the male then begins to chew the opercular area of the female, mounts her, and inserts sperm into her genital opening using the fixed fingers of his chelicerae. The two sexes then separate (release phase) and usually move quickly away from one another. In some instances, the female will attack the male. In a study of mating behaviour in *E. palpisetulosus* (Punzo, 1997), 28% of the males were seized and killed by the female during the release phase. In the present study, 19% of the males were killed by females.

In the laboratory, most females deposited their eggs in burrows constructed in the soil at the bottom of the holding containers. Some females simply deposited their eggs on the surface of the substrate. In the field, egg masses were deposited in burrows and under rocks. These solifuges frequently constructed burrows which an individual may occupy for a period of three days to several weeks (pers. obs.). There were several types of burrows associated with these solifuges. Some females ($n=21$ out of a total of 74 burrows; 28%) constructed a circular, vertical tube-shaped burrow, 6–13 cm in depth; these were usually found in adobe substrates. Sandy substrates were associated with another type of tube-shaped burrow. These burrows ($n=46$; 62%) extended to a depth of 2–3 cm and then exhibited a right-angle bend and extended for a length of 7–13 cm (parallel to the ground surface). Only female solifuges were found in this type of burrow as well. These tube-shaped burrows were deeper and may provide more adequate protection for eggs and early-instar nymphs. None of these burrow entrances was plugged, even in the hottest months. Male solifuges utilised a simple, bowl-shaped depression (usually found under a rock or decaying vegetation), 2–5 cm in depth ($n=7$; 9%). These represented more temporary types of shelter and were frequently abandoned within 48 h and re-occupied by other individuals (determined by slight differences in size or body coloration patterns). I did not find any solifuges associated with abandoned snake or rodent burrows, or occupied tarantula burrows at this study site. These types of burrows were usually re-occupied by other rodents and snakes, or scorpions, which would most likely react to a solifuge as a potential food source or in some other agonistic way. In one case, I found a solifuge and toad (*Bufo punctatus*) simultaneously occupying a deep, tube-shaped burrow (45 cm in depth) with no apparent conflict. The type of faecal pellets found at the bottom of this burrow indicated that at one time it had been occupied by rodents and snakes.

All of these types of burrows not only afford some degree of protection from potential predators, but they also provide microhabitats which can help an individual to survive under the harsh conditions associated with desert habitats. This has been verified for other species of solifuges (Cloudsley-Thompson, 1961a, 1977; Muma, 1966b,c, 1980; Wharton, 1987). The humidity within the burrow is significantly higher than that found at the surface, resulting in more favourable conditions for embryological development and postembryonic survival. Burrows also provide shelter for individuals during the moulting cycle, a time when they are most vulnerable to predation.

With respect to habitat preference, *E. marathoni* adults seemed to prefer arroyos characterised by a sandy substrate, open areas, and scattered clumps of vegetation, or adobe flats which have a harder, more compact surface with scattered vegetation. This coincides with observations that I have made on the feeding behaviour of these solifuges. I have often observed adults capturing a prey item in an open area (no vegetation). Shortly after capture, the solifuges frequently carried their prey to a location under a creosote bush, mesquite, lechuguilla plant, etc. where ingestion took place. These solifuges were least associated with alluvial fans, adobe flats, and sandy arroyos that contained very little if any vegetation. Scattered clumps of vegetation probably afforded cover and protection from potential predators which included birds (such as night hawks and roadrunners), mammals (ring-tail cats, badgers, etc.), and arthropods (scorpions, and other solifuges). Their preference for a

sandy substrate is not surprising, since solifuges frequently construct burrows (Muma, 1966c; Gore & Cushing, 1980) and are well adapted for locating prey beneath the surface of sand (Brownell & Farley, 1974; Cloudsley-Thompson, 1977; Punzo, 1994b, 1995b).

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On the widespread species *Zelotes schmitzi* (Araneae: Gnaphosidae)

Norman I. Platnick
Department of Entomology,
American Museum of Natural History,
Central Park West at 79th Street,
New York, NY 10024, USA

and

John A. Murphy
323 Hanworth Road,
Hampton, Middlesex, TW12 3EJ

Summary

Zelotes schmitzi (Kulczyński), originally described on the basis of a single female from Madeira, is newly recorded from Spain, the Canary Islands, and California; the male is described for the first time.

Introduction

When the American spiders of the genus *Zelotes* were revised by Platnick & Shadab (1983), a few species were found that did not seem to have any close relatives in the New World and were judged instead to be introductions from the Mediterranean region. Among these was *Zelotes nilicola* (O.P.-Cambridge), a species found from the Canary Islands to Egypt and also in California and Arizona. At the time, a single female was also found of a species that seemed closely related to *Z. nilicola*. A search for specimens conspecific with this female, also from California, turned up only a single female (from Spain). A search of the literature turned up only one likely candidate for an existing name for this species: *Zelotes schmitzi* (Kulczyński), originally described on the basis of a single female from Madeira.

Unfortunately, none of the modern workers who have dealt with the taxa that Kulczyński (1899) described from Madeira seem ever to have succeeded in locating the type material of any of those taxa, and we had no greater luck in attempting to find the holotype of *Z. schmitzi*. Over the intervening years, we have searched new collections for additional material of this species from Madeira or nearby islands, to no avail. In a recent collection from the Canary Islands made by M. Askins, however, we finally found a female that matches the two previously known specimens, accords well with Kulczyński's description of *Z. schmitzi*, and was taken with a male that seems closely related to that of *Z. nilicola*. We therefore present here the first reconsideration of *Z. schmitzi* since its original description nearly a century ago.

We thank M. Askins for making these specimens available for study, C. Griswold of the California Academy of Sciences (CAS) for lending material, and M. U. Shadab of the American Museum of Natural History (AMNH) for help with illustrations. The format of the description follows that of Platnick & Shadab (1983). All measurements are in mm.

Zelotes schmitzi (Kulczyński) (Figs. 1–4)

Prosthesima schmitzii Kulczyński, 1899: 359, pl. 6, fig. 32 (female holotype from Madeira, no specific locality, depository unknown).
Zelotes schmitzi: Reimoser, 1919: 204. Bonnet, 1959: 4949.
Zelotes schmitzii: Roewer, 1955: 458.

Diagnosis: The only species likely to be confused with this taxon is *Z. nilicola*, which has a similarly coiled embolar tip and a similarly shaped epigynum (see Platnick & Shadab, 1983: figs. 263–268). Males of *Z. schmitzi* can be distinguished by the basally thicker embolus (Fig. 1) and distally wider retrolateral tibial apophysis (Fig. 2), females by the more rectangular epigynal septum (Fig. 3) and distally recurved anterior epigynal ducts (Fig. 4).

Male: Total length 2.57. Carapace 1.10 long, 0.76 wide. Femur II 0.59 long. Eye sizes and interdistances: AME 0.02, ALE 0.04, PME 0.04, PLE 0.04; AME-AME 0.03, AME-ALE 0.01, PME-PME 0.02, PME-PLE 0.02, ALE-PLE 0.05; MOQ length 0.12, front width 0.07, back width 0.11. Palp with intercalary sclerite v-shaped, embolus long, distally coiled, with translucent portion broadest at base (Fig. 1); retrolateral tibial apophysis relatively short, wide (Fig. 2). Leg spination: femora: I, II p0-0-0; IV p0-0-0, r0-0-0; metatarsi: I, II v0-0-0; III v2-1p-0.

Female (from Grand Canary): Total length 3.10. Carapace 1.36 long, 0.95 wide. Femur II 0.69 long. Eye sizes and interdistances: AME 0.02, ALE 0.04, PME 0.04, PLE 0.04; AME-AME 0.06, AME-ALE 0.01,