

Dispersion, temporal patterns of activity, and the phenology of feeding and mating behaviour in *Eremobates palpisetulosus* Fichter (Solifugae, Eremobatidae)

Fred Punzo

Department of Biology,
University of Tampa,
Tampa, Florida 33606, USA

Summary

Field studies were conducted on dispersion, temporal and seasonal patterns of locomotor activity, diet composition, and the phenology of feeding and mating behaviour in the solifuge *Eremobates palpisetulosus* Fichter. Populations from three different study sites exhibited a clumped pattern as described by the standardised Morisita index of dispersion ($I_p=0.579-0.647$). No significant difference in seasonal and diel surface activity was found between males and females. These solifuges were most active from April through June. No surface activity was recorded during November to February inclusive. The peak period for mating occurred in May and June. An analysis of diel activity patterns showed that these animals are most active between 1900 and 0100h (CST). Activity declined abruptly after 0400h. This species is clearly nocturnal. The diet of *E. palpisetulosus* consisted primarily of orthopteran (21.7%) and coleopteran (15.8%) insects, as well as arachnids (7.9%). Undetermined prey taxa comprised 42.4% of the total prey sample. Seasonal patterns in feeding indicated that Orthoptera represent the major prey taxon during May, June and July. Arachnids were the least numerous prey item throughout the study period. The mating behaviour of *E. palpisetulosus* is also discussed.

Introduction

Although solifuges represent an important component of the arachnid fauna associated with deserts, few detailed studies exist concerning life history parameters, behavioural ecology or population characteristics for any particular species (Muma, 1951, 1980; Wharton, 1987; Punzo, 1993a, 1995a). Over the past several years, I have been studying parameters associated with diet (Punzo, 1993a, 1994a,b), optimal foraging (Punzo, 1994a, 1995b), activity patterns (Punzo, 1994b) and neurobiology (Punzo, 1993b, 1994c) of several species of eremobatid solifuges. In this study, I report on the distribution, temporal and seasonal patterns of activity, and phenology of feeding and mating in *Eremobates palpisetulosus* Fichter.

Description of study site

Studies were conducted on solifuges located within a 5 km radius of Lajitas (Brewster County, Texas; 32°24'N, 103°11'W; elevation 900–925 m), located within the northern region of the Chihuahuan Desert in Trans Pecos Texas. A detailed description of the geology and vegetational zones of this area is given by Tinkam (1948). The soils of this region are a mixture of sand, gravel and adobe and they support a predominantly sotol-lechuguilla plant community. The dominant vegetation of the desert floodplain (shrub desert) includes

lechuguilla (*Agave lechuguilla*), sotol (*Dasyliirion leiophyllum*), tarbrush (*Flourensia cernua*), black brush (*Acacia rigidula*), creosote (*Larrea divaricata*), catclaw (*Acacia roemeriana*), mesquite (*Prosopis glandulosa*), ocotillo (*Fouquieria splendens*), saltbush (*Atriplex canescens*), candelilla (*Euphorbia antisyphilitica*), false agave (*Hechtia texensis*), and scattered clumps of chino grass (*Bouteloua brevifolia*). The western edge of the area is bounded by the Rio Grande River, a permanent source of water. Owing to the increased moisture of the soil, the river banks are characterised by denser vegetation, and support a wider variety of plant species including the common reed (*Phragmites communis*), button bush (*Cephalanthus occidentalis*), yew-leaf willow (*Salix taxifolia*), and black willow (*S. nigra*).

The solifuge *Eremobates palpisetulosus* occurs throughout this area, where it either excavates its own burrow, or occupies burrows abandoned by rodents or theraphosid spiders (pers. obs). Less frequently, it will seek shelter in rock crevices. Although it prefers sandy substrates with scattered rocks and clumps of vegetation (Punzo, 1994d), it can also be found on gravel and boulder-strewn slopes and along the river banks. In this area, total body length ranges from 18–26 mm for adult females, and 16–22 mm for adult males. It is a univoltine species (pers. obs.) as are all of the Solifugae studied to date (Muma, 1951, 1966; Cloudsley-Thompson, 1961, 1977; Wharton, 1987).

Methods

I conducted studies to determine the distributional pattern of these solifuges (dispersion: random, uniform, or clumped) during March–September 1994. I chose two sites (sites A and B) on the floodplain and another adjacent to the river (site C). At each site, I used wooden stakes to mark ten square 0.25 ha plots chosen at random from a topographical grid map of the area (U.S. Geographical Survey). Within each plot, animals were sampled using pitfall traps (0.5 l plastic cups) over a 24 h period on ten days per month, at 3 h intervals beginning at 0400 Central Standard Time (CST). I used a cross-shaped grid (10 × 10 m) as described by Bradley (1989) which consisted of 19 traps with the centre trap shared between the lines; a distance of 0.5 m separated each trap within the grid. I recorded the following data for each adult solifuge collected: sex; total body length; time, date and location of capture; and ambient air temperature.

Only data on solifuges collected in pitfall traps were used in the analysis of dispersion. From the number of solifuges (nymphs and adults) found at each plot (10 plots/site), I used the standardised Morisita index (I_p) (derived from Morisita's index of dispersion, I_d) (Morisita, 1962), to determine their dispersion pattern at each site:

$$I_d = n[\sum x^2 - \sum X / (\sum x)^2 - \sum x]$$

where I_d = Morisita's index of dispersion, n = sample size, and $\sum x$ = sum of plot counts. Then the Chi Square (χ^2) test statistic can be used to test for randomness:

$$\chi^2 = I_d(\Sigma x - 1) + n - \Sigma x$$

Once this is done, two significance points ($\chi^2_{0.975}$ and $\chi^2_{0.025}$) for the Morisita index are calculated from the following expressions:

$$M_u = \chi^2_{0.975} - n + \Sigma x / (\Sigma x) - 1$$

$$M_c = \chi^2_{0.025} - n + \Sigma x / (\Sigma x) - 1$$

where M_u =uniform index, and M_c =clumped index. These parameters can then be used to improve Morisita's index (I_d) by expressing it on an absolute scale known as the standardised Morisita index (I_p) (Krebs, 1989):

$$I_p = 0.5 + 0.5 [(I_d - M_c) / (n - M_c)]$$

If $I_p=0$ the population sample has a random distribution (dispersion) pattern; if $I_p<0$ (uniform pattern); if $I_p>0$ (clumped pattern).

Using the same sampling plots and procedure and the data on date of capture, I determined the seasonal surface activity for adult males ($n=425$) and females ($n=397$). For these analyses, I used the data on animals collected from pitfall traps as well as those solifuges observed on the surface but not captured. I expressed the data as the percent surface activity (locomotor activity) for males and females on a monthly basis for a 12-month period.

I also used the data on time of capture to assess temporal (diel) patterns of locomotor activity in this species. I determined the percentage of adult males and females that were active over a 24 h period during April through July 1994, based on previous data which showed that peak periods of surface activity occur during these months. The data collected showed that there was no significant difference between males and

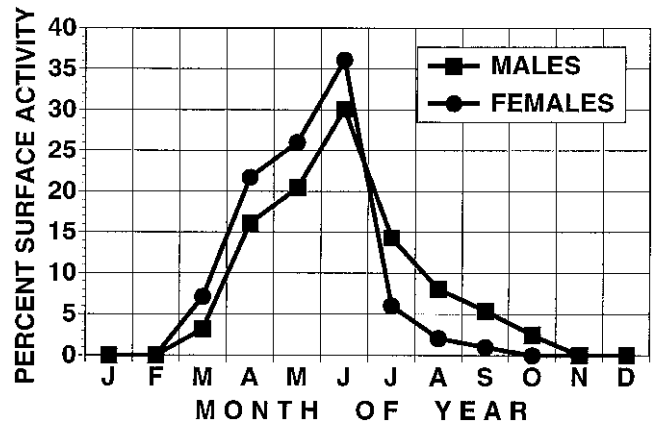


Fig. 1: Seasonal patterns of locomotor activity at the ground surface for adult males ($n=425$) and females ($n=397$) of *Eremobates palpisetulosus* over the course of one year. Data are expressed as percentage of total surface activity (see text for details).

females with respect to this parameter. Whenever an adult was observed actively moving over the surface, it was collected and the time of capture (CST) recorded. Data were collected for a total of 356 solifuges and the results expressed as the percentage of animals active at the surface at various times of the day (3 h intervals; i.e. 0400–0659, etc.). Data were tested for significance using the log frequency analysis procedure discussed by Sibley *et al.* (1990).

Mating activity was also monitored at site A during the course of this study. From March through September, I kept a record of the number of times a male and female were observed in courtship/mating activities. The results were expressed as percent mating activity for a given month based on the total number of courtship/mating bouts observed ($n=78$). Based on previous descriptions of mating behaviour in Solifugae (Heymons, 1902; Cloudsley-Thompson, 1961), I considered courtship/mating activities to be present if any one of the following behaviours was exhibited: (a) the male touching or stroking the body of the female with his front legs or pedipalps; or (b) the male grasping the female with his chelicerae while she tilts her body away from the ground.

I also studied the feeding phenology of this species using observations made at study sites A, B and C. A helmet-mounted light provided with a red filter (Punzo, 1993a) was used to locate and observe solifuges as they moved across the surface of the ground during May through August 1994. A total of 516 animals were observed, 84 of which (16.3%) had a prey item in their chelicerae. The prey item from each solifuge was placed in a vial containing 70% ethanol for subsequent identification. These data were used to determine seasonal fluctuations in diet for this species at this study area.

Results

Solifuges from the three study sites all exhibited a clumped pattern of dispersion according to Morisita's standardised index (all values for $I_p>0$, Table 1). Individuals from study site C (adjacent to the river) exhibited the most strongly clumped pattern.

Plot	Site A	Site B	Site C
1	4	2	1
2	0	7	0
3	20	0	1
4	5	34	2
5	2	5	25
6	30	0	3
7	3	12	1
8	4	35	0
9	0	0	32
10	28	4	4
M_u	1.105	1.102	1.147
M_c	0.934	0.936	0.907
I_d	2.361	2.672	3.583
I_p	0.579	0.596	0.647

Table 1: Total numbers of solifuges (*Eremobates palpisetulosus*, nymphs and adults) found at each plot (plots 1–10) for three study sites (A, B and C) during March–September 1994. Study sites A and B were located on the desert floodplain; site C was adjacent to a river. Only those solifuges captured in pitfall traps are included in these data. M_u =uniform index; M_c =clumped index; I_d =Morisita's index of dispersion; I_p =standardised Morisita index (terminology after Krebs, 1989; see text for details).

The phenology of locomotor activity patterns is shown in Fig. 1. These solifuges were most active on the surface of the ground between April (16.1–21.7%), May (20.4–26%), and June (30.1–36%). There was no difference in the seasonal activity patterns between the three study sites. Activity levels in July (6.0–14.3%) decreased significantly ($G=12.7$, $p<0.01$, Sokal & Rohlf, 1981) from those recorded in June. In March, female activity (7.1%) was higher than that of males (3.2%, $p<0.05$), indicating that females begin to move around and search for food earlier than males. Males are more active than females from July to September. No solifuges were observed at the ground surface during January, February, November and December at these sites.

These arachnids are clearly nocturnal and are most active between 1900 to 0100h (CST) (Fig. 2). Log frequency analysis (Sibley *et al.*, 1990) indicated that locomotor activity increases significantly during these time periods ($F=14.9$, $p<0.01$). Percent activity increases from a level of 2.3% for the 1600–1859h interval to 34.6% over the next three hours (1900–2159). I have never observed adults or nymphs that were active on the ground surface during daylight hours. The only individuals that I have encountered during the day were either located on the outside (shaded) or inside walls of a building, or clinging to the sides of shaded rocks, and then only infrequently.

Mating occurs with the greatest frequency in May (39.7%) and June (48.7%), and then drops off sharply during July (11.6%) (Fig. 3). No mating behaviour was observed between individuals of this species during any other month. Based on 78 observations of mating bouts, I noted that the male usually initiated courtship by slowly approaching the female and then stopping within a distance of 1.5–2.5 cm from the anterior end of her body. Males approached the female using either a head-to-head orientation (57 out of 78, 73%), or a lateral orientation (27%). Most females (63%) held their ground during a male's approach while some (37%) displayed an agonistic posture by opening their chelicerae. Some

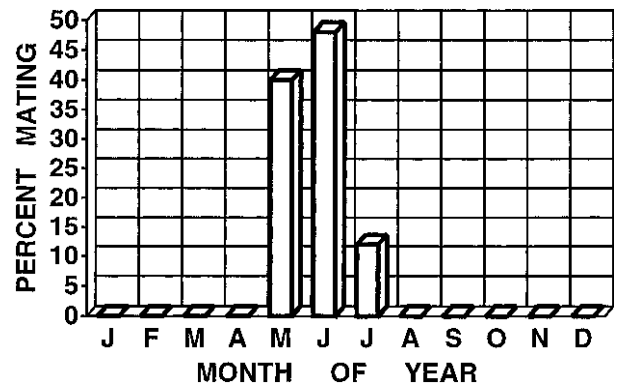


Fig. 3: Seasonal pattern of mating activity in *Eremobates palpisetulosus*. Values represent the percentage of mating bouts observed on a monthly basis over the course of one year ($n=78$).

females (37%) moved backwards, away from the male, for a distance of 3–6 cm. This was followed by a rapid forward movement by the male in which he grasped the female (usually at the posterior end of her opisthosoma). When held in this way, the female usually responded by relaxing her legs, closing the chelicerae and folding the palps against the body. The male used his chelicerae to open the genital orifice of the female and introduced droplets of seminal fluid into this structure. He then released her and usually escaped (65%) by retreating in a backward motion and then moving rapidly away from the female. In other cases the male was either seized by the female and killed (28%), or he escaped by autotomising a leg (7%).

Eremobates palpisetulosus feeds on a wide variety of prey (Fig. 4). No significant difference was found between the diets of males and females ($p<0.5$). Identifiable prey items including insects and arachnids. Orthopteran insects comprised 21.7%, followed by Coleoptera (15.8%) and Hemiptera (7.3%). Other arachnids (scorpions and spiders) together comprised 7.9% of identifiable prey. Undetermined prey constituted 42.4% of the total prey sample.

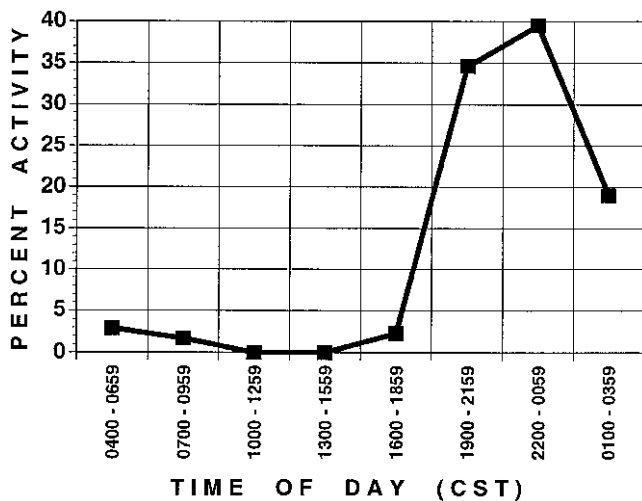


Fig. 2: Temporal (diel) pattern of locomotor activity in *Eremobates palpisetulosus* ($n=356$) expressed as the percentage of adults active at various 3-hourly intervals. CST=Central Standard Time.

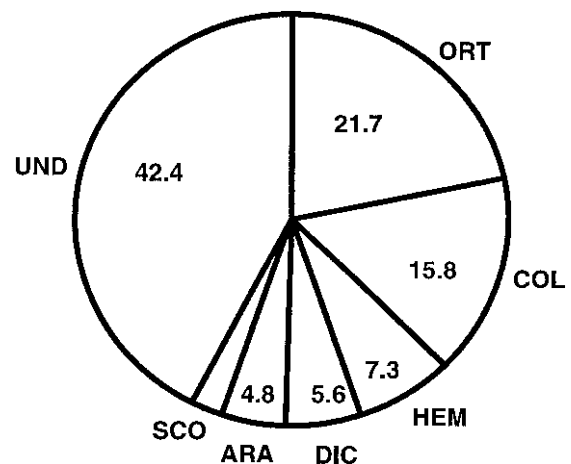


Fig. 4: Diet composition for *Eremobates palpisetulosus*. Values represent the frequency of occurrence (percent) for each prey taxon based on an analysis of prey items found in the chelicerae ($n=84$). ORT (Orthoptera); COL (Coleoptera); HEM (Hemiptera); DIC (Dictyoptera); ARA (Araneae); SCO (Scorpions); UND (Undetermined).

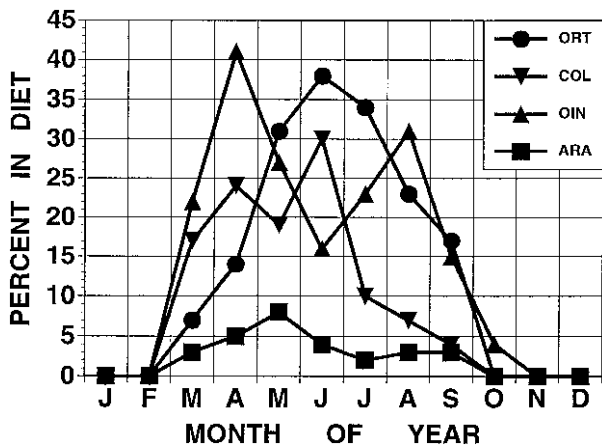


Fig. 5. Percent composition of prey taxa in the diet of *Eremobates palpisetulosus* on a monthly basis over the course of one year. ORT (Orthoptera); COL (Coleoptera); ARA (Arachnida — spiders and scorpions); OIN (other insects, including Dictyoptera, Hemiptera, Homoptera, Lepidoptera). Undetermined prey items not shown.

The phenology of the major prey taxa is shown in Fig. 5. Orthoptera (grasshoppers, locusts and crickets) represent the major prey taxon for May (31%), June (38%) and July (34%). Coleoptera (beetles) also represent a significant portion of the diet during March through June (17–30%). Other insects (OIN) which include cockroaches (Dictyoptera), bugs (Hemiptera), adult moths and caterpillars (Lepidoptera), and cicadas and planthoppers (Homoptera) were the most frequent prey items earlier in the growth season (March and April). Arachnids were the least numerous prey item throughout the year. No feeding was observed for the months of November to February inclusive, since *E. palpisetulosus* is not active at this location during those months.

Discussion

Eremobates palpisetulosus is a nocturnal species that is most active during April through June in this region of the Chihuahuan Desert. The rainy season usually starts with sporadic precipitation at the end of May, and peaks in July. These solifuges are active during one of the driest months (May) as well as in those months of highest rainfall (June and July). In this area, the nymphs of many species of Orthoptera are actively feeding during May (Tinkam, 1948). Thus, it is not surprising that this insect group represents a high proportion of the diet of *E. palpisetulosus* during this month. Females exhibit a higher level of locomotor and feeding activity earlier in the season (March). This may result in faster growth rates and the accumulation of nutrient reserves necessary for egg production later in the summer. On the other hand, Muma (1963, 1974) reported the seasonal appearance of males before females in other species of Solifugae from Nevada and New Mexico.

My observations indicate that males and females of *E. palpisetulosus* are extremely active and travel over considerable distances when above-ground. This appears to be a common behavioural trait in this group

(Cloudsley-Thompson, 1961; Lawrence, 1965; Muma, 1966; Wharton, 1987; Punzo, 1994b,c) and may be due in part to the widely dispersed pattern of prey characteristic of desert regions (Cloudsley-Thompson, 1968). This cursorial predator moves quickly over the surface, repeatedly and rapidly tapping the ground with its pedipalps. It typically moves in a rapid forward motion for 15–25 cm before suddenly changing direction. After this zig-zag movement is repeated for 0.5–2 min, the solifuge stays still for a variable period of time before starting the sequence over again. What causes these animals to stop locomotor activity at regular intervals? It may be due to fatigue resulting from the energetic costs of rapid movement. Another possible explanation may involve cues used to detect prey. It has been suggested that Solifugae are capable of detecting vibrations resulting from the below-ground movements of potential prey (Muma, 1966). Thus, a solifuge may stop locomotor activity when it senses such vibrations. Solifugae may also use chemoreceptors (malleoli) to detect kairomones emanating from potential prey beneath the surface (Brownell & Farley, 1974; Wharton, 1987). In several instances ($n=8$) I have observed solifuges locate prey beneath the surface. The predator would typically stop, tap the ground with the pedipalps and front legs, and then use its chelicerae to dig and grasp the prey item (usually coleopteran larvae or blattid nymphs).

These solifuges are generalist predators that feed on a wide variety of insects and arachnids. This is in general agreement with previous studies on the feeding habits of Solifugae. Although their generalised insectivorous habits have been mentioned repeatedly in the literature (Turner, 1916; Muma, 1966; Cloudsley-Thompson, 1977; Wharton, 1987), few studies have documented the specific prey items that comprise the diets of these arachnids. Punzo (1993a) reported a similar dietary profile for a population of *E. palpisetulosus* located 24 km to the south, near Terlingua, TX. In the Terlingua population, Lepidoptera (13.1%) and arachnids (15.2%) comprised a significantly higher proportion of the diet than in the present study (<2% and 7.9%, respectively). I found no evidence of cannibalism or predation on vertebrates of any kind in the Lajitas population. However, geckonid lizards comprised 2.2% of the diet at Terlingua. The nocturnal gecko *Coleonyx brevis* is common at both sites. *Eremobates mormonus*, which is sympatric with *E. palpisetulosus* in this area, prefers more soft-bodied arthropod prey such as blattid and gryllid nymphs as well as spiders (Punzo, 1994b). Hard-bodied prey such as Coleoptera comprised only 2% of its diet compared with 17–30% for *E. palpisetulosus*.

On several occasions ($n=17$) I observed adult solifuges in the act of capturing prey. In most cases (75.5%), the solifuges remained at the site of capture while ingesting their prey, even if it was located on open ground with little or no vegetative cover. In the remaining cases (24.5%), the solifuges moved from the site of capture to a location under a bush or within a rock crevice before initiating ingestion.

Mating behaviour has been described for only a few species of Solifugae. In *Galeodes caspius* (Galeodidae)

from Baku, the male initiates courtship by stroking the female with his pedipalps, which causes her to become lethargic (Heymons, 1902). This stroking behaviour has also been reported for *G. sulfuripes* (Amitai *et al.*, 1962) and *G. granti* (Cloudsley-Thompson, 1967), and appears to be characteristic of the Galeodidae. This type of stroking behaviour is not seen in eremobatid solifuges. Once the female acquiesces, the male then grasps her with his chelicerae. This occurs in all species of Solifugae for which mating behaviour has been described (Junqua, 1962; Cloudsley-Thompson, 1967, 1977). Galeodid males release a spermatophore and then use their chelicerae to insert it into the genital orifice of the female (Cloudsley-Thompson, 1967). In *E. palpisetulosus*, the male releases a seminal fluid which is then forced through the genital operculum of the female via the chelicerae.

Once sperm has been transferred, the female becomes active and will often attack and kill the male (Heymons, 1902; Cloudsley-Thompson, 1961, 1967, 1977). In the present study, most of the males (72%) completed the mating process without loss of life. However, 28% of the males were seized and killed by the female. Some of the males achieved their escape by autotomising a leg (7%). Leg autotomy is known to be a common anti-predator strategy in spiders and other arachnids (Foelix, 1982) but it has not received much attention in solifuges.

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