

Natural history of the Iberian solifuge *Gluvia dorsalis* (Solifuges: Daesiidae)

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Abstract. In this paper we present a detailed study of the natural history of *Gluvia dorsalis* (Latreille 1817), a representative of the family Daesiidae, the only solifuge species known to occur in southwestern Europe. We studied its distribution, habitat preference, circadian activity, seasonal occurrence, burrowing, predatory and post-mating behavior, prey, fecundity, ontogenesis, and sexual dimorphism. *Gluvia dorsalis* occurs in lowlands across the entire Iberian Peninsula, preferring grassland or similar open-ground habitats with little summer rain. According to pitfall trap data, the species was active on the surface from May until the beginning of November. It is a nocturnal epigeal predator, feeding principally on ants and spiders. However, under laboratory conditions, specimens captured and consumed a variety of arthropods. *G. dorsalis* seems to hide in underground burrows only when molting, overwintering, or laying eggs. Reproduction occurred in early summer, and females usually produced a single egg clutch containing, on average, 84 eggs, and died soon after. Our results indicate that the *G. dorsalis* is a biennial species. There was sexual dimorphism in several morphological structures that might be used for sex matching in juvenile instars.

Keywords: Camel-spider, activity, prey, reproduction, sexual dimorphism

Solifuges are one of the most important predators of arid environments (e.g., Polis & McCormick 1986; Cloudsley-Thompson 1977; Punzo 1997). Despite being locally very abundant, their natural history remains largely enigmatic, as researchers have investigated only a very few species so far. Out of 12 families and slightly more than 1,000 solifuge species currently recognized (Harvey 2003), scientists have performed a thorough natural history studies on only eight species in three families: four eremobatid (e.g., Muma 1966a, 1967; Punzo 1997, 1998a); three galeodid (Heymons 1902; Cloudsley-Thompson 1961a, b; Junqua 1966; Hrušková-Martišová et al. 2007); and one solpugid species (Wharton 1987). Biologists have studied only particular aspects of behavior, such as prey and predatory behavior (e.g., Dean & Milton 1991), reproductive behavior (Perreti & Willemart 2007), or burrowing behavior (Gore & Cushing 1980). Yet, even these data are largely fragmented. With the exception of three species (Junqua 1966; Muma 1966a; Punzo 1998a), the postembryonic development or life cycle of solifuges is virtually unknown. Only Punzo (1998a) documents the number of instars, duration of intermolt intervals, and lifespan in a single species.

Solifuges are restricted to arid regions of the world with the exception of Australia, where they do not occur. In Europe, 18 species from 4 families have been found so far (Harvey 2003). The majority of the species occur in the eastern Mediterranean, but a single species, *Gluvia dorsalis* (Latreille 1817) (Daesiidae), is endemic to the Iberian Peninsula (Fig. 1). This species was originally only described from Spain, but later collectors found it in different places across the Iberian Peninsula (Pablos 1967; de Matos 1978; Schenker 1980; Grosso-Silva 1998).

Our aim in this study is to provide a detailed natural history account of *G. dorsalis*, found to be locally quite abundant,

particularly in southern Portugal. We know of no other natural history studies of any species of the Daesiidae. We performed field and laboratory investigations in order to predict its distribution, to reveal seasonal and circadian activity, habitat preference, burrowing, foraging and post-mating behavior, fecundity, and ontogenetic development. Further, our goal has been to identify morphological characters correlated with sexual dimorphism in order to find measures that could be used to identify the sex of juvenile specimens.

METHODS

Field collection.—From February to November we monitored pitfall traps (see Cardoso et al. 2004, 2007 for details) in 11 different sites across Portugal over three different years: in 2001 in the northern part (Douro Internacional Nature Park), in 2002 in the central part (Serras de Aire e Candeeiros Nature Park), and in 2003 in the southern part of Portugal (Vale do Gadiana Nature Park). Solifuges occurred in three different habitat types: pseudosteppe or pasture with solitary trees, scrubland, and forest (Table 1). We emptied traps in two-week intervals. Further, we collected solifuges by hand in a garden in Valverde da Mitra (near Évora), southern Portugal. We preserved all captured specimens in 70% ethanol and deposited them in the collection of arachnids at the Department of Botany and Zoology, Masaryk University, Brno.

Altogether, we collected 702 individuals of *G. dorsalis* in the field over the research period, with most of them (78%) coming from southern Portugal, followed by 8% from central, and 14% from northern Portugal. We classified each collected individual to a developmental stage (juvenile or adult) and sex (only adults). Additionally, for each individual, we measured the following four morphological characters: length and the width of propeltidium, number of malleoli (on the ventral side

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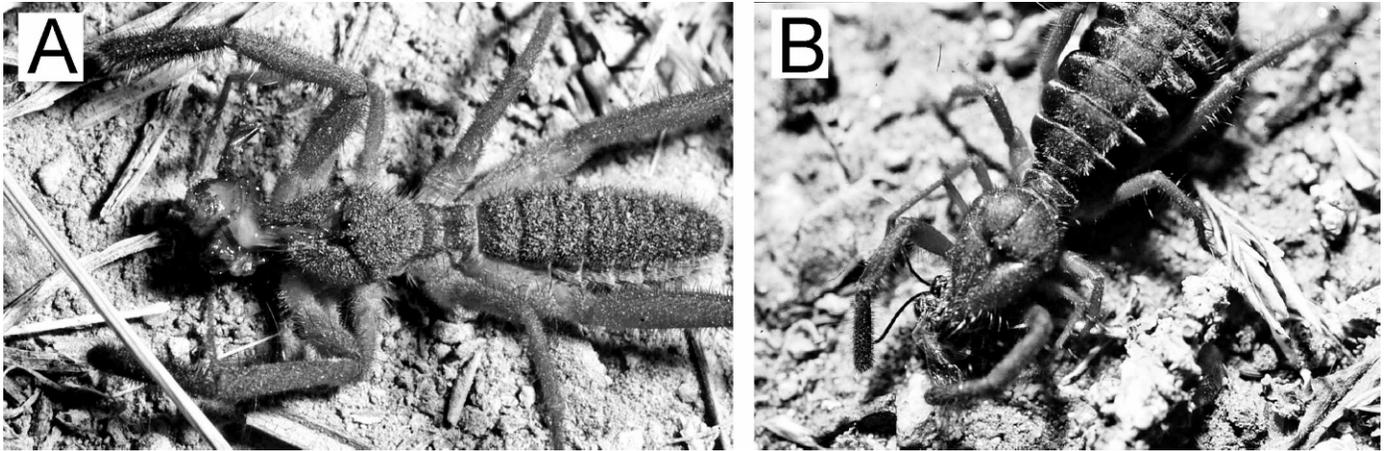


Figure 1.—Adult male (A) and adult female (B) of *Gluvia dorsalis* consuming their prey.

of coxa, trochanter, and femur of the fourth leg), and width of the fourth malleolus at the distal end. These characters were used to distinguish probable instars, to estimate developmental trajectory, and to find sexually dimorphic characters. We chose these characters because they were found to change during development, and their size is constant within intermolt intervals (Junqua 1966).

Potential distribution.—There are a large number of techniques proposed for modeling the predicted potential distribution of species based on presence data for a restricted number of points in space and environmental data for an entire region. In general, they are based on the principle that species are restricted by the environmental conditions they can survive. If we know a number of sites where a species is present, it is possible to create a “suitable climatic envelope” for the species. This climatic envelope is then translated to space through geographic information systems, making it possible to obtain spatial suitable maps for the species. It should be noted, however, that such maps usually only reflect the potential distribution of species, not their true distribution, which may be smaller. This is due to historical (e.g., local extinction, inability to disperse to many regions) or biological (e.g., competition from ecologically similar species) factors. Such factors may limit the effective distribution of species in areas that should be environmentally adequate for their populations. We used the Maxent method (Phillips et al. 2006; Phillips & Dudik 2008) because it uses presence-only data, and because it is considered the most accurate method available (Hernandez et al. 2006). The map of distribution is based on González-Moliné et al. (2008) and unpublished data

from the authors (total of 254 records). One-fifth of the records were randomly chosen for a test dataset, not used in the training of the algorithm. The spatial variables used in the modeling were eight bioclimatic variables available from the Worldclim database (Hijmans et al. 2005): annual precipitation, precipitation of the driest and wettest months, precipitation seasonality (coefficient of variation of monthly values), average annual temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, and temperature seasonality (standard deviation of monthly values). Additionally, we used a digital elevation model. All variables had a resolution of one square kilometer.

Field observations.—We investigated circadian activity in June 2005 in Valverde da Mitra, Portugal, for 9 days by censusing active solifuges for 20 min/h from 05:00 to 03:00 h in four 100 m² areas. We observed burrowing and prey hunting behaviors in July and September 2006 at the same site.

We obtained data on potential prey by censusing representatives of invertebrate orders occurring on the ground during the major activity period (20.00–24.00 h) on 3 days in June in two 100 m² areas. Additionally, we observed natural prey by witnessing prey capture, inspecting the prey, and identifying its remnants to order. Only 15 individuals of 196 inspected were found to have prey in their chelicerae.

Laboratory observations.—To determine diet breadth, we brought 62 individuals (20 males, 20 females, 22 juveniles) into the laboratory and put them in individual dishes (8 cm diameter, 4 cm tall) with a thin layer of sand substrate and a lightly moistened piece of gauze. We offered solifuges various arthropods (Table 2) found in the study site. The prey was

Table 1.—Overview of 11 study sites in three nature parks in Portugal according to their habitat classification.

Habitat type	Nature park		
	Douro Internacional	Serras de Aire e Candeeiros	Vale do Guadiana
Pseudosteppe or pasture	Vila Chã da Braciosa	–	Algodôr Braciais
Scrubland	Picote	Vale Garcia	Corredoura Ribeira de Limas
Forest	Fonte d’Aldeia	–	Cerro das Antenas, São Domingos, Perímetro Florestal de Mértola

Table 2.—Attack and feeding frequencies on a variety of prey offered to large juvenile and adult specimens of *G. dorsalis* in the laboratory. *n* = sample size, Size = length of prey.

Order	Family, Genus, Species	<i>n</i>	Size [mm]	Attack [%]	Feeding [%]
Acari	<i>Trombidium</i> sp.	10	2.5–3.5	20	0
Solifuges	<i>G. dorsalis</i>	38	15–22	100	100
Araneae	Agelenidae, Araneidae, Corinnidae, Filistatidae, Gnaphosidae, Lycosidae, Theridiidae	62	15–22	83.9	83.9
Opiliones	<i>Leiobunum</i> sp.	5	2	100	100
Isopoda	<i>Armadillidium</i> sp. <i>Porcelio</i> sp.	10 10	7–11 10	20 70	0 70
Diplopoda	Julidae	14	16–21	16.7	0
Thysanura	<i>Lepisma</i> sp.	9	7.5–9	77.8	77.8
Ephemeroptera	unidentified	11	7.5–11	27.3	27.3
Dermaptera	<i>Forficula</i> sp.	2	9	100	100
Ensifera	<i>Acheta domestica</i>	52	6–25	100	100
Caelifera	unidentified	45	5	93.3	93.3
Isoptera	<i>Reticulitermes</i> sp.	10	3.5–4	80	80
Heteroptera	<i>Coreus</i> sp., <i>Lygus</i> sp.	35	4–12	88.6	80
Coleoptera	<i>Tenebrio molitor</i> larvae <i>Brachinus crepitans</i> adults other Carabidae	41 12 42	5 9 4.5–16	100 0 47.6	100 0 45.2
Diptera	Muscidae	10	5.5–9	90	90
Hymenoptera	<i>Tapinoma</i> sp. <i>Camponotus</i> sp. <i>Messor</i> sp.	8 10 17	2–3 9–13 6–9	100 20 64.7	100 0 64.7
Lepidoptera	Noctuidae adults	10	8.5–15	60	50

offered to each solifuge in a random order in one-day intervals. For each feeding trial we recorded the size of prey, whether it was attacked and consumed, and noted the predatory behavior. We replaced a prey item that was not attacked within 5 min with another one. Once the prey was consumed, we cleaned the prey remnants from the dishes.

Adult males ($n = 39$) and adult females ($n = 21$) were captured in the field in June and then mated in the laboratory (see Hrušková-Martišová et al. 2010). We paired each female successively with one to four males until it mated. After successful copulation, we placed female solifuges singly in vials (5 cm diameter, 8 cm tall) with a sand layer (2 cm deep) with darkened sides, to lay eggs. The vials were kept in a chamber at 23° C (humidity was not measured) until hatching. The sand substrate was moistened once a week by few drops of water. We checked egg clutches every day during the three following months. We counted and measured (diameter) 10 eggs in each clutch. Larvae were kept in conditions similar to the eggs until molting to the first instar, for which we measured morphological characters similarly to the adults (see above).

Data analysis.—We studied the effect of average monthly precipitation and average monthly temperature on seasonal activity using multiple regression within Generalized Linear Models with Poisson errors (GLM). Data on long-term average monthly temperatures and average monthly precipitation were those for Évora, because most of the material came from Alentejo and this was the nearest place for which meteorological data were available at www.worldclimate.com. We compared the relative composition of potential and actual prey using chi-square tests. We used the Spearman correlation to study the relationship between the size of eggs and the clutch size. For the analyses of sexually dimorphic characters, we used specimens from all study sites, because there was no significant difference in the propeltidium width of adult males

or females between locations (ANOVA, $F < 0.8$, $P > 0.46$). Models of the relationship between selected morphological characters for juveniles, males, and females were compared by means of ANCOVA. We performed all analyses in R (R Development Core Team 2009). We present means and their standard errors in the text. We estimated confidence intervals (CI₉₅) using normal approximation.

RESULTS

Distribution and habitat preference.—*Gluvia dorsalis* specimens have been collected throughout most of the Iberian Peninsula (Fig. 2). This is reflected in its predicted presence in all but the northern and northwestern regions and the highest mountain chains. As previously mentioned, the output of Maxent, or any other technique, are maps of predicted distribution based on current climate suitability and not realized distributions, which can be smaller due to historical or biological reasons. The AUC (area under curve) of the ROC (Receiver Operating Characteristic) plot of the test dataset was 0.815 in a scale of 0 to 1, where 0.5 represents a random prediction, indicating that the maps can be considered as relatively accurate. The variable found to be most strongly driving the species distribution was the precipitation of the driest month.

According to our abundance data collected in Portugal, the species shows a strong preference for open-grass plains with low vegetation, such as pseudosteppes or pastures (55%, $n = 643$) or slopes with low-height shrub cover (39%). Only 6% of the individuals were found in forested (*Quercus* or *Eucalyptus*) areas.

Seasonal and circadian activity.—Solifuges were found to be active from late May until the beginning of November (Fig. 3). Their activity was negatively correlated with monthly average precipitation (GLM, $X^2 = 227$, $df = 1$, $P < 0.0001$,

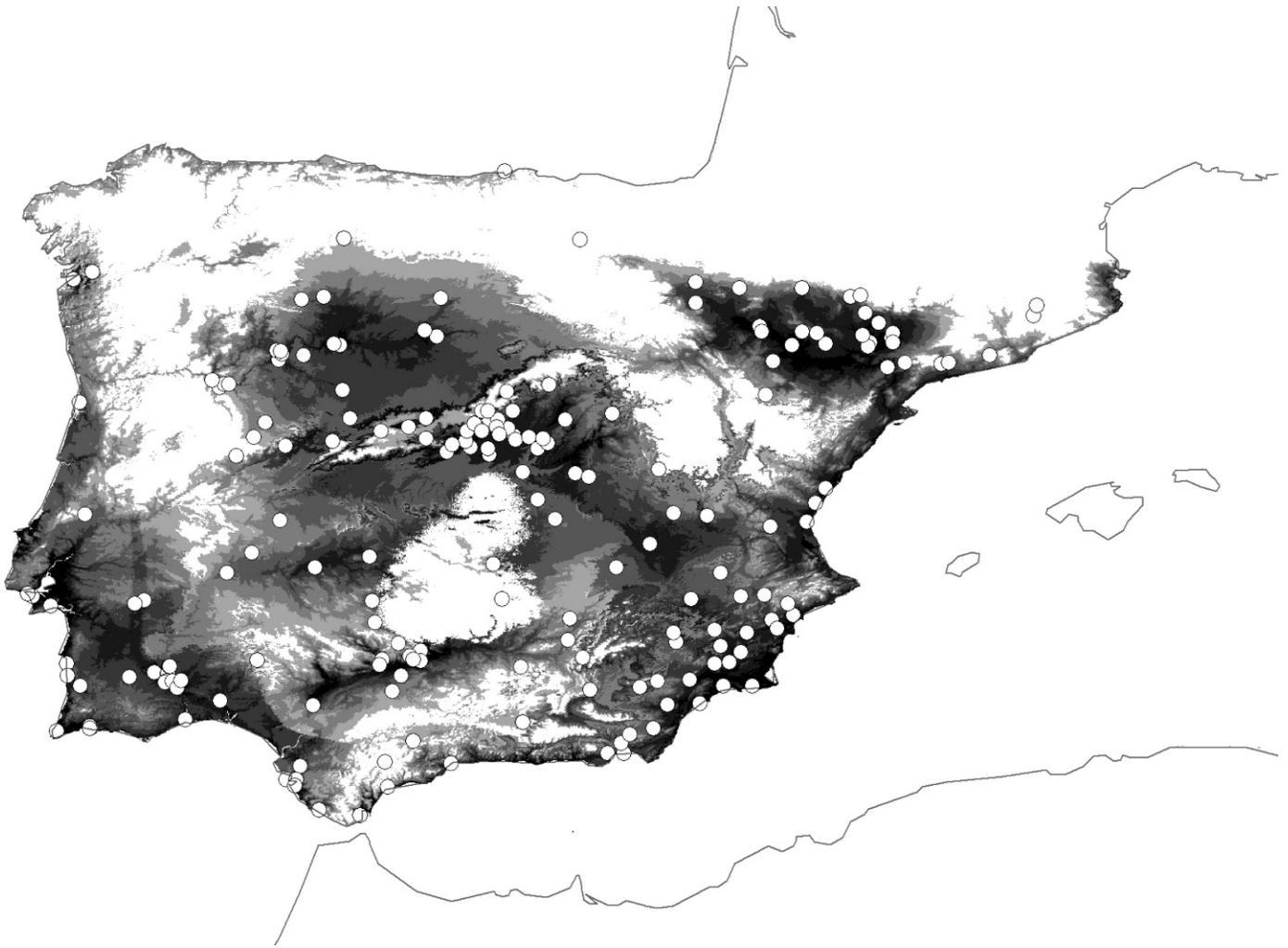


Figure 2.—Potential distribution of *G. dorsalis* on the Iberian Peninsula. Darker shades represent higher suitability for the species. Points represent actual records.

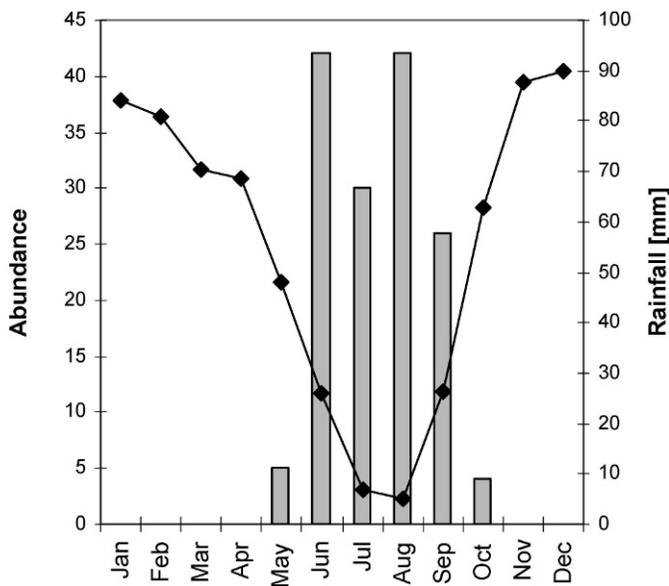


Figure 3.—Seasonal activity (i.e., total abundance per month [bars]) of *G. dorsalis* and the mean monthly precipitation (points).

Fig. 3) and positively correlated with monthly average temperature (GLM, $X^2 = 8.5$, $df = 1$, $P = 0.004$). The adult males and females appeared in late May and were most abundant in June and July. Males disappeared in mid-August, and females disappeared a month later. The average sex ratio (males: females) was highly skewed in favor of females (0.38, $n = 157$) in the field (Binomial test, $P = 0.004$).

G. dorsalis are strictly nocturnal (Fig. 4). Individuals emerge after sunset and are active until midnight, with an activity peak between 21:00 and 22:00 ($n = 68$). Principal activities observed included prey-capturing or burrow-digging. During the rest of the day solifuges hid in stonewall crevices, in shallow depressions under stones, or in the debris. Two individuals that we observed running on the ground during the day were presumably disturbed when we stepped on the rocks where they had hidden.

Burrowing behavior.—We observed females ($n = 20$) and juveniles ($n = 9$), but no males, digging burrows between 22:00 and 24:00 h in sandy soil. Solifuges dug and raked the loose sand, mainly with the second pair of legs. Chelicerae, pedipalps, and the first pair of legs were shaped into a basket to push sand heaps aside to a distance of a few centimeters.

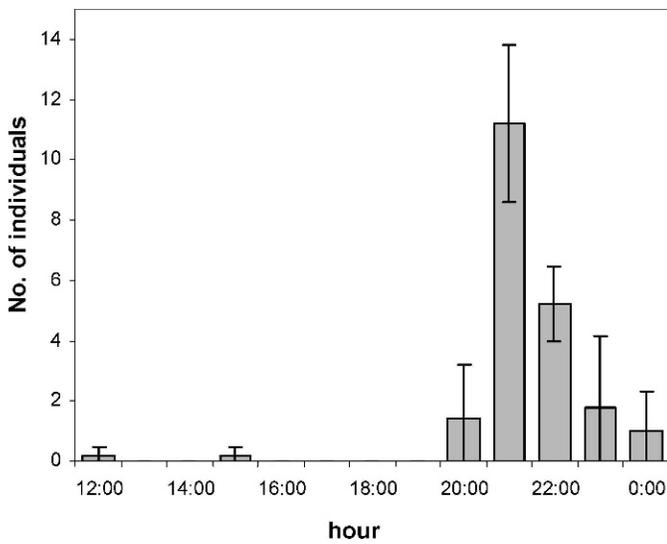


Figure 4.—Mean number (\pm SE) of individuals per hour found during 20 min in Mitra. Time of inactivity (01:00–11:00 h) are not shown.

They repeated these movements until completing the burrow. All burrows had open entrances.

Prey and prey capture.—Hunting solifuges, juvenile or adult, ran quickly over the ground with the pedipalps and first pair of legs stretched forward. The movement appeared haphazard, with frequent changes in direction. Once prey was encountered, solifuges seized it quickly by means of the sucking organs on the pedipalpal tips, and subsequently grasped it with the chelicerae. Solifuges grasped bodies of small prey, but legs of large prey (e.g., grasshoppers). The prey sometimes escaped by pulling away from its own leg. In all cases we observed, the solifuges remained at the site of capture while eating the prey.

In the field, we found the main available (potential) prey on the ground to be ants (42%, $n = 325$), woodlice (32%), and beetles (10%), but we observed solifuges catching mainly ants and spiders in such conditions. The captured prey, therefore, differed from the available options ($\chi^2 = 47.4$, $df = 9$, $P < 0.0001$, Fig. 5).

In the laboratory, solifuges accepted and consumed a wide variety of arthropods ranging in size from 2 to 25 mm (Table 2), so that the relative size (prey to solifuge) was between 0.2 and 1. Solifuges rejected or attacked but did not consume mites, some woodlice, millipedes, large ants, and carabid beetles. Male solifuges further rejected hard sclerotized beetles. In the laboratory, solifuges accepted a wider prey variety than was available in the field.

Oviposition and ontogenetic development.—In June, on average 11 days (SE = 0.7, $n = 11$) after mating, females produced one clutch of spherical, whitish eggs. They deposited a mass of eggs on the surface of the sand in the vials. The clutch size varied from 47 to 163 eggs (mean = 83.4, $n = 11$), and the eggs had an average diameter of 1.78 mm (SE = 0.09, $n = 96$). The size of the eggs was not related to the clutch size (Spearman correlation, $\rho = -0.3$, $S = 26$, $P = 0.68$). The females died on average 9 days (SE = 2.5, $n = 11$) following the oviposition. In one case, the female was observed laying

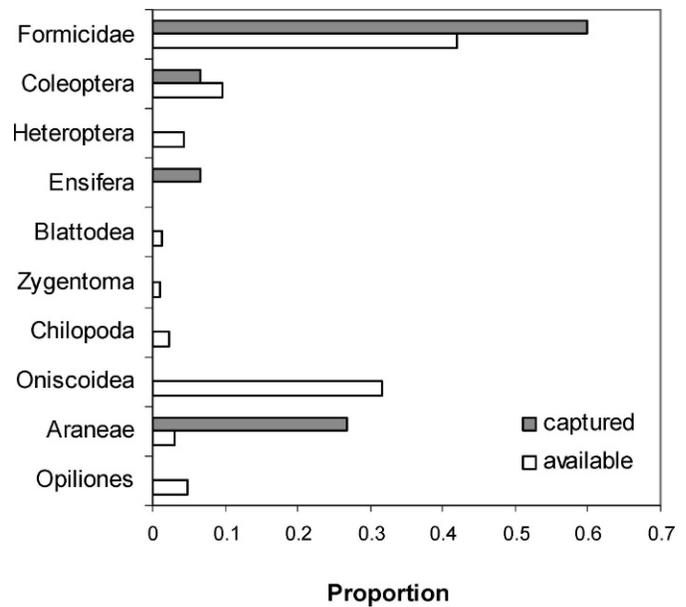


Figure 5.—Comparison of available and captured prey. Bars represent proportion of individuals. There were 3,254 prey individuals available and 15 prey captured.

another clutch (10 eggs) one week after the first one (137 eggs) had been deposited.

On average, 56 days (SE = 4, $n = 85$) after laying eggs, pale yellow immobile larvae hatched. These inactive individuals molted into the first non-feeding instar, on average in 17 days (SE = 0.9, $n = 25$). Measurements of the morphological characters of the first instar are shown in Table 3. Juveniles captured in the field were separated into two ontogenetic categories based on the number of malleoli: as early juveniles with 3 malleoli, and later juveniles with 5 malleoli. In the field, the smallest early instars (propeltidium width <1 mm) occurred from mid-July to mid-October (Fig. 6). The occurrence of early and late juveniles overlapped, as they occurred every month from May to October.

Because we sampled early juveniles, late juveniles, and adult stages each month from June to August, we assume that the life cycle is biennial, with a longevity of about 700 days. We suggest two extreme developmental trajectories. Specimens that hatched into the first instar in mid-July (dashed line in Fig. 6) would probably pass through 2–3 instars before overwintering to reach about 1.8 mm (propeltidium width). Next season, these specimens would pass through several instars to reach about 3.7 mm (propeltidium width) before the onset of winter, so that the following season they would reach maturity in the beginning of June. Specimens that hatched into the first instar later, in late September, did not molt and overwintered at 1.2 mm (propeltidium width). Next season they would pass through a few instars to reach 3 mm (propeltidium width). In the following season they would pass through another few instars to reach adulthood in August.

Sexual dimorphism.—Adult males ($n = 55$) were smaller and had a narrower propeltidium and wider malleoli than adult females ($n = 66$) (Table 3). Male sclerotized body parts (prosomatic parts and appendages) were densely covered with

Table 3.—Measurements (mean ± SE) of some body traits in the first-instar specimens, adult males and adult females of *G. dorsalis*.

Character	First instars (n = 10)	Males (n = 55)	Females (n = 66)
Length of propeltidium [mm]	0.797 ± 0.047	2.024 ± 0.363	2.728 ± 0.441
Width of propeltidium [mm]	1.061 ± 0.087	2.778 ± 0.405	4.495 ± 0.701
Number of malleoli	3	5	5
Width of the fourth malleolus [mm]	0.230 ± 0.040	0.945 ± 0.129	0.835 ± 0.128
Malleolus to propeltidium width ratio	0.216 ± 0.030	0.355 ± 0.038	0.188 ± 0.026

spines, while those of females were not (Fig. 1). The relationship between the width of propeltidium and width of malleoli was isometric for females, but allometric for males (Fig. 7A). The malleoli size of females increased with propeltidium size in similar fashion to juveniles (ANCOVA, $F_{2,650} = 0.91, P = 0.4$). But in males the relationship was significantly steeper than in juveniles (ANCOVA, $F_{2,652} = 1021, P < 0.0001$, Fig. 7A), suggesting that the size of malleoli increased markedly at the last molt of males. The relationship between the width and length of propeltidium was, in turn, isometric for males, but allometric for females (Fig. 7B). For juveniles, this relationship was significantly different from that of females (ANCOVA, $F_{2,527} = 13.3, P < 0.0001$) as well as males (ANCOVA, $F_{2,527} = 72.5, P < 0.0001$, Fig. 7B). Clearly, there was a change in the shape of propeltidium at the last molt in both sexes. The ratio of width to length of propeltidium was 1.62 ($CI_{95} = 1.59, 1.65$) in females and 1.37 ($CI_{95} = 1.32, 1.41$) in males.

DISCUSSION

We found that *Gluvia dorsalis* is widespread on the Iberian peninsula, but has a quite restricted seasonal activity. It feeds on a variety of epigeal arthropods that are captured only during the first three hours of the scotophase. Its reproduction occurs at the beginning of summer, and the life cycle is probably biennial. Several morphological characters revealed apparent sexual dimorphism at maturity, such as shape of the propeltidium or size of malleoli. We will now compare traits studied with those from other solifuge families, as there are few comparative data.

Our results strongly suggest that the distribution of the solifuge *G. dorsalis* is mostly limited to areas of the Iberian Peninsula with scarce summer rain. This supports the fact that solifuges are restricted to arid environments of the world at variable altitudes and temperatures. Similar to other solifuge species (Griffin 1990; Punzo 1998b), *G. dorsalis* has a marked preference for habitats of a semi-desert character (González-

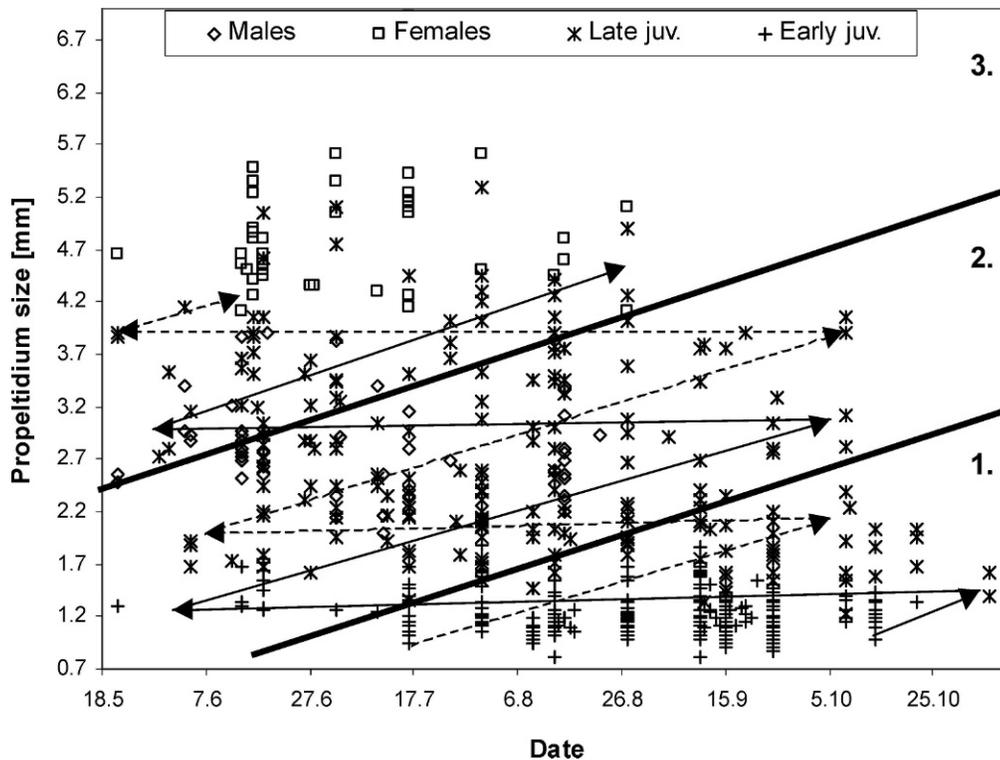


Figure 6.—Relationship between the size of propeltidium (width) and the occurrence of adult males, adult females, late juveniles (with 5 malleoli), and early juveniles (with 3 malleoli) during season from May until October. Bold lines mark the hypothesized borders between three consecutive seasons (1., 2., 3.). The slopes of the bold lines are parallel with two extreme hypothesized developmental trajectories displayed by thin solid (for late hatchlings) and thin dashed (for early hatchlings) lines with arrows.

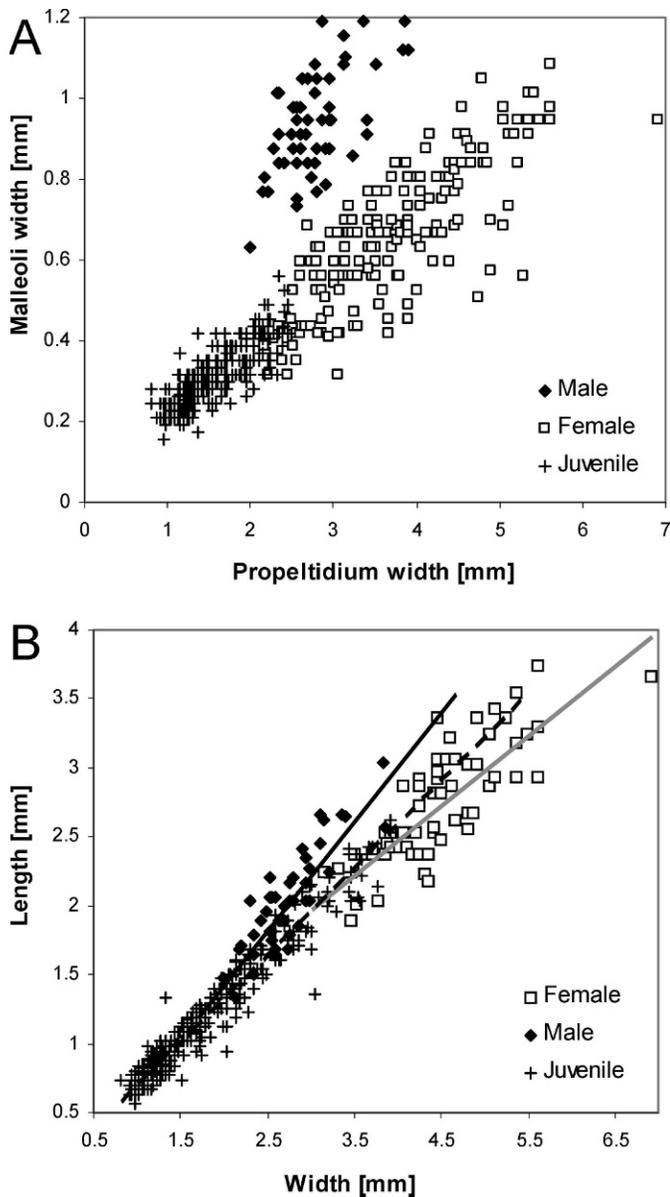


Figure 7.—A. Relationship between the width of malleoli and the width of propeltidium for juveniles, adult males and females. B. Relationship between the length and width of propeltidium for juveniles, adult males and females with linear models. Males = solid line, females = gray line, juveniles = dashed line.

Moliné et al. 2008; this study): sand substrate, rocks, and low and sparse vegetation cover. Females and juveniles can easily dig burrows in the sand, whereas stones, grass and shrubs provide cover and protection for the males. Although the use of burrows as retreats during the periods of inactivity and oviposition is widespread among solifuges (Muma 1966b; Cloudsley-Thompson 1977; Punzo 1998b; Hrušková-Martišová et al. 2007), our field observations show that solifuges sheltered mainly under stones, in debris and rock crevices while resting during the day and as a protection during ecdysis. Burrows were excavated exclusively by juveniles and females; thus, we expect that burrows function for overwintering and for egg deposition. Similar observations were made

by Punzo (1998c) of *Eremobates marathoni* Muma 1951 (Eremobatidae), where females were found in the non-plugged burrows, while males utilized simple depressions under a rock or decaying vegetation. The burrowing behavior of *G. dorsalis* was generally similar to that reported for other solifuge species (Hingston 1925; Junqua 1966; Muma 1966b; Cloudsley-Thompson 1977; Gore & Cushing 1980).

Their preference for dry habitats is also reflected in their restricted seasonal activity. As revealed by previous studies (Rambla & Barrientos 1986; González-Moliné et al. 2008), *G. dorsalis* was active during months with the highest temperature and very few summer rains, like many other solifuge species (Heymons 1902; Cloudsley-Thompson 1961a; Wharton 1987; Chandra 1989; Punzo 1997). Although both these variables are strongly correlated, rainfall was found to be a better predictor of their seasonal activity pattern than temperature. It is not clear why rain can limit the seasonal occurrence of solifuges. We have observed that on rainy nights in late summer, the density of their prey, such as ants, decreased dramatically. So solifuges may avoid wet days due to low profitability resulting from a low capture rate.

High abundance of prey must be very important for *G. dorsalis*, because its foraging activity period is very short, lasting only about three hours. Whether such a short period is an adaptation to avoid desiccation or predators is not clear. Berland (1932) and Lawrence (1956), however, suggested that *G. dorsalis* is a day-active species, because it is small. Nocturnal activity is very common in many other solifuge species (e.g., Turner 1916; Lawrence 1955; Cloudsley-Thompson 1961a; Hrušková-Martišová et al. 2007; Punzo 1998b), as well as many other animals inhabiting arid environments (Cloudsley-Thompson 1991; Rose & Mueller 2006).

The majority of solifuge species has been reported to be extremely active and extraordinarily voracious predators (Muma 1966c); however, researchers have made only a few observations on solifuge foraging behavior and feeding habits under natural conditions (Turner 1916; Bolwig 1952; Wharton 1987; Hrušková-Martišová et al. 2007). In most of those studies, juveniles and/or adults were observed to search and hunt their prey on the ground. Our observations indicate that hunting, capturing, and handling prey in *G. dorsalis* are similar to descriptions for other solifuge species (Hutton 1843; Turner 1916; Bolwig 1952; Cloudsley-Thompson 1961b; Punzo 1995). *G. dorsalis* is clearly a polyphagous predator, as are other solifuge species (Turner 1916; Muma 1967; Cloudsley-Thompson 1977; Wharton 1987; Punzo 1994, 1997). In the field, the diversity of captured prey was lower than in the laboratory, reflecting the restricted availability. *Gluvia dorsalis* seems to prefer soft-bodied prey smaller than itself, refusing arthropods with chemical or other types of defenses like in other solifuge species (Punzo 1993, 1994). It is probable that there is frequent cannibalism of small specimens by larger ones.

The longevity of solifuges is largely unknown. Some authors have suggested that they are univoltine and do not live for more than one year (Muma 1963, 1966a; Punzo 1998a). But Wharton (1987), using data from pitfall traps and field observations, concluded that *Metasolpuga picta* (Kraepelin 1899) is biennial. Junqua (1966) observed in the laboratory that *Othoes* molted once a month. Having 8–10 instars, this

species lived for ~3 yr. Lawrence (1963), studying change in the cheliceral teeth, concluded that *Zeria monteiroi* (Pocock 1895) live for several years. Our data suggest that the longevity of *G. dorsalis* is about 2 yr. Although it is as large as *E. marathoni* (Punzo 1998a), *G. dorsalis* has longer life cycle, likely due to longer hibernation period.

In the laboratory we observed that the embryological development lasted almost 2 mo. We assume that in natural conditions development is much shorter because the ambient temperature is much higher than it was in laboratory. Based upon our previous experience, we avoided using higher temperature to avoid egg desiccation (if kept in dry conditions) or attack by fungi (if kept in humid conditions), both conditions accelerated by higher temperatures. As mating takes place in mid-June and the first instars were found in pitfall traps in mid-July, it appears that the incubation period together with the larval development takes about one month in nature. In a similarly large *E. durangomus* Roewer 1934, the average duration of intermolt interval was 25 days at 20° C. Assuming a similar duration for *G. dorsalis* and considering the temperature records over the season in Portugal, we expect that individuals that hatched in mid July would molt about 2–3 times before overwintering, then continue to molt next season about 4–5 times, finally molting into the adult stage the next season. There would thus be 7–9 juvenile instars altogether. This corresponds closely to the rate observed for *E. marathoni* (i.e., increase in propeltidium length by 37% on average [Punzo 1998a]).

We were not able to distinguish particular juvenile instars due to the large variation in all measured morphological traits. The only discrete character was the number of malleoli: three in early stages and five in later juvenile stages and in adults. Junqua (1966) and Muma (1966a) observed that the juveniles of the first to the fourth instars exhibit three pairs of malleoli and the fifth to the ninth instars possess five pairs. Our data appear to be in agreement with their conclusions.

In most of the solifuge species studied to date, males and females differ in body size, in the presence of sex-specific structures, and in shape and size of some body structures (Punzo 1998b). In *G. dorsalis*, we found conspicuous sexual dimorphism in total body setosity, propeltidium, and malleoli size. We suspect that some features might already be dimorphic in the juvenile stages. However, the size of malleoli and the shape of propeltidium (expressed as width to length ratio) become clearly dimorphic only in the adult stage. However, certain differences in the shape of propeltidium were already apparent in the juvenile stage. This character deserves further investigation because it might be used for the recognition of sex in juvenile instars.

By revealing basic natural history data of *G. dorsalis*, we raise many questions, such as why their foraging activity is so short, what portion of their diet involves cannibalism, or how long is their life cycle. These remain to be addressed in future studies. Unfortunately, the scarcity of individuals in nature and the difficulty of observing and rearing them makes investigation of these remarkable arachnids infeasible.

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LITERATURE CITED

- Berland, L. 1932. Les Arachnides. In *Encyclopédie Entomologique* (A). Volume XVI. Pp. 1–485. Paul Lechavalier & Fils, Paris.
- Bolwig, N. 1952. Observations on the behavior and mode of orientation of hunting Solifugae. *Journal of the Entomological Society of Southern Africa* 15:239–240.
- Cardoso, P., I. Silva, N.G. Oliveira & A.R.M. Serrano. 2004. Higher taxa surrogates of spider (Araneae) diversity and their efficiency in conservation. *Biological Conservation* 117:453–459.
- Cardoso, P., I. Silva, N.G. Oliveira & A.R.M. Serrano. 2007. Seasonality of spiders (Araneae) in Mediterranean ecosystems and its implications in the optimum sampling period. *Ecological Entomology* 32:516–526.
- Chandra, H. 1989. Some observations on the predatory behaviour of *Galeodes* sp. (Solifugae: Galeodidae) on acridids. *Plant Protection Bulletin (Faridabad)* 40:23–24.
- Cloudsley-Thompson, J.L. 1961a. Observations on the natural history of the 'camel-spider', *Galeodes arabs* C.L. Koch (Solifugae: Galeodidae) in the Sudan. *Entomologist's Monthly Magazine* 97:145–152.
- Cloudsley-Thompson, J.L. 1961b. Some aspects of the physiology and behaviour of *Galeodes arabs*. *Entomologia Experimentalis et Applicata* 4:257–263.
- Cloudsley-Thompson, J.L. 1977. Adaptational biology of Solifugae (Solpugida). *Bulletin of the British Arachnological Society* 4:61–71.
- Cloudsley-Thompson, J.L. 1991. *Ecophysiology of Desert Arthropods and Reptiles*. Springer-Verlag, Berlin.
- Dean, W.R.J. & S.J. Milton. 1991. Prey capture by *Solpuga chelicornis* Lichenstein (Solifugae: Solpugidae). *Journal of the Entomological Society of South Africa* 54:266–267.
- González-Moliné, A.L., A. Melic & J.A. Barrientos. 2008. Taxonomía, distribución geográfica e historia natural del endemismo Ibérico *Gluvia dorsalis* (Latreille, 1817) (Solifugae: Daesiidae). *Boletín Sociedad Entomológica Aragonesa* 42:385–395.
- Gore, J.A. & B.C. Cushing. 1980. Observations on temporary foraging areas of the sun spider *Ammotrechula peninsulana* (Banks) (Arachnida: Solpugida). *Southwestern Naturalist* 25:95–102.
- Griffin, E. 1990. Seasonal activity, habitat selection and species richness of Solifugae (Arachnida) on the gravel plains of the central Namib Desert. *Transvaal Museum Monograph* 7:77–82.
- Grosso-Silva, J.M. 1998. Sobre a presença do solifugo *Gluvia dorsalis* (Latreille, 1817) (Arachnida, Solifugae, Daesiidae) no concelho de Vila Nova de Foz Coa (NE de Portugal). *Boletín de la SEA* 21:23.
- Harvey, M.S. 2003. *Catalogue of the Smaller Arachnid Orders of the World*. CSIRO Publishing, Collingwood, Victoria, Australia.
- Hernandez, P.A., C.H. Graham, L.L. Master & D.L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modelling methods. *Ecography* 29:773–785.
- Heymons, R. 1902. *Biologische Beobachtungen an asiatischen Solifugen*. *Abhandlungen der Königlich Preussischen Akademie der Wissenschaftern* 1901:1–65.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hingston, R.W.G. 1925. *Nature at the Desert's Edge*. Studies and Observations in the Bagdad Oasis. Witherby, London.

- Hrušková-Martišová, M., S. Pekár & A. Gromov. 2007. Biology of *Galeodes caspius subfuscus* (Arachnida: Solifugae). *Journal of Arachnology* 35:546–550.
- Hrušková-Martišová, M., S. Pekár & T. Bilde. 2010. Coercive copulation in two sexually cannibalistic camel-spider species (Arachnida: Solifugae). *Journal of Zoology*. In press. DOI: 10.1111/j.1469-7998.2010.00718.x.
- Hutton, T. 1843. Observations on the habits of a large species of *Galeodes*. *Annals and Magazine of Natural History* 12:81–85.
- Junqua, C. 1966. Recherches biologiques et histophysiologiques sur un solifuge saharien *Othoes saharae* Panouse. *Memoires du Museum National d'Histoire Naturelle Paris, Séries A* 43:1–124.
- Lawrence, R.F. 1955. Solifugae, scorpions and Pedipalpi, with checklists and keys to South African families, genera and species. *South African Animal Life* 1:152–262.
- Lawrence, R.F. 1956. Solifugae (Chelicerata) from Afghanistan. *Videnskabelige Meddelelser fra Danske Naturhistorisk Forening i Kjøbenhavn* 118:115–140.
- Lawrence, R.F. 1963. The Solifugae of South West Africa. *Cimbebasia* 8:1–28.
- Matos de, A. 1978. Nota sobre a existência do solifugo *Gluvia dorsalis* Latr. (Arachnida, Solifugae, Daesiidae). *Arquivos Museu Bocage* 2:319–323.
- Muma, M.H. 1963. Solpugida of the Nevada test site. *Brigham Young University Science Bulletin, Biological Series* 3(2):1–15.
- Muma, M.H. 1966a. The life cycle of *Eremobates durangonus* (Arachnida: Solpugida). *Florida Entomologist* 49:233–242.
- Muma, M.H. 1966b. Burrowing habits of North American Solpugida (Arachnida). *Psyche* 73:251–260.
- Muma, M.H. 1966c. Feeding behavior of North American Solpugida (Arachnida). *Florida Entomologist* 49:199–216.
- Muma, M.H. 1967. Basic behavior of North American Solpugida. *Florida Entomologist* 50:115–123.
- Pablos, F. 1967. Sobre la presencia de *Gluvia dorsalis*, var. *conquensis* en los puertos de Contreras (Cuenca). *Publicaciones del Instituto de Biología Aplicada* 43:45–48.
- Peretti, A.V. & R.H. Willemart. 2007. Sexual coercion does not exclude luring behavior in the climbing camel-spider *Olticola chacoensis* (Arachnida, Solifugae, Ammotrechidae). *Journal of Ethology* 25:29–39.
- Phillips, S.J., R.P. Anderson & R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- Phillips, S.J. & M. Dudik. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Polis, G.A. & S.J. McCormick. 1986. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. *Oecologia* 71:111–116.
- Punzo, F. 1993. Diet and feeding behavior of the solpugid, *Eremobates palpietosus* (Solpugida: Eremobatidae). *Psyche* 100:151–162.
- Punzo, F. 1994. An analysis of feeding and optimal foraging behaviour in the solpugid *Eremobates mormonus* (Roewer) (Solpugida, Eremobatidae). *Bulletin of the British Arachnological Society* 9:293–298.
- Punzo, F. 1995. Feeding and prey preparation in the solpugid, *Eremorhax magnus* Hancock (Solpugida: Eremobatidae). *Pan-Pacific Entomologist* 71:13–17.
- Punzo, F. 1997. Dispersion, temporal patterns of activity, and the phenology of feeding and mating behaviour in *Eremobates palpietosus* Fichter (Solifugae, Eremobatidae). *Bulletin of the British Arachnological Society* 10:303–307.
- Punzo, F. 1998a. Natural history and life cycle of the solifuge *Eremobates marathoni* Muma & Brookhart (Solifugae, Eremobatidae). *Bulletin of the British Arachnological Society* 11:111–118.
- Punzo, F. 1998b. *The Biology of Camel-Spiders* (Arachnida, Solifugae). Kluwer Academic Publishers, Boston.
- Punzo, F. 1998c. The effects of maternal nest guarding behaviour by *Eremobates marathoni* Muma & Brookhart on the survivorship of offspring (Solifugae, Eremobatidae). *Bulletin of the British Arachnological Society* 11:54–56.
- R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. Online at <http://www.R-project.org>.
- Rambla, M. & J.A. Barrientos. 1986. Nuevos datos sobre *Gluvia dorsalis* (Latreille, 1817) (Solifugae, Daesiidae). Pp. 213–218. *In* Proceedings of the Ninth International Congress of Arachnology. (W.G. Eberhard, Y.D. Lubin & B.C. Robinson, eds.). Smithsonian Institution Press, Washington.
- Rose, M.R. & L.D. Mueller. 2006. *Evolution and Ecology of the Organism*. Pearson Prentice Hall, Upper Saddle River, New Jersey.
- Schenker, R. 1980. Erster Nachweis einer Solifugae-Art (*Gluvia dorsalis* Latreille 1817) (Arachnida) in Portugal. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 53:283–284.
- Turner, C.H. 1916. Notes on the feeding behavior and oviposition of a captive American false-spider (*Eremobates formicaria* Koch). *Journal of Animal Behavior* 6:160–168.
- Wharton, R.A. 1987. Biology of the diurnal *Metasolpuga picta* (Kraepelin) (Solifugae, Solpugidae) compared with that of nocturnal species. *Journal of Arachnology* 14:363–383.

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