

## Adaptational biology of Solifugae (Solpugida)

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### Summary

Mythology and allegedly poisonous attributes are discussed; then the burrowing behaviour, circadian rhythms, exploratory behaviour, water and thermal relations, food and feeding behaviour, fighting, enemies, mating behaviour, life cycle and phenology of Solifugae are reviewed. In many of these categories, it can be seen that the animals are well adapted for life in desert conditions.

### Introduction

A review of the adaptational biology of desert scorpions has recently been published in the *Journal of Arachnology* (Hadley, 1974). It is the purpose of the present article to provide a somewhat similar service to the second order of Arachnida that dominates the desert wastelands of the world. The biology of the Solifugae, however, is far less well known than is that of scorpions; yet these impressive animals must be quite familiar to everyone who has travelled in desert areas. Indeed, they have been cited as worldwide, endemic indicators of deserts (Schmoller, 1970), since most species occur in hot, arid environments (Berland, 1932; Cloudsley-Thompson, 1958; Millot and Vachon, 1949; Muma, 1951). In southern Nevada, for example, Solifugae are common only in desert-scrub areas, few occurring at higher altitudes or in more humid situations (Muma, 1963). These animals require warmth and are never found in cold or temperate regions. One species, *Gylippus rickmersi* Krpln., nevertheless, inhabits the Pamir Mountains, north of the Hindu Kush, at an altitude of 3,000 m (Millot and Vachon, 1949). Even in the environments where they thrive, Solifugae usually make themselves apparent only during the hot season. They avoid oases and other fertile places, seeming to prefer utterly neglected regions where the soil is broken and bare (Cloudsley-Thompson, 1958; Hingston, 1925). At night, they frequently enter the tents of travellers to catch flies and other insects, circulating so rapidly that it almost makes one dizzy to watch them. The

order Solifugae is not represented in Madagascar, Australia or New Zealand (Berland, 1932; Kaestner, 1968; Millot and Vachon, 1949; Warburton, 1909).

### Mythology and allegedly poisonous attributes

Like many other impressive and speedy animals, Solifugae are known by several colloquial names. These include "false-spiders", "wind-scorpions", "wind-spiders", "sun-spiders", "jerry-munglums" and "jerry-manders"; "Scorpion-spinne", "Gift-kanker" (poison-spider) and "Walzenspinnen" in German; "vetvreter" (fat-eater) and "haarskeerder" (hair-cutter) in Afrikaans. The last name is based on the belief that, should a solifugid become entangled in a girl's long hair, it cannot be dislodged until it has shorn her locks with its strong fangs (Lawrence, 1965).

According to Aelianus (*De Natura Animalium*) an area of "Ethiopia" was deserted by its inhabitants on account of the appearance of an incredible number of scorpions or "Phalangia" but Pliny (*Historia Naturalis*) in quoting the same story, replaced "Phalangium" by "Solfuga".

There has been some controversy as to whether there is any truth in the evil reputation of Solifugae for inflicting poisonous bites. Lichtenstein (1797) endeavoured to show that the mice, which plagued the Philistines when they captured the Ark of the Covenant (1 Samuel v. 6, vi. 5), may have been camel-spiders! He also suggested that the "emerods", with which the Philistines were afflicted, were the sores caused by the bites of these animals, chiefly on the "pudenda". Lichtenstein supported this odd interpretation by the claim that camel-spiders still inflict similar bites either in the same place — especially in the case of women — or on the lips of people or animals sleeping on the ground. Then he quoted a long passage from Agatharchides to the effect that a populous district on the shores of the Indian ocean was deserted owing to swarms of Solifugae which appeared after a very long rainy season. I do not believe a word of it!

In contrast, Olivier (1807) likewise disbelieved the awful reports of the Arabs, who were terrified at the sight of the wind-scorpions which appeared in their tents at night, and who told yarns, each more horrible than the last, as to their dangerous bites. He did admit, however, that with such jaws the results would

probably be most painful. People have been bitten accidentally by the animals getting under their clothes and the effect is sometimes severe. According to Warburton (1909), the inhabitants of Baku on the Caspian Sea believe that a local species, which they call "Falanga", is especially poisonous after its winter sleep and, in order to neutralise the effects of the venom, they rub the wound with the carcase of the animal after first steeping it in boiling oil. On the other hand, he wrote, the Somalis do not regard them as noxious – indeed, they have no name in their language for anything so unimportant! (This last statement, however, is not true). Hutton (1843) recorded the case of a lizard bitten by a *Galeodes* which recovered in three days, and he used this as an argument against there being any venom in the bite. Distant (1892) also thought that Solifugae were not poisonous because, when attacked by birds, they flee before their assailants. On the other hand, Bernard (1897) suggested that poisoning might result from a simple exudation of toxic excretory matter through the setal pores which, he believed, could be traced along the tips of the jaws. In Mexico, a species of *Gluvia*, known locally as "Genisaro" is thought to be excessively venomous (Muma, 1967).

Phisalix (1922) recorded a number of cases of Solifugae biting men and concluded that, in view of the severity of the effects, which might occasionally result in death, the possibility of poison could not entirely be eliminated. It is now generally assumed, however, that the Solifugae are not venomous since several authors have searched in vain for poison glands – such as those in the jaws of spiders – and a number of people have actually allowed themselves to be bitten without experiencing any ill effects (Heymons, 1902; Lönnberg, 1899; Pocock, 1898; Savory, 1928). On the few occasions that poisoning does occur, it is most probably due to infection of the wound.

### Behavioural mechanisms

#### *Burrowing*

The burrowing habit is extremely common among desert Arthropoda being exhibited in nearly all of the major orders and families. Solifugae are no exception. The camel-spider *Galeodes granti* Pocock (incorrectly designated *G. arabs* C. L. Koch in Cloudsley-

Thompson (1961a, 1961b)), a characteristic inhabitant of the northern Sudan, for instance, is nocturnally active and spends the day in a deep burrow, the mouth of which is often closed with a plug of dead leaves (Cloudsley-Thompson, 1961a). The burrow usually follows a convoluted course at a depth of 10-20 cm, and often extends for several metres into the soil. In cooler, damp weather at the time of the annual rains, *G. granti* may be found near the entrance of its burrow but, during the hot dry season, it retreats to the innermost depths (Cloudsley-Thompson, 1961b). Young specimens are occasion-

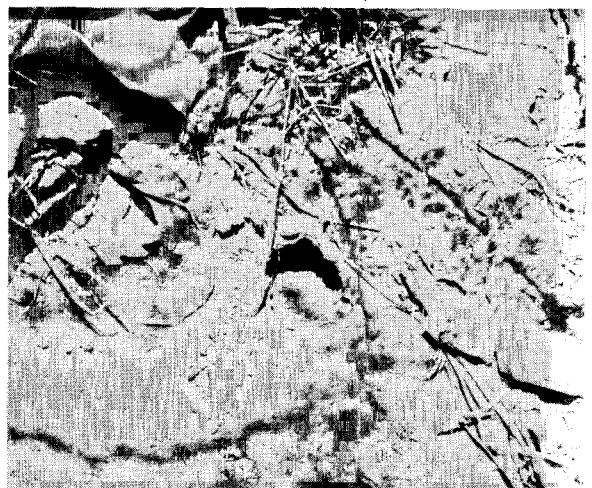


Plate 1: Typical solifugid burrows in northern Sudan (reduced).

ally to be found underneath rocks.

The general features of solifugid burrowing have been described by Hutton (1843), Turner (1916), Hingston (1925) and Fichter (1940), while a comparative study of the burrowing habits of North American species (Muma, 1966d) demonstrates a broad similarity in behaviour. All species use their chelicerae to bite at the substrate, raking loosened particles back under the body with the second and, less often, the third pair of legs. The chelicerae, sometimes assisted by the pedipalps and first, or first and second pairs of legs, plough excavated materials out of the burrow; while the palps are also used to flatten the material thus removed. Variations indicate the existence of specific and generic differences. Not only are burrows used for resting in during the daylight hours, but they are also constructed for digestion, ecdysis, hibernation and the deposition of eggs

(Muma, 1967). An individual solifugid of the family Eremobatidae may, during its lifetime, dig 40 or more burrows (Muma, 1966d).

Despite their comparatively short limbs, the Rhagodidae are extremely active and run very quickly. Although most species of the South African family Hexisopodidae lack such speed and agility, they are able to move through dune sand with surprising rapidity (Lawrence, 1965). Their greatly shortened limbs are armed with rows of long, rake-like spines for digging.

#### *Circadian rhythms*

While the larger Solifugae are strictly nocturnal, some of the smaller species are day-active. The latter are sometimes called 'sun-spiders', and include variegated and a few brightly coloured and con-

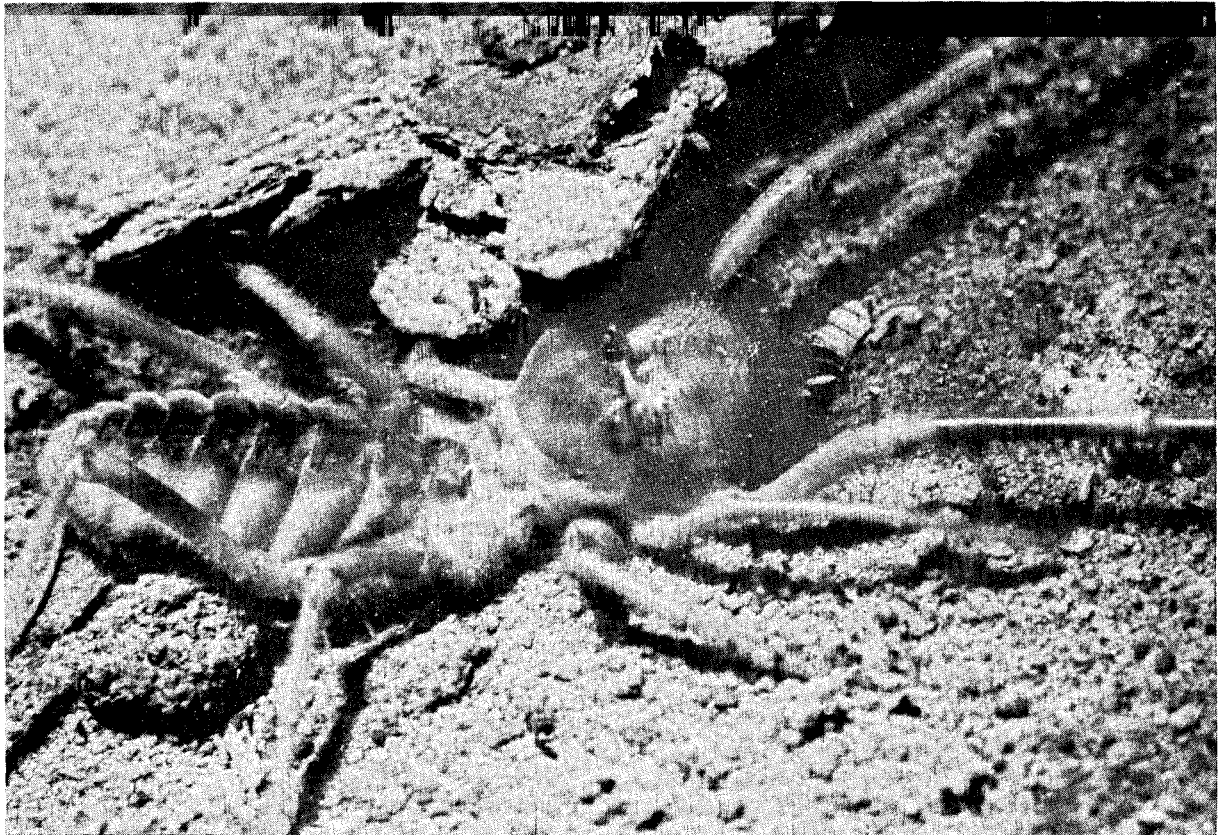


Plate 2: *Galeodes granti* Pocock burrowing (natural size).

spicuous forms, such as *Gluvia dorsalis* (Latr.) of Spain, and the South American *Mummucia variegata* (Gerv.) and *Pseudocleobis morsicans* (Gerv.). In contrast, the nocturnal camel-spiders are mostly a rather dingy yellow or earthy brown (Berland, 1932; Lawrence, 1965). Nocturnal solifugids are aptly named. They spend most of the daytime in their burrows, and emerge only after dark, when they are sometimes attracted by light. *Galeodes granti* Pocock is inactive for three or four days after ecdysis but, subsequently, shows a marked 24-hour periodicity (Cloudsley-Thompson, 1961a). All North American solifugids, with the possible exception of small species of *Therobates* and *Hemerotrecha* (e.g. *H. californica* (Banks)), are nocturnal according to Muma (1966a). In view of the marked resistance of these animals to high temperatures and low humidities (see below), it has been argued that, like scorpions, they may be nocturnal mainly in response to biotic factors in the environment. On account of their large size, they are especially vulnerable to vertebrate predators (Cloudsley-Thompson, 1960; 1977).

#### Exploratory behaviour

Solifugae are extremely active and, when not engaged in hunting, feeding, burrowing, sexual activities or resting, spend much of their time exploring their surroundings (Muma, 1967). When confined in laboratory terraria, they soon become tame.

#### Water and thermal relations

Lethal temperatures and rates of water loss of Solifugae indicate that many of these animals are unusually tolerant of heat and drought. Experiments have shown that the lethal temperature of *Galeodes granti* Pocock (for an exposure of 24 hours at a relative humidity below 10 per cent) is 50°C. This is higher than that of sympatric desert scorpions and tenebrionid beetles. In addition, the rate of water loss by transpiration is comparatively low (Cloudsley-Thompson, 1962).

When placed in water, Solifugae cease to struggle almost immediately. After removal, however, they quickly recover (Lawrence, 1949; Muma, 1967). The ability to survive submersion, when subjected to sudden rain or flash floods, is clearly of adaptive value in desert countries.

#### Food and feeding habits

Solifugae are exclusively predatory and carnivorous, having an extraordinary voracity. Several workers have recorded them as feeding until their abdomens were so distended that they could scarcely move (Bernard, 1897; Cloudsley-Thompson, 1958; Fichter, 1940; Hingston, 1925; Hutton, 1843; Lawrence, 1949; Pocock, 1898). The capture of prey, feeding behaviour, drinking and diet have also been described on several occasions (Bolwig, 1952; Cloudsley-Thompson, 1958; Cook, 1898; Cretin, 1896; Fichter, 1940; Hingston, 1925; Hutton, 1843; Lawrence, 1949, 1963; Marx, 1892; Muma, 1966b; Pocock, 1897, 1898; Putnam, 1883; Turner, 1916). Food searching behaviour involves random running, and congregating in areas where prey is likely to occur, such as the neighbourhood of lights at night and the nests of prey. The prey may be located by orientation to tactile and visual stimuli, and by vibrations of the substrate (Bolwig, 1952; Cloudsley-Thompson, 1961a). Most species appear to chase and ambush their prey, but some stalk it. *Hemerotrecha californica* (Banks) congregates in places — such as termite nests — where the density of the prey is high. The termites are picked up by the pedipalps and placed in the chelicerae. In general, either the pedipalps or the chelicerae may make first contact, depending on the size and nature of the food (Muma, 1966b). Most species also hunt their prey on the ground, but *Ammotrechella stimpsoni* (Putnam) is regularly found under bark and in termite burrows within dead trees, while *Therobates larreae* Muma has been collected from blooming creosote bushes (Muma, 1967).

Although insects, including even bees (Cook, 1898) and hard beetles, appear to form their staple diet, large solifugids do not necessarily take large prey. Smaller species, however, are naturally restricted to what they are able to overcome. According to Putnam (1883), *Eremobates pallipes* (Say) hunts bed bugs (*Cimex lectularius*), which comprise its favourite food. In Texas, *Eremobates sulfureus* (Simon) and *Eremobates geniculatus* (Simon) are truly nocturnal, running with great activity about houses at night. They are attracted to light, and sometimes to trees sugared by lepidopterists (Muma, 1967). Species of Galeodidae and Rhagodidae in various regions of the Sahara, likewise, not infre-

quently come to the lights of camp fires, where they catch the insects that are also enticed there.

Most North American species of Solifugae specialise on termites. They include *Eremobates durangonus* Roewer, which may take 20-40 at a meal, and *Ammotrechella stimpsoni* (Putnam) which, as already mentioned, lives under the bark of tree stumps inhabited by these insects. In contrast, *Eremorhax striatus* (Putnam) will eat almost any insects except termites, while *Eremorhax magnus* (Hancock) feeds on earthworms and beetles (Kaestner, 1968; Muma, 1966b). The South African *Solpuga sericea* Pocock and *S. lineata* C. L. Koch also feed mainly on termites (Pocock, 1897).

Solifugae have been observed to kill and eat large spiders, scorpions, lizards, mice and small birds (Banta and Marer, 1972; Bernard, 1897; Cloudsley-Thompson, 1958; Fischer, 1910; Hingston, 1925; Lawrence, 1963; Pocock, 1898). Apart from termitophilous species, most Solifugae will accept a wide range of diet. Preference data of North American species are listed by Muma (1966b).

Cannibalism is almost inevitable if more than one specimen is confined in the same terrarium, females usually overpowering the weaker males (Cloudsley-Thompson, 1958, 1961b; Fichter, 1940; Hingston, 1925; Hutton, 1843; Muma, 1966b, e). It apparently takes several forms: egg-cannibalism, communal-cannibalism, mating-cannibalism (stag fights), and contact-cannibalism (Muma, 1966b). Communal feeding, which seems to be restricted to second instar nymphs, has also been reported (Hingston, 1925; Muma, 1966b).

When living prey has been caught, it is held crossways in both jaws and masticated by alternate movements of the scissor-like chelicerae. At the same time it is ground between the inner surfaces of the two chelicerae which move alternately backwards and forwards. The reduction or absence of cheliceral teeth in the Hexisopodidae is correlated with a specialised diet of termites.

According to Hingston (1925) the sense of taste in *Galeodes* spp. is not well developed, but more recent experiments have shown that camel-spiders, while readily biting a wet or dry wad of cotton wool, will seldom do so when the wad has first been soaked in 70% alcohol, as they usually sample it first with their pedipalps. If they do bite it, they soon let go and

make cleaning movements with their chelicerae (Cloudsley-Thompson, 1961b).

Although drinking sometimes occurs when free water is available (Cloudsley-Thompson, 1961b; Fichter, 1940; Hingston, 1925; Muma, 1966b; Pocock, 1898), it seems probable that Solifugae normally obtain sufficient water for their needs from the body fluids of their prey (Cloudsley-Thompson, 1961b; Pocock, 1898). This ability is essential to desert arthropods.

The anus is terminal, and liquid excretory matter can be ejected forcibly – for a distance of up to 3 cm in the case of *Eremobates durangonus* Roewer – according to Muma (1967). In this way the animals are not contaminated by their own waste products.

### Fighting

The ferocious fighting behaviour of Solifugae is well known. It has been described among Asian and African species by Cloudsley-Thompson (1961a), Hingston (1925), Hutton (1843) and Pocock (1898), and in American solifugids by Fichter (1940), Muma (1966b, e; 1967), Putnam (1883) and Turner (1916). These accounts are basically similar, and indicate that the agonistic behaviour of all species is somewhat alike. The reactions of *Galeodes granti* Pocock have been classified as sleep, alertness, low intensity threat (the chelicerae move soundlessly and the animal rocks or sways on its legs), high intensity threat (usually accompanied by stridulation), leading to attack or flight (often accompanied by displacement sand-digging) (Cloudsley-Thompson, 1961a). Agonistic behaviour by North American species, however, is not so readily described in states of intensity, although some species fight more fiercely than others (Muma, 1967). Threat is strikingly exaggerated in species with long legs which permit accentuated rocking movements. Agonistic behaviour and feeding responses are obviously related, and the victor of a fight usually devours the loser.

Although adult solifugids are so aggressive and carnivorous, the first and second instars exhibit a peculiar form of allomimetic behaviour – first observed by Hutton (1843), and subsequently described by Hingston (1925) in *Galeodes arabs* Pocock. More recently, it has been discussed by Muma (1967) with reference to *Eremobates durangonus* Roewer. Second

instar sibling nymphs gather into loose clusters in which the movement of a single individual causes a slight shift or progression of the entire group. Continued mild stimuli may result in the cluster moving away from the source of irritation, but stronger stimulation may cause it to disperse altogether. As mentioned above, second instar nymphs may show communal feeding behaviour.

### Enemies

Little is known of the natural enemies of Solifugae although these probably include reptiles, birds and

small mammals (Cloudsley-Thompson, 1958; Distant, 1892; Millot and Vachon, 1949; Pocock, 1898), as well as other Solifugae. Encounters with scorpions usually result in destruction of the latter, unless the solifugid is very much smaller than its adversary.

Solifugae are able to raise their abdomens almost vertically. This, no doubt, protects that vulnerable portion of the anatomy (Walter, 1889). At the same time, it has been suggested (Cloudsley-Thompson, 1949) that such behaviour may represent a form of mimicry, since it results in a scorpion-like appearance, particularly in the short-legged Rhagodidae (Plate 3).



Plate 3: *Rhagodessa melanocephala* Simon. Male (enlarged).



Solifugae also stridulate when annoyed and this may serve as a threat to deter an attacker (Cloudsley-Thompson, 1961a; Pocock, 1898; Warburton, 1909).

The only parasite so far recorded is an Indian pompilid wasp (*Salius sycophanta*) (Bingham, 1900). Algerian solifugids have been reported to be exempt from the attacks of mason wasps which frequently destroy large spiders (Dufour, 1861).

## Reproduction

### *Mating behaviour*

The mating of Solifugae was first observed in *Galeodes caspius* Birula by Heymons (1902). Subsequently it has been described in *Galeodes granti* Pocock by Cloudsley-Thompson (1961b), in *G. sulfuripes* Roewer by Amitai, Levy and Shulov (1962), in *Othoes saharae* Panouse by Junqua (1962) and in species of *Eremobates* by Muma (1966e). Although the procedure is essentially similar in each case, minor differences occur. In *G. caspius* the male courts his mate by stroking her until she becomes lethargic. Then he inserts a spherical spermatophore with his chelicerae (Heymons, 1902). In *G. sulfuripes*, the female becomes inert when the pedipalps of the two partners meet (Amitai *et al.*, 1962), in *G. granti* the male merely touches the female with his pedipalps, in reply to which she lifts her abdomen and allows him to grasp her with his jaws (Cloudsley-Thompson, 1961b). In *Eremobates* spp., seminal fluid is emitted directly from the genital opening of the male onto that of the female, after which the male inserts the sperm with his chelicerae (Muma, 1966e).

The most significant difference between mating in Solifugae, and in scorpions or false-scorpions, consists in the immediate transfer of the spermatophore which is not fixed to the ground. This form of indirect copulation, using a spermatophore, probably represents an intermediate stage between indirect sperm transfer *via* the substrate, and indirect free sperm transfer as found in spiders (Cloudsley-Thompson, 1967, 1976). There are no distinct spermathecae in the Galeodidae (Birula, 1893; Dufour, 1861; Vachon, 1945). The spermatophore is not an adaptation to terrestrial conditions, since it first evolved in aquatic animals (Cloudsley-Thompson, 1976). Nevertheless, it is especially useful to desert animals, as it helps to prevent desiccation of the semen.

The flagella are curious organs of unknown function, situated on the dorso-distal region of the male chelicerae (male Eremobatidae lack a cheliceral flagellum, which is replaced by flagellar bristles). Junqua (1966) investigated their possible importance in courtship and mating; he found that severance of the shaft at the base had no observable effect on such behaviour. More recently, Lamoral (1974) has presented evidence suggesting that the flagellum operates for the temporary storage and emission of an exocrine secretion, possibly a pheromone, which may play a rôle in brief displays of territoriality among males during the mating phase. Brownell and Farley (1974) have recently studied the sensory system of the malleoli and suggest that the sense organs in the sensory groove may be chemoreceptors. If this is correct, the malleoli might respond to the exocrine secretion of the flagellum. It has also been suggested that they may serve to detect vibrations of the substrate, and this could account for the greater sensitivity of males in which sex they are significantly larger (Cloudsley-Thompson, 1961a).

The pedipalpal organ was at one time believed to be a receptor for airborne odours (Bernard, 1896; Lichtenstein, 1797), and Heymons (1902) suggested that it might have been used by male solifugids to detect and recognise females. Lönnberg (1899), however, had already kept *Galeodes araneoides* (Pallas), a Central Asian species, in glass boxes, and found that they could climb by means of their pedipalps whose terminal organs are now known to be suckers used for climbing and in the capture of prey. This had previously been suggested on anatomical grounds by Dufour (1862) and has subsequently been confirmed by further observations (Cloudsley-Thompson, 1954; Fichter, 1940; Hingston, 1925; Millot and Vachon, 1949). In their natural environments, some species of Solifugae are known to climb trees, no doubt assisted by their pedipalpal suckers.

### *Life cycle*

Egg deposition, incubation and hatching have been described on a number of occasions (Birula, 1893; Cloudsley-Thompson, 1961b; Croneberg, 1887; Heymons, 1904; Hingston, 1925; Hutton, 1843; Junqua, 1958, 1962; Lawrence, 1947, 1949; Muma, 1963, 1966a, 1966c; Turner, 1916). The number of eggs

produced is related to the size of the mother, as in spiders. They usually hatch in three or four weeks. Newly hatched post-embryos are translucent, white, and almost immobile: they moult in about a week to non-feeding, first-instar, nymphs which resemble their parents in shape and appearance. These complete development in a further week and moult to burrowing, feeding, second-instar nymphs. The existence of nine instars in *Eremobates durangonus* Roewer has been established by Muma (1966c). Males mature early and live for an average of only two weeks; females mature later, and live about five weeks.

#### *Protection of the young*

North American Solifugae of the genera *Ere-*

*morhax*, *Eremobates* and *Therobates* (Eremobatidae), and of *Ammotrechella* and *Ammotrechula* (Ammotrechidae), deposit their eggs in nests at the ends of deep burrows which are abandoned after the entrances have been plugged and concealed. The eggs are thus protected from predation, and provided with a relatively uniform and equable microclimate (Muma, 1967). In contrast, the females of species of *Galeodes* (Galeodidae) protect their newly hatched offspring. Hutton (1843) reported that a female *Galeodes vorax* Hutton guarded her offspring: she repeatedly attacked insects dropped into the burrow, but did not harm any of her young that had been removed and afterwards thrown back. Young *Galeodes granti* Pocock and other congeneric species are likewise protected by their mother in a haphazard

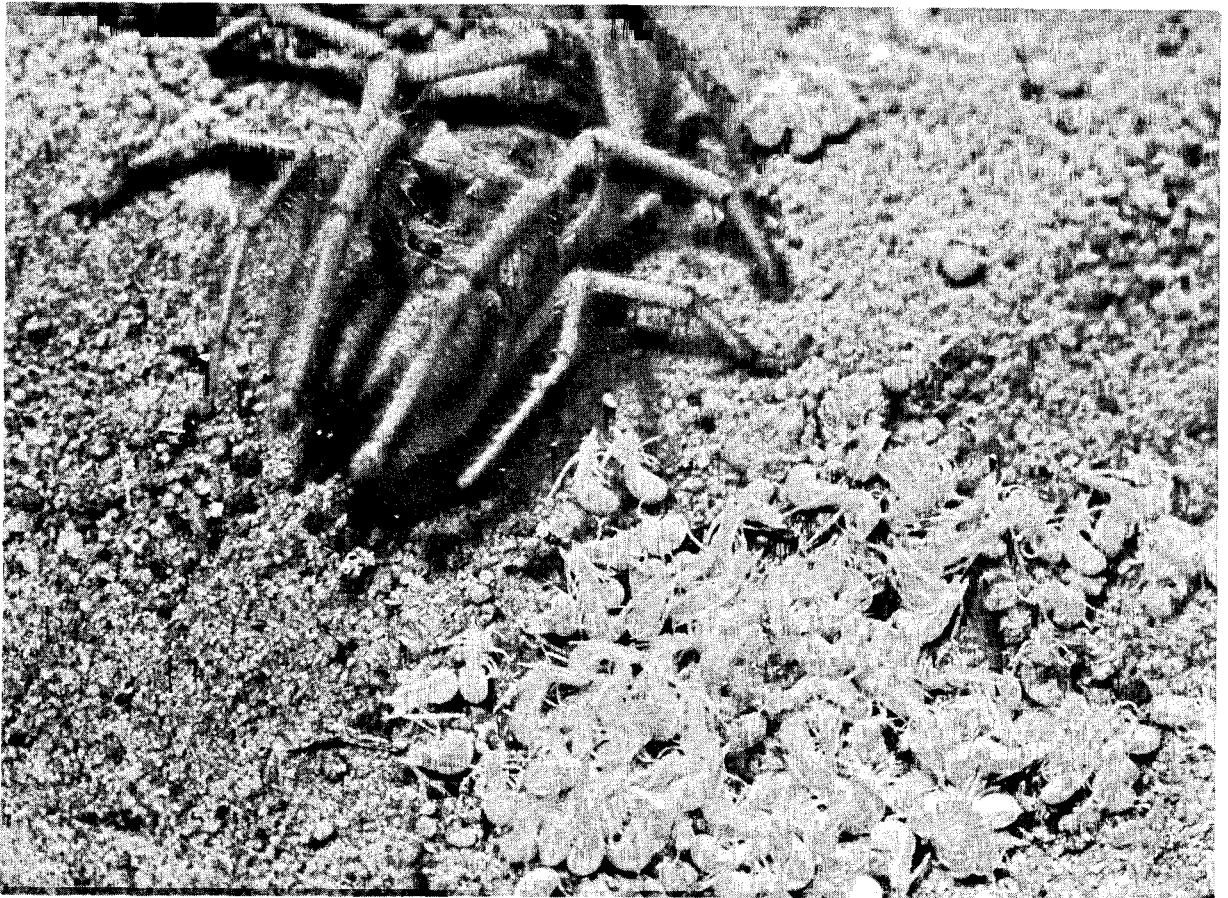


Plate 4: *Galeodes granti* Pocock. Female guarding first instar young (natural size).



sort of way (Cloudsley-Thompson, 1967) – and the same is probably true of *Solpuga caffra* Pocock, in which species the female does not immediately leave her eggs after laying them (Lawrence, 1949).

### Phenology

Despite their large size, Solifugae appear to live for only a year in the Sahara (Cloudsley-Thompson, 1961b), and the same is true of American species (Muma, 1963). It probably applies to all species. The life cycle has, however, been studied in very few species. In the Sudan, as in North America, the young are produced in summer, at the time of the annual desert rains, when there is plenty of food. It is not known where the juvenile instars pass the winter, for they are seldom to be found. It seems likely, never-

theless, that they may secrete themselves in the nests of termites, where they would obtain plenty of food, even though the desert outside is somewhat lifeless at that time of year. Seasonal changes in respiratory function probably result from thermal acclimation, as in other desert arthropods (Carlisle and Cloudsley-Thompson, 1968).

### References

- AMITAI, P., LEVY, G. and SHULOV, A. 1962: Observations on mating in a solifugid *Galeodes sulfuripes* Roewer. *Bull. Res. Coun. Israel (B) Zoology* **11**: 156-9.
- BANTA, B. H. and MARER, P. J. 1972: An attack by a solpugid on an iguanid lizard hatching. *Br. J. Herpetol.* **4**: 266.
- BERLAND, L. 1932: *Les arachnides*. 33-43. Paris: Lechevalier.

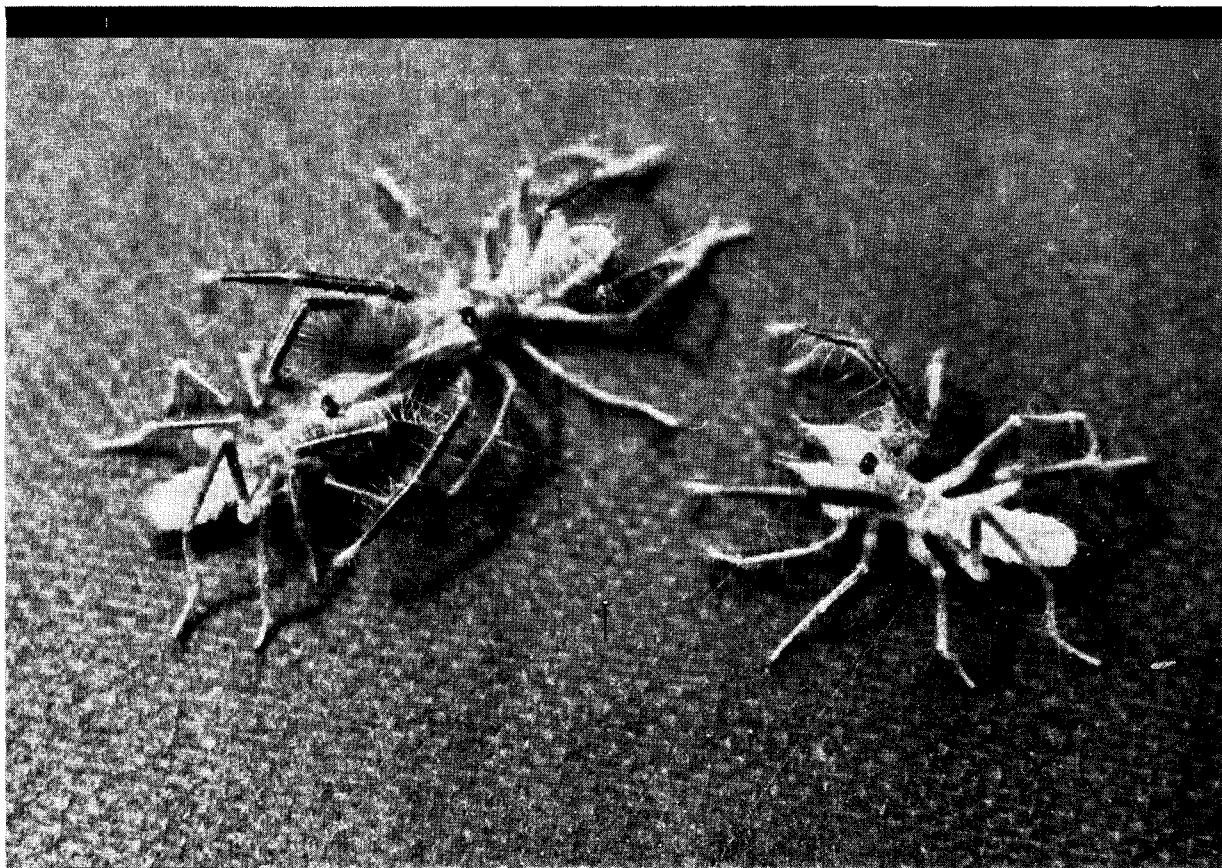


Plate 5: *Galeodes granti* Pocock. Second instar young (enlarged).

- BERNARD, H. 1892: Are the Solpugidae poisonous? *Nature, Lond.* **46**: 223.
- BERNARD, H. M. 1896: The comparative morphology of the Galeodidae. *Trans.Linn.Soc.Lond.* (2) **6**: 305-417.
- BERNARD, H. M. 1897: 'Wind scorpions', a brief account of the Galeodidae. *Sci.Prog.* (N.S.) **1**: 317-43.
- BINGHAM, C. T. 1900: Account of a remarkable swarming for breeding purposes of *Sphex umbrosus* Christ, with notes on the nests of two other species of *Sphex* and of certain of the Pompilidae. *J.Bombay nat.Hist.Soc.* **13**: 177-80.
- BIRULA, A. 1893: Untersuchungen über den Bau der Geschlechtsorgane bei den Galeodiden. *Trudy russk. ent.Obshch.* **18**: 289-326.
- BOLWIG, N. 1952: Observations on the behaviour and mode of orientation of hunting Solifugae. *J.ent.Soc.sth.Afr.* **15**: 239-40.
- BROWNELL, P. H. and FARLEY, R. D. 1974: The organization of the malleolar sensory system in the solpugid, *Chanbria* sp. *Tissue & Cell* **6**: 471-485.
- CARLISLE, D. B. and CLOUDSLEY-THOMPSON, J. L. 1968: Respiratory function and thermal acclimation in tropical invertebrates. *Nature, Lond.* **218**: 684-5.
- CLOUDSLEY-THOMPSON, J. L. 1949: Notes on Arachnida, 9. - Do Solifugae mimic scorpions? *Entomologist's mon.Mag.* **85**: 47.
- CLOUDSLEY-THOMPSON, J. L. 1954: Notes on Arachnida, 22. - The function of the palpal organ of Solifugae. *Entomologist's mon.Mag.* **90**: 236-7.
- CLOUDSLEY-THOMPSON, J. L. 1958: *Spiders, scorpions, centipedes and mites*. 87-98 (Revised Ed., 1968, 105-23). Pergamon, Oxford.
- CLOUDSLEY-THOMPSON, J. L. 1960: Adaptive functions of circadian rhythms. *Cold Spring Harb.Symp.quant. Biol.* **25**: 345-55.
- CLOUDSLEY-THOMPSON, J. L. 1961a: Some aspects of the physiology and behaviour of *Galeodes arabs*. *Entomologia exp.appl.* **4**: 257-63.
- CLOUDSLEY-THOMPSON, J. L. 1961b: Observations on the natural history of the 'camel-spider' *Galeodes arabs* C. L. Koch (Solifugae: Galeodidae) in the Sudan. *Entomologist's mon.Mag.* **97**: 145-52.
- CLOUDSLEY-THOMPSON, J. L. 1962: Lethal temperatures of some desert arthropods and the mechanism of heat death. *Entomologia exp.appl.* **5**: 270-80.
- CLOUDSLEY-THOMPSON, J. L. 1967: Reproduction in Solifugae. *Entomologist's mon.Mag.* **103**: 144.
- CLOUDSLEY-THOMPSON, J. L. 1976: *Evolutionary trends in the mating of Arthropoda*. 50-52. Meadowfield, Sheldon, Co. Durham.
- CLOUDSLEY-THOMPSON, J. L. 1977: *Man and the biology of arid zones*. 71-72. Arnold, London.
- COOK, A. J. 1898: The nature and habits of Pliny's Solpuga. *Nature, Lond.* **58**: 247.
- CRETIN, E. 1896: Habits and distribution of *Galeodes*. *Nature, Lond.* **54**: 366-7.
- CRONEBERG, A. 1887: Ueber ein entwicklungsstadium von *Galeodes*. *Zool.Anz.* **10**: 163.
- DISTANT, W. L. 1892: Are the Solpugidae poisonous? *Nature, Lond.* **46**: 247.
- DUFOUR, L. 1861: Anatomie, physiologie et histoire naturelle des Galeodes. *Mém.prés.div.Sav.Acad. Sci.Inst.Fr.* **17**: 1-109.
- FICHTER, E. 1940: Studies of North American Solpugida 1. The true identity of *Eremobates pallipes* (Say). *Am. Midl.Nat.* **24**: 351-60.
- FISCHER, C. E. C. 1910: Observations on the spider *Galeodes indicus*. *J.Bombay nat.Hist.Soc.* **20**: 886-7.
- HADLEY, N. F. 1974: Adaptational biology of desert scorpions. *J.Arachnol.* **2**: 11-23.
- HEYMONS, R. 1902: Biologische Beobachtungen an asiatischen Solifugen. *Abh.preuss.Akad.Wiss.* **190**: 1-65.
- HEYMONS, R. 1904: Ueber die Entwicklungsgeschichte und morphologie der Solifugen. *Proc. 6th Int.Congr.Zool.* (Berne): 429-36.
- HINGSTON, R. W. 1925: *Nature at the desert's edge*. 230-80. Witherby, London.
- HUTTON, T. 1843: Observations on the habits of a large species of *Galeodes*. *Ann.Mag.nat.Hist.* **12**: 81-5.
- JUNQUA, C. 1958: Observations préliminaires sur la mue et la croissance chez les solifuges. *Bull.Soc.zool.Fr.* **83**: 262-4.
- JUNQUA, C. 1962: Données sur la reproduction d'un solifuge: *Othoes saharae* Panouse. *C.r.hebd.Séanc.Acad. Sci., Paris* **255**: 2673-5.
- JUNQUA, C. 1966: Recherches biologique et histophysiologiques sur un solifuge saharien *Othoes saharae* Panouse. *Mém.Mus.natn.Hist.nat., Paris* (A) **43**: 1-124.
- KAESTNER, A. 1968: *Invertebrate Zoology* (transl. Levi, H. W. and Levi, L. R.) **2**: 218-28, Interscience, New York.
- LAMORAL, B. H. 1974: The structure and possible function of the flagellum in four species of male solifuges of the family Solpugida. *Proc.6th Int.Congr.Arachnol.* 136-41.
- LAWRENCE, R. F. 1947: Some observations on the eggs and newly hatched embryos of *Solpuga hostilis* White (Arachnida). *Proc.zool.Soc.Lond.* **117**: 429-34.
- LAWRENCE, R. F. 1949: Observations on the habits of a female solifuge, *Solpuga caffra* Pocock. *Ann.Transv. Mus.* **21**: 197-200.
- LAWRENCE, R. F. 1963: The Solifugae of South West Africa. *Cimbebasia* **8**: 1-27.
- LAWRENCE, R. F. 1965: Sun-spiders. *Animals* **6**(9): 232-5.
- LICHTENSTEIN, A. A. H. 1797: Naturgeschichte der Insekten-Gattungen *Solpuga* und *Phalangium*, in Herbst, J. F. W. *Natursystem der ungeflügelten Insekten*. Berlin. (Quoted from Bernard, 1895).
- LÖNNBERG, E. 1899: Some biological observations on *Galeodes* and *Buthus*. *K.Vetensk.Akad.Förh.* **56**: 977-83. (Quoted from Berland, 1932).
- MARX, G. 1892: Contributions to the knowledge of the life history of Arachnida. *Proc.ent.Soc.Wash.* **2**: 252.

- MILLOT, J. and VACHON, M. 1949: Ordre des Solifuges, in Grassé, P.-P. (ed.), *Traité de Zoologie* 6: 482-519. Paris: Masson.
- MUMA, M. H. 1951: The arachnid order Solpugida in the United States. *Bull.Am.Mus.nat.Hist.* 97 (2): 35-141.
- MUMA, M. H. 1963: Solpugida of the Nevada test site. *Sci.Bull.Brigham Young Univ.* (Biol.Ser.) 3 (2) 13pp.
- MUMA, M. H. 1966a: Egg deposition and incubation of *Eremobates durangonus* with notes on the eggs of other species of Eremobatidae (Arachnida: Solpugida). *Fla.Ent.* 49: 23-31.
- MUMA, M. H. 1966b: Feeding behaviour of North American Solpugida (Arachnida). *Fla.Ent.* 49: 199-216.
- MUMA, M. H. 1966c: The life cycle of *Eremobates durangonus* (Arachnida: Solpugida). *Fla.Ent.* 49: 233-42.
- MUMA, M. H. 1966d: Burrowing habits of North American Solpugida (Arachnida). *Psyche, Camb.* 73: 251-60.
- MUMA, M. H. 1966e: Mating behaviour in the solpugid genus *Eremobates* Banks. *Anim.Behav.* 14: 346-50.
- MUMA, M. H. 1967: Basic behaviour of North American Solpugida. *Fla.Ent.* 50: 115-23.
- OLIVIER, G. A 1807: *Voyage dans l'Empire Othoman, l'Égypte, et la Perse* 3: 441. Paris. (Quoted from Bernard, 1897).
- PHISALIX, M. 1922: *Animaux venimeux et venins* 1: 300-2. Paris: Masson.
- POCOCK, R. I. 1897: On the genera and species of tropical African Arachnida of the order Solifugae, with notes upon the taxonomy and habits of the group. *Ann.Mag.nat.Hist.* (6) 20: 249-72.
- POCOCK, R. I. 1898: On the nature and habits of Pliny's Solpuga. *Nature, Lond.* 57: 618-20.
- PUTNAM, J. D. 1883: The Solpugidae of America. *Proc. Davenport Acad.Sci.* 3: 195-314.
- SAVORY, T. H. 1928: *The biology of spiders.* 328-30. Sidgwick and Jackson, London.
- SCHMOLLER, R. R. 1970: Terrestrial desert arthropods: fauna and ecology. *Biologist* 52: 77-98.
- TURNER, C. H. 1916: Notes on the feeding behaviour and oviposition of a captive American false spider. *J.Anim. Behav.* 6: 160-8.
- VACHON, M. 1945: Remarques sur les organes génitaux de quelques solifuges (Arachnides). *Bull.Mus.natn.Hist.nat.Paris* (2) 17: 476-82.
- WALTER, A. 1889: Transcaspische Galeodiden. *Zool Jb.* (Syst.) 4: 1094-1109.
- WARBURTON, C. 1909: Solifugae (Solpugae). *Cambridge Natural History* 4: 423-9. London: Macmillan.
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