Ecophysiology of Desert Arachnida

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RIASSUNTO

I fattori che hanno principalmente determinato il grande successo degli Aracnidi deserticoli di maggiori dimensioni - Scorpioni, Solifugi e Migalomorfi - sono: (a) un rapporto superficie/volume inferiore a quello presentato dalle forme di minore mole, (b) elevati valori delle temperature critiche cuticolari e basse velocità di traspirazione, (c) estrema tolleranza termica, (d) cure parentali, (e) una grande efficienza predatoria abbinata alla capacità di sopportare prolungati periodi di digiuno, (f) elusione dei predatori mediante abitudini fossorie e concentrazione dell'attività nella fase notturna.

Altri fattori, quale la dissuasione dei predatori o il mimetismo, sembrano essere meno decisivi.

Parole chiave: Aracnidi, Ecofisiologia, Deserti.

SUMMARY

The factors principally responsible for the conspicuous success of the larger desert Arachnida - Scorpions, Solifugae and Mygalomorphae - are: (a) lower surface-to-volume ratios than those of smaller arachnids, (b) high critical cuticular temperatures and low rates of transpiration, (c) extreme thermal tolerance, (d) brood care, (e) a very efficient predatory mode of life coupled with tolerance of starvation for long periods, (f) avoidance of predators by burrowing habits and strictly nocturnal activity.

Deterrence of predators, mimicry, and so on are less important.

Key words: Arachnids, Ecophysiology, Desert.

Introduction

Scorpions are among the best known and most successful of desert animals. At first sight this may appear surprising because their ancestors were among the first of the terrestrial arthropods. They almost certainly evolved from the early Eurypterida, for Palaeozoic scorpions and eurypterids have much in common and share the following morphological characters: external book gills, flap-like abdominal appendages, and masticatory structures on the coxae of the first limbs. KJELLESVIG-WAERING (1986) has indicated that scorpions and eurypterids are sister groups.

Marine scorpions appeared alongside Eurypterida in the Middle Silurian (425-450 m.y.a.) but, whereas the latter may have remained aquatic (although this has been questioned by SELDEN, 1985) and died out at the end of the Permian, the scorpions invaded the land during the Devonian or early Carboniferous (325-350 m.y.a.) when enclosed lung-bodies evolved in place of external book-lungs. Apart from this, land-living scorpions have changed little from their aquatic ancestors.

Large Mygalomorphae (Orthognatha), numerous in the Australian and North American deserts, are virtually absent from the Great Palaearctic desert where their ecological niche is apparently occupied by Solifugae (CLOUDSLEY-THOMPSON, 1986). Whereas scorpions and Mygalomorphae are long-lived animals, however, the life span of Solifugae does not exceed one year. The latter represent r-selection forms in a r-K continuum. The important correlates of r-selection are associated with an unstable environment, unpredictable resources, catastrophic mortality, highly variable population size, rapid development, a short life cycle, and high productivity. Most r-selection species are small in size: Solifugae are exceptional in this respect. In contrast, K-selection is mainly correlated with the converse condition of large size, long life cycle, slow development, low productivity and so on. Clearly, therefore, the length of the life cycle is not an important factor contributing to the success of large desert arachnids.

The ecophysiology of desert arachnids, in general, has attracted considerable attention in recent years (see CLOUDSLEY-THOMPSON, 1991). The present discussion is therefore focussed upon those characters that appear to be chiefly responsible for their success in arid environments, *viz*: size and water conservation, thermoregulation, reproduction, and mode of life, predation and defence.

Size and water conservation

The basic problem for all desert organisms is the maintenance of an equable temperature without the expenditure of water for evaporative cooling. To smaller animals, such as arachnids and other arthropods (whose surface to volume ratio is correspondingly high), this problem - always present on land - becomes especially acute.

It is, however, less severe in larger than in very small species. This may help to account for the dominance of relatively large arachnids - scorpions, Solifugae and/or Mygalomorphae - in arid environments. It is significant that the integuments of desert arachnids possess unusually impervious cuticular wax layers (HADLEY, 1972). There is also a positive correlation between the high critical temperatures (at which the monomolecular layers of epicuticular wax of these arthropods become disoriented) and the high ambient temperatures that the animals experience in their natural habitats. Below this critical temperature, the rate of water loss by transpiration is especially low in scorpions (EDNEY, 1977). Moreover, the spiracles and lung books of desert arachnids are often sunken and hidden below the surface of the integument, which helps to reduce respiratory water loss (HADLEY, 1972).

Arachnids lay cleidoic eggs (or are secondarily ovoviviparous) and excrete guanine. This, like uric acid, is extremely insoluble, and can be excreted with minimum loss of water. The ability to eliminate nitrogenous excretory products and excess electrolytes with an extremely small volume of water is particularly important in hot dry environments. Moreover, scorpions (HALEY, 1990) and Solifugae (CLOUDSLEY-THOMPSON, 1977) are able to tolerate temporary losses of body water exceeding 30 per cent of their original weight. The success of large desert arachnids must be due, in no small part, to their extreme powers of water conservation and marked tolerance of temporary dehydration.

Response to heat and cold

Arachnids are ectothermal, their metabolic rates are exceptionally low, and most of their body heat is obtained from the environment. Although some small desert species, such as *Metasolpuga picta* (Solifugae: Solpugidae) (WHARTON, 1987) and some of the small Araneae are day-actyve (CLOUDSLEY-THOMPSON, 1983), presumably,

like day-active beetles and lizards, they maintain equable body temperatures by shuttling between sunshine and shade. All larger arachnids, however, appear to be nocturnal (CLOUDSLEY-THOMPSON, 1961, 1977, 1978). I have always attributed this to their vulnerability to predation by larger vertebrates rather than to especial sensitivity to heat. Indeed, lethal temperatures (LT_{50}) for exposures of 24h below 10% relative humidity as high as 50° C have been recorded in the Sudanese solifugid *Galeodes granti* (Galeodidae) and 47° C in the scorpion *Leiurus quinquestriatus* (Buthidae) (CLOUDSLEY-THOMPSON, 1962). These temperatures are apparently well above the high lethal temperatures of day-active tenebrionid beetles and lizards (CLOUDSLEY-THOMPSON, 1991).

At the other extreme, desert scorpions have supercooling points quite as low as those of arthropods from temperate environments. A Supercooling point of -5.8° C has been recorded for *Vaejovis* sp. (Vaejovidae) (CLOUDSLEY-THOMPSON and CRAWFORD, 1970) and of -7.4° C for *L. quinquestriatus* (CLOUDSLEY-THOMPSON, 1973) - temperatures to which these species are never subjected under natural conditions (see discussion in HADLEY, 1990). Clearly, desert arachnids, especially scorpions, owe much of their success to extreme thermal tolerance.

Reproduction

Many desert arthropods are able to survive in their austere environment as a result of social behaviour and the care of their offspring. The woodlouse *Hemilepistus reaumuri* (Isopoda: Oniscidea) provides a classic example.

Parental care is also characteristic of many desert arachnids including scorpions, Solifugae, Lycosidae and some other spiders. Although more typical of K-selection species, it is probably significant that brood care is also found in Solifugae (CLOUDSLEY-THOMPSON, 1977), the females of which guard their eggs and young until after the first moult.

Two types of development occur in scorpions: apoikogenic and katoikogenic. The ova of apoikogenic scorpions contain variable amounts of yolk, while those of katoikogenic scorpions are yolkless and the embryos are nourished orally in specialized diverticula from the female oviuterus. The length of gestation varies in different species from one to 18 months, and the young are fully developed at birth. Apoikogenic scorpions (Bothriuridae, Buthidae, Chactidae, Chaerilidae,

Iuridae and Vaejovidae) are born surrounded by a membrane, from which they soon wriggle free; but katoikogenic scorpions (Diplocentridae, Ishnuridae, and Scorpionidae) do not have this membrane. After birth, the young immediately climb onto their mother's back. Their limbs are able to maintain a grip there because the tarsal claws do not develop until after the first moult (POLIS and SISSON, 1990). Young Lycosidae also mount their female parent, unlike first instar mygalomorphs and Solifugae which have to be content with being guarded by their mother. Brood care undoubtedly contributes to the success of desert Arachnida, while true social behaviour is found in *Stegodyphus* spp. (Eresidae) which benefit in a number of ways from their colonial habits.

The timing of reproduction may be well defined in deserts where the rainfall is seasonal. For istance, in the North American *Paruroctonus mesaensis* (Vaejovidae), birth is synchronized with pulses in the numbers of available prey following precipitation (POLIS and FARLEY, 1979). Solifugae reproduce in late summer on the southern fringe of the Sahara, while the breeding season of Sonoran desert Theraphosidae is likewise in summer.

Predation

A predatory mode of life seems to be especially rewarding in the desert environment (CRAWFORD, 1981), and arachnids are most efficient predators. Furthermore, although their nutritional supply tends to be sporadic in time and clustered in space, desert arachnids are able to tolerate long periods of starvation and often survive for surprisingly long periods without feeding. The larger desert Arachnida are mostly sit-and-wait predators. Sand apparently transmits vibrations well, and BROWNELL and FARLEY (1979a, b) have shown that scorpions are able to locate approaching insects by detecting the compressional and surface waves they set up in the sand. The trichobothria comprise an effective sensory apparatus enabling certain scorpions to localize their prey, while chemoreceptive sensilla on the tips of the chelae, the tarsi of the legs, and the pectines, release specific feeding responses. The vision of Solifugae seems to be little better than that of scorpions, and the prey is detected mainly by touch. The limbs are covered with long sensory hairs which facilitate this. Some Theraphosidae move about until they come across potential prey, while the more sedentary Ctenizidae lift their trap-doors

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at night, and stretch out their front legs, into which the prey wanders. Substrate vibrations are probably detected by slit sensilla and lyriform organs (FOELIX, 1982).

Avoidance of predators

The three factors of the desert environment that influence its inhabitants most are heat, drought, and exposure to enemies. During their daily sojourn in retreats and burrows, nocturnal animals avoid the extremes of all these parameters. Even so, they do not escape them entirely, for the desert may still be hot at night, or it can be cold. It can be very dry, or even flooded, and enemies are never absent. Nor is there security in darkness, for light from the stars and moon in the clear desert sky is so bright that adaptive colouration is important at all times.

As already mentioned, the larger desert arachnids are nocturnal and secrete themselves away from view during the day. Most dig extensive burrows which enable them to avoid extreme temperatures and low humidity (see discussion in CLOUDSLEY-THOMPSON, 1989). Even more important, however, is the protection afforded against predation.

Adaptations for burrowing include the unusually thick and heavy pedipalps (claws) of scorpions of the families Diplocentridae, Vaejovidae, Chactidae and Scorpionidae although, even among these, digging is carried out mainly by the legs - the pedipalps being used chiefly for support. Most members of the family Buthidae, in which the claws are slender, do not burrow. Instead, they inhabit scrapes beneath rocks and surface litter. Exceptions include *Leiurus quinquestriatus* which ranges throughout the eastern part of the Sahara and the Middle East, and *Parabuthus hunteri* of the Sudan. These normally dwell in holes dug deeply into the ground (CLOUDSLEY-THOMPSON, 1991). Four different life styles, with appropriate morphological adaptations, are recognized among scorpions: (a) lithophiles, adapted to life in cracks and crevices in rocks. These have flattened, elongated bodies and curved claws which provide the legs with a strong grip on rough surfaces; (b) psammophiles with long tarsal claws for digging in loose sand; (c) fossorial scorpions which spend almost their entire existence in burrows, from the entrances to which they ambush their prey and grab it with their massive pedipalps; and (d) errant scorpions, which move actively whilst foraging. These have large, slender bodies and pedipalps (POLIS, 1990). Emergence from burrows and retreats, with their equable microclimates (which give little

clue regarding conditions outside) is controlled by 'biological clocks' which synchronize the activities of burrow-dwellers with changing conditions in the outside world (APPLIN *et al.*, 1987). Most arthropods show circadian rhythms of locomotory activity, but those of desert species tend to be especially well marked. This subjective impression is difficult to prove experimentally, but there is evidence to show that desert centipedes, scorpions and mygalomorph spiders (Theraphosidae) are not only more strictly nocturnal than are temperate and tropical forest species, but that they are generally much more active (CLOUDSLEY-THOMPSON, 1981). The physiology of rhythmic locomotory activity in desert arthropods has been reviewed in many books and reviews (see CLOUDSLEY-THOMPSON, 1991), so I will not discuss it again.

Deterrence of predators

Most of the inhabitants of arid regions are either black or pale - resembling the background colour of the desert in which they live. This applies almost equally to nocturnal and day-active species, no doubt as a result of predatory selection at all times. The hypothesis is supported by the fact that more scorpions are active on nights with little or no moon than on nights when the moon is full (HADLEY and WILLIAMS, 1968; POLIS, 1990). Of distasteful desert arthropods with black warning coloration, the most conspicuous are large tenebrionid and scarabaeid beetles. Nearly all arachnids, apart from some scorpions are, in contrast, sandy coloured and apparently avoid the attention of potential predators by their crypsis. Scorpions present a problem. As already mentioned, some are yellow, some black. Some are extremely venomous, others only mildly toxic to mammals, but all desert species appear to be nocturnal. Also, as already mentioned, I believe this to result from the vulnerability of these large, edible arthropods to vertebrate predators (CLOUDSLEY-THOMPSON, 1961). So, why are some yellow and some black? There is no correlation between colour and venom, so one cannot justifiably argue that, in one case, black is aposematic, while, in the other, yellow is cryptic. Even congeneric, sympatric species may differ in colour. For instance the Palaearctic Buthidae *Androctonus australis* and *A. amoreuxi* are yellow, while *A. aeneas, A.bicolor, A. crassicauda* and *A. mauritanicus* are dark brown or black. They are all very large, with massive tails and slender claws, all are extremely poisonous and capable of delivering large quantities of venom, yet their ranges frequently over-

lap, even though their habitats may differ (VACHON, 1952). I am unable to offer any explanation for this apparent paradox.

It is worth remembering that, of almost 1500 known species of scorpions, there are less than 50 whose venom can be dangerous to human beings, and all of these are Buthidae with slender claws. Colour is no guide as to toxicity of the venom. *Leiurus quinquestriatus* has probably the most toxic venom of any scorpion in the world. Fortunately, the amount of poison that it produces is so small that adult human lives are seldom endangered, although *L. quinquestriatus* is a significant cause of death among young children (SIMARD and WATT, 1990).

Apart from their relatively enormous jaws which could, presumably, inflict a sharp bite, Solifugae are relatively defenceless against larger vertebrate enemies (although they often kill scorpions and eat them). In fact, Solifugae seldom attempt to bite but, instead, resort to flight. Theraphosid spiders are armed with urticating hairs (COOKE *et al.*, 1972) which may be a greater deterrent to small mammalian aggressors than is the poisonous bite. In conclusion, deterrence does not appear to be greatly developed amongst desert arachnids.

Mimicry

As in other environments, examples of protective resemblance and mimicry are to be found in the arachnid fauna of deserts. Many Salticidae are batesian mimics of ants (Formicidae) or, to a lesser extent, of Mutillidae. The males of *Cosmophasis nigrocyanea* resemble ants, while the females look like mutillid wasps (CLOUDSLEY-THOMPSON, 1991). When threatened, Solifugae raise the opisthosoma until it is almost vertical, giving a remarkably scorpion-like appearance, particularly to the short-legged Rhagodidae. Scorpions of the families Scorpionidae and Diplocentridae, Solifugae, and Theraphosidae are able to stridulate. The warning sound is probably only a threat display and its function deimatic rather than aposematic. Neither deterrence nor mimicry, in my opinion, are of a level of significance approaching that of the other characters discussed earlier.

Discussion

Large arachnids - especially scorpions, Solifugae and Mygalomorphae - are uniquely successful desert animals, not so much on account of specific environmental adaptations as of their innate characters which preadapt them to life in hot, dry regions. They tend to avoid the extremes of the midday heat behaviourally by escaping into shelter or deep burrows, while conservation of water is primarily physiological. It can truly be argued that the ecology of these, as of other desert animals, is affected less by thermal instability and the scarcity of water than it is by environmental unpredictability (SAFRIEL *et al.*,1989).

The factors principally responsible for the conspicuous success of large desert arachnids - scorpions, Solifugae and Mygalomorphae - are lower surface to volume ratios than those of smaller species, high critical cuticular temperatures and low rates of transpiration, extreme thermal tolerance, brood care, a very efficient predatory mode of life coupled with tolerance of starvation for long periods, avoidance of predators by burrowing habits and strictly nocturnal activity. Other adaptations of desert arachnids, common also to non-desert forms, contribute to the dominance especially of comparatively large forms in the desert environment.

REFERENCES

APPLIN D.G., CLOUDSLEY-THOMPSON J.L. AND CONSTANTINOU C., 1987 - *Molecular and physiological mechanisms in chronobiology - their manifestations in the desert ecosystem.* Journal of Arid Environments, **13**: 187-197.

BROWNELL P.H. AND FARLEY R.D., 1979a - *Detection of vibrations in sand by tarsal sense organs of the nocturnal scorpion,* Paruroctonus mesaensis. Journal of Comparative Physiology, A **131**: 23-30.

BROWNELL P.H. AND FARLEY R.D., 1979b - *Orientation to vibrations in sand by the nocturnal scorpion* Paruroctonus mesaensis: *mechanism of target localization.* Journal of Comparative Physiology, A **131**: 31-38.

CLOUDSLEY-THOMPSON J.L., 1961 - *Adaptive functions of circadian rhythms.* Cold Spring Harbor Symposia on Quantitative Biology (1960), **25**: 345-355.

CLOUDSLEY-THOMPSON J.L., 1962 - *Lethal temperatures of some desert arthropods and the mechanism of heat death.* Entomologia Experimentalis & Applicata, **5**: 270-280.

CLOUDSLEY-THOMPSON J.L., 1973 - *Factors influencing the super-cooling of tropical Arthropoda, especially locusts.* Journal of Natural History, **7**: 471-480.

CLOUDSLEY-THOMPSON J.L., 1977 - *Adaptational biology of Solifugae (Solpugida).* Bulletin of the British Arachnological Society, **4**: 61-71.

CLOUDSLEY-THOMPSON J.L., 1978 - *Biological clocks in Arachnida.* Bulletin of the British Arachnological Society, **4**: 61-71.

CLOUDSLEY-THOMPSON J.L., 1981 - *A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species.* Journal of Arid Environments, **4**: 327-334.

CLOUDSLEY-THOMPSON J.L., 1983 - *Desert adaptations in spiders.* Journal of Arid Environments, **6**: 307-317.

CLOUDSLEY-THOMPSON J.L., 1986 - *Desert adaptations in arachnids.* Proceedings of the 9th International Congress of Arachnology (Panama, 1983). Washington, D.C.: Smithsonian Institute Press, pp. 29-32.

CLOUDSLEY-THOMPSON J.L., 1989 - *Behavioural adaptations of desert Arthropoda.* Bollettino dell'Accademia Gioenia di Scienze Naturali 1987, **20** (332): 283-293.

CLOUDSLEY-THOMPSON J.L., 1991 - *Ecophysiology of desert arthropods and reptiles.* Heidelberg, Berlin, Tokyo: Springer-Verlag. 203 pp.

CLOUDSLEY-THOMPSON J.L. AND CRAWFORD C.S., 1970 - *Lethal temperatures of some arthropods of the southwestern United States.* Entomologist's Monthly Magazine, 106: 26-29.

COOKE J.A.L., ROTH V.D. AND MILLER F.H., 1972 - *The urticating hairs of theraphosid spiders.* American Museum Novitates, No. 2498: 43 pp.

CRAWFORD C.S., 1981 - *Biology of Desert Invertebrates.* Berlin, Heidelberg, New York: Springer-Verlag. 314 pp.

EDNEY E.B., 1977 - *Water Balance in Land Arthropods.* Berlin, Heidelberg, New York: Springer-Verlag. 282 pp

FOELIX R.F., 1982 - *Biology of Spiders*. Cambridge, Mass., London: Harward University Press. 306 pp.

HADLEY N.F., 1972 - *Desert species and adaptations*. American Scientist, **60**: 338-347.

HADLEY N.F., 1990 - *Environmental physiology*. pp. 321-340 *in* Polis G.A. (Ed.) *The Biology of Scorpions*. Stanford, California: Stanford University Press. 588 pp.

HADLEY S.F. AND WILLIAMS S.C. 1968 - *Surface activities of some North American scorpions in relation to feeding*. Ecology, **49**: 726-734.

KJELLESVIG-WAERING E.N., 1986- *A restudy of the fossil Scorpionida of the world*. Palaeontographica Americana No. **55**. 287 pp.

POLIS G.A., 1990 - *Ecology*. pp.247-293 *in* Polis G.A. (Ed.). *The Biology of Scorpions*. Stanford, California: Stanford University Press 588 pp.

POLIS G.A. and FARLEY R.D., 1979 - *Characteristics and environmental determinates of natality, growth and maturity in a natural population of the desert scorpion, Paruroctonus mesaensis (Scorpionida: Vaejovidae)*. Journal of Zoology, London, **187**: 517-542.

POLIS G.A. AND SISSON W.D., 1990 - *Life history*. pp. 161-233 *in* Polis G.A. (Ed.) *The Biology of Scorpions*. Stanford, California: Stanford University Press. 588 pp.

SAFRIEL U., AYAL Y., KOTLER B.P., LUBIN Y., OKVIG-WHITTAKER L. AND PINSHAW B., 1989 - *What's special about desert ecology?* Journal of Arid Environments, **17**: 125-130.

SELDEN P.A., 1985 - *Eurypterid respiration*. Philosophical Transactions of the Royal Society, B **309**: 219-226.

SIMARD J.M. AND WATT D.D., 1990 - *Venoms and toxins*. pp. 414-444 *in* Polis, G.A. (Ed.). *The Biology of Scorpions*. Stanford California: Stanford University Press. 588 pp.

VACHON M., 1952 - *Études sur les scorpions*. Alger: Institut Pasteur d'Algérie. 482 pp.

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.