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Biological clocks in Arachnida*

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Summary

Apart from investigations of photoperiod in the regulation of reproduction and diapause in Acari, little attention has so far been paid to the study of biological clocks and circadian rhythms in Arachnida. These are apparently concerned mainly with cycles of locomotory activity, physiological rhythms and time-compensated celestial orientation. Diapause induction through photoperiodic responses has not been demonstrated. The nocturnal behaviour of scorpions and solifugids is probably related mainly to the avoidance of vertebrate enemies, although fluorescence in ultraviolet light suggests that radiation could have harmful effects on their integuments. The existence of circannual clocks has not been demonstrated even in long-lived species.

Introduction

The traditional, somewhat insular, approach of scientists to their own disciplines is, at last, beginning to break down. The study of biological clocks, in particular, offers unique opportunities for fruitful collaboration between biologists trained in different fields, as well as between them and biochemists, physicists and mathematicians. Nevertheless, apart from investigations of the measurement of photoperiod for the regulation of diapause among Acari, little attention has so far been paid to the study of biological clocks and circadian rhythms in Arachnida. By comparison, the rhythms of insects have been studied extensively (cf. Beck, 1968; Cloudsley-Thompson, 1961b; Saunders, 1976; Sollberger, 1965). It is the purpose of this paper to review the work so far undertaken on the physiology and adaptive functions of biological clocks in Arachnida (excluding Acari), so that this can be related to the knowledge already obtained from other groups of animals.

Biological clocks are interpreted as endogenous, self-sustained oscillations which persist under constant conditions. The phases of the rhythms they engender are not necessarily restricted to any particular time or season, but can be entrained by environmental synchronizers. Of these, light is by far the most important, although thermal fluctuations may also sometimes be effective. The periods of biological rhythms are relatively independent of ambient temperature. Diurnal rhythms have been reported in a wide variety of organisms, from unicellular Algae and Protozoa to the most highly evolved plants and animals; and it may be that the circadian clock controls circalunadian and circannual rhythms through frequency demultiplication. Arachnid material has been little used as a medium for studies of the fundamental nature of biorhythms, however, and we shall be concerned here mainly with the adaptive functions of such rhythms in members of the Class.

Activity rhythms

Diurnal rhythms of activity are especially important to the inhabitants of arid regions where contrast between the physical conditions of day and night are so marked. Elsewhere they are less significant but, even so, play an important part in arachnid ecology.

Scorpions

A dominant faunal element of tropical and, especially, of hot arid places, scorpions exploit burrowing and nocturnal habits which enable them to avoid extreme temperatures and low humidity. Vertical movements between the surface and the depths of the burrow provide a wide choice of microclimates throughout the night and day (Cloudsley-Thompson, 1956; Hadley, 1970a, 1974). Yet desert scorpions, like Solifugae, are usually resistant to high temperature (Cloudsley-Thompson, 1962, 1963; Hadley, 1970b, 1974). Moreover, they have extremely low transpiration rates, and their epicuticular wax layers show remarkably high critical temperatures (Abushama, 1963; Cloudsley-Thompson, 1956; Hadley, 1970b). For these reasons, the suggestion has been made that ecological factors, such as the avoidance of predators, may be more significant than physiological requirements in the nocturnal behaviour

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of these animals, even in desert regions (Cloudsley-Thompson, 1961a). Several species of birds, for instance, are known to feed on scorpions (Lourenço & Dekeyser, 1976). Furthermore, scorpions come out into the open less frequently in bright moonlight than on dark nights (Hadley & Williams, 1968). At the same time, as discussed on p. 187, the fact that they are fluorescent in ultra-violet light suggests that scorpions may be somewhat vulnerable to solar radiation.

The species of scorpion whose activity rhythms have been tested experimentally by means of aktograph apparatus, coupled with their rates of water loss in dry air at various temperatures, are listed in Table 1. No direct correlation is evident, however, between the degree of nocturnalism shown by scorpions and their rates of water loss by transpiration (Toye, 1970), although there is a relationship between the rates of water loss and geographical distribution (Cloudsley-Thompson, 1963). The only species so far not found to be strictly nocturnal under experimental conditions are *Pandinus gregoryi* (Pocock) and *P. imperator* (C. L. Koch).

By means of aktograph apparatus, it has been shown that maximum locomotory activity in *Buthotus minax* (C. L. Koch) takes place in darkness when the temperature is rising. These factors entrain the circadian rhythm of the species, which is neither accelerated nor retarded in constant darkness, and therefore, does not follow the 'circadian rule' (Cloudsley-Thompson, 1973). The circadian locomotory rhythm of *Babycurus buttneri* Karsch (= *B. centrurimorphus* Birula) is likewise entrained by transitions from light to dark and vice versa, and by rising or falling temperatures. Transitions from light to dark, darkness to light, and regularly falling temperatures can entrain different rhythms simultaneously in the same individual scorpion. The rhythm tends to be accelerated in constant darkness (Cloudsley-Thompson, 1975). These observations are in agreement with those made by Wuttke (1966) on *Euscorpius carpathicus* L., in which species a bimodal curve of activity was obtained, with a maximum during the first hour after the onset of activity. The free-running period of *E. carpathicus* tends to be shorter in constant darkness than in constant light, as it is in *B. buttneri.*

Field observations in New Mexico have revealed that, during warmer months, nocturnal extra-rock surface activity is greater in *Centruroides sculpturatus* Ewing than in *Diplocentrus spitzeri* Stahnke which tends to remain beneath rocks and near to the openings of its burrow. During the day, *C. sculpturatus* also uses rocks for shelter, and clings to their

Species	Temperature (°C)	Rate of water loss (mg cm^{-2} h^{-1})	Source
Androctonus australis (L.)	30	0.20	Cloudsley-Thompson (1956)
Babycurus buttneri Karsch (= *B. centrurimorphus* Birula)	–	–	Cloudsley-Thompson (1975)
Buthotus minax (C. L. Koch)	33	0.037	Cloudsley-Thompson (1963, 1973)
Buthotus hottentota (Fabr.)	25 ± 1	0.108	Toye (1970)
Buthus occitanus (Am.)	30	0.20	Cloudsley-Thompson (1956)
Centruroides sculpturatus Ewing	–	–	Crawford & Krehoff (1975)
Diplocentrus spitzeri Stahnke	–	–	Crawford & Krehoff (1975)
Euscorpius carpathicus L.	–	–	Wuttke (1966)
Hadogenes bicolor Purcell	–	–	C. Constantinou (pers. comm.)
Hadrurus hirsutus (Wood)	33 ± 1	0.025	Cloudsley-Thompson (1968)
Leiurus quinquestriatus (H. & E.)	–	–	Abushama (1963)
	33 ± 2	0.021	Cloudsley-Thompson (1961e)
Pandinus exitialis (Pocock)	33 ± 2	0.51	Cloudsley-Thompson (1963)
Pandinus gregoryi (Pocock)	–	–	C. Constantinou (pers. comm.)
Pandinus imperator (C. L. Koch)	25 ± 1	0.233	Toye (1970)
Scorpio maurus L.	30	0.20	Cloudsley-Thompson (1956)

Table 1: Species of scorpion on which aktograph experiments have been carried out, with rates of water loss in dry air where known.

under surfaces. Aktograph studies showed both species to be nocturnally active when imposed photoperiod was the sole variable, but only *D. spitzeri* displayed an endogenous circadian rhythm in constant darkness (Crawford & Krehoff, 1975).

Most scorpions tested under laboratory conditions have been found to be negatively phototactic and to avoid high temperatures; *Opisthophthalmus latimanus* C. L. Koch, however, shows a striking photopositive response to directed light, but this becomes photonegative at high temperatures when 'stilting' is no longer effective (Alexander & Ewer, 1958).

Solifugae

With the exception of a few small, brightly coloured forms, such as *Gluvia dorsalis* (Latr.), *Hemerotrecha californica* (Banks), *Mummucia variegata* (Gerv.) and *Pseudocleobis morsicans* (Gerv.), solifugids are strictly nocturnal, like scorpions. As described on p. 188 they are also fluorescent in ultraviolet light. A similar argument – that their nocturnal habits may be related to vulnerability to day-active predators, such as reptiles and birds – is therefore probably valid (Cloudsley-Thompson, 1977). Field observations on the time of locomotory activity in Solifugae have been confirmed experimentally only in the case of *Galeodes granti* Pocock which, in aktograph apparatus, has been found to be strictly night-active (Cloudsley-Thompson, 1961d).

Uropygi

Whipscorpions (*Mastigoproctus giganteus* (Lucas)) are efficient nocturnal predators that survive, without drinking, on a diet of insect prey which provides them with adequate moisture although, due to abrasion of their epicuticular wax layers, they lose water rapidly through transpiration. They are ardent burrowers, especially when desiccated, and are seldom found in the open except after rain. Although they respond positively to moist air, they show no preference for light or darkness (Crawford & Cloudsley-Thompson, 1971).

Opiliones and Araneae

Although harvestmen may be active at all times, most of their movement takes place at night, or during the day if they are hungry and the humidity is high – a combination of factors that occurs more often in scrub than in woodland. When a species is found over a wide range of environments, its diel periodicity is most sharply circumscribed in more favourable habitats (Williams, 1962). In a laboratory study, 90 per cent of the activity of *Phalangium opilio* L. and 70 per cent of that of *Leiobunum* spp. took place during the hours of darkness. The rhythm persisted under constant conditions (Edgar & Yuan, 1968).

Aktograph experiments have shown that British spiders of the genus *Amaurobius* (= *Ciniflo*) are strictly nocturnal. Although *A. ferox* (Walck.) loses water by transpiration much more rapidly than *A. similis* (Bl.) or *A. fenestralis* (Stroem), over 90 per cent of the activity of all three species takes place in darkness (Cloudsley-Thompson, 1957). It seems probable, therefore, that nocturnal behaviour may be related more to biotic than to physical factors of the environment. The same may well be true of the North American mygalomorph spiders *Aphonopelma* (= *Eurypelma*) spp. which are strictly night-active (Cloudsley-Thompson, 1968) and spend the days in self-constructed burrows at a depth sufficient to reduce temperature variations substantially (Seymour & Vinegar, 1973). Humphreys (1975) has pointed out that, by remaining at ambient temperature instead of thermoregulating, the Australian wolf-spider *Geolycosa godeffroyi* (L. Koch) could save from 50 to 70 per cent of its total water loss. Were moisture a limiting factor, the spider might be expected to exploit a different behavioural strategy. Although the influence of biotic factors predominates in determining the time of spider activity, physical factors may also be involved.

Physiological rhythms

Scorpions

Rhythms of locomotory activity are naturally paralleled by physiological rhythms. Several species of scorpion exhibit circadian rhythms of oxygen consumption which persist for many days in constant temperature and darkness. These species include *Euscorpius italicus* (Herbst) and *E. carpathicus* L. according to Dresco-Derouet (1961) and *Centruroides sculpturatus* Ewing. This latter remains in bark crevices or under some form of cover during the day and, soon after sunset, does not walk about but merely comes to the surface where it sits motionless, awaiting potential prey (Hadley & Hill, 1969). Abrupt changes in illumination, as occur at sunset, initiate brief but large outbursts of respiratory activity which may signify such movement onto the surface rather than prolonged locomotory activity. Chengal Raju, Bashamohideen & Narasimham (1973) have demonstrated a circadian rhythm in the blood glucose and liver glycogen levels of *Heterometrus fulvipes* (C. L. Koch): this reflects various levels of use in activities such as the synthesis of acetylcholine and the circadian rhythm of heartbeat (Devarajulu Naidu, 1969). Levels of muscle dehydrogenase are highest in this species at times of increased locomotor activity and oxygen consumption (Rao & Govindappa, 1967), while a positive correlation has been obtained between spontaneous electrical activity of the ventral nerve cord and cholinesterase activity which show a regular circadian rhythm coinciding with nocturnal activities of the scorpion as observed in nature (Venkatachari & Dass, 1968). Recordings of electroretinogram amplitudes by means of implanted electrodes have shown that, in constant darkness, the median eyes of *Androctonus australis* (L.) change their sensitivity endogenously between that of the state of subjective day and that of subjective night: the sensitivity of the lateral eyes is much lower. This transition compensates for diminishing light at dusk (Fleissner, 1977).

Fluorescence in ultra-violet light

Scorpions

It is now well known that scorpions emit a fluorescent glow when exposed to ultra-violet light. They can easily be collected in open country at night with the aid of an ultra-violet lamp (Honetschlager, 1965; Lawrence, 1954; Williams, 1968). Experiments on museum specimens, either dried or preserved in alcohol – in some cases for many years – have shown that this quality is not lost after death. In some cases, however, the preserving fluid becomes fluorescent, suggesting that a solvent may also be involved. The phenomenon is presumably caused by the molecular constitutions of the scorpion's integument. It suggests that, in daylight, scorpions could absorb a degree of radiation that might have a deleterious effect upon their cuticles, just as sunlight does on many man-made polymers. Several species of scorpions and other arachnids from the writer's collection were therefore tested in the darkroom in ultra-violet light to determine whether any correlation could be drawn between fluorescence in ultra-violet light and nocturnal habits. Newly moulted scorpions do not fluoresce (B. Betts, pers. comm.).

When exposed to ultra-violet light, scorpions of 18 different species belonging to the families Buthidae, Scorpionidae, Vejovidae and Chactidae, all exhibited fluorescence. Yellow desert Buthidae, such as *Hadrurus hirsutus* (Wood), *Buthus occitanus* (Am.), *Androctonus australis* (L.) and *Oiclus purvesii* (Becker) fluoresced brightly, as did *Androctonus aeneas* C. L. Koch, *Parabuthus hunteri* Pocock, *Tityus trinitatis* Pocock, *Scorpio maurus* L., *Pandinus imperator* C. L. Koch and *P. exitialis* (Pocock) – despite their dark pigmentation. *Palamnaeus fulvipes* (C. L. Koch) fluoresced very strongly indeed.

Most of these species are known to be strictly nocturnal (Cloudsley-Thompson, 1956, 1963), but *P. imperator* is crepuscular or day-active (Toye, 1970). Aktograph experiments have shown that 69 per cent of its locomotory activity occurs during the daytime but, of course, it is normally restricted to subtropical forests where the heavy canopy and dense undergrowth present lighting conditions during the day which are similar to those of more exposed habitats at night (Hadley, 1974).

The situation with regard to *Euscorpius flavicaudis* (Deg.) is different. According to Wanless (1977) *E. flavicaudis*, which has been established at Sheerness, Sheppey, for over a century, can be seen basking in the sunlight on warm days. Indeed, its ability to survive so far north of its normal environment may well be associated with this behavioural trait. Very little fluorescence could be observed from this species when inspected under ultra-violet illumination except from the yellow spot on its tail. The remainder of the body appeared dark grey, like that of *E. italicus* (Herbst) and *E. germanus* Schaeffer under similar conditions. In his account of the zoology of Trabzon, Deryugin (1899) stated that *E. italicus* is attracted by light, and frequently crawls into rooms at night.

Other orders

The fluorescent responses of other orders of arachnids to ultra-violet light were varied. (Insects did not fluoresce). No fluorescence was observed among Araneae (including the primitive *Liphistius batuensis* Abraham), Pseudoscorpiones, Schizomida (*Schizomus latipes* Hansen), or Phrynichida (*Tarantula marginemaculata* C. L. Koch). Various Opiliones showed extremely faint fluorescence from the body but not from the limbs, while the black *Mastigoproctus giganteus* (Lucas) (Thelyphonida) showed no fluorescence except from the pale intersegmental membranes which glowed quite brightly.

Although perhaps not so fluorescent as scorpions, all the Solifugae tested glowed to some extent in ultra-violet light. *Galeodes granti* Pocock emitted less visible radiation than most scorpions, and the same was true of *Ammotrechella stimpsoni* (Putnam), for instance. But even black *Rhagodes* spp. emitted some fluorescent light. The body of *Rhagodessa melanocephala* Simon showed almost none, although the legs glowed even more brightly than did those of *G. granti* or *A. stimpsoni.*

When it is remembered that Solifugae are markedly nocturnal except, as mentioned above, for a few small brightly coloured species, it becomes apparent that there may be some evidence for the correlation suggested earlier, viz. that species which fluoresce in ultra-violet light tend to show nocturnal activity while day-active arachnids do not exhibit fluorescence.

Lawrence (1954) obtained fluorescence from *Uroplectes formosus* Pocock (Scorpiones), *Solpuga hostilis* (White) (Solifugae), *Damon variegatus* Perty (Amblypygi), the large spider *Harpactira* sp., very slight reactions from Diplopoda, Chilopoda, Isopoda, and some insects (cf. Pope & Hinton, 1977), but none from Onychophora.

The circadian clock in orientation

Araneae

Time-compensated celestial orientation and navigation is probably widespread among arachnids, but has so far been investigated only in wolf-spiders (Lycosidae). When placed on the surface of the water, riparian species of the genus *Arctosa* orientate themselves by means of the sun towards an azimuth which, near the river bank where they live, corresponds to a direction towards the shore. They can also orientate themselves correctly under a clear sky, by means of the polarized light, even when placed in such a position that they are unable to see the sun directly. If they were to find themselves accidentally in the water near their normal habitat, it is by moving in this direction that they would most rapidly escape and regain the shore. Analogous experiments with individuals of different populations show that each one of these has its own direction of flight which corresponds with the lie of the shore that it inhabits (Papi, 1955 a, b, 1959; Papi & Serretti, 1955; Papi & Tongiorgi, 1963 a, b; Tongiorgi, 1961). Specimens kept in the dark for several days orientated correctly at whatever hour the experiment was carried out, indicating that the spiders must make allowance for the movement of the sun (Papi, Serretti & Parrini, 1957).

Solar orientation during the night, studied in an Italian population of *Arctosa cinerea* (Fabr.) by altering the phase of rhythms of illuminations, showed that the animals were incapable of orientation at that time. On the other hand, Finnish populations of the same species, living within the Arctic Circle, navigated correctly at all times on the days around the summer solstice. Between sunset and dawn, the animals orientated themselves by polarized light. Specimens of *Lycosa fluviatilis* Bl., however, were capable of orientation by the sun throughout the 24 hours (Papi & Syrjamaki, 1963).

Phenology

Although scorpions are long-lived animals, very little research has been carried out on their phenology and survival during unfavourable times of the year, apart from a study of the overwintering physiology of *Diplocentrus spitzeri* Stahnke by Crawford & Riddle (1975). These authors concluded that, although winter cold is a common cause of death, seasonal changes in supercooling ability are not clearly related to cold hardiness in this species. On the other hand, tolerance of prolonged cold varies seasonally, as does the rate of oxygen consumption. The existence of an endogenous circannual clock in scorpions has neither been confirmed nor disproved.

In general, even the largest species of Solifugae live no longer than a year (Cloudsley-Thompson, 1961c, 1977; Muma, 1963), so the question as to the existence of a circannual clock does not arise. In cooler weather, the activity rhythm of *Galeodes granti*

Pocock is less rigid than it is when hot, and aktograph records may then indicate a certain degree of movement during the daytime (Cloudsley-Thompson, 1961d). Seasonal changes in respiratory function probably result from thermal acclimation (Carlisle & Cloudsley-Thompson, 1968).

The autecology and phenology of other orders, such as Opiliones and Araneae, have been investigated by many authors (e.g. Braun & Rabeler, 1969; Cloudsley-Thompson, 1955; Edgar, 1971; Williams, 1962), but no evidence of a circannual clock has been reported, even in long-lived species. Seasonal changes of prey appear to be related to availability rather than to changes in preference (Edgar, 1969).

Diapause induction

Obligatory diapause is induced by changes of temperature in the harvestman *Mitopus morio* F. Egg deposition takes place at the end of July, in Germany. Embryological development then proceeds at summer temperatures until it is arrested at a genetically determined stage; hatching occurs the following spring. Three phases can be distinguished during embryogenesis: the first and last take place only at higher temperatures, whereas the middle one demands a significantly lower temperature. Consequently, it is not possible to rear *M. morio* in the laboratory at constant temperatures. In nature, dormancy is initiated in summer during the second embryonic phase. Development remains arrested until low winter temperatures engender completion of the second phase of embryogenesis, but the third stage of development cannot take place until the advent of warm spring weather. In this way, untimely hatching in autumn and winter is prevented, and the nymphs do not appear until adequate food is available in spring (Tischler, 1967).

Induction of diapause by changing day lengths implies the existence of a circadian clock to monitor photoperiod. It is a striking adaptation of the life-cycles of insects and Acari to seasonally changing environments, but it has not yet been demonstrated in the case of other Arachnida.

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The web of *Paraneus cyrtoscapus* (Pocock, 1899) (Araneae: Araneidae) in Ghana*

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Summary

Paraneus cyrtoscapus was found in Ghana on two types of web. One was a normal, almost vertical, araneid web. The other was basically horizontal, but with the hub pulled up by threads attached to the vegetation above, so that it formed a shallow cone. The latter was smaller both in diameter and mesh size than the normal web, and occurred closer to the ground. It had a defective frame, radii being attached to the vegetation or to very short frame threads. Both types of web were found mainly in grassy, sunny areas. Only mature females were found on vertical webs. Juveniles, mature males and a few mature females were found on horizontal webs. The most likely explanation is that all spiders spin horizontal webs until they are mature, but that shortly after reaching maturity females change to building vertical webs.

Introduction

Whilst studying the ecology of Araneidae and Tetragnathidae at Legon (near Accra), Ghana, between February 1971 and August 1973, I occasionally saw the webs of what I assumed to be two species of Araneinae, though the spiders were similar in appearance. One type of web was an almost vertical normal araneid web, and the other was an almost horizontal cone-shaped web. Spiders from both types of web have since been identified as *Paraneus cyrtoscapus* by Dr M. Grasshoff (pers. comm.). The vertical web was not common; the horizontal web was easily overlooked as it occurred low in the grass. However, the spider was probably common as one individual of the wasp *Chalybion fuscipenne* Smith stocked 11 cells with 78 *P. cyrtoscapus* out of 93 araneids and a total of 112 spiders. Because of the difficulty in finding the spiders, observations were not as extensive as they would have been if I had realised during the field work that there was a single species building two types of web.

P. cyrtoscapus is an African species (M. Grasshoff, pers. comm.). All individuals were entirely brown with some mottling on the abdomen, especially ventrally; mature specimens were dark reddish brown, juveniles normally yellowish or greyish brown. For three mature females the weight varied from 230-481 mg and measurements were:– total length: 11.0-14.0 mm; carapace length: 5.0-7.0 mm; length of first leg: 18.0-22.5 mm. Males were on average slightly smaller,

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