

- MILLIDGE, A. F. 1985: Some linyphiid spiders from South America (Araneae: Linyphiidae). *Am. Mus. Novit.* **2836**: 1–78.
- MILLIDGE, A. F. 1991: Further linyphiid spiders (Araneae) from South America. *Bull. Am. Mus. nat. Hist.* **205**: 1–199.
- MILLIDGE, A. F. 1993: Further remarks on the taxonomy and relationships of the Linyphiidae, based on the epigynal duct conformations and other characters (Araneae). *Bull. Br. arachnol. Soc.* **9**: 145–156.
- OROMI, P., MARTIN, J. L., MEDINA, A. L. & IZQUIERDO, I. 1991: The evolution of the hypogean fauna in the Canary Islands. In E. C. Dudley (ed.) *The unity of evolutionary biology*: 380–395. Dioscorides Press, Portland, Oregon.
- PECK, S. B. 1990: Eyeless arthropods of the Galapagos Islands, Ecuador: composition and origin of the cryptozoic fauna of a young, tropical, oceanic archipelago. *Biotropica* **22**: 366–381.
- RIBERA, C., FERRANDEZ, M. A. & BLASCO, A. 1985: Araneidos cavernícolas de Canarias II. *Mém Biospéol.* **12**: 51–66.
- SOUTHWOOD, T. R. E. 1962: Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.* **37**: 171–214.
- TAITI, S. & FERRARA, F. 1991: Two new species of terrestrial Isopoda (Crustacea, Oniscidea) from Ascension Island. *J. nat. Hist.* **25**: 901–916.

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## The activity cycle of the social spider *Phryganoporus candidus* (Araneae: Desidae)

Michael F. Downes

Zoology Department,  
James Cook University, Townsville,  
Queensland 4811, Australia\*

### Summary

Regular observations of *Phryganoporus candidus* (= *Badumna candida*) (L. Koch) colonies over a two-year period showed that colony activity began at sunset and fell off between 2200 and 2400 h. Three components of activity were measured: web work, predation and extra-nest activity. Web work peaked before predation each evening. The activity cycle of *P. candidus* appears to be both exogenous and endogenous.

### Introduction

Spiders of the genus *Amaurobius*, to which *Phryganoporus candidus* was previously referred (Gray, 1983), undertake more than 90% of their activity during the hours of darkness (Cloudsley-Thompson, 1957). Moreover, all of the permanent-social spiders, such as *Agelena consociata* Denis, are more or less nocturnal in habits (Cloudsley-Thompson, 1986), and this seems to be true also for colonial orb-weavers such as *Eriophora bistrata* (Renger) (Fowler & Diehl, 1978), but very few studies on any spiders have considered whether these daily rhythms are exogenous, endogenous or composite (an example of the latter is the 24-hour cycle of photoreceptor physiology in the posterior median eyes of *Deinopsis subrufa* L. Koch (Blest, 1978)). If circadian (endogenous) rhythms follow and reflect monophyletic and very ancient lineages in animals (Pittendrigh, 1966), then most 24-hour activity cycles of animals are likely to be composite, in so far as the cycles will also relate to extrinsic factors. For example, spiders of the genera *Dictyna* and *Mallos* become active in the early evening, a time when dipterans and other insect prey are themselves most active (Jackson, 1978).

Biological clocks in general (and in the present context, circadian rhythms in particular) have been classified in various ways. One such classification recognises “pure”

rhythms (e.g. colour change in crabs), interval timers (e.g. pupal eclosion) and continuously consulted clocks (e.g. time-compensated sun orientation in bees) (Pittendrigh, 1958, in Saunders, 1982). These kinds of classifications reflect the fact that various behavioural and physiological activities of organisms will differ in their responses to photoperiodic and other environmental cycles in nature. Hence we might expect feeding activity to be more opportunistic, and less endogenous, in many animal species, than some other functions. Among spiders, web-spinning activity seems to be an especially finely-tuned circadian rhythmic behaviour (Tietjen, 1986).

This paper describes how feeding, spinning and extra-nest activity (defined below) relates to the 24-hour cycle in *Phryganoporus candidus* (L. Koch). As *Badumna candida* this is one of three species that together form what Gray (1983) has called the *candida* species group of the genus *Badumna*. A current revision, unpublished at the time of writing, proposes that *B. candida* revert to *Phryganoporus candidus* (L. Koch) (M. R. Gray, pers. comm.). Consequently, the latter name is used throughout this study.

Nests of this species are founded early in the year by individual females, and are subsequently enlarged by the female and her offspring (Main, 1971). Average colony size is about 100 spiders; most dispersal occurs between December and February in the Townsville area. Full details of the life cycle will be published separately.

### Methods

Some observations were carried out in an area of open dry sclerophyll woodland surrounding James Cook University, Townsville, Queensland, in locations selected mainly for proximity and/or convenience of access, especially when working in the dark. Most observations, however, were carried out on 20 nests transported from the field to my garden, where they were housed in hanging wire-mesh frames. Five nests were relocated in this way in August 1987 and were disposed of in March 1988. Ten newly-collected nests then took their place from April 1988 until March 1989. Another five nests followed, between April 1989 and February 1990.

Observations were informal in the first year. In the second year, the following three main components of

\*Present address: Dept. of Zoology, Universitetsparken B135, DK8000 Aarhus C, Denmark.

activity were recorded: web construction/repair, predation/feeding, and extra-nest activity (ENA). The latter included the construction of a swathe of silk extending clear of the normal extent of the nest, walking to and fro over the swathe and (rarely) broadcasting single silk strands into the surrounding air.

Each observation lasted 15 minutes, but directly adjacent nests could often be observed simultaneously. Night observations were made by torchlight.

Observations were made at (or close to) all even-hour times of the day and night, i.e. 0200, 0400 h, etc. The numbers of observations for given times differed, however, ranging from 10 (0200 h) to 75 (2000 h). Observations were made in all months of the year except February and March. The minimum and maximum numbers of observations for given months were 12 (January) and 116 (December). The total number of observations was 431 (i.e. 107.75 hours).

In 1989 records included a scale of intensity for each of the three activities (web work, predation and ENA). This scale was an estimate of the proportion of the total nest population engaged in each activity. The proportional categories used were zero, 1–3%, 3–10%, 10–25% and >25%; previously each activity had simply been recorded as present or absent.

Sufficient observations (26% of the total of 431) were made on nests in the field study area to ensure that behaviour in natural and transplanted nests was similar (the three homogeneity tests applied all gave  $p > 0.1$ ). The field and garden-based data were therefore not treated separately.

## Results

*P. candidus* was found to be primarily nocturnal, and normally ignored insects caught in the web in daylight.

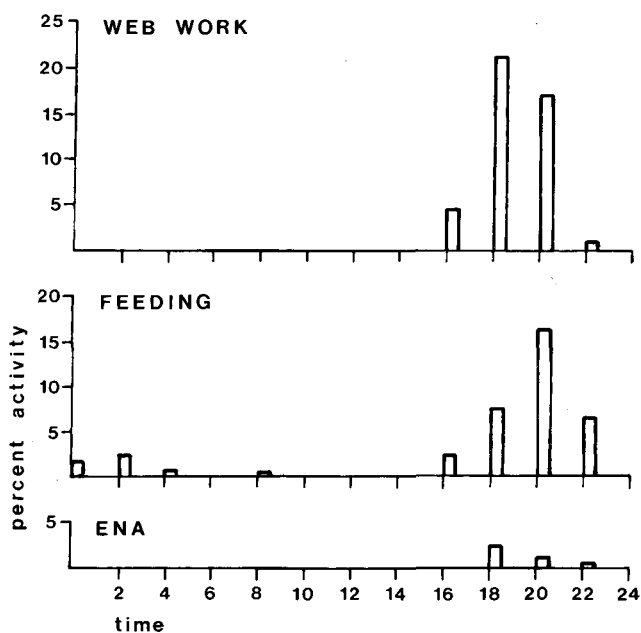


Fig. 1: The daily activity cycle of *P. candidus*: web work, feeding and extra-nest activity. Mean proportion (%) of spiders active during 15-minute observation periods at two-hour intervals. Sunset time is between 1800 and 1900 h.

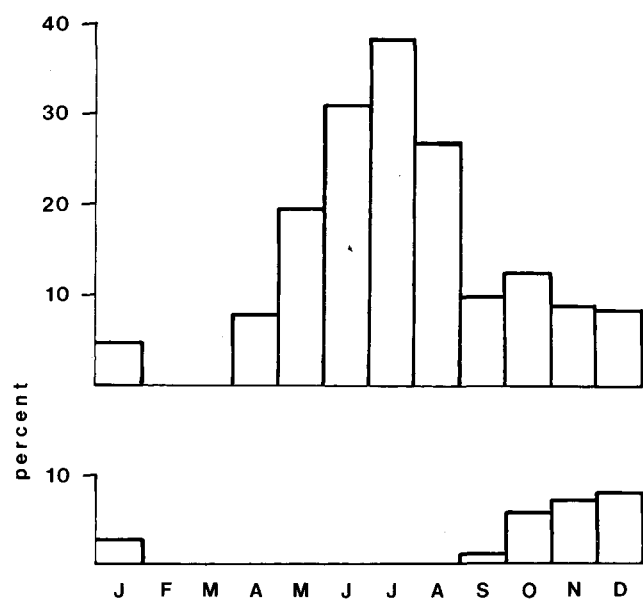


Fig. 2: Mean proportion (%) of *P. candidus* spiders engaging in web work (top) and extra-nest activity (bottom), in different months of the year. No data available for February or March.

Occasionally, however, prey struggling in the web induced some spiders to leave the retreat to feed well after sunrise (Fig. 1). During the early afternoon — as a rule the hottest part of the day — they were almost invariably inactive, and characteristically accumulated just beneath, and in the shadow of, the retreat area. The spiders did not stand far from the underside of the retreat at these times and thus did not expose themselves unduly to predation. They took on a very limp aspect in this situation, hanging motionless with their abdomens dangling almost vertically down, often in small clusters like bunches of grapes.

Activity got under way at or just before sunset, peaked during the early to middle evening and fell off between 2200 and 2400 h (Fig. 1).

Web work (repairs, alterations and extensions) began as soon as the spiders became active, but successful predation and feeding did not usually occur so promptly; hence web work tended to peak before the feeding period each evening (Fig. 1). The peak feeding period was not followed by any substantial bout of web work to repair damage arising from the activity of trapped prey.

Occasionally a large prey item was the focus of a feeding peak for most or all of the night, and feeding activity recorded at 0600 h was thus usually the finger-licking stage of a meal begun eight hours earlier.

The intensity of web work varied over the year, peaking between June and August (Fig. 2). Extra-nest activity was not prominent compared with web work and feeding (Fig. 1). This reflected partly the fact that it did not occur at all between about March and August (Fig. 2), and partly the fact that most nests were not displaying ENA even on nights when some were doing so.

## Discussion

The crepuscular/nocturnal pattern of activity detailed here for *P. candidus* is probably composite (i.e. both endogenous and exogenous) in nature. Studies under

constant light and constant dark conditions would be necessary to demonstrate any endogenous component of the behaviour. There are probably two main factors reducing daytime activity in *P. candidus*. One is higher day temperatures, which will produce a direct avoidance response that operates physiologically. The other is predation pressure from day-active birds such as the black-faced cuckoo shrike *Coracina novaehollandiae* (Gmelin) and the spangled drongo *Dicrurus bractiatus* Gould, both of which I have observed feeding on *P. candidus*. This is an ecological factor that will presumably operate on the circadian clock by selection against daytime activity. Even in the absence of such factors, however, the same activity pattern may occur if it optimises the balance between energy expenditure and predation success, given that the spiders' prey itself peaks in availability in the evenings.

This activity cycle is typical of many social spiders. The resid *Stegodyphus sarasinorum* Karsch, for instance, shows an almost identical pattern in so far as its activity peaks in the early to mid-evening, and web-spinning is the earlier activity (Jambunathan, 1905; Kullmann *et al.*, 1972; Jacson & Joseph, 1973). *Mallos gregalis* (Simon), on the other hand, has a single midday period of inactivity and a single peak of activity (recorded as movement events) at about 0400h (Tietjen, 1982). Evidence from the behaviour of isolated *M. gregalis* individuals suggests that the relatively regular daily activity pattern of the colony as a whole may obscure fluctuating periods of high and low activity, over several days, of the individual spiders (Tietjen, 1982).

The seasonal variation in web work reflected the fact that cohorts of newly-emerged *P. candidus* spiderlings did not begin to appear in nests until April, and even then they did not contribute much to the web until they had moulted to second instar. The decline in attention to web work after August coincided with the rising incidence of ENA, and with an increasing prevalence of dispersal.

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#### References

- BLEST, A. D. 1978: The rapid synthesis and destruction of photoreceptor membrane by a dinopid spider: a daily cycle. *Proc. R. Soc. (Ser. B.)* **200**: 463–483.
- CLOUDSLEY-THOMPSON, J. L. 1957: Studies in diurnal rhythms. V. Nocturnal ecology and water-relations of the British cribellate spiders of the genus *Ciniflo* (Bl.). *J. Linn. Soc. (Zool.)* **43**: 134–152.
- CLOUDSLEY-THOMPSON, J. L. 1986: The biorhythms of spiders. In W. Nentwig (ed.), *Ecophysiology of spiders*: 371–379. Berlin, Springer.
- FOWLER, H. G. & DIEHL, J. 1978: Biology of a Paraguayan orb-weaver, *Eriophora bistriata* (Rengger) (Araneae, Araneidae). *Bull. Br. arachnol. Soc.* **4**: 241–250.
- GRAY, M. R. 1983: The taxonomy of the semi-communal spiders commonly referred to the species *Ixeuticus candidus* (L. Koch) with notes on the genera *Phryganoporus*, *Ixeuticus* and *Badumna* (Araneae, Amaurobioidea). *Proc. Linn. Soc. N.S.W.* **106**: 247–261.
- JACKSON, R. R. 1978: Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae): III. Prey and predatory behavior. *Psyche, Camb.* **83**: 267–280.
- JACSON, C. C. & JOSEPH, K. J. 1973: Life-history, bionomics and behaviour of the social spider *Stegodyphus sarasinorum* Karsch. *Insectes soc.* **20**: 189–203.
- JAMBUNATHAN, N. S. 1905: The habits and life history of a social spider (*Stegodyphus sarasinorum* Karsch). *Smithson. misc. Collns* **47**: 365–372.
- KULLMANN, E., NAWABI, St. & ZIMMERMANN, W. 1972: Neue Ergebnisse zur Brutbiologie cribellater Spinnen aus Afghanistan und der Serengeti (Araneae, Eresidae). *Z. Kölner Zoo* **14**: 87–108.
- MAIN, B. Y. 1971: The common 'colonial' spider *Ixeuticus candidus* (Koch) and its synonyms (Dictynidae: Araneae). *J. Proc. R. Soc. West. Aust.* **54**: 119–120.
- PITTENDRIGH, C. S. 1966: The circadian oscillation in *Drosophila pseudoobscura* pupae: a model for the photoperiodic clock. *Z. PflPhys.* **54**: 275–307.
- SAUNDERS, D. S. 1982: *Insect clocks*. Oxford, Pergamon Press.
- TIETJEN, W. J. 1982: Influence of activity patterns on social organization of *Mallos gregalis* (Araneae, Dictynidae). *J. Arachnol.* **10**: 75–84.
- TIETJEN, W. J. 1986: Social spider webs, with special reference to the web of *Mallos gregalis*. In W. A. Shear (ed.) *Spiders: webs, behavior and evolution*: 172–206. Stanford, Stanford University Press.