

## Arthropod nest associates of the social spider *Phryganoporus candidus* (Araneae: Desidae)

Michael F. Downes

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

### Summary

Nests of the social spider *Phryganoporus candidus* (= *Badumna candida*) (L. Koch), sampled over a two-year period, yielded information on arthropod parasites, parasitoids, predators, scavengers, boarders and others that utilised the nests and/or the spider hosts. Prominent among these associates were mealybugs (Hemiptera: Pseudococcidae), oecophorid moths, and the scelionid parasitoid *Ceratobaeus setosus* Dodd (Hymenoptera) which infests some 20% of the egg masses of *P. candidus* in the Townsville region. *Stathmopoda platynipha* Turner (Lepidoptera: Oecophoridae) lived intimately with the spiders in the nest retreat, was immune to attack by them, and sometimes caused great damage to the nest structure. Other notable associates included gryllacridid orthopterans, psocopterans, the diaspidid *Quadrapsidiotus perniciosus* (Comstock) (Hemiptera), the mealybug-mimicking coccinellid *Cryptolaemus montrouzieri* Mulsant (Coleoptera), the mirid *Tytthus mundulus* (Breddin) (Hemiptera), the mantispid *Austromantispa imbecilla* (Gerstaecker) (Neuroptera), the gnaphosid spider *Lampona fasciata* L. Koch and dewdrop spiders (*Argyrodes* sp.).

### Introduction

The nests of vertebrates and invertebrates are utilised by many small arthropods, providing shelter for itinerants, a source of food for scavengers and predators, and the tissues of the host and/or its eggs for parasites and parasitoids. Despite the catholic carnivorous habits of the hosts, the nests of spiders — especially social spiders — are habitats for complex communities of this kind (Auten, 1925; Jackson & Griswold, 1979; Lopez, 1987), and the diversity of the nest associates of the cribellate spider *Phryganoporus candidus* (L. Koch) has been noted by New (1974). The present study, derived from an investigation of the life history of *P. candidus* (Downes, 1993), describes this diversity and reveals some of the interspecific interactions between the host spider and its nest associates.

*Badumna candida* (L. Koch) is one of three species that together form the *candida* species-group of the genus *Badumna* (Gray, 1983; Colgan & Gray, 1992). A current revision, unpublished at the time of writing, proposes that *Badumna candida* revert to *Phryganoporus candidus* (M. R. Gray, pers. comm.). Consequently, the latter name is used throughout this study. *P. candidus* is widespread on the Australian mainland. Its nests are irregular constructions of leaves, twigs and debris bound together by silk and containing an anastomosing network of tunnels; the whole structure is divisible into an inner retreat area and an outer area of prey-capture

webbing. Colonies are univoltine and may consist of more than a hundred spiders, all the progeny of a single female (Main, 1971; Gray, 1983).

Meikle-Griswold (1986), referring to the nest associates of South African eresid spiders, proposes a fivefold classification of these associates, viz: predators and parasitoids of the host, kleptoparasites, scavengers, boarders, and predators and parasitoids of the first four classes. This classification is adopted here.

That individuals are more vulnerable to parasites and parasitoids when they live in groups rather than solitarily is believed to be one of the disadvantages of sociality (Williams, 1966; Smith, 1982). This was tested by Hieber & Uetz (1990) who found that the rate of parasitism increases with colony size in the colonial araneid *Metepeira incrassata* F. O. Pickard-Cambridge, but not in an undescribed colonial congener. However, some of the detrimental effects that parasitic species have on their hosts may be mitigated in unexpected or expected ways. An unexpected “benefit” of this kind involves the scelionid egg parasitoid *Baeus* sp.: the emergence of the wasps from egg sacs of the theridiid spider *Achaearanea tepidariorum* (C. L. Koch) stimulates spiderlings to cannibalise their weaker siblings, thus utilising an otherwise lost resource (Valerio, 1975). The importance to dispersing spiderlings of having harvested undeveloped eggs or any otherwise lost food supply is emphasised by Downes (1988). An expected “beneficial” effect of parasites is as selective agents in the maintenance of genetic variability in eusocial insect populations: the correlation of parasite transmission with genetic relatedness of the hosts promotes outbreeding (Shykoff & Schmid-Hempel, 1991). Since this enhances genetic variability but undermines the benefits of kin-selected social behaviour, it further complicates the definition of a parasite.

### Materials and methods

Except in October 1988 and March 1989, nests of *P. candidus* were collected each month from July 1987 to June 1989 inclusive, from a 400 ha area of open dry sclerophyll woodland surrounding James Cook University, Townsville. Each collecting location was selected at random and the five nests nearest to the chosen location were collected, after their host plants were recorded (if unknown, a sample was taken for later identification, though this did not always prove possible). The maximum and minimum numbers of nests collected in any month were 35 (March) and 15 (December); the total was 280.

Each nest was enclosed singly in a large (1.0 × 0.5 m) plastic bag and brought to the laboratory where it was dissected, either the following day or within the two subsequent days. All arthropods seen, other than mites, were collected. The central parts of the nests, dense with silk and rich in prey remains and spider exuviae, were dissected under a microscope. A Tullgren extraction, as employed by New (1974), was not used because a record of the number, location and contents of the spiders' egg sacs was essential, making a manual search of the nests

\*Present address: Dept. of Zoology, Universitetsparken B 135, DK 8000 Aarhus C, Denmark.

unavoidable; fragmentation of egg sacs, however, sometimes prevented accurate counts. Also, it was desirable to secure the living immature stages of associates from which adult specimens could be reared. Any such immatures were kept in glass containers with perforated plastic stoppers until hatching or metamorphosis took place.

Moribund nests (i.e. failed nests which no longer contained spiders, or those past the end of their annual cycle and from which all the spiders had dispersed) were excluded from the above sampling programme because the latter was intended primarily to determine the absolute and relative numbers of the age and sex classes of the spiders. All (23) moribund nests that would have been included had they been thriving were however dissected in the laboratory in the way described above, to confirm the absence of spiders and to record the nest associates present. Unless otherwise stated, all arthropods referred to in the following account were encountered in thriving nests.

### Results and discussion

Table 1 gives a list (mostly at the family level) of all the associates found. Known or assumed relationships listed there generally follow the five classes of Meikle-Griswold's (1986) scheme, but the categories of the latter are not mutually exclusive — nor do they give sufficient allowance for jointly beneficial functions of the association. The families encountered most frequently were the Oecophoridae (Lepidoptera) and the Scelionidae (Hymenoptera). In numbers of individuals the Pseudococcidae (Hemiptera) and, again, the Scelionidae were dominant.

Collembolans (like psocopterans) are largely detritivores and thus, like several of the associates to be discussed below, may benefit the whole community within the nest.

With one exception, all the blattids came from moribund nests, as did seven of the gryllacridids, some of the psocopterans and ants, and a few of the thrips. That the cockroaches were virtually confined to moribund nests may reflect their relative vulnerability to predation by the spiders; even the single exception was from a late-cycle nest containing only two spiders. Main (1988), however, reports that thriving nests of the social thomisid *Diaea socialis* Main, in Western Australia, are invariably inhabited by an unidentified species of cockroach which is never attacked by its hosts. The gryllacridids — one unknown, the other probably *Hyalogryllacris* sp. (D. Rentz, pers. comm.) — were in several cases very large insects which, in occupied or moribund nests, hollowed out silk-lined retreat chambers for themselves within the central part of the nest. They fed voraciously on *P. candidus* in captivity.

There were seven species of psocopterans, from three families. These included two unidentified species of *Liposcelis*, four ectopsocids of which two were new and have since been described by Smithers (1990), and one pseudocaeciliid. The psocopterans were apparently catholic scavengers, mostly found in association with

prey remains or within spent egg sacs, many of which contained little or no debris, presumably as a result of the action of these and other insects.

The diaspidid was the San José scale *Quadraspidotus perniciosus* (Comstock), of which 55 emergent adult males were collected. Presumably, adult females and nymphs of both sexes were also present, in unknown ratio, concealed by the numerous scales. *Q. perniciosus* was once regarded as the most damaging diaspidid pest of pome and other fruit trees in Australia and other countries (Brookes & Hudson, 1969).

The pseudococcids included at least three species: *Paracoccus solani* Ezzat & McConnell, *Ferrisia virgata* (Cockerell) and *Nipaeococcus viridus* (Newstead). Host plants of the specimens used for identification were *Petalostigma pubescens* Domin for *P. solani*, *Sida subspicata* F. Mueller for *F. virgata* and *Zizyphus mauritiana* Lamarck for *N. viridus*. *Z. mauritiana*, the chinee apple, was the most common host plant involved, accounting for 39 of the 66 instances of mealybugs in association with the nests of *P. candidus*; it has not previously been recorded as a host plant of any mealybug in Australia (Williams, 1985). Mealybugs were most often on (or close to) green, living leaves, but were sometimes encountered in the dry central part of the nest in rolled-up dead leaves, occasionally close to the host spider's egg sacs, and once among the debris within one of the egg sacs. Every sampling month yielded all life history stages of mealybugs (other than adult males which were encountered twice only — in March 1988 and May 1988), but because many of the specimens were unidentified juveniles, details of annual patterns of occurrence cannot be given for any of the three known species.

Mealybugs were apparently immune to predation by *P. candidus*, probably owing to their waxy filaments and defensive secretions (Cox & Pearce, 1983). Clusters of mealybugs were often found in the nests without any evidence of their presence elsewhere on the host plant, so the nest habitat may be especially favourable for them, perhaps through its advantages as a protective shelter and/or the effects of a benign microclimate. Although spider nests have not previously been recorded as a habitat for the mealybugs identified in this study, Browning (1959) found that two-thirds of the summer population of the long-tailed mealybug *Pseudococcus adonidum* Linnaeus in South Australia live under the webs of certain spiders. Pupae (more rarely, adults) of the mealybug mimicking coccinellid beetle *Cryptolaemus montrouzieri* Mulsant, which in its larval stage is a predator of these pseudococcids (Britton, 1970), were found in eleven of the nests containing mealybugs.

The mirid bug *Tytthus mundulus* (Breddin) was encountered frequently — more often in the nymphal than the adult stage. This mirid had red nymphs and black adults, as did the phlaeothripid thysanopterans that were common nest occupants. The mirid *Ranzovius contubernalis* Henry is a commensal in nests of the social theridiid *Anelosimus studiosus* (Hentz) (Wheeler & McCaffrey, 1984). Vollrath (1986) has seen mirids of the genus *Ranzovius* (which, according to Wheeler & McCaffrey (1984) may be commensals, kleptoparasites

ORDER/Family	Individuals	Species	Number of nests	Assumed relationship
COLLEMBOLA				
Isotomidae	1	1	1	Scavenger
Entomobryidae	56	2	24	Scavenger
BLATTODEA				
Blattidae	83	3	19	Scavenger/prey
ORTHOPTERA				
Gryllacrididae	10	2	10	Boarder/predator
PSOCOPTERA				
Liposcelidae	5	2	3	Scavenger
Ectopsocidae	8	4	6	Scavenger
Pseudocaeciliidae	1	1	1	Scavenger
Unknown (nymphs)	>10 <sup>2</sup>	?	40	Scavenger
HEMIPTERA				
Cicadellidae	1	1	1	?
Aphididae	>10 <sup>2</sup>	2	2	Boarder
Psyllidae	1	1	1	?
Diaspididae	>10 <sup>2</sup>	1	2	Boarder
Pseudococcidae	>10 <sup>3</sup>	4?	66	Boarder
Miridae	>10 <sup>2</sup>	1	31	Egg predator
Pentatomidae	1	1	1	?
Tingidae	2	1	1	?
Unknown	>10 <sup>3</sup>	15	56	?
THYSANOPTERA				
Phlaeothripidae	108	1	28	Scavenger
NEUROPTERA				
Mantispidae	47	1	34	Egg predator
Unknown	39	1	1	?
COLEOPTERA				
Scaphidiidae	2	1	2	?
Elateridae	1	1	1	Potential prey
Coccinellidae	44	2	15	Scavenger/Boarder
Chrysomelidae	2	2	2	?
Curculionidae	12	1	10	?
Unknown (adults)	>10 <sup>2</sup>	16	23	Potential prey
Unknown (larvae)	25	5	9	?
DIPTERA				
Unknown (adults)	28	1	4	?
LEPIDOPTERA				
Oecophoridae	>10 <sup>2</sup>	3	96	See text
Unknown (adults)	1	1	1	?
Unknown (pupae)	5	3	4	?
Unknown (larvae)	33	5	10	?
HYMENOPTERA				
Scelionidae	>10 <sup>3</sup>	2	78	Parasitoid
Chalcididae	9	2	3	Parasitoid
Encyrtidae	4	1	2	?
Sphecidae	13	1	2	Predator
Formicidae	>10 <sup>2</sup>	9	13	Scavenger
Unknown (adults)	21	5	5	?
UNKNOWN INSECTS				
(Larvae)	1	1	1	?
(Exuviae)	1	1	1	?
(Cocoons)	1	1	1	?
(Eggs)	>10 <sup>2</sup>	5	5	?
ARANEAE				
Gnaphosidae	19	1	15	Predator
Clubionidae	21	1	20	Predator?
Salticidae	13	9?	11	Boarder
Theridiidae	37	8	11	Kleptoparasites
Thomisidae	2	2	2	Boarder
Sparassidae	4	2?	4	Predator/Boarder
Oxyopidae	2	1	2	?
Araneidae	3	3	3	?
Unknown (juveniles)	42	25	30	?
Unknown (egg sacs)	33	?	25	?
Unknown (retreats)	9	3?	9	?
ACARI			Most	Scavengers
PSELAPHOGNATHA	1	1	1	?

Table 1: Arthropod associates of 280 thriving and 23 moribund nests of *Phryganoporus candidus*.

or predators, but are all obligate associates of web-building spiders) eating dead *A. eximius* (Keyserling). *T. mundulus* is a known egg predator of the sugar cane leafhopper *Perkinsiella saccharicida* Kirkaldy (Hemiptera: Delphacidae), and is also known to eat the eggs of tetranychid mites (Woodward *et al.*, 1970), so it may consume the eggs of *P. candidus*.

Some species of mantispid neuropterans also eat spider eggs in their larval stages, and complete their development within spider egg sacs (see, for example, McKeown & Mincham, 1948; Hoffman & Brushwein, 1990; Rice & Peck, 1991). Those in Table 1 are included, not for the presence of adults — which were never seen (although developing ones, close to the adult condition, were found twice) — but for the 47 instances of their cocoon remains within the host spiders' egg sacs. An adult was obtained, however, from a field-collected *P. candidus* nest that was not part of the sampling programme on which this study was based, and it proved to be *Austromantispa imbecilla* (Gerstaecker). This specimen was collected in April 1989 and emerged from the sac the following month. The cocoon remains of all the mantispids were typical, in their form and their effect upon the host sac, of *A. imbecilla* which is common in Townsville and has been recorded from egg sacs of *Achaearanea decorata* (L. Koch), *A. tepidariorum*, *Latrodectus hasselti* Thorell, *Mopsus penicillatus* (Karsch) and *Theridion rufipes* Lucas (Austin, 1985; Downes, 1985). It is remarkable that so few developing mantispids were encountered. There may be a restricted season of activity (as there appeared to be for *Ceratobaeus setosus* Dodd — see below), leaving the empty cocoons in nests that continued to thrive for most or all of the year. Despite there being 3–27 *P. candidus* egg sacs within the nests in which these mantispids occurred, only one egg sac (rarely two) was affected. This reflects the fact that a single larva (rarely two) is normally ectoparasitic on the female spider before the construction of egg sacs. Destruction of host eggs within affected egg sacs was always total, though spiderlings of *A. tepidariorum*, *Lycosa poliostrata* C. L. Koch and *L. rabida* Walckenaer have been known to survive the development of mantispids within their cocoons (Valerio, 1971; Capocasale, 1971; Rice, 1985).

Other than the coccinellid *C. montrouzieri*, already mentioned, most of the beetles found in *P. candidus* nests may have been casual entrants whose relatively hard cuticles protected them from predation. However, colonies of the "mosquero" (*Mallos gregalis* [Simon]) are inhabited by a symbiotic scavenging beetle (Digue, 1909), and some tenebrionid beetles may have more than a casual association with *Agelena consociata* Denis (Furey & Riechert, 1989).

There were three species of oecophorid moth. One, *Xylorycta candescens* Lower, was found once (in December 1987); the others, *Eochrois chrysius* (Lower) and *Stathmopoda platynipha* Turner, were the most frequently encountered nest associates of *P. candidus*. Sometimes *E. chrysius* and *S. platynipha* occurred simultaneously within the same nest; their larvae were indistinguishable, so a species name could be assigned to

them only when adult moths (which were never found in the nests) were reared from larvae or pupae taken from nests. From records gathered in this way, both species were found to occur in most months of the year without any seasonal pattern. Infestation of nests by oecophorid larvae was at times massive, causing great damage to the nest structure. Larval excreta, and occasionally the larvae themselves, were sometimes observed inside riddled and empty host spider egg sacs. Whether any benefits to the hosts offset these costs, for instance by the scavenging of organic remnants throughout the nest retreat performing a sanitation role, is unknown. Beneficial behaviour of this kind has been noted for lepidopteran larvae associated with social spider nests (Pocock, 1903; Robinson, 1977). Furey & Riechert (1989) have commented on the occurrence of caterpillars in the retreats of *Agelena consociata*: the spiders apparently never interfere with these visitors. On one occasion during the present study a group of middle-instar *P. candidus* spiders was observed feeding on a small oecophorid larva, but this was the rare exception since at all other times the spiders ignored these larvae, which exuded apparently repugnant secretions in droplets when disturbed. Larvae of these moths were very frequently found in close association with the spiders, several of them often clustered together with a number of spiders within a single rolled-up leaf. The unprovoked larvae, then, were not offensive to the spiders, but the latter would move away from any provoked larva that secreted its scarlet repellent.

The genus *Stathmopoda* includes species whose larvae are known to feed on spiders' eggs (Austin, 1985); in Australia, *S. arachnophthora* (Turner) is the best-known of these (Turner, 1917), but even this species has only a single definite host record, namely *Cyrtophora hirta* L. Koch (Elgar *et al.*, 1983). *Eochrois chrysius* almost certainly feeds on green plants (E. Nielsen, pers. comm.) and, if so, may use the spider nest as a shelter during development.

Apart from a single specimen of an unidentified scelionid taken from a nest in August 1987, the listing for Scelionidae in Table 1 refers to *Ceratobaeus setosus*. *Ceratobaeus* is one of several scelionid genera that consist of species that exclusively parasitise spider eggs, often with marked host specificity (Austin, 1984a). *C. setosus* was second only to the two oecophorids in the frequency of its occurrence in sampled nests. It was encountered as adults, as developing stages within the host eggs, or as a characteristic combination of host egg chorions and empty parasitoid pupal cases within abandoned egg sacs. Table 2 shows for each sampling month the proportion of sampled egg sacs that was parasitised, the number of parasitised eggs per sac and the number of adults of *C. setosus* encountered. No developing parasitoids were present between November and March inclusive; the records for these months refer to empty *C. setosus* pupal cases, the occupants of which had emerged the previous season.

The pattern of occurrence of *C. setosus* adults in association with *P. candidus* nests follows the pattern of production of eggs by the host spider over the cooler

months of the year in Townsville. The host spider largely restricts its nest founding, maturation and mating to between December and March. Egg sac construction begins around March but founding females continue to oviposit up to September. Later in the year very few founding females are present in nests and all eggs have hatched — most long since (Downes, 1993). The data in Table 2 suggest that some 20% of the egg masses of *P. candidus* are infested by *C. setosus* in the Townsville region.

*P. candidus* egg sacs most often occurred in contiguous clusters of 2–13. When affected by *C. setosus*, such clusters normally contained totally parasitised and unparasitised egg sacs. Only 18% of parasitised sacs left one or more unaffected host eggs; the development of these unaffected eggs into spiderlings did not appear to be affected by the presence of the parasitoids. They were sometimes, however, the victims of the mantispid *Austromantispa imbecilla* (see above) which was found on four occasions to be sharing the spoils of an egg sac with *C. setosus*. In many of the sacs examined, one or more dead adult wasps were found, usually with spent chorion/pupal case combinations; on one occasion, however, a dead adult female wasp was found within an apparently unbreached sac along with a brood of half-developed wasp pupae. This suggests that female *C. setosus* may die after oviposition, and may sometimes enter the host sac to oviposit, rather than oviposit through the sac wall. Austin (1984b) draws similar conclusions from his observations of *C. masneri* Austin. That certain egg sacs of a given sac cluster of *P. candidus* were untouched by *C. setosus* while adjacent ones were totally parasitised probably meant that *C. setosus*, like

*C. masneri*, only uses relatively freshly-laid eggs. Austin (1984b) found that *C. masneri* does not oviposit into host eggs more than two days old.

Sphecid wasps (*Pison* sp.) were found in two nests, in one of which the wasp's mud cocoons, hanging in the web silk, contained several juveniles of the host spider. All species of Sphecidae prey on spiders and most build mud nests (I. Naumann, pers. comm.).

Ants were unexpectedly scarce in the nests. Several of those that did occur were associated with mealybugs, probably on account of the honeydew produced by the latter. Ants are far more abundant, and play an important cleaning role, in nests of *Agelena consociata* (Furey & Riechert, 1989).

Among the araneid nest associates, the gnaphosid *Lampona fasciata* L. Koch showed the closest relationship with *P. candidus* (or at least with its nests), in so far as specimens were always taken from within the retreat areas where they would necessarily be in close contact with their hosts most of the time. *L. fasciata* is a predator of *P. candidus* (R. Raven, pers. comm.). The (commensal?) gnaphosid *Poecilochroa convictrix* Simon, which lodges with *Mallos gregalis*, was among the first spiders ever to be recorded from the webs of social spiders (Simon, 1909; Diguët, 1909). The clubionid *Cheiracanthium tenue* L. Koch was found in the present study more frequently than the gnaphosid, but mostly in peripheral parts of the web, in curled leaves. It was not observed to prey upon its host, but clubionids are predators of the social thomisid *Diaea socialis* (Main, 1988). Clubionids and gnaphosids are by far the commonest nest associates of the salticid *Phidippus johnsoni* (Peckham & Peckham) (Jackson & Griswold, 1979), but

Month & year	Host egg sacs			$\bar{x}$ parasitoids per host sac	Adults			
	Samp	Para	P (%)		F	E	H	T
July 87	64	12	19	12.1	7	6	1	14
August 87	133	23	17	11.9	10	27	3	40
September 87	71	16	23	14.2	—	48	29	77
October 87	37	9	24	19.8	—	—	1	1
November 87	171	34	20	14.6	—	—	—	—
December 87	81	18	22	9.4	—	—	—	—
January 88	20	7	35	21.8	—	—	—	—
February 88	53	14	26	14.3	—	—	—	—
March 88	15	1	7	2.0	—	—	—	—
April 88	30	4	13	10.2	4	7	18	29
May 88	47	5	11	21.1	12	3	15	30
June 88	42	16	38	22.9	7	10	24	41
July 88	36	7	19	16.0	1	9	12	22
August 88	34	9	26	19.7	4	28	23	55
September 88	75	11	15	17.8	2	26	1	29
October 88	0	—	—	—	—	—	—	—
November 88	61	12	20	8.7	—	—	—	—
December 88	72	16	22	10.1	—	—	—	—
January 89	56	10	18	15.6	—	—	—	—
February 89	23	2	9	19.4	—	—	—	—
March 89	0	—	—	—	—	—	—	—
April 89	10	0	0	0.0	—	—	—	—
May 89	44	9	20	13.5	2	—	24	26
June 89	50	15	30	11.0	18	10	26	54

Table 2: Seasonality and frequency of *Ceratoabaes setosus*, scelionid parasitoid of *Phryganoporus candidus*. Abbreviations under Host egg sacs are as follows: Samp = number sampled that month; Para = number parasitised in the month's sample; P (%) = proportion (percent) parasitised for that month. Abbreviations given for *C. setosus* adults are as follows: F = free living within the nest; E = emerging from host eggs as sample was taken; H = hatched from host eggs subsequently; T = total.

are not among the 12 families of spider symbionts recorded by Vollrath (1986) from the nests of *Anelosimus eximius*.

Other than *L. fasciata*, the only spider that was unequivocally associated with the nest retreat was one of the sparassids, a large *Isopeda* sp. that had hollowed out the interior of the retreat of one of the nests and had probably been feeding on the host spiders, few of which remained. Jackson (1987) describes the cohabitation of another sparassid, *Olios diana* (L. Koch), with *P. candidus* in North Queensland.

Relatively few of the (unfortunately unidentified) salticids occurred in the retreat area. Salticids of the genus *Simaetha* are known to associate with the webs of *P. candidus* (Jackson, 1985), and Jackson (1986) has also described the cohabitation of communal jumping spiders with other communal spiders in Kenya.

As many as 11 dewdrop spiders (*Argyrodes* sp.) were taken from the upper webbing of a single nest (almost all of the theridiids listed in Table 1 are of the genus *Argyrodes*). They may use their own silk in these locations and avoid contacting the cribellate silk of the hosts (R. Jackson, pers. comm.). The host spiders were never observed to chase or otherwise interfere with these fringe-dwellers, as *Anelosimus eximius* does to *Argyrodes ululans* O. Pickard-Cambridge (Cangialosi, 1990). Spiders of the genus *Argyrodes* are primarily kleptoparasites (Vollrath, 1976, 1981; Cangialosi, 1991), but the repertoire of some species is wider: *A. antipodiana* (O. Pickard-Cambridge) is known to be a predator of its host *Araneus pustulosus* (Walckenaer) (Whitehouse, 1986), and there are several reports of predation by *Argyrodes fictilium* (Hentz), *A. baboquivari* Exline & Levi and *A. trigonum* (Hentz) on their hosts (Archer, 1947; Exline & Levi, 1962; Smith Trail, 1980; Wise, 1982).

Other arthropod associates found in the present study included a solitary pselaphognath myriapod and a bewildering number and variety of mites; attempts to collect the latter were abandoned early in the study.

This account of the associates of the nests of *P. candidus* not only confirms that here is a complex community demonstrating interactions worthy of further study, but also suggests that populations of *P. candidus* may be reservoirs of both harmful and beneficial insect species. The mealybug *Ferrisia virgata*, for example, is a plant disease vector (Bigger, 1981; Nguyen-Ban, 1984) that has caused damage to many crops including cotton (Al-Azawi, 1979) and cocoa (Campbell, 1983), and has been recorded on pineapple in North Queensland (Carter, 1942). By contrast, the mirid bug *Tytthus mundulus* and the coccinellid beetle *Cryptolaemus montrouzieri* have both been employed successfully in crop protection measures in Hawaii (Britton, 1970; Woodward *et al.*, 1970).

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