Notes on the ecology and behaviour of *Physocyclus globosus* (Araneae, Pholcidae)

William G. Eberhard
Smithsonian Tropical Research Institute

and

Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica

Summary

Webs of *Physocyclus globosus* apparently function in prey capture as snares as well as signalling devices to guide attacks on walking and flying prey. Viscous adhesive is not present on web lines, but occurs on wrapping silk. Females stay with their offspring during the egg, prelarva, prenymph, and part of the first nymph stage. Females with egg sacs and recently emerged young rarely changed websites, while those without offspring moved very frequently compared with other sheet-weaving species. Population densities in man-made tunnels were greater near openings to the outside, perhaps because of greater numbers of available prey. Females with eggs and young tended to occur deeper in the tunnels than those without offspring.

Mature males cohabited with mature females with and without egg sacs, as well as with immature nymphs. They did not usually stay long in the webs of other spiders, and migrated distances of up to 50 m. They fought other males, using stereotyped threat behaviour. Anterior legs of males were more often missing than posterior legs, and smaller males lacked legs more often than larger males.

Introduction

Despite their striking abundance in many tropical forest sites (Eberhard & Briceño, 1985; Deeleman-Reinhold, 1986), spiders of the family Pholcidae are relatively poorly studied. Aside from short descriptions of the behaviour of the tropical *Calapnita* and *Belisana* (Deeleman-Reinhold, 1986) and *Blechroscelis* sp. and *Modisimus* spp. (Eberhard & Briceño, 1983, 1985; Eberhard, in press), nearly all published accounts of pholcid natural history are restricted to the temperate species *Pholcus phalangioides* (Fuesslin) (Bristowe, 1958; Maughan, 1978; Nentwig, 1983; Kirchner, 1986; Jackson & Brassington, 1987; Jackson & Rowe, 1987; Jackson, 1990; Jackson, Brassington & Rowe, 1990) and *Physocyclus simoni* Berland (Bristowe, 1958). The present study concerns *Physocyclus globosus* (Taczanowski), an anthropophilic species distributed widely throughout the New World tropics (Brignoli, 1981).

Methods

Spiders were observed in the field during July 1990 in the extensive tunnels associated with large gun emplacements on Naos Island, Panama. Built in 1916 to defend the Panama Canal, these tunnels offer several advantages for studying *P. globosus*. Their walls are smooth, and many of the sites inhabited by spiders were easily-inspected areas such as the intersections of walls and ceilings. In addition, the walls and ceilings are white; the dark spiders stand out clearly, permitting rapid and complete surveys of spiders over extensive areas. The tunnels are also laid out in regular patterns, making it easy to relocate websites. The white walls made the spiders' webs difficult to observe, however, and their presence or absence was generally not noted.

Residence times and movements between sites by spiders were determined by writing labels on the walls to mark sites, then revisiting sites daily between 1000 and 1700. Spiders in one 71 m tunnel were checked for 22 consecutive days; those in four other shorter sections of tunnel were checked for 12 consecutive days. A total of 452 websites were marked. Individual identities of mature males were determined by estimating their relative sizes, noting which legs if any they lacked, and, on first sighting, by marking portions of different legs with airplane dope. Painted segments of legs were observed by illuminating the spider laterally, causing the marks to show more clearly. Newly hatched eggs were distinguished from the uniformly coloured unhatched eggs by the combination of bright white discarded chorions and dark prelarva spiderlings inside the sac (Fig. 4).

Aggressive interactions between males were staged at night by placing two males in the web of a female which was holding eggs. Behaviour was observed in captivity in an approximately 50 × 40 × 40 cm cardboard box, using a red light through a glass plate that formed the floor of the box. Behaviour in the field, which was not perceptibly different, was observed with a dim white light. Aggressive interactions were between males of approximately equal sizes.

Fig. 1: Web of female *Physocyclus globosus* in a wall-ceiling corner (spider at upper left). The sheet was attached at many points to both surfaces (scale line = approximately 5 cm) (photo by Carl Hansen).

Terminology for the early stages of life outside the egg follows that of Galiano (1969). Means are followed by standard deviations. Two-tailed Chi-squared tests were used to judge statistical significance.

Results

Web design and prey

Web design varied substantially. At sites such as corners between walls and in corners near the floor, webs were readily seen, and often had a clearly defined, approximately horizontal sheet that was usually slightly domed in the middle. The spider hung under the lower surface of the sheet, as described for other pholcids (e.g. Bristowe, 1958; Eberhard & Briceño, 1983). Lines in one sheet examined under a microscope had no sign of the thin lines with balls seen in webs of *Modisimus* species (Briceño, 1985; Eberhard, in press). Many of the lines were curly, like the "screw threads" in *Pholcus* webs (Kirchner, 1986).

Webs in corners between a wall and the ceiling did not have horizontal sheets. Instead, an inclined sheet was stretched between the two surfaces, with some mesh above it where the spider rested (Fig. 1). Webs at easily-observed sites remained more or less intact for periods of several days after the resident spider moved away, since wind velocities in the tunnels were generally low, and there was no rain damage. Abandoned webs were often subsequently occupied for extended periods by a different conspecific individual, sometimes much smaller than the original resident. At some sites there were numerous, unoccupied, more or less intact webs. Some females that laid eggs in captivity made a relatively dense mesh of lines which contained numerous small white masses (presumably accumulations of loose silk) around the point where the female rested.

Some prey seen being fed upon by spiders had probably walked into the web (four worker ants, one millipede, and two other spiders). Others probably flew into the web (one winged termite, one sarcophagid fly, and one stratiomyid fly). Spiders responded to vibrations such as sudden loud sounds in the tunnel or the touch of a vibrating tuning fork on the web by running rapidly across the web. The extreme quickness of their attacks on prey was illustrated by a spider which appeared to snatch a small fly from the air. Spiders in captivity that captured tephritid flies which were walking on the substrate appeared to lift them off the substrate with their legs III as they began wrapping them in silk with legs IV. In one case (an attack by a mature female on a mature male observed under a dissecting microscope) it was clear that there were relatively large blobs of presumably adhesive liquid on the wrapping silk.

Distribution of spiders in tunnels

Although spiders were found throughout the tunnel system, the population density was consistently greater in areas near openings to the outside (e.g. Fig. 2), perhaps because of greater prey availability, since spiders near openings fed more often. In the first 9 m at each end of the tunnel shown in Fig. 2, 53 captured prey were seen during 603 visits to spiders at 68 websites (females with eggs and young were excluded as they almost never captured prey), as compared with 29 prey during 945 visits to spiders at 140 websites in the middle 53.3 m ($0.02 > p > 0.01$).

Movement between websites

Both males and females changed sites often. Mature females without offspring were observed to remain at a given site (both arrival and departure observed) for a mean of 2.6 ± 2.7 days (range 1–21), and nearly half (49.4%) stayed only a single day. Penultimate nymphs that could be identified as females (swollen epigynal area) showed similar website tenacity (2.5 ± 1.6 days, $n = 19$, range 1–5), although in those cases in which their stay as a penultimate ended with their moulting, they stayed longer (4.1 ± 0.8 days as a nymph, $n = 8$, range 3–5).

Mature females with offspring stayed at sites two to three times as long as those without. The mean number of days at a site for those females with unhatched eggs that
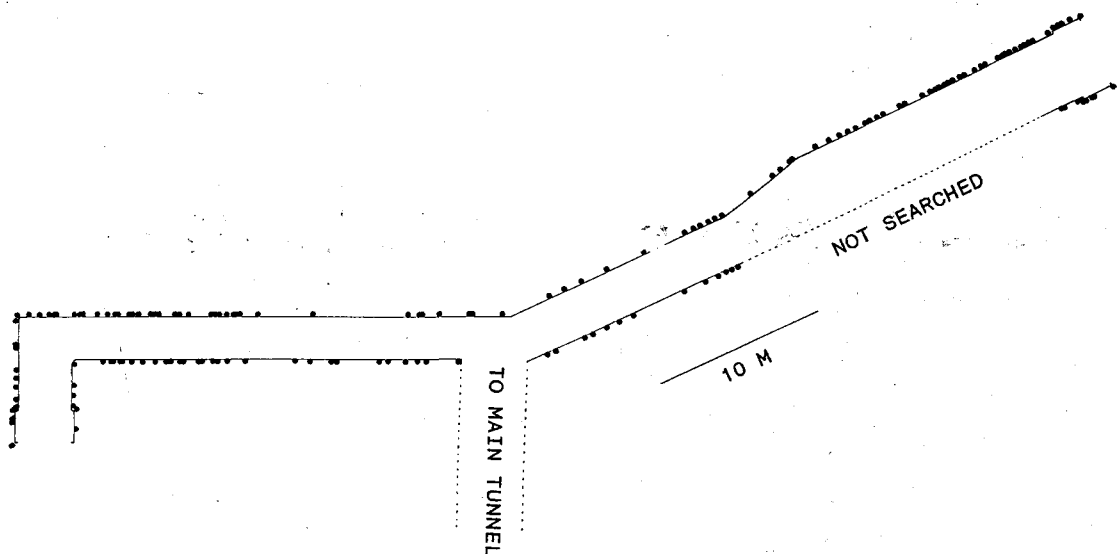

Fig. 2: Distribution of sites along the wall-ceiling intersection where spiders were seen during 22 days in a tunnel which opened to the outside at both right and left. Website density was greater near the openings to the outside (dotted lines indicate areas which were not exhaustively searched for spiders; the tunnel in the middle ran for about 30 m before intersecting another tunnel) (scale line = 10 m).

moved away before the eggs hatched was 5.7 ± 3.9 (n = 9, range 2–12); it was 7.9 ± 4.1 days (n = 12, range 2–13) for females which stayed until their eggs hatched. Not a single female with first instar larvae in the sac changed location (number of days 6.3 ± 1.7, n = 15, range 2–8). It is possible that these figures are slight overestimates, since females were not marked and occasionally one female may have replaced another.

Males were more mobile than females. Those accompanying females without offspring (Fig. 3) were present for a mean of only 1.45 ± 0.75 days (n = 47, range 1–3). Males accompanied mature females holding unhatched eggs, mature females holding prelarvae, and penultimate instar female nymphs for similar lengths of time (respective means 1.49 ± 0.76, n = 39, range 1–4; 1.60 ± 0.95, n = 35, range 1–5; 1.65 ± 1.48, n = 51, range 1–7). Males not accompanying other spiders were even less likely to stay at a given site (mean 1.11 ± 0.37, n = 223, range 1–3) (differ from males accompanying mature females p < 0.001 comparing stays of 1, 2 and > 2 days). Males probably moved substantial distances. One individual was found 50–60 m from the site where he was originally marked.

Oviposition and care of offspring

Females used their chelicerae and palps to hold their spherical egg masses, which were scantily wrapped with silk. Application of silk, observed in two cases, resembled prey wrapping; the egg mass was held with legs III while legs IV pulled silk from the spinnerets and applied it to the eggs. Egg masses were held during both the egg and pre-larva stages (Fig. 4). In nine cases a female apparently stayed at a site for at least one day (mean 3.4 ± 1.7, range 2–13) before ovipositing there (a site at which a female with a strongly inflated abdomen was present on one day had a female with a small abdomen holding unhatched eggs the next day).

Females may tend to move deeper into tunnels before ovipositing. Of the 70 cases in which a mature female was present at a given site for one or more days in the outer 9 m at either end of the long study tunnel, in only 14% was the female accompanying offspring; corresponding numbers for the interior 53.3 m portion of this tunnel were 37.5%
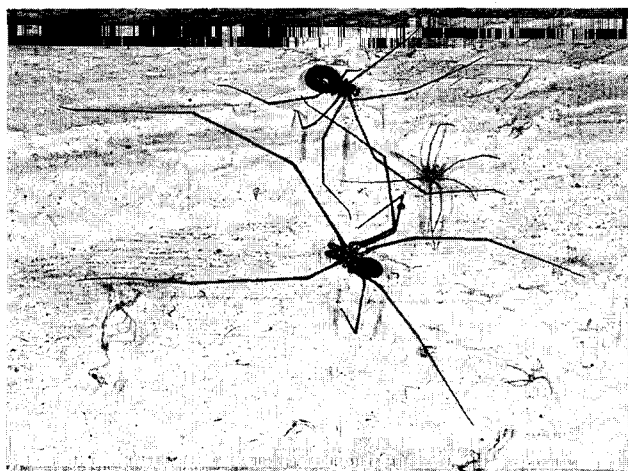

Fig. 3: Mature male (below) cohabiting with a mature female *P. globosus* (photo by Carl Hansen).
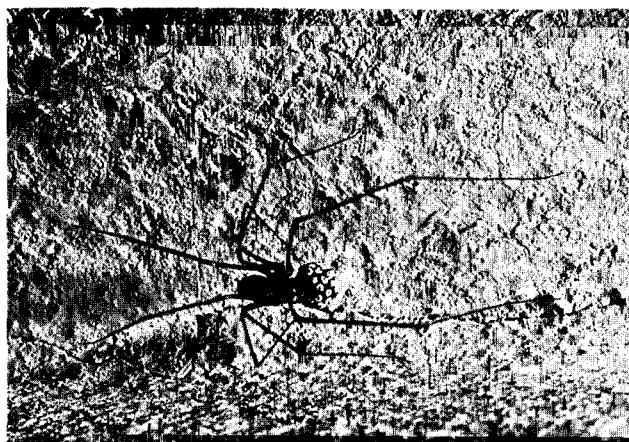

Fig. 4: Mature female *Physocyclus globosus* carrying an egg sac with prelarvae. The white spots are discarded chorions of eggs (photo by Carl Hansen).

of 80 females (Fig. 5) (p < 0.005 comparing ends vs. middle portion).

In no case (145 female days) was a female with an egg-sac observed feeding. The presence of the eggs may inhibit predatory behaviour, since females from which I removed the eggs in captivity attacked prey as little as three hours later. On only five occasions was a female with an egg mass in the field observed not holding it in her chelicerae: one of these females was mating, one was being courted, another was cleaning her legs in her chelicerae, and the other two were wrapping the eggs (perhaps recently laid).

The mean duration of the egg stage was 11.3 ± 1.0 days (n = 8), and that of the prelarva stage 7.0 ± 0.8 days (n = 8). This is similar to the average of 20 days for these two stages in *Pholcus muralicola* Maughan & Fitch (Maughan, 1978).

When the spiderlings moulted to the prenymphal instar they left the eggsac, and dispersed slightly in the web lines just above the female. In two cases the deserted egg sac was seen fastened to the mesh on the first day after the spiderlings emerged, then it disappeared. The female stayed in place directly under the group of spiderlings for the duration of this instar (mean 4.3 ± 0.7 days, n = 14), but probably occasionally left them briefly, as in two cases a female with prenymphs was observed feeding on prey. The spiderlings stayed together briefly after moulting to the first nymph. The female stayed with first nymphs (Fig. 6) a mean of 2.8 ± 1.2 days (n = 18) before leaving; often many of the first nymphs remained in the web for 1–2 more days after the female had left. Females in captivity produced multiple egg sacs. Bonnet (in Bristowe, 1958) found that females of the temperate *Physocyclus simoni* live for several years, and produce several clutches of eggs.

Male aggressive behaviour

Ten different aggressive interactions were seen between males. The following composite description includes different behaviour patterns that occurred repeatedly.

Sometimes the resident male responded immediately to the introduction of another male by moving towards him, jerking the web with his legs and/or bouncing his entire body. In other cases the resident was immobile, and the
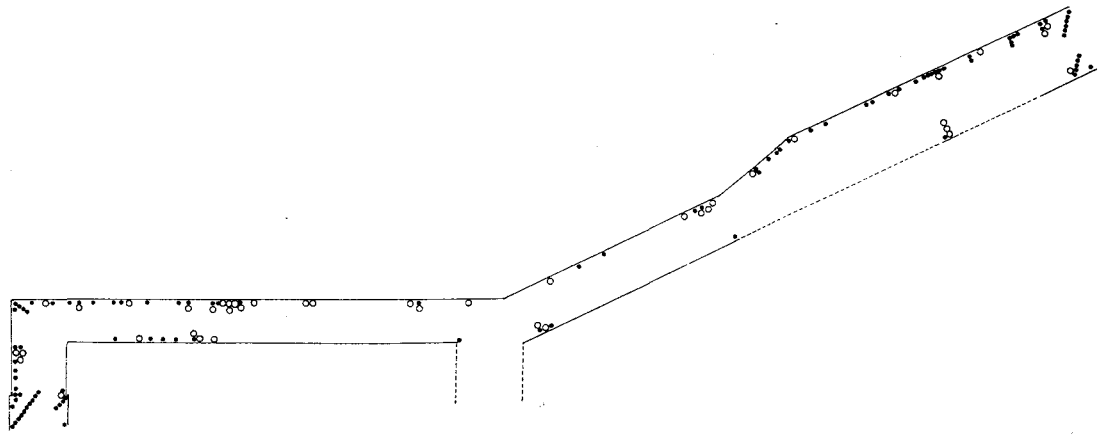
Fig. 5: Distribution of sites at which mature females were seen with offspring (open circles) and without offspring (dots) during 22 days in a tunnel opening to the outside at both right and left. Females with offspring tended to be farther from the openings to the outside (dotted lines indicate areas which were not exhaustively searched for spiders) (scale as Fig. 2).

invader moved slowly across the web, sometimes extending his front legs straight forwards to tap in an apparently cautious manner. Occasionally one of the males left without further interactions, but usually the males ended up squaring off in what appeared to be ritualised threats. They aligned themselves face-to-face, and each spread and extended his long anterior legs laterally. Then each spider leaned forwards, vibrating his body intermittently and perhaps pushing at least slightly against the opponent. In some cases a male contacted his opponent with at the least the basal portions of his extended legs I as well as with the anterior portion of his cephalothorax. Following each push the male leaned back and vibrated his entire body strongly before leaning forwards again. A forward–backward cycle lasted in the order of 1–2 s, and several interactions included 5–20 such cycles. Even when two males made forward lunges more or less synchronously, as was often the case, their chelicerae did not meet, since the males were always slightly misaligned laterally. In some cases the pedipalps or the anterior portion of a male's body appeared to catch briefly on the dorsal surfaces of the other male's front legs, and then snap free.

If neither male turned away after a series of lunges, the males then engaged in one or several mutual embraces, each wrapping his legs I–III around the other and apparently pulling his opponent briefly towards him. An embrace sometimes ended with a brief scramble of legs, and usually signalled the end of the interaction. One male turned and walked away to the edge of the web or off it, while the other vibrated his body strongly. In no case did I see a fighting male either vibrate his pedipalps (as in courtship — see Eberhard, in prep.) or bob his abdomen dorso-ventrally (as was common in both immature and mature individuals moving in their webs).

Missing legs

Of 163 mature males marked in the field, 24.5% had lost one leg, 10.4% had lost two, and 0.6% lacked three. The legs most often missing were, in order, legs I (46.5% of those lost), legs II (21.1%), legs III (19.7%) and legs IV (12.7%) ($p < 0.001$ comparing rates of loss of different legs).

Smaller mature males were more likely to have lost legs.

Of a sample of 147 males which were classified in the field as being in one of four sizes, 59.1% of small males ($n = 22$) were missing at least one leg; corresponding figures were 39.5% for medium-small ($n = 43$), 27.0% for medium-large, and 18.2% for large males ($n = 44$) ($p < 0.005$ comparing males having 8 vs. < 8 legs for different sizes). The same trend for smaller males to have fewer legs was seen in comparing males with seven legs against those with six or less: 50% of small males which had lost a leg had lost two or more; similar figures for other males were 35.3%, 10.0%, and 12.5% ($p = 0.025$ comparing the two lower vs. two upper size categories).

Discussion

Capture of walking prey by pholcids in webs has also been observed in *Pholcus* (Maughan, 1978; Nentwig, 1983; Kirchner, 1986; Jackson & Brassington, 1987; Lopez, 1987). It appears that, as in *Pholcus phalangioides* (Jackson & Brassington, 1987), the webs of *Physocyclus globosus* are best considered traps for both flying and walking prey. The spiders' extreme rapidity of movement, effective wrapping behaviour, and ability to attack prey
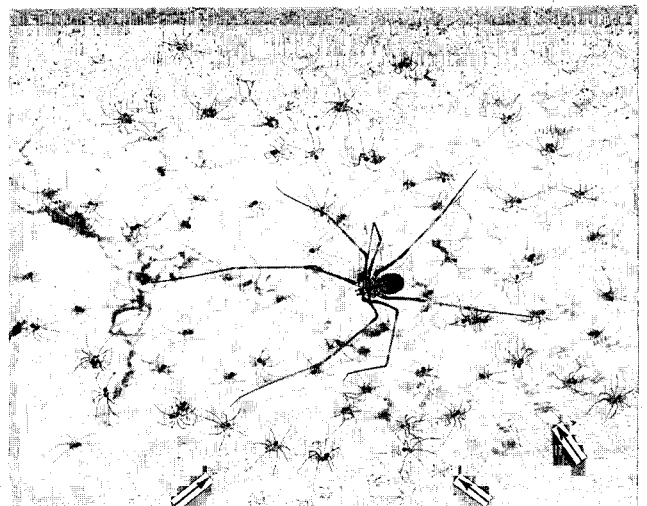

Fig. 6: Mature female *Physocyclus globosus* hanging just below a cluster of first nymph spiderlings. Some of their moulted skins are visible (arrows) (photo by Carl Hansen).

much larger than themselves, all of which are probably direct results of their long legs (Bristowe, 1958; Jackson & Brassington, 1987; Lopez, 1987), make them quite effective predators.

Since webs were not removed by spiders when they changed websites and remained more or less intact even when untended for extended periods in the sheltered tunnels, it was not uncommon for a spider to utilise a web built by another individual. Lack of reingestion of the web when changing websites may be common in some families of spiders (e.g. Eberhard & Briceño, 1983 on Pholcidae; S. Guzmán-Gómez pers. comm. on Diguetidae), and probably affects the balance between the costs and benefits of changing websites.

Changing websites may be unusually inexpensive for *P. globosus*. In addition to reuse of abandoned webs, predation risk during movement from one site to another may be relatively low in sheltered habitats such as tunnels and caves, owing to a scarcity of predators, as compared with open forest. The hypothesis that tendency to change websites is inversely related to the cost to the spider of making such a change (Janetos, 1982; Riechert & Gillespie, 1986) would predict that, all else being equal, *P. globosus* would show a greater tendency to change websites than do other pholcids which build at exposed sites where intact, abandoned webs are more rapidly damaged and thus less often available. The prediction is not supported by available data. Mature female *P. globosus* without offspring left websites only slightly more often (31% of 310 spider-days) than did females of the forest-living species *Blechroscelis* sp. (24% of 97) or *Modisimus* sp. A (23% of 70) (Eberhard & Briceño, 1983); neither of these differences is statistically significant.

Janetos (1982) found that orb-weavers stayed at websites for shorter periods (means of 2.2 and 2.4 days in different years) than did sheet-weaving species (means of 4.8 and 5.0 days). The mean duration at a website of *P. globosus* females without offspring $(2.6 \pm 2.7$ days) was more similar to the website tenacity of orb-weavers than sheet-weavers. This indicates the lack of consistent correlation between web type and website tenacity which has already been noted by others (Shelly, 1984).

The distributions of spiders in the tunnels and the frequency of observations of feeding in different parts of a tunnel suggest that spiders may stay longer at sites where they feed more, as occurs in other species (Turnbull, 1964). The trend for females to oviposit deeper in the tunnels suggests, on the other hand, that dangers from parasites or predators may be reduced deeper in the tunnels.

The greater tendency to lose legs in smaller males, and the tendency to lose anterior rather than posterior legs may result from battles with other males, but leg loss can also occur during moulting (Maughan, 1978).

Acknowledgements

References

BRICEÑO, R. D. 1985: Sticky balls in webs of the spider *Modisimus* sp. (Araneae, Pholcidae). *J. Arachnol.* **13**: 267–269.

BRIGNOLI, P. M. 1981: Studies on the Pholcidae, I. Notes on the genera *Artema* and *Physocyclus. Bull.Am.Mus.nat.Hist.* **170**: 90–100.

BRISTOWE, W. S. 1958: *The world of spiders.* London, Collins.

DEELEMAN-REINHOLD, C. 1986: Leaf-dwelling Pholcidae in Indo-Australian rain forests. *In* W. G. Eberhard, Y. D. Lubin & B. Robinson (eds.), *Proceedings of the ninth international congress of arachnology, Panama 1983:* 45–48. Washington, Smithsonian Institution Press.

EBERHARD, W. G. & BRICEÑO, R. D. 1983: Chivalry in pholcid spiders. *Behav.Ecol.Sociobiol.* **13**: 189–195.

EBERHARD, W. G. & BRICEÑO, R. D. 1985: Behavior and ecology of four species of *Modisimus* and *Blechroscelis* (Araneae, Pholcidae). *Revue arachnol.* **6**: 29–36.

EBERHARD, W. G. in press: Web construction by *Modisimus* sp. (Araneae, Pholcidae). *J.Arachnol.*

EBERHARD, W. G. in prep.: Courtship and copulation by *Physocyclus globosus* (Araneae, Pholcidae).

GALIANO, M. E. 1969: El desarrollo postembrionario larval de *Diguetia catamarquensis* (Mello-Leitão, 1941) (Araneae, Diguetidae). *PhysisB.Aires* **28**: 395–405.

JACKSON, R. R. 1990: Predator-prey interactions between jumping spiders (Araneae, Salticidae) and *Pholcus phalangioides* (Araneae, Pholcidae). *J.Zool., Lond.* **220**: 553–559.

JACKSON, R. R. & BRASSINGTON, R. J. 1987: The biology of *Pholcus phalangioides* (Araneae, Pholcidae): predatory versatility, araneophagy and aggressive mimicry. *J.Zool., Lond.* **211**: 227–238.

JACKSON, R. R., BRASSINGTON, R. J. & ROWE, R. J. 1990: Anti-predator defences of *Pholcus phalangioides* (Araneae, Pholcidae), a web-building and web-invading spider. *J.Zool., Lond.* **220**: 543–552.

JACKSON, R. R. & ROWE, R. J. 1987: Web invasion and araneophagy by New Zealand and Australian pholcid spiders. *N.Z.Jl Zool.* **14**: 139–140.

JANETOS, A. C. 1982: Foraging tactics of two guilds of web-spinning spiders. *Behav.Ecol.Sociobiol.* **10**: 19–27.

KIRCHNER, W. 1986: Das Netz der Zitterspinne (*Pholcus phalangioides* Fuesslin) (Araneae: Pholcidae). *Zool.Anz.* **216**: 151–169.

LOPEZ, A. 1987: Observations sur le proies des Pholcidae (Arachnida: Araneae). *Bull.Soc.Arach.Béziers* (6 Ser.) **3**: 47–53.

MAUGHAN, O. E. 1978: The ecology and behavior of *Pholcus muralicola. Am.Midl.Nat.* **100**: 483–487.

NENTWIG, W. 1983: The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linyphiidae, Pholcidae, Agelenidae). *Oecologia* **56**: 132–139.

RIECHERT, S. E. & GILLESPIE, R. G. 1986: Habitat choice and utilization in web-building spiders. *In* W. A. Shear (ed.), *Spiders, webs, behavior, and evolution:* 23–48. Stanford, Stanford University Press.

SHELLY, T. E. 1984: Prey selection by the neotropical spider *Micrathena schreibersi* with notes on web-site tenacity. *Proc.ent. Soc.Wash.* **86**: 493–502.

TURNBULL, A. L. 1964: The search for prey by a web-building spider, *Achaearanea tepidariorum* (C. L. Koch) (Araneae: Theridiidae). *Can.Ent.* **96**: 568–579.