

A knife in the back: use of prey-specific attack tactics by araneophagic jumping spiders (Araneae: Salticidae)

D. P. Harland¹ & R. R. Jackson^{2,3}

¹ Canesis Network Ltd, Christchurch, New Zealand

² School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

³ The International Centre of Insect Physiology and Ecology, Nairobi, Kenya

Keywords

predation; araneophagy; spiders; *Portia*; *Badumna*; *Pholcus*.

Correspondence

Duane P. Harland, Canesis Network Ltd, Private Bag 4749, Christchurch, New Zealand.

Email: duane.harland@canesis.com

Received 4 May 2005; accepted 23 September 2005

doi:10.1111/j.1469-7998.2006.00112.x

Abstract

Three species of *Portia* (*Portia africana* from Kenya, *Portia fimbriata* from Australia and *Portia labiata* from the Philippines) were tested with flies *Drosophila immigrans* and *Musca domestica* and with web-building spiders *Badumna longinquus* and *Pholcus phalangioides*. *Badumna longinquus* has powerful chelicerae, but not especially long legs, whereas *Ph. phalangioides* has exceptionally long legs, but only small, weak chelicerae. Typically, *Portia* sighted flies, walked directly towards them and attacked without adjusting orientation. However, *Portia*'s attacks on the spiders were aimed primarily at the cephalothorax instead of the legs or abdomen. *Portia* usually targeted the posterior-dorsal region of *B. longinquus*' cephalothorax by attacking this species from above and behind. When the prey was *Ph. phalangioides*, attack orientation was defined primarily by opportunistic gaps between this species' long legs (gaps through which *Portia* could contact the pholcid's body without contacting one of the pholcid's legs). *Portia*'s attack strategy appears to be an adjustment to the different types of risk posed by different types of prey.

Introduction

Most jumping spiders (family Salticidae) are insectivorous hunters characterized by their vision-directed attacks on motile prey (Forster, 1982; Jackson & Pollard, 1996), but salticids from the genus *Portia* are exceptions. The species in this genus build prey-capture webs, in addition to stalking prey away from webs, and they invade the webs of other spiders. Although they eat insects, *Portia*'s preferred prey are other spiders, including other spiders that are themselves effective predators. Penetrating the web of another spider means crossing into that spider's perceptual world, where even a small *faux pas* may be fatal for *Portia* (Jackson *et al.*, 1998); however, *Portia* gets the upper hand by adopting a predatory strategy based on aggressive mimicry (Jackson & Wilcox, 1998).

After entering an alien web, *Portia* makes web signals by stretching, plucking and striking the silk with specialized leg, palp and abdomen movements (Tarsitano, Jackson & Kirchner, 2000). These signals may either lure the resident spider to within attack range or keep it pacified during *Portia*'s approach (Jackson & Wilcox, 1998). *Portia* may also synchronize its movement across the web with periods when the resident spider is distracted by its own prey or has the ability to detect web signals impaired by a light breeze hitting the web (Wilcox, Jackson & Gentile, 1996; Jackson, Pollard & Cerveira, 2002a).

Previous studies have primarily addressed questions about how *Portia* interacts with its prey in the context of entering a web and getting close enough to attack. Here we consider a

later part of the predatory sequence. We investigate *Portia*'s decisions when orienting and executing an attack. More specifically, we investigate whether *Portia*'s attack strategy is fine tuned to particular types of spiders on which it preys. Our working hypothesis is that stricter decisions are made when the prey is especially dangerous, this working hypothesis being the rationale for the prey we chose for this study.

We compared *Portia*'s tactics during encounters with dangerous prey (i.e. spiders) with its tactics during encounters with safer prey (i.e. flies). Two species of web-building spiders were chosen as case studies, *Badumna longinquus* (L. Koch) (Desidae) and *Pholcus phalangioides* (Fuesslin) (Pholcidae), both of which sometimes kill *Portia* (D. P. Harland & R. R. Jackson, unpubl. data). *Badumna longinquus* is a stocky spider with powerful chelicerae and thick, but not especially long, legs. *Badumna longinquus* typically attacks by suddenly lunging forward and biting its prey. *Pholcus phalangioides*, despite having only small, weak chelicerae, is also a formidable predator because of how it uses its exceptionally long, thin legs. With its body out of harm's way, *Ph. phalangioides* uses its legs to bundle up its prey in silk.

Materials and methods

General

Three species of *Portia* were used: *Portia fimbriata* (Doleschall) from Queensland (Australia), *Portia labiata*

(Thorell) from Los Baños (Luzon, the Philippines) and *Portia africana* (Simon) from Entebbe (Uganda). All individuals of *Portia* that we used came from laboratory cultures. *Badumna longinquus* (L. Koch) (Desidae) and *Ph. phalangioides* (Fuesslin) (Pholcidae), being common web-building spiders in New Zealand, were collected locally as needed. House flies *Musca domestica* L. (body length ~6 mm) and fruit flies *Drosophila immigrans* (Sturtevant) (body length ~4 mm) were from stock laboratory cultures.

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson & Blest, 1982; Jackson & Hallas, 1986). All testing was carried out between 08:30 and 17:30 h (laboratory photo-period 12L:12D, lights on at 08:00 h). No individuals of the prey and no individuals of *Portia* were used in more than one test. All individuals of *Portia* were either adult females or juveniles close to adult size.

Hunger level was standardized by maintaining each individual of *Portia* without prey for 7 days before being tested. The estimated body length of the prey was always 75% that of the *Portia* with which it was tested. Tests were executed in transparent plastic cages (diameter 90 mm, height 125 mm).

Data were analysed using χ^2 tests of independence, with Bonferroni adjustments being applied whenever the same data set was used in more than one analysis. As there were no significant differences between data for different *Portia* species, data were pooled for presentation.

Webs

Precise determination of the relative orientation of predator and prey was difficult when using the natural webs of *B. longinquus* and *Ph. phalangioides*, these webs being complex three-dimensional structures. What is more, there was considerable web-to-web variation in the structure of these species' webs, with the structure of any given web potentially bringing about different limitations on how *Portia* might orientate attacks and potentially complicating the interpretation of test outcomes by introducing uncontrolled variables.

Our solution to these problems was to use 'reduced webs'. These were built by *Portia* instead of by the prey spider and, in these webs, predatory sequences could be observed under uniform conditions, with the range of *Portia*'s possible attack directions not being so restricted as in normal webs. Using reduced webs was feasible because *B. longinquus* and *Ph. phalangioides* are both spiders that readily enter the webs of other species (see Jackson & Brassington, 1987).

Reduced webs were obtained by first leaving an individual *Portia* in a cage for 1 week, during which time it built a thick web that filled most of the cage (the 'testing chamber'). Immediately before testing began, *Portia* was removed and the web in the cage was reduced by using forceps and fine scissors to remove threads a few at a time until the only silk lines remaining were within 1 mm of the cage surface. We also removed any prey remains or other detritus that was in

the cage. Control tests ($n = 20$) (i.e. tests using full webs built by the prey spider) were also carried out using *B. longinquus*.

Experimental procedure

Using a small paintbrush, a prey spider was coaxed from a plastic vial (60 mm long; diameter 25 mm) into a web and, before testing began, allowed 2 min ('pre-test period') during which it wandered about before becoming quiescent. During this pre-test period in a reduced web, the *Ph. phalangioides* almost always ascended the chamber and laid a few silk lines across the cage walls and ceiling, and then came to rest hanging upside down from these lines. *Badumna longinquus*, whether in a reduced or a full web, typically settled with its ventral surface against the web.

Flies were immobilized using CO₂ gas and then allowed to recover partially. Once they began to walk, but before they began to fly, they were coaxed into webs. They typically settled at the top of the cage with their ventral surfaces against the silk.

Observation began when *Portia* began stalking the prey (for definition, see below) and continued until *Portia* captured the prey or until it turned and walked away from the prey. With the objective being to look specifically at how *Portia* orientated attacks on prey, our data came from only those sequences in which *Portia* attacked the prey. We also restricted this study to *Portia*'s first-attack decisions (i.e. we ignored all sequences in which the prey moved more than one body length in any direction after *Portia* had begun stalking). By using this simplified data set, we examined, with minimal ambiguity, our hypothesis that *Portia* makes prey-specific attack decisions.

Definitions

Fixated on the prey: *Portia* held the front of its body oriented so that the gaze of its anterior medial eyes faced directly towards the prey.

Stalk: *Portia* stepped slowly towards the prey, all the while remaining fixated.

Attack: *Portia* made a sudden, rapid lunge at the prey from close range (i.e. *Portia* extended its legs and moved its body forward, but its legs did not leave the substrate).

Capture: *Portia* ended an attack by using its forelegs and chelicerae to hold on to the prey.

Feed: *Portia* pumped digestive fluids in and out of the prey.

Data collection was simplified by defining 26 'sectors' (angular fields radiating out from the centre of the prey's body) with centres 45° apart (Fig. 1). When fixating its gaze on, stalking or attacking the prey, *Portia*'s orientation was recorded as being 'in' the particular sector it faced. For data presentation, we were primarily interested in evidence of changes in the region of the prey's body targeted by *Portia*, with left-right distinctions disregarded. This enabled us to reduce the number of sectors to 17 (i.e. pooled data from regions that were left-right mirror images of each other). For example, should *Portia* attack while facing the prey's

flank from 30° above the prey’s horizontal (dorsal–ventral) plane, the attack was to be recorded as being in the lateral–dorsal sector, ignoring whether it was in the left or the right

lateral–dorsal sector. When *Portia* attacked, we also recorded the part of the prey’s body contacted (cephalothorax or abdomen for spiders; head, thorax or abdomen for flies).

The expressions ‘usually’, ‘sometimes’ and ‘rarely’ are used, respectively, for frequencies of 80% or more, 20–80% and 20% or less.

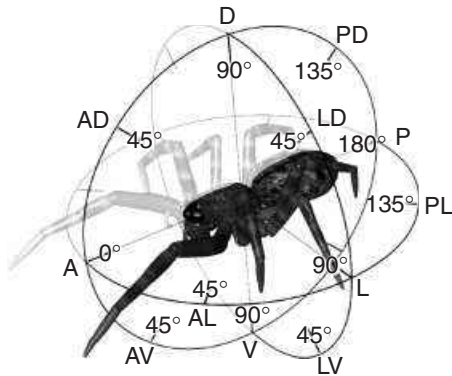


Figure 1 Sectors (26 angular fields; ambit of each, 45°; radiating out from the centre of the prey’s body). Data from sectors that are left–right mirror images were pooled, leaving 17 sectors: A, anterior; AL, anterior lateral; AD, anterior dorsal; AV, anterior ventral; ALD, anterior lateral dorsal (not shown in figure); ALV, anterior lateral ventral (not shown in figure); D, dorsal; L, lateral; LD, lateral dorsal; LV, lateral ventral; V, ventral; P, posterior; PL, posterior lateral; PD, posterior dorsal; PV, posterior dorsal; PLD, posterior lateral dorsal (not shown in figure); PLV, posterior lateral ventral (not shown in figure). The same system is used for each of three prey types (flies and two spider species). Only a spider, *Badumna longinquus*, is illustrated here.

Results

Regardless of prey type, *Portia*’s initial behaviour during a test was usually to walk slowly in the cage, intermittently pausing and moving its gaze over the surroundings. Eventually *Portia* fixated on the prey and then began stalking. The sector in which *Portia* began stalking was highly variable (Fig. 2), generally corresponding to the sector in which it initially happened to detect and fixate on the prey. Stalking in sectors radiating from the prey’s ventral side was ruled out by the way in which the prey sat on the web (i.e. the prey kept its ventral surface close to the cage surface).

When the prey was an individual of *Ph. phalangioides*, instead of a fly or an individual of *B. longinquus*, *Portia* usually began stalking in sectors radiating out from the prey’s side (Fig. 3a). However, instead of being a consequence of *Portia* deciding to stalk from the side, this finding might be accounted for by *Ph. phalangioides*’ exceptionally long, thin body (ratio of mean carapace width to mean body length for *Ph. phalangioides*, 1:4.5, $n = 10$; for *B. longinquus*, 1:2.6, $n = 10$; for *D. immigrans* and *M. domestica*, 1:2.8, $n = 10$ each).

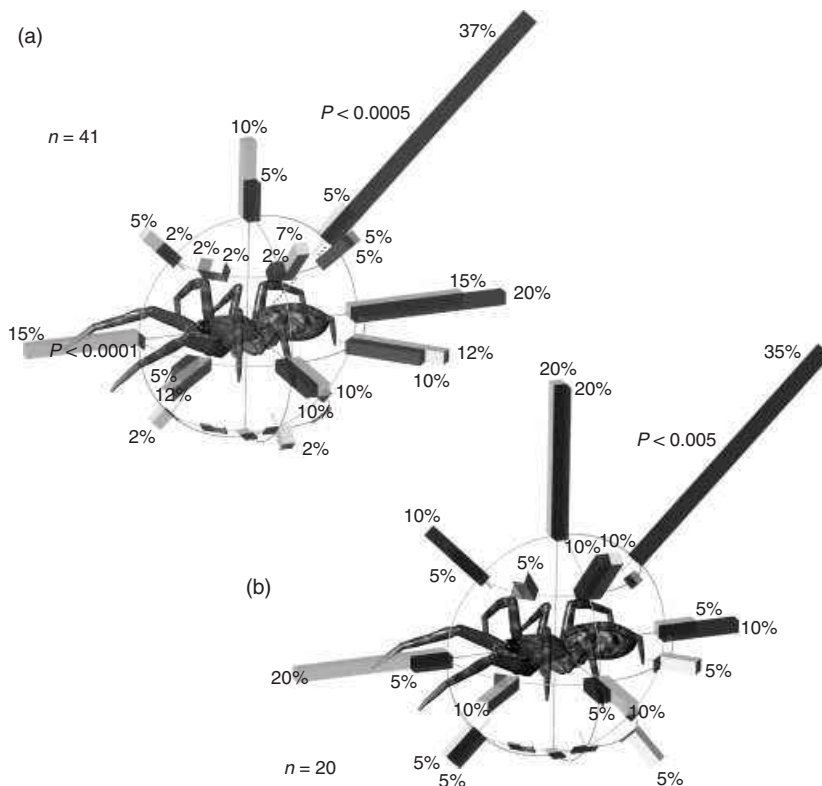


Figure 2 Number of *Portia* that began stalking *Badumna longinquus* in each sector (light bars) and number that attacked in each sector (dark bars): (a) in reduced webs; (b) in full webs.

There were two methods by which *Portia* changed sectors before attacking prey: (1) by manoeuvring around a quiescent prey and (2) by waiting while an active prey turned about. The null hypothesis for this study was that *Portia*, irrespective of prey type, was inclined simply to stalk straight towards a spider or fly and attack (i.e. we predicted that *Portia* would attack from the same sector in which it began stalking).

Portia changed sectors (Fig. 3) significantly more often during tests with *Ph. phalangioides* (50% of the 41 tests) ($\chi^2 = 11.43$, $P < 0.001$) and with *B. longinquus* (66% of 41 tests in reduced webs) (test of independence, $\chi^2 = 20.19$, $P < 0.001$) than with flies (13% of 31 tests).

How often *Portia* changed sectors when the prey was *Ph. phalangioides* (Fig. 3) was not significantly different from how often *Portia* changed sectors when the prey was *B. longinquus* (Fig. 2). However, the outcome of tests with sector changes differed, depending on whether the prey was *B. longinquus* or *Ph. phalangioides*. When the prey was an individual of *B. longinquus* in a reduced web, 82% of the orientation changes were from stalking in a more anterior sector to attacking in a more posterior sector. Notably, every individual that began stalking in sector A changed to another sector before attacking. Although stalking began in sector PD in only 5% of the tests, 37% of the *Portia* attacked in sector PD.

Findings from testing *B. longinquus* with full webs (control tests) (Fig. 2b) were comparable to findings from testing

B. longinquus with reduced webs (Fig. 2a) (i.e. most individuals that began stalking in more anterior sectors changed to more posterior sectors when they attacked, with PD usually being the sector from which attacks were launched).

When the prey was *Ph. phalangioides*, the outcome of sector changes was that *Portia* launched an attack through suitable gaps between legs (i.e. attacks were in spaces through which *Portia* could contact *Ph. phalangioides*' body without hitting a leg). These gaps appeared opportunistically and were not in any particular sector. Observations during this and numerous other studies have illustrated that, for *Portia*, contacting one of *Ph. phalangioides*' legs is dangerous (Jackson, 1990) because leg contact routinely elicits *Ph. phalangioides*' predatory response (use of its long legs to wrap up prey), sometimes with fatal consequences for *Portia* (Fig. 4).

Irrespective of the sector in which the attack was launched, *Portia* consistently aimed its attack at the cephalothorax of *B. longinquus* (in all 20 full-webs tests and in 40 out of 41 reduced-webs tests) and *Ph. phalangioides* (in 39 out of 41 tests) (Fig. 5). In the three exceptions, *Portia* grabbed hold of the prey by its abdomen. When grabbed by the cephalothorax, spiders became quiescent within 5 s, but the three spiders *Portia* grabbed by the abdomen struggled by twisting at the pedicel and intermittently flailing their legs about, becoming quiescent only after about 30 s. Attacks on flies *D. immigrans* and *M. domestica* were concentrated at the front and middle regions of the body (head, 11; thorax, 19; abdomen, 1). Although there are spiders from other

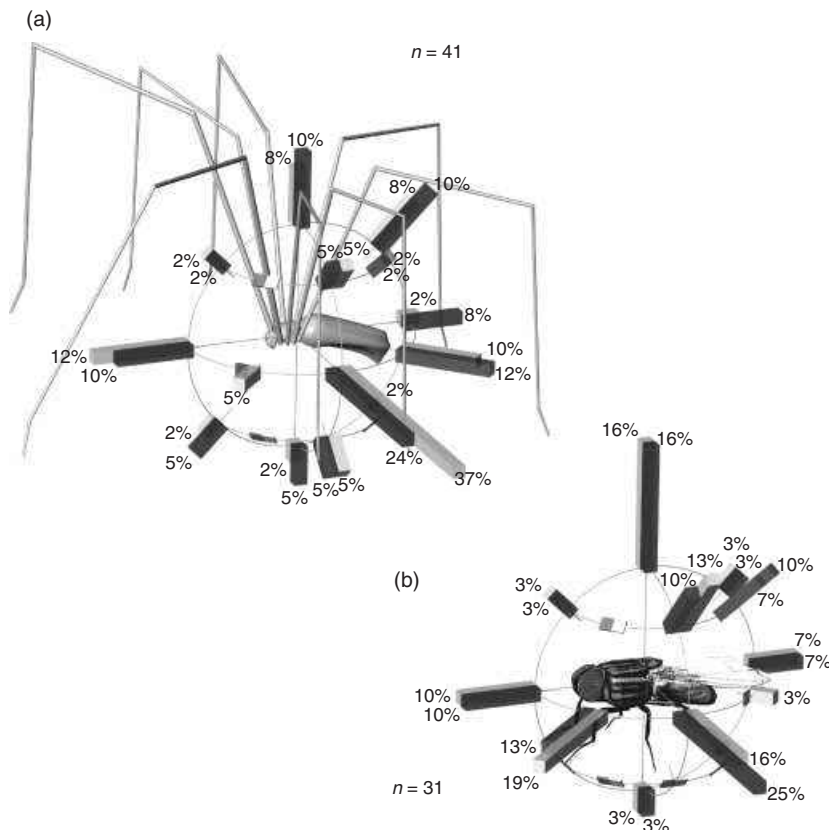


Figure 3 Number of *Portia* that began stalking prey in each sector (light bars) and number that attacked in each sector (dark bars): (a) *Pholcus phalangioides* in reduced webs; (b) flies in reduced webs.

families that routinely target their prey's legs (Foelix, 1996), *Portia* never attacked the legs of any prey.

Discussion

Spider eyes generally do not support high spatial acuity (Land, 1985), but salticids are a distinct exception, being spiders with complex eyes and intricate vision-guided behaviour (Jackson & Pollard, 1996; Harland & Jackson, 2000). Previous studies have established that, when using optical cues alone, *Portia* can discriminate conspecific individuals from other salticids, insect prey from spider prey and insects that are prey from insects that are not prey (e.g. ants), and also discriminate between various species of spider prey and, for some of these spider prey, egg carrying from eggless individuals and individuals that wrap up their own prey from individuals that are not so engaged (Jackson & Blest, 1982; Li & Jackson, 1996; Wilcox *et al.*, 1996; Harland & Jackson, 2000; Jackson *et al.*, 2002a,b). The findings from the present study suggest that *Portia* also adopts prey-specific attack tactics. We found that *Portia* actively chooses how to orientate its attacks on *B. longinquus* and on

Ph. phalangioides, using attack-orientation rules that depend on which of these two spider species is the target. No comparable regularities in orientation were evident when the prey was a fly. The two spider species we used in our experiments are, for *Portia*, particularly dangerous prey and *Portia*'s attack-orientation rules appear to be a risk-reduction strategy. A fly presents little or no mortal risk to *Portia*, and *Portia* appears to be unconcerned about how it orientates attacks on this safe prey. When the prey is another spider, however, the stakes are higher (i.e. *Portia* may lose its life instead of just losing a meal).

Evidently, rather than deploying a general-purpose tactic for attacking all spiders, *Portia* fine-tunes defence to match special risks from different kinds of spiders. *Badumna longinquus* normally uses its powerful chelicerae and legs to make forward-directed attacks. *Portia* compensates by avoiding the dangerous front end of this spider and instead aims its attacks at the prey's posterior carapace. *Pholcus phalangioides* does not lunge forward when attacking, and its chelicerae are small and weak compared with the chelicerae of *B. longinquus*. Nonetheless, *Ph. phalangioides* is dangerous because, by using its long legs, it can rapidly wrap up prey and wrap up *Portia*. *Portia* does not target any particular sector of *Ph. phalangioides*' body, but *Portia* is especially attentive to this spider's long legs, making attacks opportunistically through gaps in the pholcid's legs (i.e. through clear space that arises opportunistically between *Portia* and the pholcid's body).

Portia's attack strategy also appears to include a spider-specific decision concerning the targeted region of the prey's body. Irrespective of whether the prey was *B. longinquus* or *Ph. phalangioides*, *Portia* attacked the spider's cephalothorax (the smaller of the spider's two body regions) instead of its abdomen (the spider's larger body region). Analogy may be appropriate to a person who is skilled at handling poisonous snakes. Grabbing hold behind the snake's head limits the snake's ability to twist around and strike and *Portia* also restricts a dangerous animal's ability to twist around and strike. Besides fangs, a spider has legs. By grabbing hold of the spider's carapace, *Portia* restricts the reach of the spider's legs. *Badumna longinquus* is a particularly powerful spider and, with this particular spider, *Portia* aims especially precisely, taking hold directly behind and above this spider's fangs.

A spider's cephalothorax may also be, for *Portia*, an optimal location for venom injection. Spiders have a central nervous system (CNS) that is more compact than that of

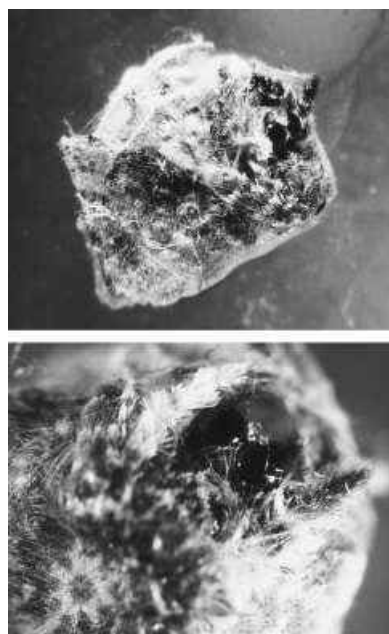


Figure 4 *Portia*'s fate (wrapped up in silk and unable to move) after contacting the leg of *Pholcus phalangioides*.

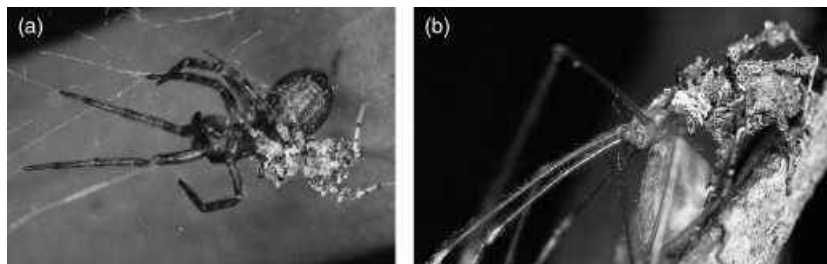


Figure 5 *Portia* holding prey spider by the posterior dorsal surface of the cephalothorax: (a) *Badumna longinquus*; (b) *Pholcus phalangioides*.

most arthropods (Bullock & Horridge, 1965), consisting primarily of two large heavily interconnected ganglia in the cephalothorax (Babu, 1985). When their cephalothoraxes were penetrated by *Portia*'s fangs, both *B. longinquus* and *Ph. phalangioides* usually became quiescent within a few seconds. On the rare occasions when *Portia*'s fangs penetrated the abdomen instead of the cephalothorax, the prey spider thrashed about for considerably longer than a few seconds. For the spider, the cephalothorax may be its 'Achilles' heel' because venom injected there quickly knocks out the CNS.

There have been frequent reports of leopards and lions targeting the necks of ungulates on which they prey (Mivart, 1881; Schaller, 1972; Bailey, 1993). The ungulate taken down by the neck typically dies quickly, either from suffocation when its windpipe is crushed or from paralysis when its spinal cord is damaged, and there is little struggling. It is interesting that *Portia*, a salticid spider, may have evolved an attack strategy with similarities to how large cats overpower their mammalian prey.

Acknowledgements

Work in Kenya was generously assisted by the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology (Mbita Point, Kenya). We thank the International Rice Research Institute for assistance with work in the Philippines. We are grateful for financial assistance provided by grants from the Marsden fund of the Royal Society of New Zealand, the National Geographic Society and the University of Canterbury.

References

- Babu, K.S. (1985). Patterns of arrangement and connectivity in the central nervous system of arachnids. In *Neurobiology of arachnids*: 3–19. Barth, F.G. (Ed.). Berlin: Springer-Verlag.
- Bailey, T.N. (1993). *The African leopard: ecology and behavior of a solitary felid*. New York: Columbia University Press.
- Bullock, T.H. & Horridge, G.A. (1965). *Structure and function in the nervous systems of invertebrates*. San Francisco: W. H. Freeman. 2v.
- Foelix, R.F. (1996). *Biology of spiders*. 2nd edn. New York & Oxford: Oxford University Press & Georg Thieme Verlag.
- Forster, L.M. (1982). Vision and prey-catching strategies in jumping spiders. *Am. Sci.* **70**, 165–175.
- Harland, D.P. & Jackson, R.R. (2000). Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. *J. Exp. Biol.* **203**, 3485–3494.
- 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. & Blest, A.D. (1982). The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilization of webs and predatory versatility. *J. Zool. (Lond.)* **196**, 255–293.
- 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. & Hallas, S.E.A. (1986). Comparative biology of *Portia africana*, *P. albimana*, *P. fimbriata*, *P. labiata*, and *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. *N. Z. J. Zool.* **13**, 423–489.
- Jackson, R.R., Li, D., Fijn, N. & Barrion, A.T. (1998). Predator–prey interactions between aggressive-mimic jumping spiders (Salticidae) and araneophagic spitting spiders (Scytodidae) from the Philippines. *J. Insect Behav.* **11**, 319–342.
- Jackson, R.R. & Pollard, S.D. (1996). Predatory behaviour of jumping spiders. *Annu. Rev. Entomol.* **41**, 287–308.
- Jackson, R.R., Pollard, S.D. & Cerveira, A.M. (2002a). Opportunistic use of cognitive smokescreens by araneophagic jumping spiders. *Anim. Cognition* **5**, 147–157.
- Jackson R.R., Pollard, S.D., Li, D. & Fijn, N. (2002b). Interpopulation variation in the risk-related decisions of *Portia labiata*, an araneophagic jumping spider (Araneae, Salticidae), during predatory sequences with spitting spiders. *Anim. Cognition* **5**, 215–223.
- Jackson, R.R. & Wilcox, R.S. (1998). Spider-eating spiders. *Am. Sci.* **86**, 350–357.
- Land, M.F. (1985). The morphology and optics of spider eyes. In *Neurobiology of arachnids*: 53–78. Barth, F.G. (Ed.). Berlin: Springer-Verlag.
- Li, D. & Jackson, R.R. (1996). Prey-specific capture behaviour and prey preferences of myrmecophagic and araneophagic jumping spiders (Araneae: Salticidae). *Rev. Suisse Zool. Vol. hors série*, 423–436.
- Mivart, G.J. (1881). *The cat: an introduction to the study of backboneed animals, especially mammals*. London: Murray.
- Schaller, G.B. (1972). *The Serengeti lion*. Chicago: Chicago University Press.
- Tarsitano, M., Jackson, R.R. & Kirchner, W. (2000). Signals and signal choices made by araneophagic jumping spiders while hunting the orb-weaving spiders *Zygiella x-notata* and *Zosis genicularis*. *Ethology* **106**, 595–615.
- Wilcox, R.S., Jackson, R.R. & Gentile, K. (1996). Spiderweb smokescreens: spider trickster uses background noise to mask stalking movements. *Anim. Behav.* **51**, 313–326.