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The web and prey-capture behaviour of *Diaea* sp., a crab spider (Thomisidae) from New Zealand

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Abstract – The prey-catching behaviour of *Diaea* sp., a thomisid from New Zealand, is documented for the first time. This is the first detailed report of web building and predatory versatility in a thomisid spider. *Diaea* sp. is neither simply a web-building spider nor simply an ambush non-web-building spider. Instead, individual spiders of this species practise both of these prey-catching methods.

INTRODUCTION

Spiders are often divided, on the basis of whether they use silk in the detection and capture of prey, into one of two groups – web builders and hunters (Foelix 1982). Web-building spiders are generally regarded as being sedentary predators that catch prey by moving about only within the confines of their web, whereas the hunting spiders are envisaged as predators that range widely within their environment in the pursuit of prey.

Thomisid spiders do not fit easily into this informal classification scheme because they are generally envisaged as spiders that neither hunt nor build webs. Instead, they are generally categorized as "ambush" or "sit-and-wait" predators that do not build webs but, instead, sit motionless on flowers or elsewhere in the vegetation and grab hold of prey that comes near (Lovell 1915; Bristowe 1958; Haynes and Sisojevic 1966; Forster and Forster 1973; Jennings 1974; Main 1976; Nelson and Lake 1976; Nentwig 1986). Perhaps, it would be more appropriate to use a different scheme for informally classifying spiders, dividing them into sedentary and motile predators, with web-builders and ambush predators being a subgroup under 'sedentary spiders'. However, this would probably still prove too simplistic because some species are known to consist of individuals that practise both web building and hunting. The most striking example might be *Portia* (Wanless 1978), a genus of salticids. Five species of *Portia* have been studied and each is known to have a complex predatory strategy in which individual spiders sometimes build prey-catching webs and the same individuals at other times hunt their prey away from webs (Jackson 1992).

Like thomisids, salticids have traditionally been envisaged as a family solely of non-web-building spiders. Recent studies have brought attention to numerous exceptions (Richman and Jackson 1992), *Portia* being a particularly striking example. The thomisids appear to be another large family of spiders with surprises in store for the behavioural researcher. The traditional view that thomisids can be regarded simply as solitary ambush spiders has already been shown to be inaccurate. In particular, recent work from Barbara Main's laboratory on *Diaea socialis*, an Australian thomisid that is social (Main 1988; Rowell and Main 1992; Evans and Main 1993), warns against premature acceptance of generalizations about thomisid behaviour.

The present paper is a report on *Diaea* sp. indet., a New Zealand congener of *Diaea socialis*. The feeding behaviour of this species has previously been investigated extensively (Pollard 1990a), especially in relation to water loss (Pollard 1988, 1989, 1990b). In the present paper, we provide the first report on the prey-catching behaviour of this species and the first detailed report of web building in a thomisid spider. We also illustrate that this spider is neither solely a web-building spider nor solely an ambush non-web-building spider. Instead, individual spiders of this species are versatile predators that practise both of these prey-catching methods.

We would like to dedicate this paper to Barbara Main who has done more than any other researcher to generate interest in the behaviour of thomisid spiders.

MATERIALS AND METHODS

Diaea (Thorell) is a large genus of thomisids, with more than 80 described species. About 70% of these are from Australia and various Pacific islands (Ono 1988). The species used in the present study is undescribed, and voucher specimens have been deposited at the Otago Museum (Dunedin, New Zealand).

Specimens of this species were collected in New Zealand from *Muehlenbeckia complexa* plants at Birdling's Flat, near Christchurch (South Island). Observations reported here are based on several hundred individuals kept in the laboratory, including all sizes of juveniles and adults of both sexes, over a period of 8 years, supplemented by observations from the field. Standard laboratory maintenance procedures for spiders were used (Jackson and Hallas 1986), except that we kept the *Diaea* in the open on plants, and artificial plants (all referred to simply as "plants"), instead of enclosed in cages. As *Diaea* was averse to contact with water, each plant was centred in a pan of water to ensure that the spider stayed on the plants.

When testing *Diaea* with prey, a large transparent plastic cylinder (closed at the top) was placed over the plant and tray to prevent prey from escaping into the laboratory. We tested *Diaea* with the following prey: vestigial winged fruitflies, *Drosophila melanogaster* Meigen; wild type fruitflies, *D. melanogaster*; and houseflies, *Musca domestica* L. About half of these tests were carried out with *Diaea* in a web, and about half were carried out with *Diaea* on the plant but without a web. To begin a test, 10 individuals of one of the three types of prey were introduced into the cylinder through a corked hole in the side by removing the cork and inserting the open end of a vial that matched the diameter of the hole. Prey then left the vial spontaneously and entered the cylinder. Observation continued for c. 4 h or until prey capture was observed.

We also tested the prey-holding ability of *Diaea*'s web, using methods described elsewhere (Hallas and Jackson 1986). These tests were carried out with the plastic cylinder in place, and the *Diaea* was removed from the web immediately before each test began. In each instance, 10 wild type fruitflies were released into the cylinder. Observation continued for 4 h or until 10 observations were made of prey contacting the web.

Escape times were recorded to the nearest second (latency from the contact with silk to escape). The minimum recorded escape time was 0 s, which included apparently instantaneous escapes. An 'escape' was recorded if the insect (1) moved off the silk (i.e. flew away from, walked off of, or dropped out of the web) or (2) remained on the web and walked about with no evident impediment. Flies that remained inactive on initial contact were not included in the analysis, nor were flies that did not struggle for more than one-third of the time they spent on the web.

RESULTS

Description of the web

All sex-age classes of *Diaea* built webs. In some cases, a single web observed in *Muehlenbeckia complexa* contained groups of *Diaea*, consisting of an adult female and several early instar juveniles. However, the descriptions here are based on webs of adult females, with no juveniles present, on flowers in the laboratory. Webs of males and juveniles appeared to be identical to those of solitary females, except smaller. Webs of females with juveniles were similar, except somewhat larger. The web (Fig. 1) was a sparse array of silk forming a nearly transparent sheet on the vegetation. It had a bridal-veil appearance, with lines of silk 60–100 mm long descending 45–90° from a horizontal, more or less circular platform 40–100 mm in diameter. The platform consisted of criss-crossed lines of silk, with the descending lines being mostly parallel (more or less up and down) and connected to foliage below the platform.

Webs in nature were found on flowers, stems and leaves of shrubs, with the platform of the web usually covering several flowers, stems and leaves. In dense vegetation in the field, these webs were very difficult to find, and once found, the boundaries of the sheet and of the descending lines were often difficult to discern. In *M. complexa*, webs were commonly located within the plant beneath the exterior leaf layer, and generally these webs contained few, if any, descending lines. However, some webs contained similar lines that extended outward from the platform and attached to surrounding vegetation. Accurate measurement in the field proved to be impracticable, but webs in nature appeared to be basically comparable to the more easily observed webs built by *Diaea* in the laboratory.

Prey capture when on the web

The web appeared to be quite non-sticky. Most flies walked unimpeded on the silk of the web or left the web soon after contact. Escape times recorded tended to be short (Fig. 2); the median was 0 s and the maximum was 45 s. Predatory sequences of *Diaea* tended to be different depending on whether or not the prey was active.

Prey active after contacting web. *Diaea* responded quickly by orienting toward, then rapidly approaching, prey up to 200 mm away. When successful, *Diaea* reached the prey within a few seconds, contacted the prey with its forelegs, then rapidly moved legs I and II over the prey. The spider flexed these legs to draw the prey in, grabbed hold of the prey with its chelicerae, then extended its legs away from the prey.

If a prey began to fly off the web just before *Diaea* reached it, *Diaea* sometimes sprang up

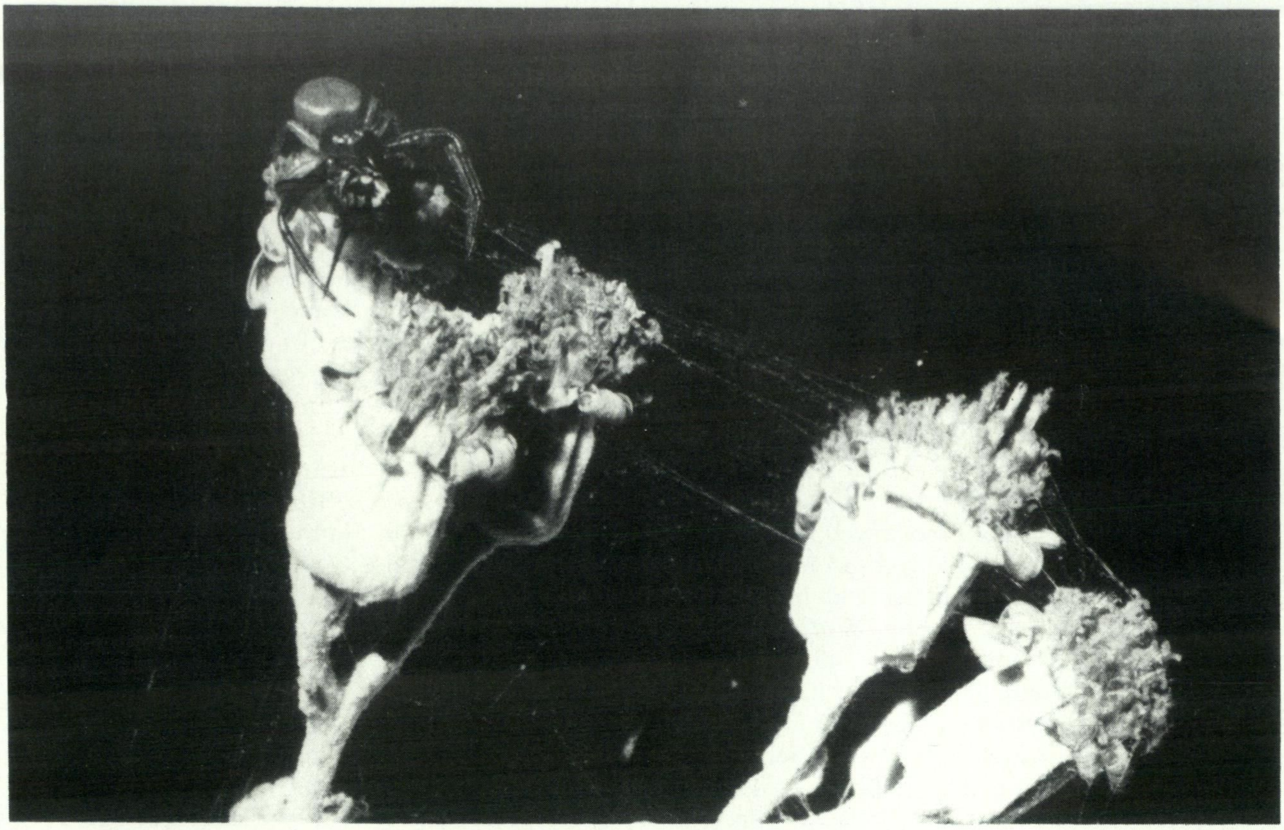

Figure 1 *Diaea* sp. on its web eating a fly (Diptera).

toward it by straightening legs III and IV, simultaneously lifting its cephalothorax off the web, and reaching up with legs I and II, striking upward at the prey. Usually the prey escaped, but occasionally the spider plucked the prey out of the air by contacting it with one or more legs and pulling it down onto the web and into its open chelicerae. Records were kept for 22 attempts; 5 were successful.

Prey inactive after contacting web. *Diaea* responded quickly by orienting toward the prey, but then approached slowly. Sometimes, after orienting toward the prey, *Diaea* paused for up to several minutes before starting to approach. During these pauses, *Diaea* sat motionless facing the prey.

Initially, the prey might be as far as 200 mm away when *Diaea* began its slow approach. *Diaea* walked slowly across the web until 30–40 mm away, then crouched and eased forward slowly so that movement was only barely perceptible. In the crouched posture, *Diaea* held its body lowered more than usual so that it appeared to be dragging the ventral surface of its body across the web. Once within 5 mm, *Diaea* made a sudden dash forward to grab the prey.

Prey capture when not on a web

Diaea often sat motionless in the vegetation with legs I and II outstretched, and ambushed prey that came near. When prey made contact with *Diaea*'s outstretched legs I and II, *Diaea* quickly flexed these legs, pulling the prey in to the chelicerae and biting it. If contacted on legs III or IV, *Diaea* made a rapid turn toward the prey and grabbed it with legs I and II. While biting prey, *Diaea* used tarsi I and II to press the prey against its chelicerae.

Usually, there was no apparent response by *Diaea* until the prey contacted or came within 5 mm of the spider, and *Diaea* generally ignored stationary flies even if they were as close as 5 mm away. However, *Diaea* did occasionally orient to flies moving past at up to 40 mm away. After orientation spiders either waited until the fly

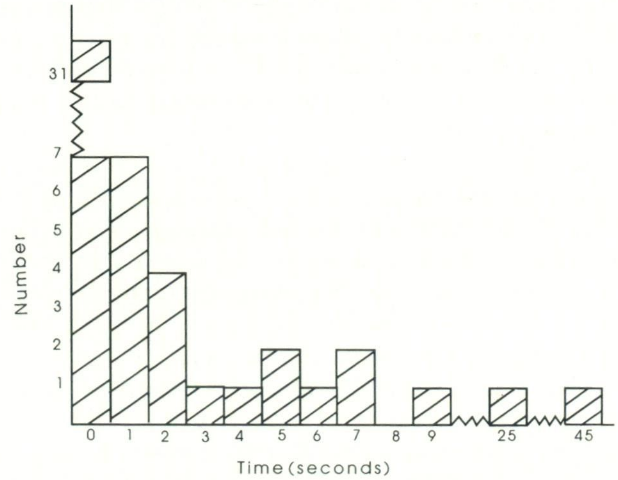

Figure 2 Escape times (s) from testing *Drosophila melanogaster* on vacant webs of *Diaea* sp. See text for details.

approached before capturing it by ambush, or moved rapidly toward the fly, lunging at it, and pulling it to the chelicerae with legs I and II.

DISCUSSION

What is the justification for calling the silk device of *Diaea* a web? The term 'web' is not strictly defined in the literature, but webs are generally thought of as silk devices that spiders use in prey capture (Shear 1986). *Diaea*'s silk edifice is only a flimsy array of silk, but there are numerous other spiders that build comparably flimsy silk arrays that function in prey capture and are called "webs" (Lubin 1986; Jackson 1986).

The flimsy structure of *Diaea*'s web may, in fact, have advantages. *Diaea*'s web is not readily detected by arachnologists in the field. If the web is comparably difficult to detect by *Diaea*'s prey, then this may be an advantage to the spider because prey may be especially likely to land inadvertently on an undetected web (see Craig 1988).

Some spiders build sticky webs which are capable of ensnaring and detaining prey for considerable periods of time (Hallas and Jackson 1986). *Diaea* and many other spiders build webs that are not sticky and appear to function not so much as a snare but more as an extension of the spider's tactile sense organs (see Witt 1975). Silk is an efficient medium for transmission of vibrations from prey to spider, alerting the spider to the prey's presence and location (Masters *et al.* 1985). That is, *Diaea*'s web appears to function as an information gathering device which extends the spider's tactile sensory range because vibratory stimuli from prey can probably travel more efficiently to the spider through silk than through the vegetation.

Non-sticky webs may also have other advantages. A sticky web might collect a great deal of debris on its surface, which might impair the spider's sensory acuity when using the web to pick up vibrations from prey. Also, non-sticky webs may be less likely to provoke escape responses in potential prey.

Our observations suggest that, not only tactile and vibrational, but also visual cues from prey are used by *Diaea*, and we are currently conducting experiments to investigate the role of vision in mediating the predatory sequences of the species.

Diaea's web may be of assistance to *Diaea* when detecting and locating prey even when using visual, instead of vibrational, cues. Because the web reduces the space on which the spider and prey interact to a two-dimensional plane, prey is less likely to be out of view behind leaves, flower petals or other vegetation when on a web than when not on a web.

A few other thomisids have also been reported to stalk prey (Gertsch 1939; Snelling 1983), and recent work on thomisid retinae suggest that thomisid spiders (Blest *et al.* 1990) might have greater visual capabilities than previously thought.

Diaea's web appears to have yet another function that is not often considered in discussions of spider webs. By covering the convoluted topography of flowers and the vegetation with a web, the spider decreases the distance, and time, it must travel in order to reach the prey. In effect, the web can be likened to a motorway over which the spider can move rapidly from its current location to the prey.

Although no other detailed reports of prey capture on webs by thomisids have been found in the literature, Main (1976) reports that *Sidymella* sp., an Australian thomisid, leaves vegetation "matted with strands of silk formed from the criss-crossing of the drag-line thread". As many thomisids seem to be territory holders, often spending considerable periods occupying the same general area (Main 1976), deposition of draglines within this area is a likely precursor of the use, and adaptive development, of a silk edifice for prey-capture. Investigation may reveal more widespread use of silken structures for prey-capture in Thomisidae.

The behaviour of *Saccodomus formivorous* Rainbow, in particular, needs to be investigated in detail. Nearly a hundred years ago, this Australian thomisid was reported to build an unusual bag-like silken nest in the vegetation (Rainbow 1900). This structure may serve as a trap for ants, which appear to be the primary prey of this unusual thomisid (Rainbow 1900). Rainbow's (1900) paper appears, in fact, be the first report of web building in a thomisid. However, as is true for so much of the Australasian spider fauna, *S. formivorous* remains a potentially exciting study animal for which details of natural history and behaviour are still lacking.

Another example of an Australian thomisid that makes an unusual silken device is *Diaea socialis*. This spider binds leaves together to make a communal nest (Main 1988). However, unlike *Diaea* sp. from New Zealand, *D. socialis* does not appear to be a web builder. Instead, it hunts from portals in the nest, and it is not known to use the silk of its nest as a tool in prey capture.

There are interesting parallels between the biology of *Diaea* sp., a thomisid, and *Portia* (Jackson 1992), a genus of salticids. Like *Portia*, *Diaea* sp. is a web builder from a family in which web building is exceptional. Also in common with *Portia*, *Diaea* sp. is a versatile predator, each individual practising two disparate types of predation: catching prey on webs and ambushing prey while away from webs. This appears to the first report of predatory versatility in a thomisid.

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