RESEARCH ARTICLE

The Influence of Ants on the Mating Strategy of a Myrmecophilic Jumping Spider (Araneae, Salticidae)

Running head: Behaviour of a myrmecophilic jumping spider

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Abstract

Phintella piatensis is an unusual jumping spider because, despite being neither myrmecophagic nor myrmecomorphic, it associates with ants, including dangerous weaver ants. Although salticids typically spin cocoon-like nests for use as shelters, *Phintella*'s nests are unusually dense. These play an important role in how *Phintella* adapts to living with ants. In experiments, intraspecific interaction and mating increased the risk of being killed by ants when there was no accessible nest, while access to a nest eliminated this risk. Additionally, while outside of nests, seeing ants made *Phintella* reluctant to mate, this being an unusual example of a small animal with exceptional eyesight compensating for predation risk when making vision-based mating decisions. On the whole, *Phintella*'s behaviour during intraspecific interaction had broad similarity to the pattern that is common in salticids, but with some of the details of courtship suggesting further adaptation to interacting in the presence of dangerous ants.

Keywords: mating strategies; risk-related decisions; display; *Oecophylla smaragdina*; myrmecophily

Introduction

Much of the study of animal behaviour is concerned with understanding decision rules (Werner and Hall 1974; Charnov 1976; Kacelnik 1984). The tradition has been to consider these rules in one context at a time (e.g., Werner and Hall 1974; Cowie 1977; Davies 1977; Elner and Hughes 1978), with research on how the decisions of foraging individuals are influenced by predation risk being a notable exception (e.g., Millinski and Heller 1978; Cooper 2000; Martín et al. 2003). Here we investigate the risk-related mating decisions of *Phintella piatensis*, a jumping spider (Salticidae) that tends to live in close proximity to ants. In particular, we consider the adaptations by which the spider may minimize the risk ants pose to courting and mating individuals, where we define 'courtship' as intersexual communicatory behaviour that forms the normal preliminaries to mating (see Jackson 1982a).

During courtship and other interactions between conspecific individuals, animals often adopt distinctive display behaviour (i.e., they use signals that appear to have been evolutionarily modified in a manner that enhances information-conveying capacity; Smith, 1977). Some of the most elaborate display behaviour described for any animal group is found in the spider family Salticidae (Jackson and Pollard 1997). As a distinguishing characteristic, salticids have a pair of large forward-facing anterior-medial eyes that support exceptional spatial acuity (Land 1969; Williams and McIntyre 1980; Land and Nilsson 2002) and it is not surprising that these spiders' vision-based courtship has been emphasized in the literature (Peckham and Peckham 1889; Bristowe 1941; Richman and Jackson 1992) Yet chemosensory, tactile, and vibrational (seismic) signals are also known to have important roles in salticid courtship (Edwards 1981; Pollard et al. 1987; Maddison and Stratton 1988; Elias et al. 2003, 2006) and courtship versatility is more pronounced in the Salticidae than in any other spider family.

'Courtship versatility' (*sensu* Jackson 1977) refers to conditional mating strategies in which males use three distinct tactics depending on the female's location and state of maturity. Males adopt vision-based displays when they encounter mature

females outside nests (type 1 courtship) and silk-borne signalling when they encounter adult females inside nests (type 2 courtship). When a male encounters a subadult female inside a nest, his tactic ('cohabitation', see Jackson 1986) is to make a second chamber fastened to the female's nest and then wait to mate with the female when she matures.

A salticid's nest is typically a cocoon-like silken structure, with a slit at either end serving as a door through which the salticid enters and leaves. Besides being a mating site, the nest serves as a shelter when the salticid is quiescent and also as an oviposition and a moulting site (Jackson 1977). Here we show that a nest can be a safe haven for salticids that mate in the company of ants.

For salticids in general, ants appear to be especially important predators (James et al. 1999; Nelson et al. 2004), and most salticids may take active measures to avoid close proximity to ants (Harland and Jackson 2001; Nelson and Jackson 2006a). Yet myrmecophilic salticids, species that associate with ants, account for a sizeable minority of the species in this family, with the familiar myrmecophilic salticids being either myrmecophagic or the myrmecomorphic. Myrmecophagic species are salticids that routinely feed on ants, adopt ant-specific prey-capture behaviour and actively select ants as preferred prey (Jackson et al. 1998; Nelson and Jackson 2006b). Myrmecomorphic salticids usually do not eat ants but they morphologically and behaviourally resemble ants, with this resemblance functioning as Batesian mimicry (Cushing 1997; Edmunds 2006; Nelson et al. 2006; Nelson and Jackson 2006a).

Phintella piatensis (hereafter shortened to '*Phintella*') is unconventional because, although neither myrmecophagic nor myrmecomorphic, this salticid is nonetheless myrmecophilic. Here we document *Phintella*'s association with ants and *Phintella*'s intraspecific interactions. We also consider, with experiments, whether *Phintella* is especially at risk of being killed by ants during intraspecific interactions and whether *Phintella*'s mating strategy includes adjustments to this risk.

General methods

Our field site was in the Philippines at the International Rice Research Institute (IRRI) in Los Baños (Laguna Province, Luzon), where *Phintella* was especially abundant. This small (adult body length c. 3-5 mm) iridescent yellow-and-black species (yellow markings dominant on females, black dominant on males) was readily identifiable to species and sex.

For laboratory studies carried out at IRRI and at the University of Canterbury (New Zealand), we established cultures derived from spiders collected from the field site. Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier salticid studies (Jackson 1982b; Jackson and Hallas 1986) and only critical details are provided here. All testing was carried out between 0800 h and 1700 h (laboratory photoperiod, 12:12; lights on at 0800 hours). No individual spider, nest or mount was used in more than one test of any type. An earlier convention (Jackson and Hallas 1986) is adopted for indicating frequencies of occurrence: "usually", "often" and "typically" indicate c. 80% or more; "sometimes" and "occasionally" indicate 20–80%; "infrequently", "rarely" and "on rare occasions" indicate 20% or less. Standard terminology (Jackson 1982b) for spider legs was followed (legs I, the anterior most pair of legs; legs II, the second most anterior, etc). "Male" and "female" are short for "adult male" and "adult female". "Subadult" refers to spiders one moult before maturity, with "juvenile" referring to spiders two moults from maturity.

For experiments requiring living ants (carried out at IRRI only), we used a laboratory colony of Asian weaver ants, *Oecophylla smaragdina*, a species known for being exceptionally dangerous to salticids (Nelson et al. 2004, 2005). This colony was maintained in a large glass terrarium and the terrarium was kept humid by placing a water-logged 40-long cotton roll on the inside floor of the terrarium and replacing it every two days.

Although most previously studied salticids (Jackson and Pollard 1997) build more or less normal nests in bare plastic cages, the nests built by *Phintella* in the absence of a leaf usually differed considerably from nests in nature by being flimsy and poorly structured. However, most

individuals of *Phintella* spun normal nests when supplied with 'natural leaves' or 'artificial leaves'. Natural leaves, collected locally, were green, waxy, slightly concave (upper-surface bent up slightly around sides), more or less ellipsoid in shape and about 140 mm long and 100 mm wide. 'Artificial leaves' were made by cutting green cardboard (c. 0.5 mm thick) into ellipses comparable in size and shape to natural leaves and bending them to give the artificial leaf a slightly concave shape like that of natural leaves (see Cerveira and Jackson 2002). A leaf (natural or artificial) was placed concave side up in a cage made from a clear plastic Petri dish (diameter 140 mm). A damp cotton roll (40 mm long) was placed inside the Petri dish, positioned to one side. Spiders usually built nests on these leaves within 1-2 days. We destroyed all nests that were occasionally built in the cage but not on the leaf.

We staged preliminary encounters between conspecific individuals on natural and artificial leaves, with the leaf either left in the cage or else taken from cage and, by using a crocodile clip on a stand, held horizontal c. 150 mm above the surface of a laboratory bench. However, as interactions appeared to be similar regardless of the methods adopted, all testing and experiments reported here were based on using artificial leaves that were left in cages. Our preliminary testing confirmed that previously mated males usually mate again and previously mated females will also mate again, but only rarely. However, we standardised our methods by using, except where stated otherwise, only virgin males and virgin females (matched for size).

It was rare that we could directly observe whether mating took place after a male joined a female inside a nest and we relied instead on an indirect method for determining whether these females mated ("isolation procedure"): once one of the two spiders left the nest, we removed the male from the cage and kept the female isolated in her cage for a minimum of 10 weeks, with the laying eggs that hatched being confirmation that a female had mated.

Data were analysed using Fisher's exact tests and 3 x 2 and 2 x 2 chi-square tests of independence, with Bonferroni alterations of alpha made whenever the same dataset was used in more than one comparison.

Field survey

Methods

From casual observation, our impression was that *Phintella* routinely associated with ants in the field and we confirmed the accuracy of this impression by undertaking a survey in an area where the dominant tree species were *Mangifera indicata* (mango) and *Theobroma cacao* (cocao). The survey was carried out over 5 successive days in January 2000 by inspecting each leaf that could be reached without using a ladder (different trees sampled on each successive day). Each daily survey began at 1500 hours and lasted for 3 h. Whenever we found an individual *Phintella* inside a nest, we recorded whether or not the leaf also had ants on it. *Oecophylla smaragdina* was readily identified in the field (see below), but we collected the other ants for later taxonomic identification.

Results

One hundred and twenty-two occupied *Phintella* nests were found during the field survey and 111 (91%) of these had at least one ant on the same leaf. The ants were: *Oecophylla smaragdina* (34.2%); indeterminate (26.1%); *Crematogaster* sp. (15.3%); *Iridomyrmex* sp. (8.1%); *Camponotus* sp. (6.3%); *Polyrachis* sp. (5.4%); *Odontomachus* sp. (2.7%); *Anoplolepsis longipes* (1.8%)

Survival of eggs in the presence of ants

Methods

Unlike more typical salticid nests, *Phintella*'s had a crisp, tough weave that was difficult to tear with fingers or forceps, but was readily cut with sharp scissors. Being densely woven, the nests were opaque or nearly opaque. Viewed from above, the nest's shape was more or less rectangular, with the length of the nest tending to be 2-6 x the width, and height being about half the width (Figure 1). There was usually a door at each end, with these doors being flaps

of silk hinged at the top such that they opened by swinging up. Previously mated females in nests with eggs (oviposited 8-10 days before testing) were assigned at random to two groups (N = 12 for each). The female was removed from both the nest and the cage (see above) 10 min before testing began, leaving the eggs intact. Testing began by putting three *Oecophylla smaragdina* workers in the cage. Group A: nests left intact. Group B: nests cut open with scissors, exposing the eggs. For each group, we recorded 60 min later whether eggs had been destroyed.

Results

All of the eggs in intact nests, but none of the eggs in cut-open nests, survived ($\chi^2 = 24$, $P < 0.001$). We saw ants in the act of destroying eggs from cut-open nests in 10 (83.3% of 12) instances. In eight (66.6% of 12) instances, we saw ants biting briefly on intact nests and then walking away.

Influence of nests and of intraspecific interaction on survival with ants

Methods

There were seven treatments, with testing beginning for each when two *O. smaragdina* workers were introduced into a cage already containing a pair of spiders. Testing continued until one of the salticids was killed or 60 min elapsed, whichever came first, except that Group F also ended if the pair stopped mating (7 instances) and Group G also ended if one of the spiders left the nest (4 instances).

Group A (male-juvenile outside nest): a male was put in a cage containing a juvenile conspecific spider (body length, 2 mm); no nest present; ants put in cage directly after male.

Group B (female-female outside nest): a female was put in a cage containing another female; no nest present; ants put in cage as soon as the females began interacting.

Group C (male-female after mating outside nest): a male was put in a cage containing a female; no nest present; in successful tests, the spiders mated and, as soon as they separated, the ants were put in the cage.

Groups A-C gave us baseline data on the risk of being attacked by ants when the two spiders were interacting only minimally: From our preliminary work, we knew there was typically little, if any, display or other overt interaction during male-juvenile encounters and that females, during female-female encounters, rarely interacted for longer than 30 s and then showed little or no overt response to each other; we also knew that there was usually little or no overt interaction between spiders after they mated.

Group D (male-female outside nest): a male was put in a cage containing a female (female mated 2 days earlier); no nest present; ants were put in cage as soon as the male and female began interacting; testing aborted whenever mating began before the test ended (3 instances). Our goal with Group D was to get an idea of the risk male-female pairs incurred when interacting outside nests and, for this, we needed pairs that would persistently interact but not mate. We achieved this by using females that had already mated, as we knew from preliminary work that, despite already-mated females being reluctant to mate again, males persistently courted them.

Group E (male-male outside nest): a male was put in a cage containing another male; no nest present; ants put in cage as soon as the males began interacting. Our goal with Group E was to ascertain whether the risk of ant attack applied specifically to courtship or was instead general to interacting. For this we paired males, as we knew males were predisposed to persistent interaction.

Group F (male-female mating outside nest): a male was put in a cage containing a female; no nest present; ants were put in cage as soon as the spiders began to mate. Group F was used for getting an indication of the risk of ant attack incurred while mating outside nests and we achieved this by waiting to introduce the ants only after a male we paired with a virgin female began to mate.

Group G (male-female mating inside nest): a male was put in a cage containing a female; nest present; in successful tests, the male entered the nest occupied by the female and mating ensued inside (determined by isolation procedure); ants were put in cage as soon as the male entered the nest; there were no instances of spiders leaving nests before testing ended. By testing whether mating inside nests incurred risk of attack, Group G served as a control for group F.

Results

Among the groups designated *a priori* as displaying little interaction (Groups A-C), there were no significant differences in survival (Figure 2; $\chi^2 = 4.19$, P = 0.123, df = 2, N = 240). Among the groups designated *a priori* as displaying persistent interaction (Groups D and E), there were no also significant differences in survival (Figure 2; $\chi^2 =$ 404, P = 0.53, N = 160). Both of these results were pooled for subsequent analysis.

When we compared tests in which spiders displayed little interaction, being killed by ants was significantly more frequent in tests in which spiders interacted persistently (Groups A-C versus Groups D-E, $\chi^2 = 22.428$, $P < 0.001$, N = 400). Risk of attack appeared to be independent of whether the interaction was between courting individuals or between males displaying toward rival males (Figure 2; Group D versus Group E, $\chi^2 = 0.404$, P = 0.53, N = 160).

When outside nests, significantly more spiders were killed while mating than after mating (Figure 2; Group F versus Group C, $\chi^2 = 18.459$, $P < 0.001$, N = 160) and significantly more were killed when mating outside than when mating inside nests (Figure 2; Group F versus Group G, ($\chi^2 = 75.462$, $P < 0.001$, N = 120).

Once Bonferroni adjustments had been made for multiple comparisons, the suggestion of a trend for interacting male-female pairs, when outside nests, to be more at risk *in copula*

than during courtship was not significant (Figure 2; Group D versus Group F, $\chi^2 = 3.956$, P = 0.094, N = 160).

Influence of seeing ants on mating decisions

Methods

In this experiment, we used mounts (made from *O. smaragdina* workers) instead of living ants. We also used mounts made from green leafhoppers (*Nephotettix nigropictusi*, available in culture at IRRI). Each mount was made by using carbon dioxide to immobilise an insect, placing it in ethanol for 60 min, mounting it in a life-like posture on the centre of one side of a disc-shaped piece of cork (diameter of the disc c. 1.25 × the body length of the ant or leafhopper) and then spraying it with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty) for preservation.

Mounts were positioned in an otherwise empty Petri dish, each mount held in place with double-sided sticky tape on the bottom of the cork disc. There were eight mounts per dish, spaced evenly in a circle (distal end of each mount 20 mm from the rim of the dish and positioned so that the insect faced the centre of the dish). Before testing began, the dish was kept closed, but the lid was removed and the dish was turned upside down immediately before testing began.

There were three treatments: all eight mounts were ants, all eight were green leafhoppers, or no mounts were present (empty dish). The empty dish was a control for the procedure of placing a dish over the testing arena. Leafhoppers were a control for the effect of seeing ant-size insects instead of specifically ants.

Three trial conditions were used for each of the three treatments: 1) no nest was present (we used forceps to remove the nest from the leaf 5 min before testing began) (N = 50 for each of the three treatments); 2) a nest was present but the female was outside the nest when testing began (we did not entice the resident out of the nest but instead relied on instances when the resident had spontaneously left the nest 5 min before testing began) (N =

50 for each of the three treatments); 3) a nest was present and the female was inside the nest when testing began (N = 20 for each of the three treatments).

To start each test, we introduced a male into the cage directly followed by turning the open dish containing the mounts (or the open empty-nest control dish) upside down and placing it over the cage. Testing ended when mating was seen outside nests, when one of a pair of spiders inside a nest left the nest or after 60 min elapsed.

Results

In cages devoid of nests, there was an overall effect of treatment on how many of the pairs mated ("propensity to mate"; $\chi^2 = 46.3$, $P < 0.001$, df = 2, N = 150). However, as there was no difference between tests with the dish empty and tests with the dish containing mounts made from leafhoppers (Figure 3, $\chi^2 = 0.59$, $P = 0.444$, N = 100), results from these two were pooled ("ants absent") and then compared with the tests with dishes containing mounts made from ants ("ants present"). Mating occurred significantly less often when ants were present than when ants were absent ($\chi^2 = 46.0$, $P < 0.001$, N = 150).

When spiders were in cages with a nest available, but with interaction beginning while the female were outside the nests, inter-treatment differences in propensity to mate were not significant (Figure 3, $\chi^2 = 1.85$, $P = 0.397$, df = 2, N = 150,). However, there was significant variation among treatments in how many pairs went into nests before mating ("propensity to enter nests"; $\chi^2 = 24.8$, $P < 0.001$, df = 2, N = 150). As the propensity to enter nests was not significantly different between the empty-nest control and the leafhopper-mount treatments ($\chi^2 = 1.45$, $P = 0.229$, N = 100), these data were pooled. Propensity to enter nests to mate was significantly higher when ants were present than when ants were absent (Figure 4, $\chi^2 = 23.6$, $P < 0.001$, N = 142).

When testing began with the female already inside a nest, most pairs mated (determined by the isolation procedure) and there was no significant effect of treatment on propensity to mate (Figure 3, $\chi^2 = 2.14$, P = 0.343, df = 2, N = 60).

Response of males to empty nests

Methods

For testing the hypothesis that nests by themselves elicit posturing by the male, we first prepared cages containing nests but no occupants (N = 10) by gently pressing the nest with a wooden stick until the female left the nest. Testing began 5 min later by putting a male in the cage. We recorded whether the male postured before contacting the nest, posturing being display behaviour salticids typically restrict to interactions in which they can see the other spider (see below). Test duration was 10 min.

Results

All males postured without first contacting the nest (mean ± SEM of latency to display (s), 71 ± 12.9; display duration (s), 98 ± 18.7). In each instance, the male was oriented to the nest while posturing. Seven of the males later contacted the nest and three desisted without coming closer than 20-30 mm.

Staged encounters between conspecific individuals in the laboratory

Methods

With one individual (the 'resident') already in a cage, an encounter was staged by putting another individual (the 'intruder') in the cage (Table I). The intruder was taken into a plastic tube (diameter, 8 mm; length, 20 mm; plugged with a stopper at each end) and kept there until it was quiescent. Next we removed one stopper and inserted this end of the tube into a hole (diameter of hole, 8 mm) in the centre top of the cage. The intruder usually entered the cage within 2 min but, whenever this failed to happen, the stopper was removed from the

opposite end of the tube and a soft paintbrush was used to nudge the spider into the cage. For intersexual encounters, the female was always the resident.

Interactions at nests began when one spider displayed at or walked on to a nest occupied by another and ended when one of the spiders fled without the other watching or following. *Phintella* entered nests by placing tarsi I at the base of the door, then lifting legs I and walking inside. The definition we adopted for the beginning of interactions away from nests was the first instance of one of the two spiders displaying while oriented towards the other. These interactions ended when both spiders became quiescent on opposite ends of the leaf and remained this way for at least 5 min or when one spider fled, with the other not watching or following.

First we define elements of behaviour that occurred during intraspecific interactions and then we provide an overview of how behaviour was organized in different types of interaction (see Table II for the contexts in which key elements of behaviour occurred). As behaviour sequences were highly variable, only the general trends are summarised.

Elements of behaviour

In the normal posture, the spider's cephalothorax and abdomen were aligned and held parallel to substrate (ventral side c. 1 mm above substrate) (Figure 5), and the spider's palps appeared to hang loosely in front of chelicerae (femur-patella joints flexed sharply; tarsi held about parallel to each other and perpendicular to substrate) (Figure 5). Various departures from the normal posture were specific to conspecific individuals interacting.

Flexed-up and flexed-down abdomen: abdomen angled up (Figure 6) or down from the cephalothorax by10-90°.

Flexed-to-side abdomen: abdomen angled 10-80° to the left or to the right of the cephalothorax.

Rotated abdomen: left or right yaw (20-75°) of the abdomen from the cephalothorax (Figure 6).

Raised cephalothorax: cephalothorax parallel to substrate and the ventral side held c. 2 mm above the substrate.

Tilted-up body: anterior end of body angled up, with cephalothorax and abdomen being more or less in alignment (Figures 7 & 8).

Tilted-down body: anterior end of body angled down, with cephalothorax and abdomen being more or less in alignment (Figure 6).

Lowered body: cephalothorax parallel to the substrate and the underside of the cephalothorax touching or almost touching the substrate; abdomen aligned with the cephalothorax (Figure 1).

Flexed-up cephalothorax: cephalothorax angled up from the abdomen by 10-60°.

Twitch abdomen: abdomen moved jerkily up and down (2-4 s^{-1}, 2-3 mm, bouts usually lasting c. 3 s), sometimes with faintly perceptible side-to-side wobbling superimposed on the up-and-down motion.

Flutter abdomen: similar to abdomen twitching, but faster, at lower amplitude, of shorter bout duration (c. 10 s^{-1}, < 1 mm, bouts usually 1-2 s) and with no superimposed side-to-side wobble (i.e., motion appeared smooth).

Raised legs (refers to legs I only): all joints distal to the patella fully extended (erect, Figure 9) or almost fully extended (semi-erect), but with femur-patella joint sometimes flexed; three modal positions defined by the angle of the tarsi with respect to body.

Position 1: legs held parallel to substrate, or angling slightly down, and either extending almost directly forward or angling slightly inward toward each other.

Position 2: legs held c. 45° to side; kept about parallel to substrate or angling up by as much as 60° (Figure 9).

Position 3: like Position 2, except legs were held c. 90° to side (Figure 10)

Sprawled posture: Legs II-IV extended widely out from the body (Figures 8 & 9), with only slight flexion evident; sometimes legs I were raised in Position 2.

Tiptoe posture: all legs, or all legs except legs I, extended almost straight down (i.e. almost perpendicular to substrate) (Figure 11), with tarsi II-IV on the substrate; one or both tarsi I on the substrate or held slightly above the substrate, or legs I were held raised (Position 1 or 2).

Posturing: maintaining raised, sprawled or tiptoe posture while standing or stepping.

Arched palps: palps held ventral to the chelicerae; femur-patella joints flexed strongly; tarsi held anywhere on a continuum from pointing down and inward by 45° to being parallel to the substrate and pointing directly toward each other so that the tips of the tarsi touched or almost touched.

Frontal palps: femora held higher than in the normal posture, and angled in so that the patellae were just under the spider's eyes (Figure 8); from the patellae to the tarsi, palps angled almost straight down or down but also slightly inward, sometimes with the two palps almost touching; palps almost completely hid the chelicerae from view.

Retracted palps: femora held flexed up and to the side of face, with the tibia and tarsus of each palp were held parallel to the closer chelicera.

Raised palps: held the two palps parallel to the substrate or angled down as much as 45° and either parallel to each other (Position 1, Figure 9) or making an angle 120-180° to each other (Position 2; Figure 10); all joints fully extended (erect) or almost fully extended (semi-erect).

Downward palps: palps were held parallel to each other and extending either straight down or down and also forward by as much as 20° (Figure 11).

Flick palps: repeatedly and rapidly switching palps between semi-erect (Position 1) and downward, with only a momentary pause between each switchover (5-10 s^{-1} switchovers per bout, bout duration 1-2 s; two palps move in matching phase).

Lunge: by extending legs III and IV, without tarsi leaving the substrate, the spider moved its body suddenly and rapidly forward several millimetres and then immediately returned to original position.

Zigzag dance: while raised, tiptoe or sprawled posturing, the spider rapidly and alternately walked in a smooth motion 5-20 mm to one side and then the other side (each cycle, 1–4 s).

Spread-apart chelicerae: basal segments of the two chelicerae positioned so that there was a gap of 20-170° between them (Figure 10).

Extended fangs: with chelicerae spread apart, fangs were positioned away from basal segments of chelicerae, sometimes extending almost straight down (Figure 10).

Embrace: two spiders approached each other, usually with legs erect in Position 3, and then embraced (Figure 10) by bringing their legs I, and often also their palps and chelicerae, into contact; the spiders usually kept their chelicerae spread apart, with fangs extended, palps erect in Position 2, cephalothoraxes raised and abdomens flexed down.

Grapple and push: while embracing with legs in erect Position 3, spiders grappled by suddenly and forcefully flexing legs I down and repeatedly repositioning legs, with one spider sometimes managing to hook one or both of its legs I over the legs of the other spider and pulling the other spider's leg I or legs II down; spider pushed by attempting to walk forward while embracing, but its progress was usually impaired by the other spider pushing back or holding its position; normally spiders grappled and pushed at the same time.

Charge: one spider suddenly ran toward another spider, and then suddenly stopped when still 5-10 mm away, after which both spiders usually fled in opposite directions; charging spider's legs were usually raised, typically in erect in Position 2, with chelicerae usually spread apart and palps retracted.

Probe with legs and palps: from close to a door, but outside the nest, the spider jerkily moved tarsi of legs I (probing with legs) or tarsi of palps (probing with palps) in alternating phase backward and forward (2 s^{-1}) on the silk for 2-5 s (Figure 1).

Stand in door: after probing from outside, a spider extended legs I, and sometimes legs II, through door and then remained quiescent in this position for several seconds or minutes before entering or backing out of the nest.

Pre-mount tapping: a male repeatedly moved legs I (held erect in Position 1 and extended over the female) up about 45° and then down (1-3 s^{-1}), contacting the female's carapace on the downstroke.

Mount: while being pre-mount tapped by a male, the female lowered her cephalothorax and then the male walked (typically in slow, intermittent steps, interspersed with pauses lasting 1-5 s) over her, veering to one side and often adopting the tiptoe posture.

Scrape with legs: the male moved his leg tarsi (or tarsi plus metatarsi) across the female's body (c 2 s^{-1}, 1-2 mm; movement primarily femoral); the male usually scraped simultaneously with both of his legs I (on rare occasions, the male scraped with only one leg I); sometimes the male also scraped with one or both of his legs II (tarsi I contacted the female's abdomen; tarsi II contacted the female's cephalothorax or legs; legs I highly flexed, but legs II only moderately flexed).

Scrape with palp: while standing over a female, with one of his palp tarsi in contact with her body, a male moved his nearer palp back and forth (c. 5 s^{-1}; c. 1 mm; femoral movement) on female's ventral abdomen in the vicinity of her epigynum.

Apply palp: the male stopped scraping and held his palpal organ stationary on a female's epigynum; while the palp was applied, there was frequent pulsation of haematodocha and intermittent twitching of the male's abdomen.

Step aside: by pivoting and stepping, a spider undertook localized movement during which net movement was no more than a few millimetres.

Flee: one spider fled by running (usually) or jumping (rarely), away from another spider; unlike when stepping aside, a fleeing spider moved at least 20 mm before stopping.

Watch: by turning, a spider kept its anterior-medial eyes aligned with another spider.

Follow: by running (usually) or leaping (rarely), remained close to a fleeing spider.

Male-female interactions away from nests (Type 1 courtship)

These interactions usually began when a male, after orienting so that he was facing a female, postured with raised legs in Position 2. The female's first response was usually to watch the male. Throughout the highly variable sequences that followed, Position 2 posturing by the male continued to be common and females also postured intermittently with raised legs in Position 2. Males interjected bouts of zigzag dancing, tiptoe posturing and sprawled posturing and, whenever the male came to within 1-2 body lengths of the female, he usually postured with erect legs in Position 1. Females often stepped aside and then continued watching the male, usually without the male interrupting his display. Males usually twitched and fluttered their abdomens intermittently, especially once they were within 1-2 body lengths of females, but females only rarely twitched and never fluttered their abdomens. While watching the male, especially if the male was only a few body lengths away, the female often held her palps frontal, abdomen flexed up and cephalothorax lowered. At any stage in a sequence, the female might suddenly flee, with this usually being the end of the interaction because males usually watched fleeing females for only a few seconds and it was rare that they followed fleeing females.

If the female did not flee, it was usual for the male to approach the female from the side while zigzag dancing and, when the female turned to face him, the male shifted to her side again. The male continued to do this until the female was quiescent and facing 20-90° away and then he manoeuvred while dancing so that he was head on and usually only 10-20 mm away from the female. Next he covered the remaining short distance by stepping directly toward the female, all the while tiptoe or erect (Position 1) posturing. As the male came closer, the female lowered her cephalothorax, the male mounted and the pair mated.

Copulation

While copulating (i.e., when one of the male's palps was applied), the male and female were oriented 180° to each other (bodies parallel; female's abdomen flexed up and rotated, her cephalothorax lowered), with the male usually standing distinctively to one side of the

female, his posture resembling the tiptoe posture, except that his body was tilted down and there was considerably more flexion of his legs I. The male's legs II-IV on the same side as the applied palp passed over the female's body (rarely touching the female) and contacted the substrate on the other side (Figure 6).

Each palp was usually applied once or twice, with the male switching palps for each successive application, although there were two instances of the same palp being applied twice in a row. Between applications, the male disengaged and, if the female remained quiescent, moved across her to the other side, keeping his body raised over hers and the tarsus of his nearer leg I firmly pressed against her abdomen. The male sometimes walked backward over the female and, on reaching her cephalothorax, stepped forward over her again (tarsus of his nearer leg I pressed against her). After switching sides, the male resumed copulating. Females normally ended copulation by fleeing.

Male-female interactions at nests (Type 2 courtship)

When approaching a female's nest, males often twitched their abdomens and postured with legs raised in Position 2 (male's body in normal posture or lowered). There were rare instances of males, while approaching the nest, zigzag dancing, posturing with raised legs in Position 1, tiptoe posturing or sprawled posturing. Once the male contacted the nest, he began probing the silk (Figure 1) with his palps, legs or both and sometimes he stood or stepped about on a nest, all the while maintaining the tiptoe posture (Figure 11).

The pattern that usually followed was for the male to stand in the door and the female to remain more or less quiescent, with the male intermittently easing further into the nest. The female became agitated (details of how females behaved inside nests not discernible) when the male eased forward and he usually then resumed standing in the door until she was again quiescent. With repetitions of these sequences, 53 of the males slowly entered the nest and the isolation procedure confirmed that 51 of 53 females then mated inside the nest. However, two

females left the nest while the male was easing through the door, ending the interaction without mating taking place.

Male-male interactions away from nests

These interactions began when one male oriented toward another, raised his body and postured with legs raised in Position 2 or 3. The other male typically faced the displaying male and displayed in kind. There was intermittent palp flicking, abdomen twitching and abdomen fluttering and occasionally a male tiptoe postured. Sometimes one male charged and the other fled. Other times, the males stepped toward each other while posturing with raised legs in Position 3 and, once close, spread their chelicerae apart, extended their fangs and flexed their abdomens to the side and then embraced, after which one or both fled.

Female-female interactions away from nests

After orienting toward each other, females postured for up to 30 s, usually with raised legs in Position 2, palps downward or retracted and bodies raised. Brief bouts of charging, lunging, abdomen twitching and embracing were sometimes seen, but grappling was rare. Interactions usually ended with the two spiders fleeing in opposite directions.

Male-male and female-female interactions at nests

Usually the intruder (female or male) contacted the nest, probed briefly and then walked away after no more than 30 s. However, four males postured briefly while facing the nest and then walked to the nest, probed and walked away. Five of the resident males, but none of the resident females, came out of nest after the intruder made contact, after which a typical outside-nest male-male-male interaction took place. All other resident males, and all resident females, remained inside their nests until testing ended.

Cohabitation

Cohabiting pairs were often found in the field and we also observed cohabitation in the laboratory when we staged encounters (N = 5) between adult males and subadult females (adult male put in a cage in which there was a nest with a subadult female inside). In these instances, the male responded much the same as to an adult female in a nest except that he did not enter the nest and instead built a second chamber alongside and contiguous with the subadult female's nest. These pairs were left together and, when the subadult female underwent their final juvenile moult a few days later (next day = 1; after 4 days = l; after 5 days = 3), the males entered the females' chambers. The isolation procedure confirmed that each of these females mated.

Encounters with ants in the laboratory

Encounters were staged by putting a spider in a cage already containing an ant worker (N = 30), *O. smaragdina*, or by putting the ant worker in a cage already containing the spider (N = 25). The spider usually watched the ant from a distance and walked away if the ant came closer than 10-20 mm. However, there were rare instances of a spider facing the ant, adopting the sprawled or raised (Position 2) posture, only to flee soon afterwards.

As long as the spider stayed a few centimetres away from the ant, no particular reaction by the ant was evident, regardless of whether the spider postured. However, when the spider came closer, the ant usually spread its mandibles apart and ran toward the spider, with the spider usually fleeing and the ant chasing. The agitated ant usually held its abdomen flexed up c 70° and held the scapes of its antennae raised almost directly up, but bent at the pedicel so that the funiculus was extended forward and almost parallel to the substrate. Sometimes *O. smaragdina* killed *Phintella* by suddenly closing its jaws over the centre of the spider's abdomen.

Discussion

The company of ants, especially weaver ants, *Oecophylla smaragdina*, can be exceedingly dangerous for salticids (Nelson et al. 2004). However, in an earlier study during which encounters with weaver ants were staged in the laboratory (Nelson et al. 2005), myrmecomorphic and myrmecophagic salticids had, when compared with "ordinary" (i.e., not myrmecomorphic or myrmecophagic) salticids, distinctly higher survival rates. *Phintella* appeared to be an intriguing exception. Instead of being like that of other ordinary salticids, the survival rate of *Phintella*, a salticid that neither resembles nor eats ants, was akin to that of myrmecomorphic and myrmecophagic salticids. In the present study, we have shown that *Phintella* is myrmecophilic. It that routinely associates with ants in the field, including *O. smaragdina*, and our laboratory findings suggest some of the behavioural mechanisms by which this species minimizes the risks incurred by associating with dangerous ants.

During staged encounters, *Phintella* responded to seeing ants by keeping its distance, and perhaps this species has refined its ability to avoid ant attacks in this way. However, our experiments showed that the risk of being attacked by ants was particularly great during courtship and during male-interactions outside nests, and this risk was even more pronounced when individuals of *Phintella* were mating outside nests, consistent with other studies suggesting that, for a many animals, increased risk of predation is a cost of mating and a cost of other interactions between conspecific individuals (Ryan 1985; Magnhagen 1991; Baker et al. 1999). There have also been studies showing that, when exposed to predators, animals may alter their mate-choice decisions (Forsgren 1992; Johnson and Basolo 2003), animals become less receptive to potential mates (Dill et al. 1999) or make safety-related adjustments in how they court, mate and carry out other interactions between conspecific individuals (Sih 1988; Magurran and Seghers 1990).

We were especially interested in clarifying the role *Phintella*'s nest might play in defence against being attacked by ants. Although it has been proposed one of the more important functions of salticid nests is to provide anti-predator protection (Jackson 1979), our work on *Phintella* is an unusual instance of providing experimental support for this

hypothesis (see also Nelson and Jackson in press). In this study, we found that eggs inside nests that we cut open with scissors, but not nests we left intact, were raided by ants. Other experimental findings supported our hypothesis that ants influence *Phintella*'s decisions concerning whether to mate or not and its decisions concerning whether to mate inside or outside nests. When no nests were available, *Phintella* was less inclined to mate when ants were visible than when no ants were visible, yet if the female was already inside a nest, whether ants were visible or not had no effect on whether mating took place. However, when both spiders were outside, but with a nest in the vicinity, the pair entered the nest to mate in safety more often when ants were visible than when ants were not visible. An alternative hypothesis, that seeing more or less any ant-size animal in the vicinity influenced *Phintella*'s behaviour, seems unlikely because "no ants visible" included having leafhoppers instead of ants visible. *Phintella*'s decisions concerning mating and entering nests appears to be triggered by seeing specifically ants Our findings also suggest that *Phintella* can identify ants by their static appearance alone because, instead of using living stimuli, we used stationary mounts made from ants and leafhoppers and the mounts were placed outside the arena in which the spiders interacted. This procedure precluded any possibility of the test spiders touching the mounts. It is also unlikely that any residual odour from the ants that might have remained on the mounts after the treatment with ethanol and might have remained detectable through the aerosol plastic adhesive would have reached the test spiders inside the closed dish.

Except for tiptoe posturing, a distinctive part of *Phintella*'s display repertoire that was unlike the posturing adopted by other salticid species that have been studied (Jackson and Pollard 1997), the elements of behaviour seen during *Phintella*'s interactions (in particular, probing with palps and legs, abdomen twitching and fluttering, flicking palps, zigzag dancing, embracing, grappling and most of the distinctive postures adopted with legs, palps and body) were similar to those of many other salticids. The basic structuring of *Phintella*'s intraspecific interactions was also similar to that of salticids in general. This included male courtship

versatility, which was evident in intersexual interactions (type 1 courtship when females were encountered away from nests, type 2 courtship when females were encountered in nests and cohabitation when subadult females were encountered in nests).

However, there were some unusual details about the intersexual interactions of *Phintella* that might be related to the intraspecific interactions of this species often taking place in the company of ants. When compared to salticids in general, the distinction between type 1 and type 2 courtship for *Phintella* was not as sharp. During salticid courtship, it is usual for posturing to be a display males adopt only when a female is in view, but we often saw *Phintella* males posturing while facing a female's nest, with the female not seeming to be in view. We also confirmed experimentally that seeing a conspecific spider is not a prerequisite for male posturing. Posturing with only a nest in sight might function for *Phintella* males as pre-emptive broadcasting of their presence to females that might be present but not seen. Possibly these vision-based signals are supplemented by associated percussion signals transmitted through the leaf (e.g., by abdomen twitching and abdomen fluttering), something that would be interesting to address in future studies. While being attentive to finding a female, males may become less vigilant of ants nearby and pre-emptive display may encourage females to respond in a way that reveals their presence and location (e.g., females may posture in return), encourage females that might be outside to enter the nest or encourage any female already inside a nest to stay there, with these outcomes potentially reducing the *Phintella* male's risk of being attacked by ants.

Other behavioural details suggest that, when interacting outside nests, *Phintella* might take unusual measures to minimize risk of being attacked by ants. During type 1 courtship of other salticid species, it is typical for a male to approach a conspecific female head on and for the female to flee repeatedly, with the male watching and following, and with the male displaying again once the female settles down. *Phintella* was atypical, as its intersexual interactions almost invariably ended when females fled because the male only briefly watched and rarely followed. However, stepping aside, which might be envisaged as an attenuated

substitute for fleeing, was common during the intersexual interactions of *Phintella*. Additionally, the approach orientation of *Phintella* males was unusual. Males of other salticid species typically approach the female head on, but *Phintella* males often manoeuvred so as to approach the female from the side. Then, only when close to the female, the male positioned himself head on. The male's efforts to delay going head on with the female may function to make females less prone to flee.

Interactions between conspecific individuals may be instances in which salticids in general are especially vulnerable to attack by ants and other predators. However, by living in close proximity to ants, the risk to *Phintella* during intraspecific interactions may be exceptionally high. Although our findings suggest that the character of *Phintella*'s intraspecific interactions can be understood as evolutionary adjustments to the special risks incurred by myrmecophily, we have not addressed more basic questions concerning the advantages *Phintella* might gain by being myrmecophilic. A hypothesis currently being investigated is that keeping close company with ants provides *Phintella* with a degree of safety from the attentions of ant-averse predators.

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Table I. Sample sizes for interactions staged in the laboratory

Resident	Intruder	Nest present	No. of interactions
Female	Male	No (Type 1 courtship)*	80
		Yes (Type 2 courtship)**	55
Male	Male	Yes	70
		No	40
Female	Female	Yes	60
		No	40

*Mated, 72

**Mated, 51

Table II. Major elements of intraspecific behaviour of *Phintella piatensis* (listed alphabetically) and types of interactions during which they occur. M-F: male behaviour in male-female interaction. F-M: female behaviour in male-female interaction. M-M: behaviour in male-male interaction. F-F: behaviour in female-female interaction.

Element of behaviour	Context in which element of behaviour occurred
Charge	F-M, M-M, F-F
Embrace	M-F, F-M, M-M, F-F
Flick palps	M-M
Flutter abdomen	M-F, M-M
Lunge	F-M, F-F
Posturing with legs raised in Position 1	M-F
Posturing with legs raised in Position 2	M-F, F-M, M-M, F-F
Posturing with legs raised in Position 3	M-M
Pre-mount tapping	M-F
Probe with legs and palps	M-F
Scrape with legs and palps	M-F
Sprawled posturing	M-F, M-M
Stand in door	M-F
Step aside	F-M
Tiptoe posturing	M-F, F-M, M-M, F-F
Twitch abdomen	M-F, F-M, M-M, F-F
Zigzag dance	M-F

Figure 1. *Phintella piatensis* male, with body lowered, probing on nest. Female in nest. Note rectangular shape of nest.

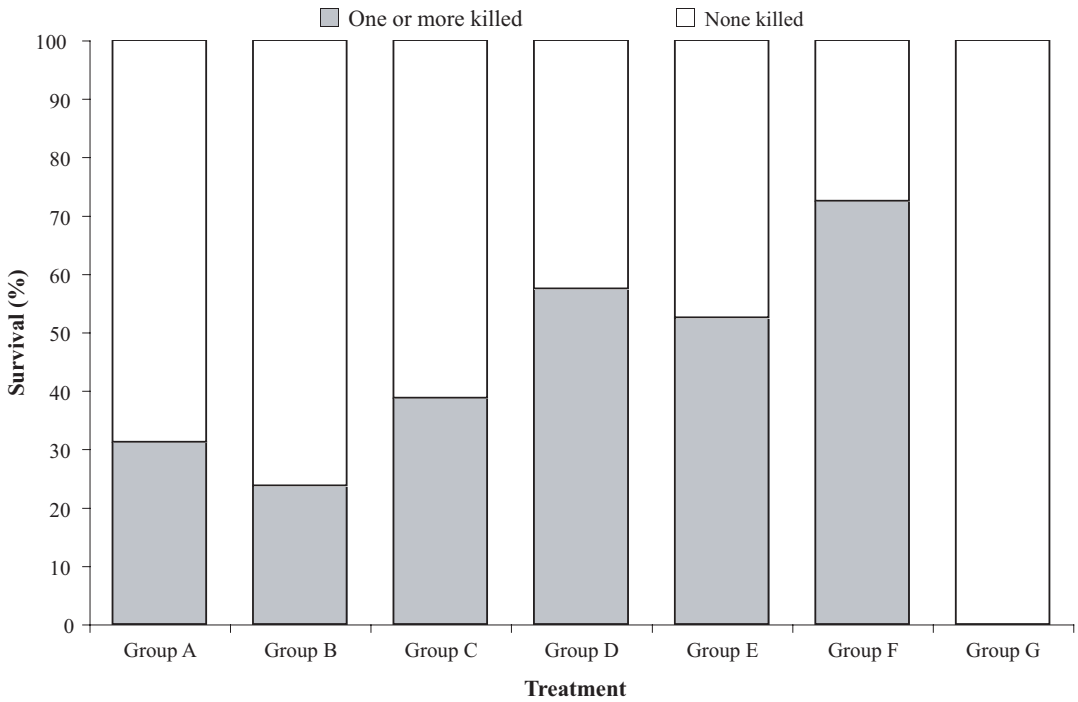

Figure 2. Influence of presence of nests and of interacting with conspecific individuals on survival of *Phintella piatensis* with ants (three *Oecophylla smaragdina* workers). Group A: male-juvenile pair, no nest. Group B: female-female pair, no nest. Group C: male-female pair, ants not introduced until mating ended, no nest. Group D: male-female pair (female mated 2 days earlier), no mating, no nest. Group E: male-male pair, no nest. Group F: male-female

pair mating, no nest. Group G: male-female pair, in nest. N = 80 for all groups except Group F (N = 40).

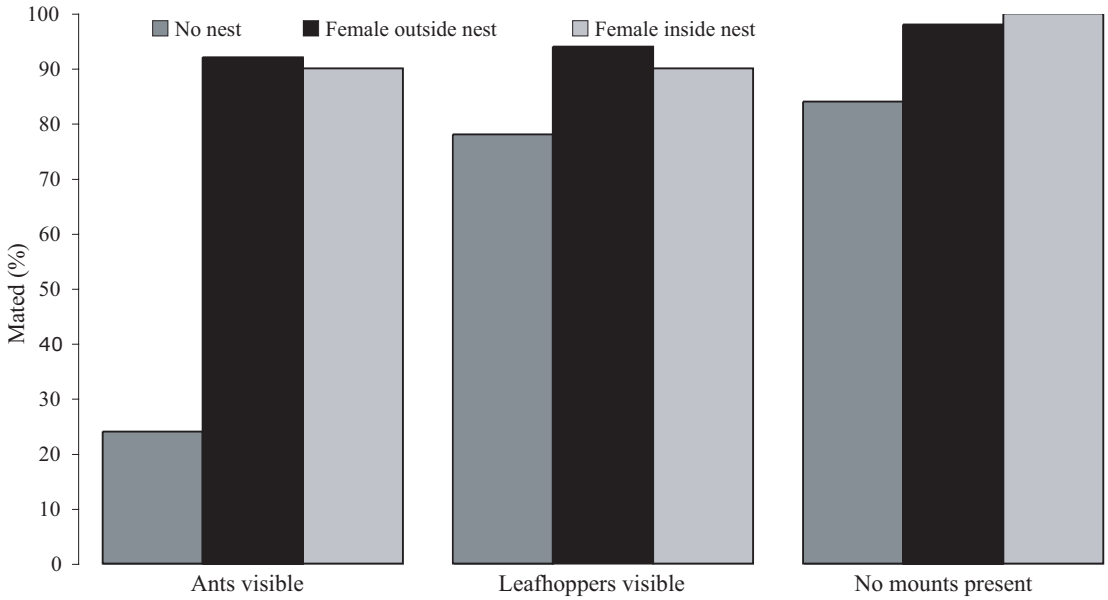

Figure 3. Influence of seeing ants on mating decisions of *Phintella piatensis*. Ants visible: mounts made from *Oecophylla smaragdina* (ants). Leafhoppers visible: mounts made from *Nephotettix nigropictus* (leafhoppers). No mounts present: empty Petri dish. For each treatment, tests were done in cages where there was no available nest, in cages where nest was available but female was outside and in cages where female was already inside nest. For testing with female already in nest, N = 20 for each treatment. For all others, N = 50.

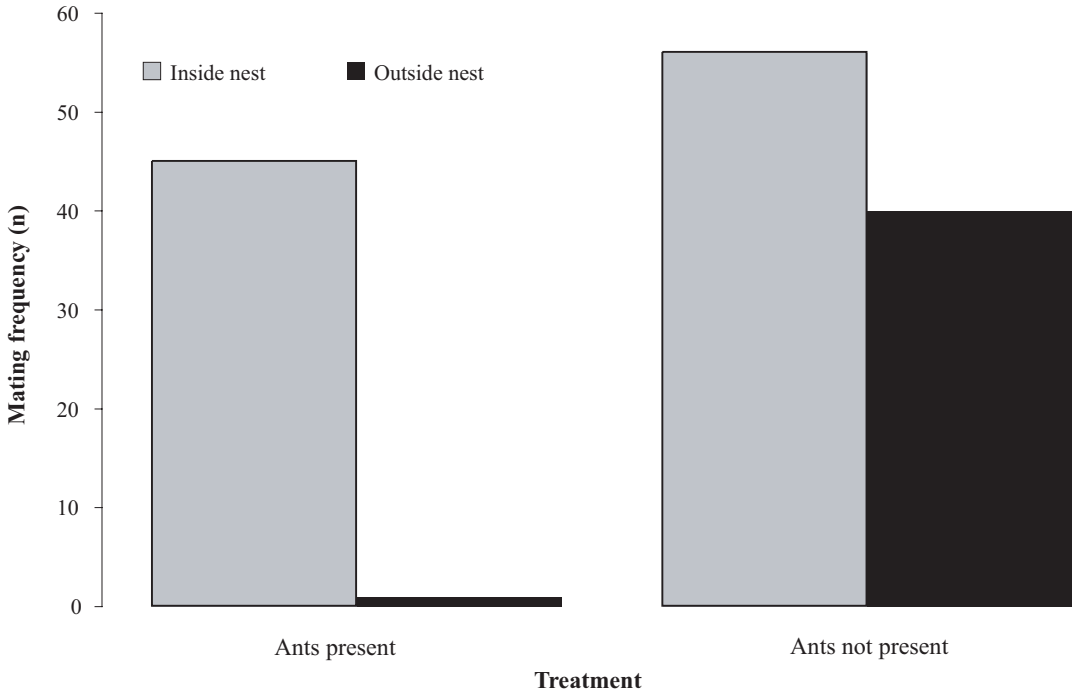

Figure 4. Comparison of number of *Phintella piatensis* pairs mating inside versus outside nest, under two different conditions. Ants present: data from testing in presence of mounts made from *Oecophylla smaragdina* workers. Ants not present: pooled data from testing in the presence of mounts made from *Nephotettix nigropictus* (leafhoppers) and testing in the absence of mounts.

Figure 5. *Phintella piatensis* female in a normal body posture holding the palps in a normal posture.

Figure 6. Mating pair of *Phintella piatensis*. Female (below; facing left) with abdomen flexed up and rotated to her left; cephalothorax lowered. Male (above; facing right and down) standing with his body to female's right side. Male's body tilted down.

Figure 7. *Phintella piatensis* male (facing right) in sprawled-legs posture with body tilted up.

Figure 8. *Phintella piatensis* male (facing diagonally forward and to the right) in sprawled-legs posture with body tilted up and palps frontal.

Figure 9. *Phintella piatensis* male (facing to right; dorsal view) in sprawled-legs posture with legs I erect in Position 2 and with palps semi-erect in Position 1.

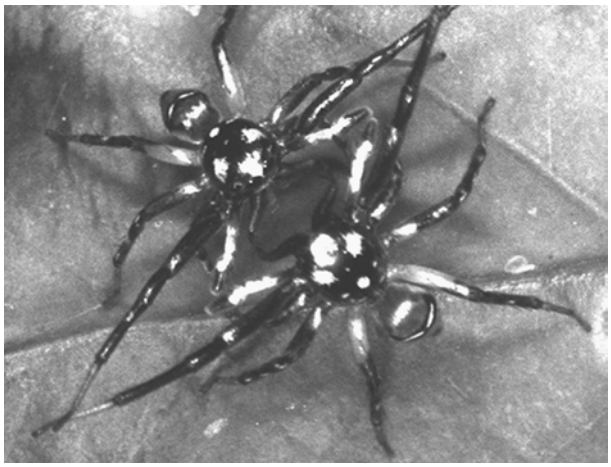

Figure 10. *Phintella piatensis* males embracing. Palps erect in Position 2. Legs I erect in Position 3. Chelicerae spread apart and fangs extended.

Figure 11. *Phintella piatensis* male (facing up and to left) in tiptoe posture while standing on female's nest. Palps downward (extend straight down). All leg tarsi contacting silk.