

Brood-defence as a function of maternal brood-attendance in *Trite planiceps* Simon (Araneae, Salticidae)

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Summary

In support of the hypothesis “brood-attendance by maternal jumping spiders (Salticidae) functions as brood-defence”, broods of *Trite planiceps* are shown to suffer increased predation in nature when maternal females are removed. Apparent predators of unattended *T. planiceps* broods are identified in nature, and that these species eat *T. planiceps* eggs and post-embryos is confirmed in the laboratory. *Trite planiceps* males and females not attending broods of their own ate the eggs and post-embryos of conspecifics in the laboratory but females with their own broods did not, indicating that predation of conspecifics’ broods is suppressed by maternity.

Introduction

Although some spiders typically abandon their eggsacs soon after oviposition, others stay with them until the juveniles disperse (Foelix, 1982). “Brood-attendance” by maternal females is widespread in jumping spiders (Salticidae), but the function of this behaviour in salticids has rarely been studied. Richman & Jackson (1992) have suggested that, like some spiders from other families (e.g. Pollard, 1984; Willey & Adler, 1989; Horel & Gundermann, 1992), brood-attendance by maternal salticids functions as brood-defence. At present, however, Richman & Jackson’s (1992) suggestion is supported only by indirect evidence from nature and laboratory studies (Eberhard, 1974; Jackson & Willey, 1994), and whether brood-attendance by maternal salticids reduces the frequency of predation on broods does not appear to have been investigated for any species.

Trite planiceps Simon is a common New Zealand salticid that appears especially well suited to an investigation of whether maternal brood-attendance can reduce the frequency of predation on broods. Most salticids shelter and oviposit inside a dense, opaque, silken cocoon (Hallas & Jackson, 1986). For these species, it is very difficult to assess the incidence of predation on the brood without damaging the cocoon and thereby increasing exposure to predation or damage from other sources. *Trite planiceps* usually does not shelter or oviposit within such a cocoon; this species instead deposits its eggs in layers that form an open platform within the cavities formed by rolled-up leaves of New Zealand flax (*Phormium tenax*) and similar plants (Forster, 1979). These leaves roll up naturally as they desiccate, and their shape is neither caused nor maintained by the spiders. When leaves containing broods are unrolled, the developing offspring of

T. planiceps are clearly visible through the thin sheet of silk that covers them. Maternal females are found standing on their nests facing the entrance to the rolled-up leaf (Fig. 1). In the present study, I investigate the hypothesis “brood-attendance by maternal *T. planiceps* functions as brood-defence” and identify some of the predators that might eat unattended broods.

Material and methods

Effects of maternal brood-attendance on survivorship of broods in nature

Ninety *Trite planiceps* broods with attendant females were located in rolled-up leaves of New Zealand flax near Christchurch, New Zealand. All broods contained 1–3 egg-batches (eggs deposited at the same time and enclosed by thin sheets of silk) when experiments began, and each egg-batch contained 8–20 eggs or post-embryos. No broods contained first instar spiderlings (dispersing stage) when experiments began.

Forty-five broods were randomly assigned to each of two experimental groups: “unattended” and “attended”. Maternal females were removed from broods in the unattended group, but were left on the broods of the attended group. Each rolled-up leaf containing a brood was marked with enamel paint for relocation and individual identification. All broods were initially located, and experiments started, between 20 November and 11 December 1993. Broods were checked for a maximum of 6 weeks, the maximum latency from oviposition to dispersal of juveniles observed in nature during the same period in the previous season (unpublished data).

To inspect a brood, the rolled-up leaf was carefully unrolled to expose the nest. When the leaf was unrolled, the maternal female usually retreated to a part of the leaf that remained rolled-up and returned to the nest later. All broods were inspected once weekly to assess whether females were present on broods in the attended group, and to assess broods for evidence of predation. Each week, the number of eggs and post-embryos in the uppermost egg-batches was counted. Absence of eggs or post-embryos that were present the previous week and physical damage to the nest was adjudged to be

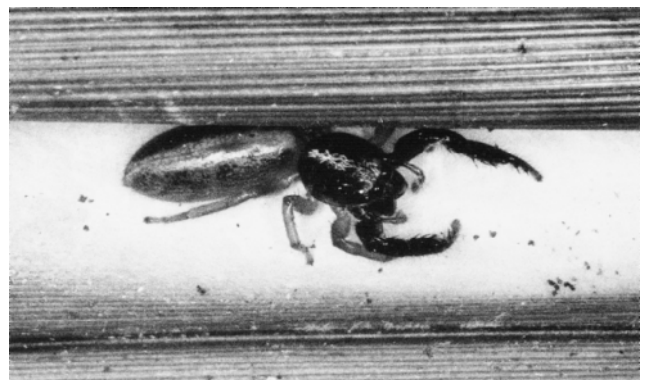


Fig. 1: *Trite planiceps* female (body 10 mm) on her nest inside a rolled-up leaf of New Zealand flax (*Phormium tenax*) (leaf unrolled to photograph).

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evidence of predation. Assessment excluded first-instar spiderlings for which it was not possible to ascertain whether disappearance was due to dispersal or predation. After inspection, the leaves rolled back to their original shape.

Inspections were always carried out within 2 h of sunset, as preliminary observations showed that maternal females that left the rolled-up leaf containing the brood during the day usually returned several hours before darkness. Dusk was therefore the most reliable time to assess whether nests in the attended group still had an attendant female. Broods were omitted from analysis if the leaves were damaged during sampling, and attended broods were omitted if maternal females went missing (never subsequently observed with the brood). To assess the effect of maternal brood-attendance on frequency of predation on broods, I compared the cumulative frequencies of predation since the previous weekly inspection for attended and unattended broods, the likelihood that a nest suffered any predation in the testing period, and the likelihood that at least some offspring survived until the dispersing stage.

Predation on T. planiceps broods in the laboratory

Species suspected to be predators of *T. planiceps* broods in nature were collected, and whether they eat undefended broods was investigated in the laboratory. Suspected predators included conspecific males, conspecific females (with and without broods of their own), *Clubiona cambridgei* L. Koch (Clubionidae), *Cheiracanthium stratioticum* L. Koch (Clubionidae), *Taieria erebus* (L. Koch) (Gnaphosidae), and *Forficula auricularia* (L.) (Dermaptera, Forficulidae).

Individual adults of each suspected predator were maintained in the laboratory for 1–2 weeks before testing, following procedures outlined by Jackson & Hallas (1986). They were given *ad libitum* access to house flies (*Musca domestica* L.) and fruit flies (*Drosophila melanogaster* Meigen) as prey. Gravid *T. planiceps* females (evident from distended abdomens) were also collected and maintained in the laboratory. After a *T. planiceps* female had deposited 2 or 3 batches of eggs and the nest contained both eggs and post-embryos, the maternal female was removed from her cage and a suspected brood-predator was released into the cage containing the brood. Whether any eggs or post-embryos had been eaten was checked 7 days later.

Results

Effects of maternal brood-attendance on survivorship of broods in nature

The presence of maternal *Trite planiceps* on broods was strongly associated with reduced frequency of predation on broods. Some eggs of broods in the unattended group were found to have been eaten since the previous week in 66 (31.6%) of 209 sampling events, whereas some eggs of broods in the attended group were found to have been eaten since the previous week in only

8 (3.3%) of 240 sampling events (test of independence with Yate's correction, $\chi^2=64.75$, $p<0.001$).

Of the 38 broods that were attended throughout the 6-week period (maternal females went missing from 5 broods, and 2 broods were omitted because the leaves split open during sampling), only 7 (18%) suffered any instances of predation. In contrast, 35 (78%) of the 45 unattended broods suffered one or more instance of predation (test of independence with Yate's correction, $\chi^2=26.71$, $p<0.001$). Some offspring from all attended broods survived until the dispersing stage, but some offspring survived this long in only 8 (18%) of the 45 unattended broods (test of independence with Yate's correction, $\chi^2=53.10$, $p<0.001$).

The clubionid spiders *Clubiona cambridgei* and *Cheiracanthium stratioticum*, and the gnaphosid spider *Taieria erebus*, were commonly seen in rolled-up leaves similar to those in which *T. planiceps* nests were usually found. Each of these nocturnal hunters was sometimes found in the remains of unattended *T. planiceps* broods that had suffered predation, although they were never observed eating eggs of *T. planiceps* in nature. An earwig, *Forficula auricularia* (Dermaptera, Forficulidae), was found on unattended broods that had suffered predation on 11 occasions, and on 3 of these occasions was observed eating eggs. Adult female *T. planiceps* were found on unattended broods on 15 occasions. On 11 of these occasions, some of the brood had been eaten. In 3 of the other 4 cases, the *T. planiceps* female apparently adopted the nest, depositing her own eggs alongside those already present.

Predation on T. planiceps broods in the laboratory

All of the suspected predators that were found in damaged nests in nature ate the eggs and post-embryos of *T. planiceps* in the laboratory (Table 1). Although conspecific males and females without broods of their own (non-brooding females) ate eggs and post-embryos in the laboratory, females with broods of their own (brooding females) did not eat each other's broods. Because none of the predators appeared to discriminate between eggs and post-embryos, data for these prey types were pooled.

	N	%
<i>T. planiceps</i> male	10	50
<i>T. planiceps</i> brooding ♀ (on conspecific's brood)	16	0
<i>T. planiceps</i> brooding ♀ (replaced on own brood)	30	0
<i>T. planiceps</i> non-brooding female	15	40
<i>C. cambridgei</i> female	10	90
<i>C. stratioticum</i> female	10	100
<i>T. erebus</i> female	10	100
<i>F. auricularia</i>	10	70

Table 1: Number of individuals tested for predation on *Trite planiceps* broods in the laboratory, and percentage that ate one or more eggs or post-embryos during the 7-day testing period. "Brooding females" were attending broods of their own whereas "non-brooding females" had not attended broods for at least 10 days before testing.

Discussion

In support of Richman & Jackson's (1992) suggestion that brood-attendance by maternal salticids functions as brood-defence, the present study showed that *Trite planiceps* broods deprived of maternal females suffer greatly increased mortality from predation. Under natural conditions, maternal females that abandoned their broods altogether, or spent insufficient time guarding, would suffer greater losses from brood predation than more attentive conspecifics.

Although this is the first direct evidence from nature, there is ample reason to suspect that brood-attendance also functions as brood-defence in other salticids. Salticids commonly share their habitats with ants, parasitic Hymenoptera, Diptera, mantispids, spiders, and various opportunistic scavengers (e.g. Dermaptera) that might attack their broods (Austin, 1985; Jackson & Hallas, 1986; Jarman & Jackson, 1986; Nyffeler *et al.*, 1990). Additionally, like *T. planiceps*, the broods of some salticids might be prone to attack by foraging conspecifics (although suppression of brood-predation by maternity may lessen this threat). With their fangs and venom, weapons otherwise employed when hunting, maternal salticids would probably present a formidable deterrent for many prospective brood predators.

In accord with a general paucity of information about salticid life-histories, little is known about how salticids detect and deal with enemies at their nests. In a rare exception, Eberhard (1974) describes maternal *Lyssomanes jemineus* Peckham, Peckham & Wheeler physically repelling diurnal intruders from the surface of their nests. In this case, the salticid could use its exceptionally acute vision (Blest *et al.*, 1990) to recognise intruders and mediate attacks. However, many of the predators reported to eat salticid broods are nocturnal (Jackson, 1976; Jarman & Jackson, 1986), attacking when the salticid's acute vision would be redundant. For example, all of the heterospecific predators of *T. planiceps* broods identified in this study are nocturnally active. Additionally, maternal salticids attacked at their nests during the day may be unable to see the attacker because their view would be obscured by the silken cocoon or because, like *T. planiceps*, they build their nests in dark places (Hallas & Jackson, 1986). How salticids detect and deter potential brood-predators when visual cues are absent warrants special attention as an unusual instance in which salticids are active whilst they are restricted to the sensory limits of spiders which lack acute vision.

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