Predation by ants on jumping spiders (Araneae: Salticidae) in the Philippines

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Abstract Using a tropical fauna from the Philippines as a case study, ant-salticid predator-prey relationships were investigated. In the field, 41 observations of ant predation on salticids were made, and the actual attack on the salticid was seen in four. In the laboratory, five of the ant genera observed in the field were tested with four categories of salticids: (1) four myrmecophagic (i.e., ant-eating) species, (2) six myrmecomorphic (i.e., ant-like) species, (3) an ant-associate species (i.e., a species that is neither myrmecophagic nor myrmecomorphic, but known to associate with ants), and (4) 14 ordinary species (i.e., species that are neither ant-eating nor ant-like, and are not known to associate with ants). In these

tests the highest survival rates were observed in the myrmecophagic salticids, followed by the myrmecomorphic salticids, the ant-associate species, and finally the ordinary species.

INTRODUCTION

In the tropics, ants (Formicidae) are the dominant insects (Hölldobler & Wilson 1990) and jumping spiders (Salticidae) are the dominant spiders (Coddington & Levi 1991), but little is known about how salticids and ants interact. Ants may often be important predators of other types of spiders (Gillespie & Reimer 1993; Vieira & Hoefer 1994; Halaj et al. 1997), but salticids have a potential advantage in ant-spider encounters. Although spider eyes generally lack the structural complexity required for acute vision (Land 1985), the unique, complex eyes of salticids (Land 1969a,b; Blest et al. 1990) support resolution abilities that have no known parallels in other animals of comparable size (Land & Fernald 1992; Land & Nilsson 2002). Whether these keen-sighted arthropods are threatened by ants requires investigation.

As a step toward clarifying the significance of ants as predators of salticids, we investigated a tropical fauna from the Philippines. We compiled records of ants feeding on salticids in the field and confirmed in laboratory tests that ants readily kill salticids. In laboratory tests, we considered four categories of salticids (myrmecophagic, myrmecomorphic, ant associate, and ordinary), investigating whether representative species from these four categories differ in their vulnerability to attacks by ants.

We reserved the term "myrmecophagic" (or "ant eaters") for a minority of salticids that feed routinely on ants in nature and have been shown in laboratory studies to prefer ants to other prey (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, 1992; Li & Jackson 1996; Li et al. 1996; Jackson et

al. 1998). There were four representative species from this group in our study (Table 1). Another minority of salticids, the myrmecomorphic species, resemble ants in gross morphology and style of locomotion (Edmunds 1974; McIver & Stonedahl 1993; Cushing 1997). The most extensively studied species in this group belong to the genus *Myrmarachne* (Wanless 1978; Jackson 1986; Jackson & Willey 1994), and we included six *Myrmarachne* species in our study (Table 1). Myrmecomorphic (or "ant mimic") salticids rarely prey on ants, and these salticids' resemblance to ants

probably has little or no role in deceiving ants (Elgar 1993) because ants, in general, lack acute vision, relying primarily on chemical and movement cues for prey detection and for discriminating colony members from intruders (Hölldobler & Wilson 1990). That myrmecomorphic salticids are Batesian mimics of ants (i.e., ant mimicry serves to reduce predation on the mimic due to its similarity to a dangerous model, in this case ants) is the most widely accepted hypothesis for these spiders' resemblance to ants (Edmunds 1974, 1978, 1993; Cutler 1991; Elgar 1993; Cushing 1997).

Table 1 Salticids used in tests with ant workers in the laboratory.

Salticid	Description	Category
Bavia sexpunctata (Doleschall)	Species that neither mimics nor eats ants	Ordinary
Chalcotropis gulosa (Simon)	Ant eater	Myrmecophagic
Chalcotropis luceroi Barrion & Litsinger	Ant eater	Myrmecophagic
Cosmophasis estrellaensis Barrion & Litsinger	Species that neither mimics nor eats ants	Ordinary
Epeus hawigalboguttatus Barrion & Litsinger	Species that neither mimics nor eats ants	Ordinary
Harmochirus brachiatus (Thorell)	Species that neither mimics nor eats ants	Ordinary
Heratemita alboplagiata (Simon)	Species that neither mimics nor eats ants	Ordinary
Lagnus sp.	Species that neither mimics nor eats ants	Ordinary
Mantisatta longicauda Cutler & Wanless	Species that neither mimics nor eats ants	Ordinary
Menemerus bivattatus (Dufour)	Species that neither mimics nor eats ants	Ordinary
Myrmarachne assimilis Banks	Ant mimic	Myrmecomorphic
Myrmarachne bakeri Banks	Ant mimic	Myrmecomorphic
Myrmarachne bellicosa (G. & E. Peckham)	Ant mimic	Myrmecomorphic
Myrmarachne bidentata Banks	Ant mimic	Myrmecomorphic
Myrmarachne maxillosa (C. L. Koch)	Ant mimic	Myrmecomorphic
Myrmarachne nigella Simon	Ant mimic	Myrmecomorphic
Orthrus bicolor Simon	Species that neither mimics nor eats ants	Ordinary
Phintella piatensis Barrion & Litsinger	Species that neither mimics nor eats ants	Ant associate
Portia labiata (Thorell)	Species that neither mimics nor eats ants	Ordinary
Plexippus petersi (Karsch)	Species that neither mimics nor eats ants	Ordinary
Siler semiglaucus Simon	Ant eater	Myrmecophagic
Telamonia masinloc Barrion & Litsinger	Species that neither mimics nor eats ants	Ordinary
Thiania sp.	Species that neither mimics nor eats ants	Ordinary
Xenocytaea sp.	Ant eater	Myrmecophagic

We also included an ant-associate species, *Phintella piantensis*, in our study (Table 1). Little is known about the biology of this species other than that it is frequently found living in the vicinity of ants. It is not myrmecomorphic, nor does it appear to be myrmecophagic. In the field, it has been seen feeding on a variety of insects, but never on ants, and it never fed on ants in laboratory trials (unpubl. data).

The majority of salticids, which we will call the "ordinary" species (Table 1), do not live in close association with ants and neither resemble nor routinely eat ants. Avoiding ants may be an ordinary salticid's best defence, but ant eaters, ant mimics and *Phintella piantensis* would not appear to have this option. Ant eaters must approach the ants on which they prey, and effective Batesian mimicry may depend on ant-like salticids living in proximity to ants. Additional research on *Phintella piatensis* is needed to clarify the adaptive significance of this species' predisposition to associate with ants, but the routine occurrence of these associations suggest that living close to ants has some overriding importance for *Phintella*.

Our hypothesis is that, among salticids, survival tactics that permit close proximity to ants have evolved especially in myrmecophagic, myrmecomorphic and ant-associate species.

MATERIALS AND METHODS

General

Our study site was in the vicinity of Los Baños (Laguna Province, Luzon), including rain forest at Mt Makiling. Between 1993 and 2000, whenever we found salticids in the field being attacked by or fed on by ants, we collected the ants and the salticids for identification (Table 2). Prey identification was taken to the lowest taxonomic level possible. However, working with a poorly known fauna and with prey often being in mediocre condition when collected, species determination was often imprecise.

The ants and salticids chosen for laboratory experiments were species from field ant-predation records. When needed, we collected ants from the field for laboratory studies, but all salticids used in experiments came from laboratory cultures and none had prior experience with ants of any species. No individual ant or salticid was tested more than once.

Table 2   Records of ants feeding on salticids in nature.

Salticid	Ant	No. of records
Bavia sexpunctata	*Oecophylla smaragdina*	3
Carrhotus sannio (Thorell)	*Odontomachus* sp.	1
Cosmophasis estreallensis	*Oecophylla smaragdina*	2
Epeus hawigalboguttatus	*Oecophylla smaragdina*	1
Gambaquezonia itimana Barrion & Litsinger	*Oecophylla smaragdina*	1
Harmochirus brachiatus	*Solenopsis geminata*	2
Heretemita alboplagiata	*Oecophylla smaragdina*	1
Icius sp.	*Odontomachus* sp.	1
Lagnus sp.	*Odontomachus* sp.	2
	Polyrachis dives	1
	Polyrachis sp.	1
Menemerus bivittatus	*Diacamma vagans*	1
Myrmarachne assimilis	*Oecophylla smaragdina*	1
Myrmarachne bakeri	*Solenopsis geminata*	1
Orthrus bicolor	*Diacamma vagans*	1
Phintella piatensis	*Solenopsis geminata*	1
Portia labiata	*Odontomachus* sp.	3
	Oecophylla smaragdina	1
Thiania sp.	*Oecophylla smaragdina*	1
Thianitara sp.	*Odontomachus* sp.	1
Unknown	*Dolichoderus bituberculatas*	1
	Oecophylla smaragdina	5
	Odontomachus sp.	4
	Solenopsis geminata	4

All salticids were juveniles (body length: 3–4 mm). Only worker ants were used, and tests were aborted whenever ants died during the course of the experiment.

Salticid maintenance procedures were the same as those used in earlier spider studies (Jackson & Hallas 1986). All tests began at c. 0800 h and lasted 10 h (laboratory photoperiod 12L:12D, lights on at 0700 h). Data were analysed using tests of independence (Sokal & Rohlf 1995).

We tested 25 salticid species belonging to four groups: ant associate (1 species); ant eater (4 species); ant mimic (6 species) and ordinary (14 species). Analysis was based on these *a priori* groupings.

One-ant tests

Tests were carried out by placing one juvenile salticid, followed 5 min later by one ant, in a cage made from a plastic petri dish (diameter 90 mm). Each test began in the morning and the fate of the salticid was recorded 10 h later. Intermittent observations were made during this period.

There were holes (diameter 5 mm) in the centre of the top and in the centre of the bottom of the cage. Ants and spiders were introduced into the cage via the hole at the top. Except when introducing ants and spiders, the top hole was plugged with a cork that fitted flush with the surface of the cage (i.e., it did not protrude into the cage). Each spider or ant to be transferred was first taken into a 40-mm long (diameter 5 mm) clear glass tube (plugged by a cork at both ends). After 10 min the corks were removed from one end of the tube and from the top hole of the cage. The open end of the tube was placed against the open top hole of the cage. If the spider or ant did not enter the cage immediately, the cork at the other end of the tube was removed and the spider or ant was gently pushed out of the tube and into the cage with a soft-hair paintbrush.

A waterlogged cotton roll (diameter 5 mm, length 40 mm) was inserted through the bottom hole. The top end of the cotton roll protruded 3 mm into the cage. The cage rested on a plastic pot (diameter 50 mm) filled with water. The cotton roll, by protruding from the bottom of the cage into the pot of water, remained waterlogged during the course of the each test and provided humidity and drinking water for the spiders and the ants.

There was nothing in the cage other than the spider, the ant, and the cotton roll. Between tests, cages were wiped clean with 80% ethanol, followed by distilled water. Transfer tubes and corks were also cleaned with 80% ethanol, followed by distilled water. The cleaning routine was a precaution against any potential influence of chemical traces from previous ants and salticids on test outcomes. Each salticid species was tested with the same five ant genera (Table 3). Equal numbers of tests ($N = 100$) were carried out with each salticid-ant combination.

Five-ant tests

These tests were identical to one-ant tests except that five ants (all of the same species) shared the petri dish with the juvenile salticid. In each instance, the five ants used were collected in close proximity to each other and were probably from the same colony.

OBSERVATIONS FROM THE FIELD

Forty-one examples of ants preying on salticids were observed (Table 2). Most of the salticids (66%) could be identified at least to genus. During four of these 41 observations, ants were attacking a living salticid: in one instance, a group of *Oecophylla smaragdina*

Table 3 Ant workers (Hymenoptera, Formicidae) used in the laboratory.

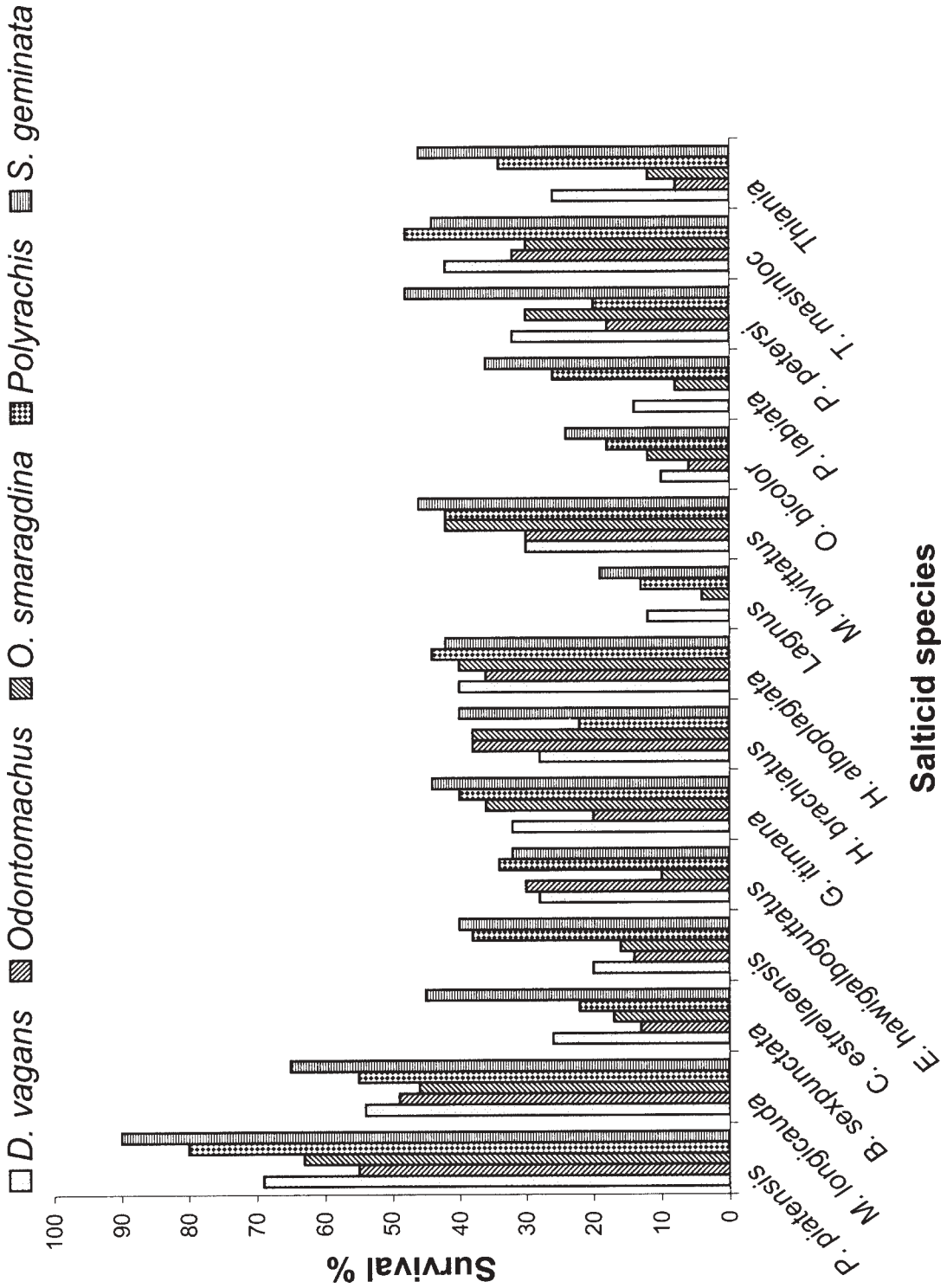| Subfamily	Tribe	Species	Body length (mm)
Formicinae	Camponotini	*Polyrachis armata* (Le Guillou), *Polyrachis dives* Smith, *Polyrachis pubescens* Mayr, *Polyrachis* spp.	5–6
	Oecophyllini	*Oecophylla smaragdina* (Fabricius)	7–8
Myrmicinae		*Solenopsis geminata* (Fabricius)	4
Ponerinae	Odontomachini	*Odontomachus* spp.	5–12
	Ponerini	*Diacamma vagans* (Fabricius)	12

Fig. 1 Survival rates of ordinary salticids and of *Phintella piatensis*, an ant-associate salticid, in one-ant tests. $N = 100$ for each salticid-ant combination.
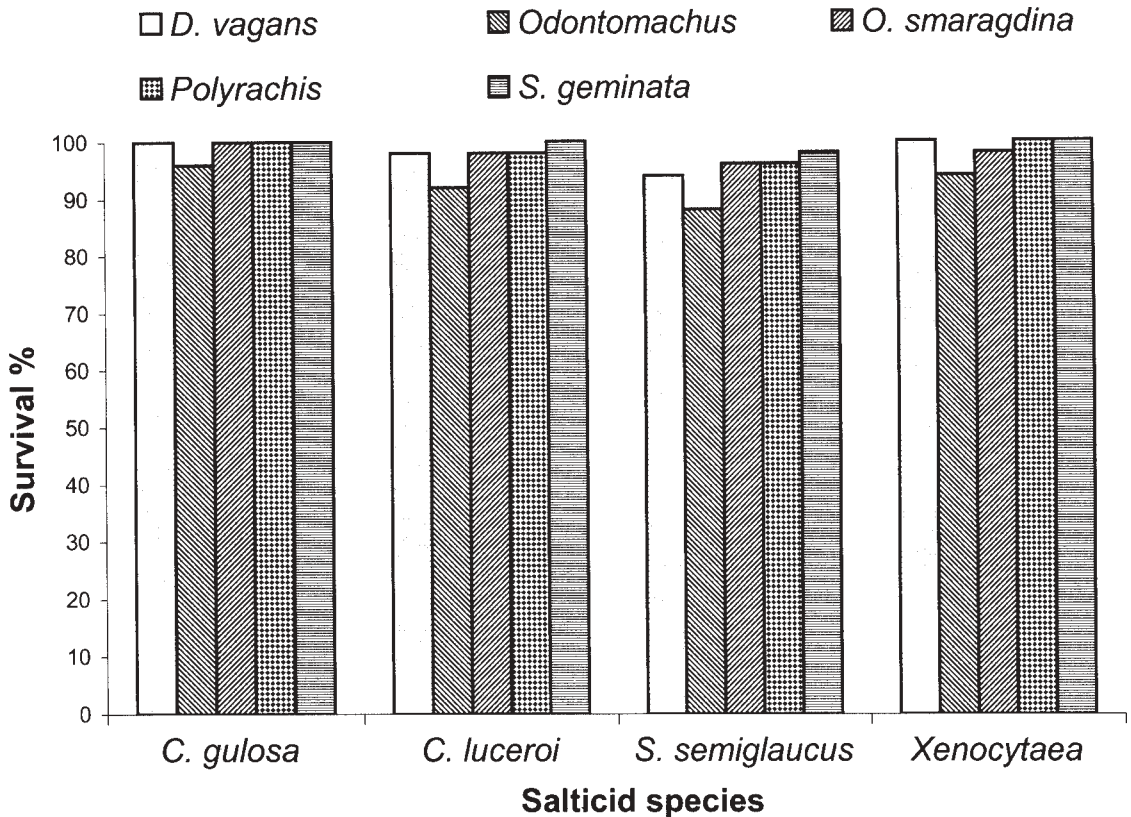
Fig. 2   Survival rates of myrmecophagic salticids in one-ant tests. $N = 100$ for each salticid-ant combination.

was seen attacking a juvenile of *Bavia sexpunctata* on a mango leaf; in another single instance, a group of *Polyrachis* sp. was seen attacking a juvenile of *Lagnus* sp. on a tree trunk; in two instances, a solitary *Odontomachus* sp. was seen attacking an adult female of *Portia labiata* (seen twice; once on a tree trunk and once on the ground).

Although most salticids are cursorial hunters rather than web builders (Jackson & Pollard 1996), *P. labiata* is unusual because it builds a large aerial web (Jackson & Wilcox 1998). However, each individual of *P. labiata* that we observed being attacked by ants was, at the time, outside its web (on a tree trunk or on the ground).

In the remaining 37 instances, the salticid was already dead when first seen. We can not rule out the possibility that some or all of these were instances of the ants scavenging on salticids that were already dead, but none of these salticids was dried up or otherwise had the appearance of having been

dead for long. In 14 instances (38% of 37), a single ant was carrying a dead salticid in its mandibles (*Odontomachus*, 9; *Oecophylla*, 2; *Diacamma*, 2; *Dolichoderus*, 1). In the other 23 instances (62% of 37), a group of ants was gathered around a dead salticid, dismembering it (*Oecophylla*, 13; *Solenopsis*, 8; *Polyrachis*, 2).

RESULTS FROM LABORATORY TESTS

One-ant tests

When confined with ants, ordinary salticids had significantly lower survival rates than any other group (Fig. 1, Table 4) and myrmecophagic species had significantly higher survival rates than any other group (Fig. 2, Table 4). This trend held for all species of ants. The survival rates of myrmecomorphic species (Fig. 3) and *P. piatensis* (Fig. 1) were similar
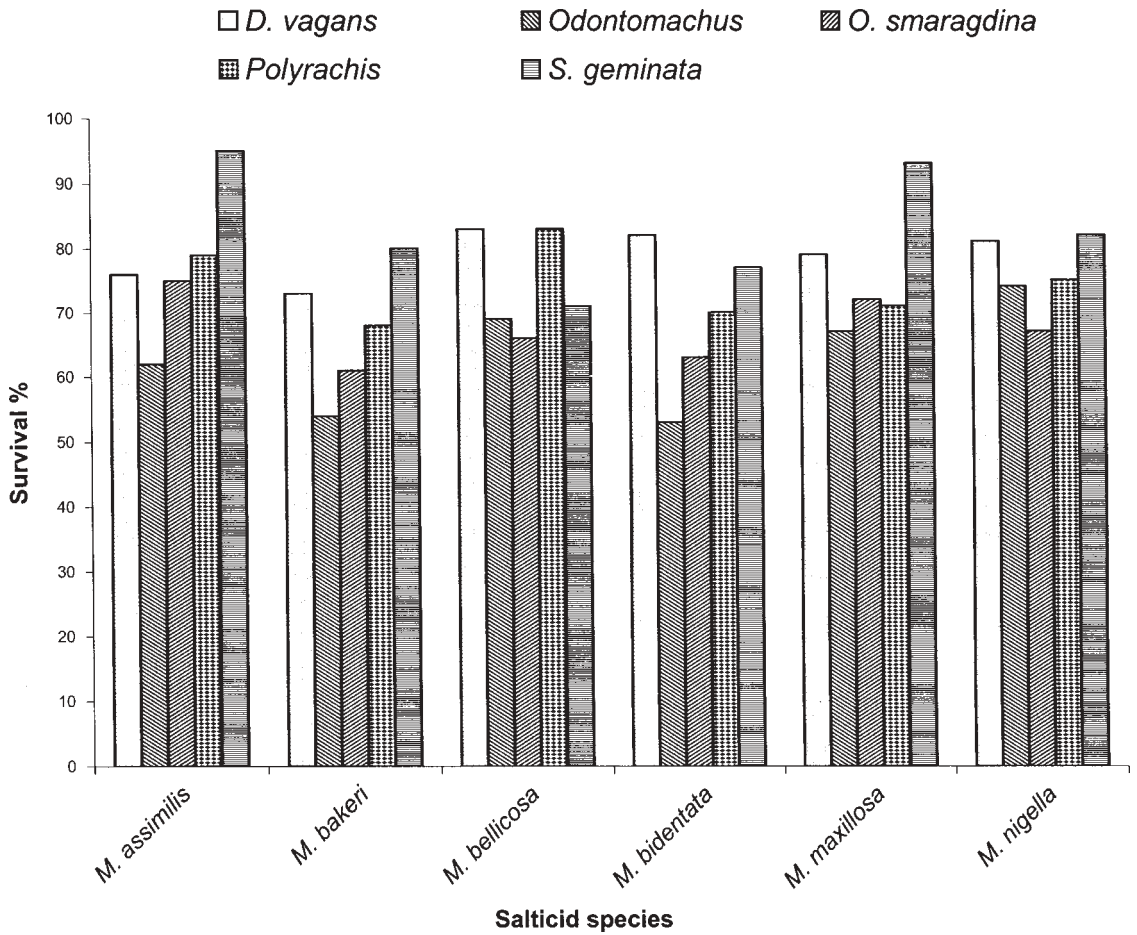
Fig. 3 Survival rates of myrmecomorphic salticids in one-ant tests. $N = 100$ for each salticid-ant combination.

Table 4 Tests of independence and results from one-ant tests.

	Phintella piatensis	Ant eaters	Ant mimics
Ordinary	$\chi^2 = 377.75***$	$\chi^2 = 2906.71***$	$\chi^2 = 1662.60***$
P. piatensis		$\chi^2 = 369.64***$	$\chi^2 = 0.84$ NS
Ant eaters			$\chi^2 = 485.79***$

***$P < 0.001$.

Table 5 Tests of independence and results from five-ant tests.

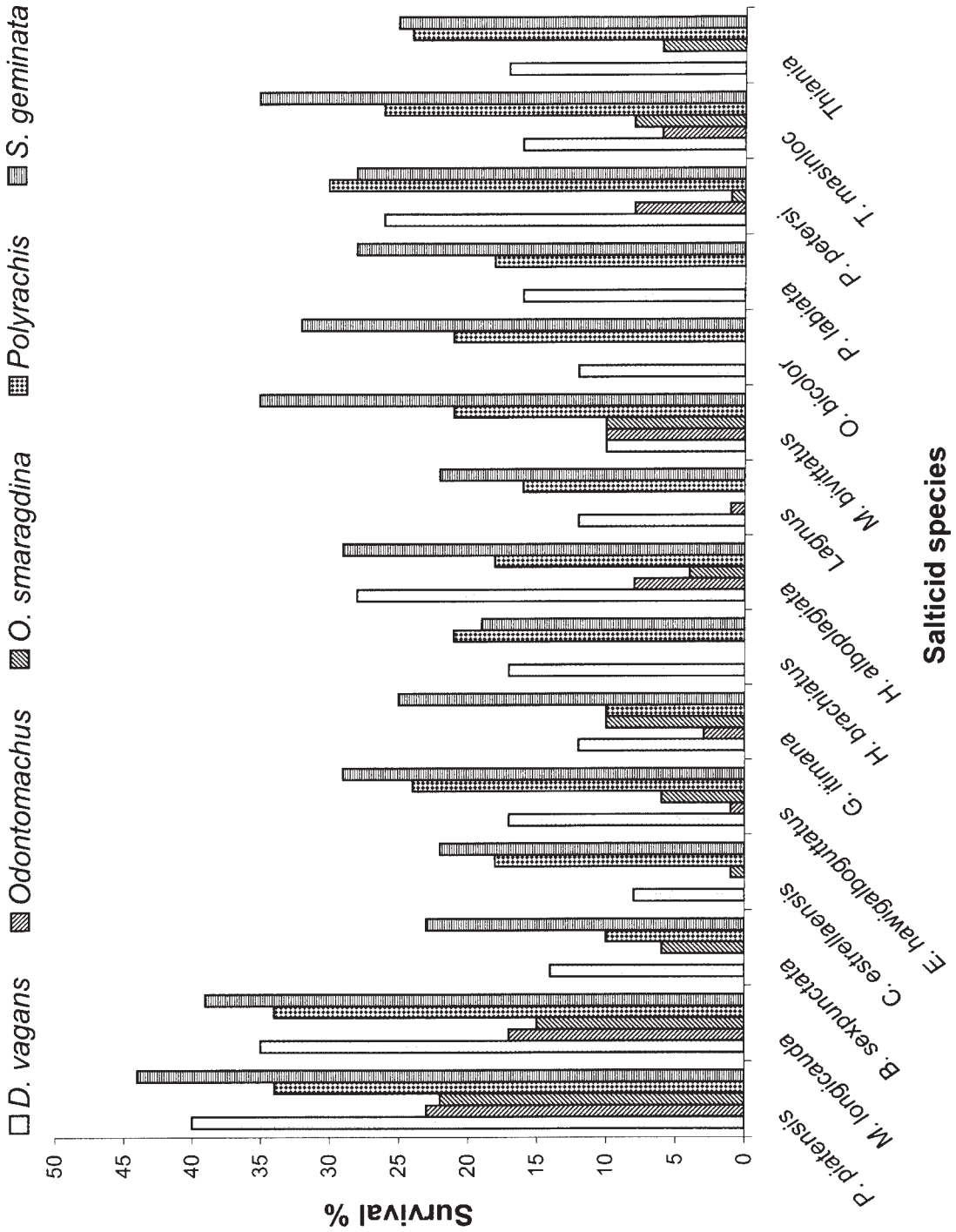|	*Phintella piatensis*	Ant eaters	Ant mimics
Ordinary	$\chi^2 = 108.34***$	$\chi^2 = 1390.81***$	$\chi^2 = 697.27***$
P. piatensis		$\chi^2 = 81.74***$	$\chi^2 = 0.16$ NS
Ant eaters			$\chi^2 = 231.69***$

***$P < 0.001$.

Fig. 4   Survival rates of ordinary salticids and of *Phintella piatensis*, an ant-associate salticid, in five-ant tests. *N* = 100 for each salticid-ant combination.
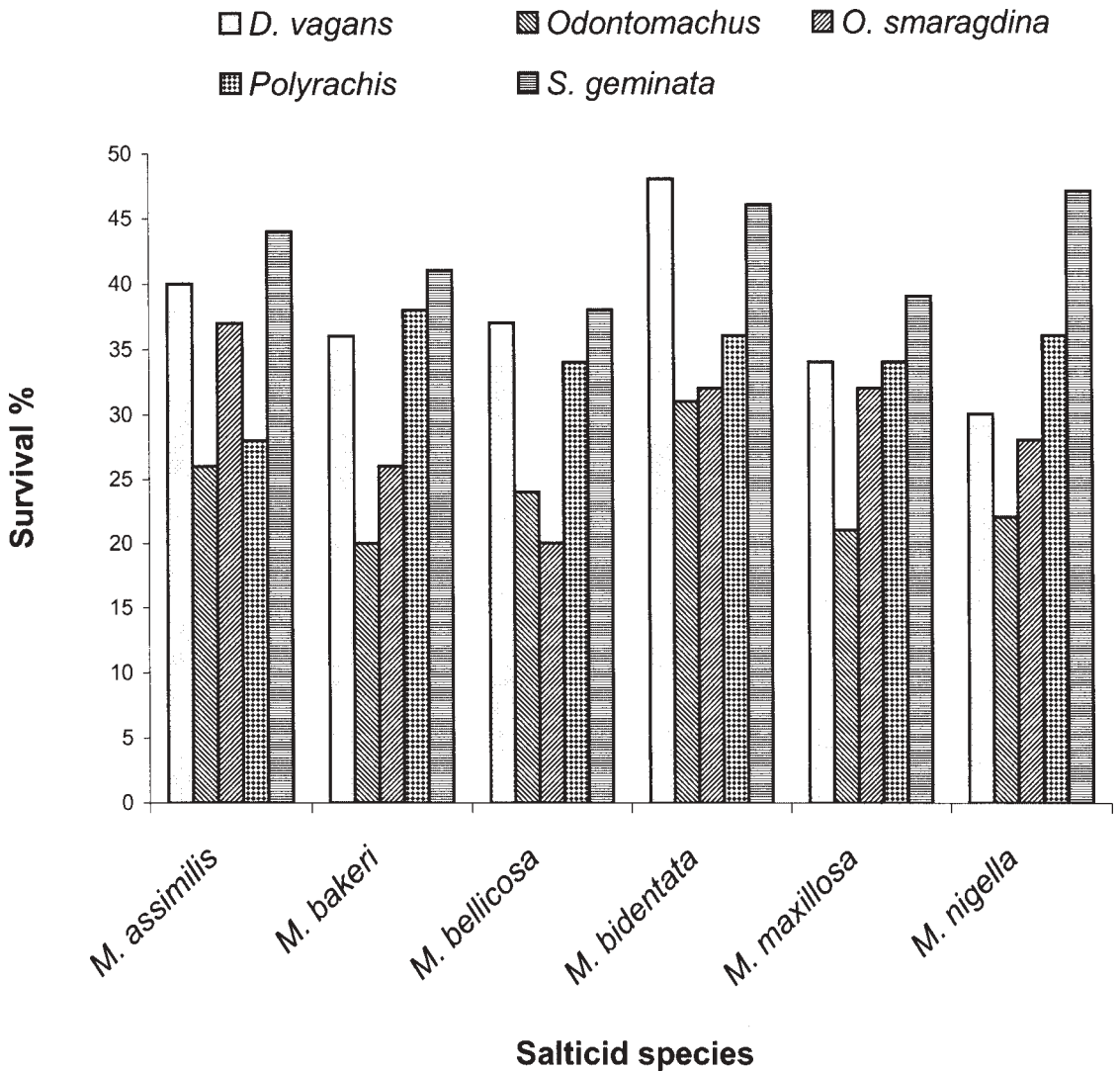
Fig. 5 Survival rates of myrmecomorphic salticids in five-ant tests. $N = 100$ for each salticid-ant combination.

and significantly higher than the survival rates of ordinary salticids (Table 4). The ratio of survival rates (myrmecophagic: myrmecomorphic: *Phintella*: ordinary) was 1.00:1.33:1.37:3.34.

Five-ant tests

The trend was the same as in one-ant tests. The survival rate for *P. piatensis* (Fig. 4) was significantly higher than the survival rates of ordinary salticids (Table 5) and similar to the survival rates of myrmecomorphic species (Fig. 5, Table 5). Myrmecophagic salticids survived at significantly higher rates than any other group (Fig. 6, Table 5). The ratio of survival rates (myrmecophagic: myrmecomorphic: *Phintella*: ordinary; 1.00:1.62:1.67:3.44), was roughly the same as in one-ant tests.
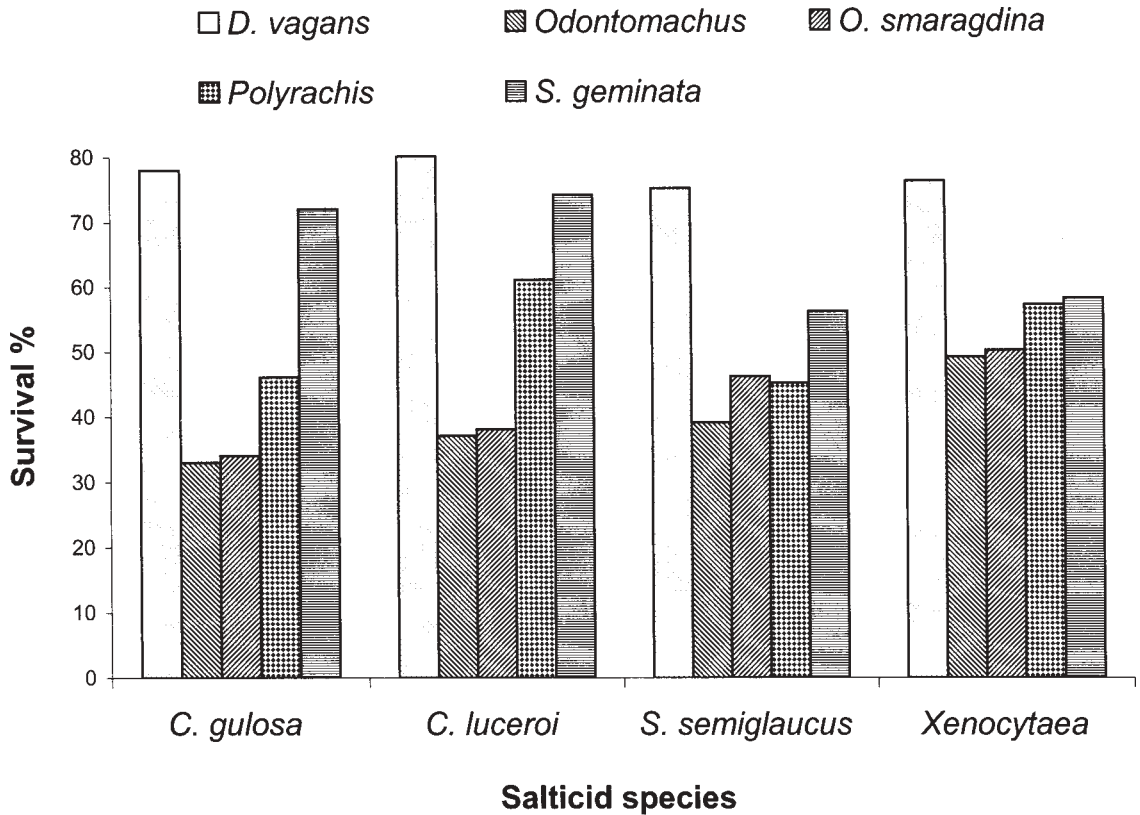
□ *D. vagans*   ▨ *Odontomachus*   ▨ *O. smaragdina*

▦ *Polyrachis*   ▤ *S. geminata*

Fig. 6 Survival rates of myrmecophagic salticids in five-ant tests. $N = 100$ for each salticid-ant combination.

DISCUSSION

Our field and laboratory data suggest interesting, but poorly understood, relationships between two dominant arthropod groups, ants and salticid spiders. In the tropics, ants are the leading predators of other arthropods, including spiders (Edmunds 1974; Oliveira 1988; Hölldobler & Wilson 1990). Ants, however, are not common prey for most spiders (Elgar 1993). The best survival tactic of an ordinary salticid in the field might be its ability to see an ant at a distance sufficient to allow time to flee. However, in the small cages we used in our laboratory tests, ordinary spiders could not move far away from the ants, and most of these salticids did not survive encounters with ants. Despite being tested in the same small-size cages that limited opportunities to flee, significantly more ant mimics, ant eaters, and *Phintella piatensis* than ordinary salticids survived.

Apparently, these salticids, but not ordinary salticids, have behavioural or other characteristics that facilitate surviving in prolonged close proximity to ants. When expressed as a ratio, the survival rates of the different salticid groups were remarkably similar in one-ant and five-ant tests. Although increased numbers of ants augmented the overall risk to salticids, this augmentation remained proportionately comparable across the groups.

Ants are especially abundant prey-size arthropods in the habitats of many spiders (Hölldobler & Wilson 1990; McIver & Stonedahl 1993), and a variety of spider species, including a sizeable minority of the Salticidae, specialise at preying on ants (Cutler 1980; Nyffeler et al. 1988; Jackson & van Olphen 1991, 1992; Allan et al. 1996). Successful predation may often depend on use of ant-specific prey-capture behaviour, but survival in prolonged close association with ants may also depend on specialised

defensive behaviour. The high survival rates of myrmecophagic salticids that we observed suggest this, but details concerning precisely how these salticids avoid being killed or injured by ants are not available.

Ant-like salticids, like the ant-eating salticids, also appear to require specialised defence against ants, but for different reasons. Being abundant and well defended, ants may frequently be the models mimicked in Batesian mimicry systems (Oliveira 1988; Hölldobler & Wilson 1990; Elgar 1993; McIver & Stonedahl 1993; Cushing 1997). For Batesian mimicry of ants to be convincing it may be necessary for *Myrmarachne* species to live near ants, but the visual character of *Myrmarachne's* mimicry suggests that ant-like appearance is of little value in protecting the spider from ants (Elgar 1993), as ants rely primarily on chemical, not visual, information for detecting other ants (Hölldobler & Wilson 1990).

Next to nothing is known about the biology of *Phintella piatensis*, the ant associate. Many ant species can be especially dangerous because they tend to mob predators that attack one of their number (Hölldobler & Wilson 1990). By avoiding the aggression of ants themselves, perhaps an ant-associate salticid gains significant protection from an aggressive army that keeps other predators away.

Possibly some form of behavioural mimicry helps *P. piatensis* and *Myrmarachne* spp. survive encounters with ants and ant-eating salticids. These salticids tend to walk especially fast, with frequent changes in direction, a pattern of movement that bears at least a crude resemblance to an active ant. Behavioural mimicry has been shown in *Eristalis tenax*, a drone fly that mimics the flight patterns of the honey bee, *Apis mellifera* (Golding & Edmunds 2000; Golding et al. 2001). The appearance of a stationary drone fly is not especially like a bee, but the behavioural mimicry of *A. mellifera* may be good enough to prevent birds from attacking drone flies when in flight. What we are suggesting for *P. piatensis* and *Myrmarachne* spp., however, is different. Rather than depending on appearance and rather than providing protection from predators such as birds, perhaps the ant-like gait of these salticids provide tactile or vibratory stimuli that, for an ant, resemble another ant. Among the ant-eaters, only *Siler semiglaucus* has a style of locomotion similar to that of *P. piatensis* and *Myrmarachne* spp. For *Chalcotropis* spp. and *Xenocytaea*, ability to survive close proximity to ants is apparently based on something other than behavioural mimicry.

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