

The role of ants, especially the fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae), in the biological control of tropical upland rice pests

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Abstract

Predatory ants are omnipresent year-round in upland (dryland) rice fields in the Philippines. At least 14 species were identified of which the very aggressive *Solenopsis geminata* (Fabricius) and also *Tapinoma* sp. nr *indicum* Forel usually predominated. Some highly aggressive species, notably *Pheidolegeton* spp. and *Bothriomyrmex dalyi* Forel were localized. *Solenopsis geminata* flourished within many fields, not only during the crop season but also throughout dry season fallows where they remained aggressively predatory. Rice plants infested with brown planthopper *Nilaparvata lugens* (Stål) were usually found within a few hours and *S. geminata* workers were quickly recruited to *N. lugens* aggregates. Predation was usually incomplete and workers began to solicit the few remaining late instar or adult *N. lugens* survivors. These oviposited but no second generation nymphs appeared. There was a surge of recruited ants at the time of *N. lugens* egg hatch when surviving adults were also killed. Initially, *S. geminata* alone killed *N. lugens* aggregates less quickly than with the whole predator complex but ultimately its sole effect was as great as that of the complex. Scattered *N. lugens* adults, corresponding to numbers that initially colonize rice plants, were eliminated as quickly by *S. geminata* alone as by the predator complex. *Tapinoma indicum* occurring separately or with *S. geminata* on the same plant contributed to predation of *N. lugens* especially on young nymphs. *Solenopsis geminata* attacked other insects on rice notably leaffolders of which 97% mortality was recorded when they were exposed throughout egg and larval stages. The role of *S. geminata* as a predator of upland rice pests is discussed in the context of known biological control of pests of non-rice dryland crops in the tropics and subtropics by *S. geminata* and other *Solenopsis* spp.

Introduction

Solenopsis geminata (Fabricius) (Hymenoptera: Formicidae) is widely present in tropical South-east Asia as well as in its native tropical America. It can remove newly sown seeds and so is sometimes regarded as a rice pest

(Litsinger *et al.*, 1987) though this can be prevented, e.g. by diversionary baits (Urbina, 1995) or adequate seed burial (Risch & Carroll, 1982b). However, it also beneficially removes weed seeds in dryland crops (Saks & Carroll, 1980; Carroll & Risch, 1983; Way & Khoo, 1992). Most significantly, *Solenopsis* spp. are recognized as important predators in some non-rice dryland crops notably in the Americas (Way & Khoo, 1992). For example, *S. geminata* decreased *Sitophilus* spp. (Coleoptera: Curculionidae) in maize by 98% (Risch &

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Carroll, 1982a). Chemical control of the ants can make pests worse (Way & Khoo, 1992), and methods of enhancing the predatory roles of *Solenopsis* spp. on eggs and active stages of non-rice dryland pests are discussed by Reagan (1986) and Risch & Carroll (1982b). Observations of *S. geminata* in upland rice fields in the tropics indicate that it 'will feed on any insect it can subdue', including eggs and even the large adults of pests such as blackbugs, *Scotinophara* spp. (Hemiptera: Pentatomidae) (Shepard *et al.*, 1987).

Although significant research has been done on the predatory role of *Solenopsis geminata* in some other crops (Way & Khoo, 1992), its impact on upland rice pests has been confined to observations. The work described here begins with studies on identification and relative abundances of predatory ants in upland rice on the island of Luzon, Philippines. This is followed by experimental work on year-round predation by *S. geminata* and other relevant ant species mostly using the easily reared brown plant hopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) as experimental prey.

Materials and methods

Over a period of four years, potted rice plants were set up in a range of many rice crops during the dry and wet seasons in the island of Luzon, Philippines. They were then infested with *N. lugens* and records made of the ants seen preying on them.

The presence of ant species and their relative abundances in rice fields during the dry fallow and rice crop seasons were determined using baits. Pairs of baits were placed on the soil surface, each comprising a cottonwool bud soaked in 20% sugar solution and a teaspoon of mashed canned tuna in oil. These were set out in transects or grid frameworks and the numbers of ants of different species were counted after 30 and 90 min. When relatively scarce, they were counted individually but otherwise were categorized (Way *et al.*, 1998). The peak counts for any particular species were selected for data analysis usually based on a minimum of 50 baits in a transect and up to 200 in a bait grid depending on field size. Ant predation was examined by planting *N. lugens* infested potted rice plants within fields during both fallow and crop seasons. Ants seen attacking and carrying away *N. lugens* prey were assessed qualitatively for frequency of occurrence and voracity.

In March experiments on predation during the fallow season, two sets of 20 rice plants were set out in transects across two unploughed fields with drying weed cover. Cages were placed over each plant, one set allowing access of ants at the base and the other excluding ants. About 200 third instar *N. lugens* were put on each plant. Crop season field experiments, particularly on *S. geminata* predation and its impact compared with that of other predators, were done using transparent Mylar ring cages each put around five rice plants which were then infested with varying numbers of *N. lugens* adults or third–fourth instar nymphs. Treatments were replicated 5 to 20 times and, when appropriate, results were analysed by t-tests or by ANOVA and multiple comparison of means using Duncan's multiple range test. The experiments which compared ant-exposed and ant-free conditions culminated in comparison of three treatments. The first, which excluded all predators, comprised 0.7 m diameter Mylar rings surmounted by sleeves of 180 micron nylon netting which also excluded parasitoids. Each Mylar

ring was taped on to an 0.4 m high metal ring that was set at least 0.2 m into the soil. This prevented *S. geminata* burrowing shallowly through the soil into the cage. The second treatment, mostly allowing sole access by *S. geminata*, comprised the same sized nylon netted cages without the metal rings but with the Mylar rings pressed a few cm into the soil. Around the periphery of each ring about eight horizontal slits 60 mm wide and about 5 mm deep were cut in the Mylar on all but the lower side which was bent inwards and downwards at an angle of c. 45°. The slits were situated such that they were about 20–30 mm above the soil surface once the ring had been set in position. They provided easy access by *S. geminata* but excluded virtually all main predators apart from a few Carabidae that were removed when seen in the cage. The third treatment comprised Mylar rings ending less than about 0.1 m above the soil and with open tops. This allowed access of all predators and other insects aerially, across plants and by crawling up from the ground over the rims of the Mylar rings. This system, like the others, also helped to retain *N. lugens*, a few of which can otherwise stray beyond the limits of the cage.

Susceptible upland rice cultivars were used in all experiments except that TN1, an *N. lugens*-susceptible irrigated rice cultivar, was used in pot experiments.

Results

Species of predatory ants in rice field habitats

At least 14 ant species (Formicidae) were recorded in upland rice sites (table 1). *Solenopsis geminata* was common and abundant as well as being highly aggressive. *Tapinoma indicum* was even more widespread, as were *Paratrechina* spp. though the latter were relatively unaggressive, sometimes merely collecting *N. lugens* that had seemingly been injured by *S. geminata*. The roles of the highly aggressive *Pheidolegeton* spp. and of the other ants, which were localized, were not studied.

Ant species distribution and abundance in fields

Experimentally, one field (table 2, nos. Ia,b) was kept completely free of vegetation into the wet season in July, eight months after the rice crop had been harvested. Even in these circumstances virtually all baits were found by many *S. geminata*. Perhaps the scarcity of other food sources made the baits particularly attractive as indicated by fierce battles at baits between different *S. geminata* colonies. Consequent mortality may partly explain fewer ants at baits in July than in May. However, the results show that *S. geminata* can remain abundant for at least eight months within bare fallow fields. In such conditions, *T. indicum* seemed unable to survive though it was common in the weedy boundaries of the field. *Tapinoma indicum* remained in vegetated, rough ploughed and uncultivated fields (table 2, nos. II–III and V–VII) where *S. geminata* also remained mostly common in the dry season. Four fields were sampled in the dry season and later in the rice-cropped wet season when there were more *S. geminata* at baits in three of the fields (table 2, nos. IV–VII). The most striking feature was where *Monomorium* spp. were common in the dry season, when they were seen displacing *S. geminata* at tuna baits, but were absent or rare at baits in the rice cropping season (table 2, nos. IV–VI).

Table 1. Ant species recorded attacking *Nilaparvata lugens* on infested rice plants in upland habitats.

	Aggressiveness	Abundance
Myrmecinae		
* <i>Monomorium</i> spp.	++	Occasionally common
<i>Myrmecaria brunnea</i> Saunders	+	Very localized – common
<i>Pheidole fervens</i> Smith	++	Locally common
<i>P. parva</i> Mayr	++	Locally common
<i>Pheidolegeton affinis</i> (Jerdon)	+++	Occasional – locally common
<i>P. diversus</i> (Jerdon)	+++	Locally common
* <i>Solenopsis geminata</i> (Fabricius)	+++	Common – very abundant
Dolichoderinae		
<i>Bothriomyrmex dalyi</i> Forel	+++	Very localized
* <i>Tapinoma</i> sp. nr. <i>indicum</i> Forel	++	Widespread – locally abundant
<i>Tetramorium smithi</i> (Mayr)	+	Scarce
Formicinae		
<i>Anoplolepis gracilipes</i> Smith	+	Locally common
<i>Camponotus chloroticus</i> Emery	+	Occasional
* <i>Paratrechina longicornis</i> (Latreille)	+	Widespread, common
* <i>P. vaga</i> Forel	+	Widespread, common

All species were also recorded on bunds of irrigated rice fields.

*Recorded on rice within irrigated rice crops (ref. Way *et al.*, 1998).

Table 2. Distribution and abundance of three ant species at baits within fields of upland rice 4–6 months into uncropped dry seasons and during rice cropping wet seasons.

Site no.	Soil conditions and vegetation	Site and date	Ant species					
			<i>Solenopsis geminata</i>		<i>Monomorium</i> spp.		<i>Tapinoma indicum</i>	
			% baits occupied	Mean no./total baits	% baits occupied	Mean no./total baits	%baits occupied	Mean no./total baits.
1a	Ploughed and harrowed, no vegetation	IRRI April 1998	100	82.8	0.0	0.0	0.0	0.0
1b	throughout	July 1998	98.2	38.3	0.0	0.0	0.0	0.0
II	Rough ploughed, sparse weed vegetation	Tanauan April 1998	36.7	35.9	0.0	0.0	13.3	5.50
III	Uncultivated, 'dry' weeds	IRRI June 1998	83.3	76.3	0.0	0.0	30.9	59.6
IVa	Uncultivated 'dry' weeds	Maravoc April 2000	74.0	94.1	16.3	89.4	0.0	0.0
IVb	Rice crop	July 2000	71.4	47.6	0.0	0.0	0.0	0.0
Va	Uncultivated 'dry' weeds	Cabolalaaan May 2000	12.5	9.1	71.2	89.4	12.5	7.48
Vb	Rice crop	July 2000	56.7	31.3	1.11	0.03	21.1	10.7
VIa	Uncultivated 'dry' weeds	Laurel May 2000	65.7	64.4	29.1	42.1	2.24	0.47
VIb	Rice crop	July 2000	87.9	52.2	7.07	1.35	0.0	0.0
VIIIa	Rough ploughed Sparse weeds	Cali July 1998	64.0	39.1	0.0	0.0	18.0	3.38
VIIIb	Rice crop	Dec. 1998	91.4	82.7	0.0	0.0	14.3	7.71

Seemingly, *Monomorium* spp. were unable to survive or otherwise displace *S. geminata* in wet soil conditions. *Tapinoma indicum* was often recorded with *S. geminata* on the same baits but mostly on sugar with *S. geminata* predominating on the tuna.

Predation in the fallow season

In an IRRI site, exposed *N. lugens* infested plants were quickly found by *S. geminata* and virtually all *N. lugens* were carried away within two days (table 3). At Tanauan, relatively few *S. geminata* and *T. indicum* arrived during the

first 12 h but *S. geminata* became particularly abundant after one day. Yet, despite the presence of up to 40–70 *S. geminata* on each plant, *N. lugens* numbers only halved between the first and fourth day – relatively little more than the 30% decline during the same period in the ant protected controls. Such limited predation by *S. geminata* was not recorded in rice-crop season experiments.

Predation in the rice season

Two sets of five plants in a transect through an upland rice crop at IRRI were each infested by 500 adult and late

Table 3. Effect of ants on third instar *Nilaparvata lugens* infesting rice plants put in unploughed fallow in March during the dry season.

Time after exposure	Numbers per plant – IRRI			Numbers per plant – Tanauan			
	Ant-exposed		Ant-protected	Ant-exposed			Ant-protected
	<i>N. lugens</i>	<i>S. geminata</i>	<i>N. lugens</i>	<i>N. lugens</i>	<i>S. geminata</i>	<i>T. indicum</i>	<i>N. lugens</i>
0	200a	–	200a	200a	–	–	200a
2–3 h	90b	17a	184b	184b	0.72a	0.40a	191b
10–12 h	24c	15a	180b	nr	nr	nr	nr
1 day	2.8d	8.1a	135bc	56.5c	70b	3.6b	176bc
2 days	0.80d	2.7b	140bc	34.4c	38b	8.7bc	160bc
3 days	0.47d	0.7c	118c	30.3c	48b	18c	131c
4 days	0.0	0.10	112c	28.4c	58b	8.8bc	126c

Numbers in each column with the same letters are not significantly different at $P < 0.05$. nr, not recorded.

Table 4. Changes in numbers of 500 adult and nymphal *Nilaparvata lugens* per artificially infested plant in relation to ant predators at two rice cropped fields.

Site	Day	Time	Numbers per plant			<i>S. geminata</i> carrying away <i>N. lugens</i>		
			<i>N. lugens</i>	<i>S. geminata</i>	Total ants			
IRRI	1	07.00	500a	–	–	–		
		09.30	230b	63	63a	39a		
		11.30	83c	8.0	8.0b	4.0b		
		13.30	79c	11	11b	0.6		
		15.30	47c	31	31c	0.0		
	2	17.30	12d	38	38c	0.0		
		07.00	14d	37	37c	0.0		
		12.00	7.6d	5.5	5.5b	0.0		
		Tanauan	1	09.30	500a	–	–	–
				11.30	348b	6.8a	19a	nr
15.30	174c			8.1a	16a	nr		
17.30	150c			12ab	13a	nr		
2	08.00	65d	11ab	13a	nr			
		12.00	26de	21b	21a	nr		
	08.00	25de	15ab	15a	nr			
		12.00	12e	4.3a	4.5b	nr		

For each site separately the numbers with the same letter in each column are not significantly different at $P < 0.05$. nr, not recorded.

nymphal *N. lugens*. Initially about 60 *S. geminata* per plant fiercely attacked and disturbed the *N. lugens*, some of which jumped off with attached ants while others were caught on the ground. Every 30 min, counts were made for 5 min of *N. lugens* seen being carried away from the plant neighbourhood (table 4). Predation then slowed such that a few adult *N. lugens* per plant still survived two days later despite a surge in plant occupation by seemingly unaggressive *S. geminata*, 7–24 h after the experiment started (table 4). In a similar grower's field experiment at Tanauan, *S. geminata* occurred less frequently together with abundant *T. indicum* sometimes foraging on the same plants. *Solenopsis geminata*, in particular, attacked the *N. lugens* and also disturbed them, when both species as well as *Paratrechina longicornis* (Latreille) collected *N. lugens* on the ground (table 4). The relatively small *T. indicum* workers mostly attacked early instar nymphs although groups of about ten sometimes cooperated in carrying away adults as well as large nymphs. *Solenopsis geminata* numbers on the plants peaked after about 26 h, but they also did not completely eliminate the adult *N. lugens* (table 4).

A more detailed experiment lasting 19 days was done on the effect of ants on caged initial populations of 500 fourth instar nymphs on 10 plants, compared with their effect on 10 females + 10 males on 10 plants, the latter approximating to a current level of natural infestation by colonizing immigrants. A grower's field was chosen where there were relatively few *S. geminata* and *T. indicum* as indicated by earlier bait counts (table 2, no. II). In each set-up, ant-protected were compared with ant-exposed *N. lugens*. The periodic rainfall and wet soil conditions prevented consistent examination and sometimes stopped ant activity. In the 500 nymph treatment, total *N. lugens* numbers fell during the first day associated with the presence of both ant species (fig. 1a,b), but subsequently there was relatively little change even on the fifth day when the *N. lugens* became adult (fig. 1b). However, where the *N. lugens* were protected from ants, nymphal progeny began hatching on day 11 and reached > 14,000 on day 19. Contrastingly, in the ant-exposed treatment no progeny were recorded although > 100 adult *N. lugens* had survived to day 11. Based on numbers on each plant, day 11 coincided with a significant

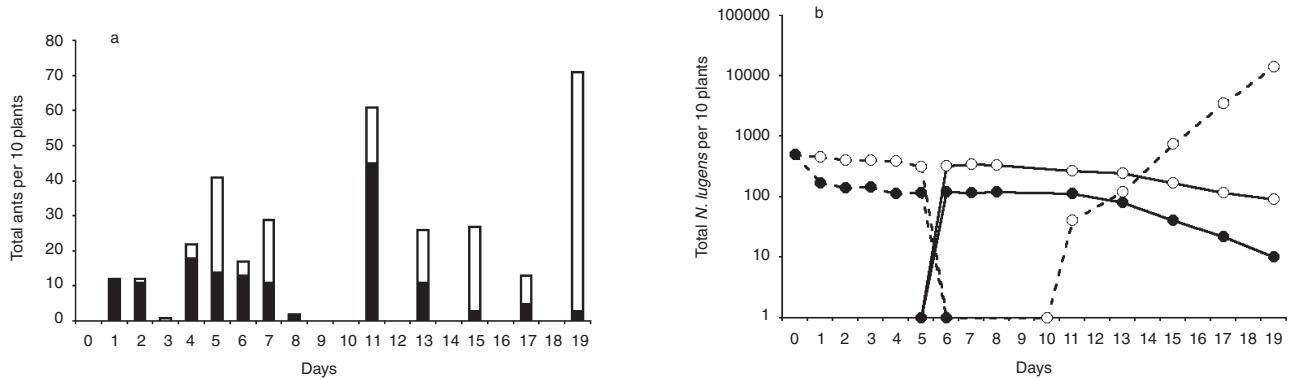


Fig. 1. (a) Numbers of *Solenopsis geminata* (■) and *Tapinoma indicum* (□) on ten rice plants and (b) their impact on an initial population of 500 fourth instar *Nilaparvata lugens* (—, adults; ---, nymphs; ○, ant-protected; ●, ant-exposed).

($P < 0.001$) increase in *S. geminata* numbers (fig. 1a), supporting evidence that workers were recruited to catch hatching *N. lugens* (cf. Way & Javier, unpublished). The large increase of *T. indicum* on day 19 is inexplicable.

Where 10 + 10 adult *N. lugens* were used, all were killed by *S. geminata* within four days (fig. 2a,b). In the controls, second generation nymphs began hatching after day 8 (fig. 2b) which coincided with an increase in *T. indicum* on day 11 ($P < 0.01$) on the ant-exposed plants (fig. 2a) indicating that this species was reacting to hatching *N. lugens* nymphs that were possibly too few to attract *S. geminata*.

Finally, the full set of replicated selective exclusion techniques was used to compare the effects of *S. geminata*, with and without other main predators, separately on third and fourth instar *N. lugens* and on adults. Predators appeared quickly in both exposed treatments, but where 250 nymphal *N. lugens* per five plants were exposed to all predators, *N. lugens* numbers decreased faster in the first 9 to 10 days than when exposed only to *S. geminata* (table 5). Other *N. lugens* predators must therefore have contributed to *N. lugens* mortality as exemplified by results on day 12 when 26 adult female *N. lugens* still survived on the *S. geminata*-only treatment, compared with 2.8 *N. lugens* on the all-predator treatment where the numbers of some

recognized *N. lugens*-predatory spiders and also *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae) had greatly increased (table 5). However, on day 12 and especially on day 15 there was also a large increase in numbers of *S. geminata* in the treatment where other predators were excluded. At this time, many second generation *N. lugens* were hatching in the predator-free controls (table 5). This suggests that, as before, *S. geminata* were recruited to catch hatching *N. lugens* in the ant-only-exposed treatment. It also coincided with a notable decrease in the remaining adult *N. lugens* numbers in the *S. geminata*-only treatment such that by day 21 no *N. lugens* were left, while only a few remained where *N. lugens* were exposed to all predators.

In the other part of this experiment, 5 female + 5 male adults were exposed per five plants to simulate approximate numbers that would be found naturally colonizing the plants. Overall, fewer *S. geminata* were recorded, but virtually all *N. lugens* adults had been taken in both treatments by day 5. *Solenopsis geminata* alone was therefore as effective as the predator complex (table 5). In the *S. geminata*-only treatment, where there were no potential prey on day 9, no ants were seen. As before, their return on day 12 would have been in response to emerging nymphs from the *N. lugens* adults that had reproduced before being killed. In

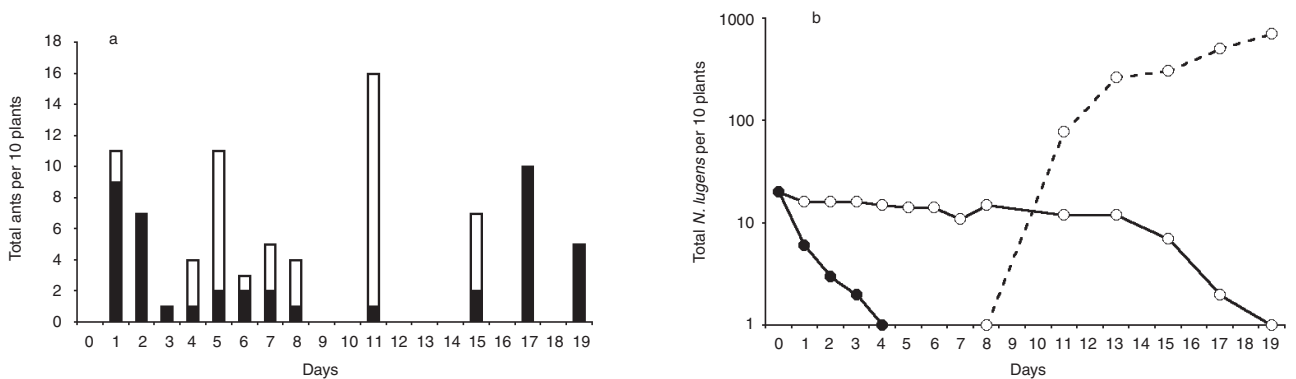


Fig. 2. (a) Numbers of *Solenopsis geminata* (■) and *Tapinoma indicum* (□) on ten rice plants and (b) their impact on an initial population of 20 adult *Nilaparvata lugens* (—, adults; ---, nymphs; ○, ant-protected; ●, ant-exposed).

Table 5. Changes in mean numbers (\pm 95% confidence limits) of third/fourth instar nymphs and adults of *Nilaparvata lugens* exposed in the field to all predators, to *Solenopsis geminata* only and to predator exclusion.

Initial <i>N. lugens</i> nos.	Time (days)	Treatments						
		All predators				<i>S. geminata</i> only		No predators
		<i>N. lugens</i>	<i>S. geminata</i>	Spiders	<i>C. lividipennis</i>	<i>N. lugens</i>	<i>S. geminata</i>	<i>N. lugens</i>
250	0	250	0	0	0	250	0	250
3rd+4th instars	1	53 \pm 23	9.0 \pm 1.4	1.5 \pm 0.7	0.51 \pm 0.22	96 \pm 27	6.5 \pm 3.5	217
	5	21 \pm 9.4	8.0 \pm 1.3	4.9 \pm 1.4	3.2 \pm 1.1	68 \pm 15	5.0 \pm 1.6	184
	9	8.7 \pm 3.0	2.6 \pm 1.7	3.0 \pm 1.3	0.80 \pm 0.69	59 \pm 18	3.8 \pm 1.8	159
	12	2.8 \pm 1.8	5.7 \pm 2.7	7.3 \pm 2.0	11.8 \pm 2.8	26 \pm 7.2	12.0 \pm 4.2	251
	15	0.25	13.2 \pm 1.8	2.5 \pm 0.9	5.7 \pm 1.6	3.2 \pm 1.9	36.2 \pm 11.2	6303
	21	0.30	3.5 \pm 1.1	0.8 \pm 0.5	0.0	0.0	5.8 \pm 1.7	6722
5 males +	0	10	0	0	0	10	0	10
	1	2.8 \pm 1.1	5.0 \pm 1.8	0.8 \pm 0.87	2.5 \pm 1.4	3.7 \pm 2.0	7.3 \pm 2.1	7.0
5 females	5	0.3	2.5 \pm 0.8	5.0 \pm 2.1	7.0 \pm 2.1	0.3	2.5 \pm 1.8	8.0
	9	0.0	2.5 \pm 1.2	5.5 \pm 1.8	1.5 \pm 0.9	0.0	0.0	24
	12	0.0	7.5 \pm 2.3	7.5 \pm 2.5	10.0 \pm 1.9	0.0	3.7 \pm 0.59	159
	15	0.0	8.0 \pm 2.6	5.8 \pm 0.9	1.3 \pm 1.0	0.0	4.7 \pm 1.3	1003
	21	0.0	4.5 \pm 2.0	0.3	0.0	0.0	1.7 \pm 0.42	1225

the all-predators treatment, spider numbers increased during the first 12 days and *C. lividipennis* notably increased significantly on days 5 and 12 (table 5), seemingly attracted by egg laying *N. lugens* and hatching nymphs, respectively.

Predation on leaffolders in the rice crop

Solenopsis geminata were seen attacking leaffolder *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) eggs and larvae in leaf folds. The ants crawled into the folds and sometimes made holes through the folded rice leaves, biting and disturbing larvae which dropped out and were attacked and stung, with the paralysed larvae carried away. The leaffolders were usually attacked by individual foraging workers. Such predation also occurred in irrigated rice after partial drainage when larvae of several Lepidoptera were seen being carried along trails to the ants' nests (Way, Javier & Heong, unpublished).

In the first experiment, two third instar larval leaffolders were put on each of five plants in three treatments using the selective predation technique for exposure to ants only, to ants and other predators, and predator-excluded. Initially, 10–15 dispersed *S. geminata* were seen foraging over a total of 50 plants. Where other predators were admitted, no more than three spiders and three predatory Coleoptera were seen. At pupation, leaffolder losses were 97%, 95% and 36% in the ants only, in ants plus other predators, and in the predator-free controls, respectively. In a second experiment, a similar procedure was used with second instar larvae but without the all-predators treatment. Mortalities were 91% and 23%, respectively, in the ant-exposed and control treatments. In a third experiment using another crop, 100 leaffolder adults were put in each of three sets of ant-free 2 \times 2 m net cages, allowed to oviposit for 24 h and then removed. One cage was then immediately exposed to *S. geminata* by raising the net at the base of the cage a few cm above ground level. The second cage was not exposed until after hatched larvae had completed leaffolding. The third was ant-protected throughout. At the time of pupation, the mortalities (based on survivorship of 388 leaffolders in the protected cage) were 97% where the leaffolders were

exposed from the egg stage and 79% when exposed only after larval leaffolding.

Discussion

Although needing confirmation in other upland systems in South-east Asia, our evidence shows that *S. geminata*, in particular, and *T. indicum* are common and widely distributed in upland rice and other dryland annual crops. *Solenopsis geminata* can survive abundantly in disturbed land, and even on completely bare soil which had been fallow for six months, the ants remained voraciously predatory on artificially established *N. lugens* and on baits at which there was often fierce competition between workers from competing colonies. The survival of *S. geminata* in bare rice fallows is characteristic of *Solenopsis* species which are known to be invaders of disturbed habitats (Risch & Carroll, 1982b; Saks & Carroll, 1980).

During the rice cropping wet season, *S. geminata* quickly found *N. lugens*-infested plants and showed an immediate density-dependent response to relatively large aggregates. Otherwise, when adult *N. lugens* prey were not aggregated and, like leaffolders, were relatively sparsely distributed, there was still effective predation by the few individual *S. geminata* workers that in daytime forage continuously over the rice plants. 'Casual' predation by individual foraging *S. geminata* must therefore be regarded as importantly controlling colonizing *N. lugens* and also leaffolders, particularly when the latter are exposed from the egg stage. In these circumstances, there are evidently too few prey to trigger density-dependent recruitment to the food source though in the laboratory and often in the field, several workers were seen cooperating in dragging adult *N. lugens* and leaffolder larvae to the nest.

A notable feature of *S. geminata* and *T. indicum* predation on aggregates of *N. lugens* was the initial ferocity of attack but failure to eliminate some of the original later instar and adult *N. lugens*, even though at a later stage more *S. geminata* sometimes remained on the plants than during the initial phase of intense predation. This is partly because initially they were quickly departing with prey, but other critical

experiments (Way & Javier, unpublished) showed that at this stage some workers began soliciting *N. lugens* for honeydew. Later, however, they recruited heavily in response to impending prey, namely hatching second generation *N. lugens* progeny. At this time, predation sometimes re-started on surviving adults. This explains why no second generation nymphs were recorded and no *N. lugens* survived, in sharp contrast to ant-protected conditions.

In several experiments, *S. geminata* workers usually quickly found and killed adult *N. lugens*, as many as two to three per plant that are comparable to numbers of natural *N. lugens* immigrants at any one time. In such circumstances, the mortality from *S. geminata* alone was as successful as when other predators were not excluded. Contrastingly, in one experiment with relatively large aggregates of *N. lugens* nymphs the mortality from *S. geminata* alone was initially less than by the whole predator complex, though ultimately *S. geminata* alone was equally successful. Nevertheless, the key question is what is the value of *S. geminata* and other predatory ants relative to that of the many other species in the natural enemy complex of upland rice pests? Present evidence shows that ants are widespread in upland rice fields with *S. geminata* remaining abundant even during the fallow season. They are already in the fields before rice planting so can react immediately to arrival of prey and, by recruitment, are rapidly responsive to prey density (Risch & Carroll, 1982b; Way & Khoo, 1992). In this respect they are therefore a unique component of the natural enemy complex although some other predator species such as spiders begin to arrive as plants grow older while the egg and early instar *N. lugens* predator, *C. lividipennis*, can also immigrate quickly in response to ovipositing *N. lugens* (Way & Heong, 1994). However, *S. geminata* preys on a much wider range of species than other main predators, including egg to adult stages as well as on prey such as leafhopper and also stemborer larvae that within rice stems are apparently inaccessible to some other predators (Shepard *et al.*, 1987). Its role against some major underground pests of upland rice grown in mixed cropping systems remains to be determined, but it is significant that, against corn rootworms *Diabrotica adelphe* Harold and *D. balteata* Le Conte, (Coleoptera: Chrysomelidae), it removed 80% of eggs in the soil (Risch, 1981). On other dryland crops *Solenopsis* species may (Lee *et al.*, 1990) or may not (Sterling *et al.*, 1979) affect other natural enemies. The roles of *S. geminata* and other ants as part of the overall biological control community and in the context of upland and irrigated rice crop biodiversity are discussed in detail separately (Way, Javier & Heong, unpublished).

Acknowledgements

The authors gratefully thank Cedric Collingwood and Dr A. Barrion for the ant identifications, and Messrs J. Angeles, E. Rico and A. Salamatín for technical assistance and M.E. Cammell for the figures and statistical analysis; also Isobel Way for data handling and manuscript preparation, and the

IRRI farm staff for the field experiments. M.J.W. deeply appreciates the generous support of the IRRI Administration and the welcome and encouragement from Dr T.W. Mew and other senior staff of the IRRI Division of Entomology and Plant Pathology.

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(Accepted 17 May 2002)
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