

Significance of the tropical fire ant *Solenopsis geminata* (hymenoptera: formicidae) as part of the natural enemy complex responsible for successful biological control of many tropical irrigated rice pests

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Abstract

The tropical fire ant *Solenopsis geminata* (Fabricius) often nests very abundantly in the earthen banks (bunds) around irrigated rice fields in the tropics. Where some farmers habitually drain fields to the mud for about 3–4 days, the ants can quickly spread up to about 20 m into the fields where they collect food, including pest prey such as the eggs and young of the apple snail *Pomacea caniculata* (Lamarck) and insects such as lepidopterous larvae and hoppers, notably *Nilaparvata lugens* (Stål) the brown planthopper (Bph) and green leafhoppers *Nephotettix* spp. Even in drained fields, the activity of *S. geminata* is restricted by rainfall in the wet season. The relatively few ant workers that forage characteristically into drained fields and on to the transplanted clumps of rice plants (hills) kill the normally few immigrant Bph adults but are initially slower acting than other species of the natural enemy complex. However, larger populations of Bph are fiercely attacked and effectively controlled by rapidly recruited ant workers; whereas, in the absence of the ant, the other natural enemies are inadequate. In normal circumstances, there is no ant recruitment in response to initially small populations of immigrant Bph and no evidence of incompatibility between ant foragers and other natural enemies such as spiders. However, when many ants are quickly and aggressively recruited to attack large populations of Bph, they temporarily displace some spiders from infested hills. It is concluded that, in suitable weather conditions and even when insecticides kill natural enemies within the rice field, periodic drainage that enables *S. geminata* to join the predator complex is valuable for ant-based control of pests such as snails and Lepidoptera, and especially against relatively large populations of Bph. Drainage practices to benefit ants are fully compatible with recent research, which shows that periodic drainage combats problems of 'yield decline' in intensively irrigated tropical rice and is also needed in South East Asia to make better use of seriously declining water supplies for irrigation.

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Introduction

Solenopsis geminata (Fabricius) and some other predatory ant species can nest abundantly within fields of upland (dryland) tropical rice (Way *et al.*, 2002). The ants may also establish nests within the fields during dryland phases between irrigated rice crops, particularly during the long fallow season of single cropped flooded rice. During flooding, the ants are largely limited to the earthen banks (bunds) used to confine water in each field. Here, the numbers of workers in *S. geminata* nests may exceed 500,000 per 100 m of bund (Way *et al.*, 1998). In continuously flooded rice fields, *S. geminata* can forage across a closed leaf canopy once this has overlapped the bund (Way *et al.*, 1998), but most only reach the peripheral 2–3 m of the crop. However, as discussed later, some farmers periodically drain cropped fields to mud level for several days, during which predatory *S. geminata* quickly spread across wet mud and forage on the rice plants.

This paper describes experimental studies on the behaviour and impact of *S. geminata* compared with that of other natural enemies, notably spiders, mostly using *Nilaparvata lugens* (Stål) the brown planthopper (Bph) as a target pest species. Interactions between *S. geminata* and spiders are also examined in order to assess possible impairment of biological control by the diverse natural enemy community, which is potentially very important in the control of many crop pests (Sunderland *et al.*, 1997) and recognized as sometimes crucial in the suppression of at least one key pest of tropical irrigated rice, notably Bph (Kenmore *et al.*, 1984; Way & Heong, 1994).

Materials and methods

Some studies on foraging behaviour of *S. geminata* were done on a private farm within 10 km of IRRI, where no insecticides had been used for at least ten years. Otherwise, most field experiments were at the IRRI Experimental Farm in pesticide-free areas, apart from a single pre-emergence non-insecticidal herbicide as used also on the private farm.

At IRRI, transplanted rice seedlings were established using bunches (hills) of 3–5 rice seedlings reared in the nursery, which were transplanted in flooded fields 0.2 m apart. The rice cultivar was the Bph resistant IR72. This is only partly resistant because adapted strains of Bph can colonize and multiply though more slowly than on susceptible cultivars. The adapted Bph were reared in a glasshouse and then established as target pests for experimental studies in the field.

Experiments on *S. geminata* predation and its impact compared with that of other natural enemies, notably spiders, were done using 0.7-m diameter and 0.6-m-high transparent Mylar ring cages with two 0.2 m² netting windows, each usually put around five rice hills artificially infested with Bph adults or 3rd–4th instar nymphs. The cages were designed to compare the impact of all predators and parasitoids including ants with that of ants only and with non-ant natural enemies, as well as with complete natural enemy exclusion. All predators and parasitoids were excluded by Mylar rings pressed into the mud around the rice hills and surmounted by sleeves of 180 µ nylon netting. All natural enemies were given access through unsleeved open top cages with the bases lifted about 0.1 m above the soil surface. Such cage frames did not impair herbivore or predator access (see table 1). The treatment for sole access of *S. geminata* involved sleeved cages with about six 0.1-m-wide and 5-mm-high slots cut into the sunken bases of the Mylar rings about 10 mm above the level of the mud. Such slots were quickly found by *S. geminata*. In the treatment with ants excluded, the non-ant predators and parasitoids were given access through the unsleeved tops of Mylar cages set into the mud. Based on total spider numbers, these selective exclusion procedures proved satisfactory. For example in one experiment (table 2), the numbers of spiders in the all predator and non-ant predator treatments in the first five days were, respectively, 8.6 and 7.4 per two cages, which did not differ significantly ($P > 0.05$); but in the first five days their species composition was different, with 18.2% per hill *Lycosa pseudoannulata* (Böesenberg & Strand) of total spiders in the ant plus other predator treatment compared with 5.8%

Table 1. Changes in numbers of the natural population and of 400 introduced Bph per hill on five uncaged hills and on five caged hills, all given access to both *S. geminata* and spiders during four days when a field of IR72 rice was kept drained in rainy weather.

Bph numbers	Caging	Distance from bund(m)	Highest individual hill counts during the four-day period		No. of Bph	
			<i>S. geminata</i>	Spiders	Day 1	Day 4
Natural population	Not caged	2	3	4	2	2
	Caged	12	0	12	6	3
		2	5	9	2	1
		12	0	12	3	2
400 introduced	Not caged	2	15	7	360	1
	Caged	12	0	16	350	260
		2	50	16	370	38
		12	0	18	400	290

Table 2. Changes in Bph numbers beginning with (a) 400 initially introduced 3rd–4th instar Bph nymphs or (b) ten gravid females and of naturally occurring Glh on groups of five caged hills given access either to *S. geminata* and other predators, or to other predators only, or to no predators on a wet season crop of Bph resistant IR72 rice.

(a)						
Predator exposure	Species	Mean nos per hill for each five-day period				
		Days				
		1–5	6–10	11–15	16–20	21–25
Ants and other predators	Bph	202 ± 58	76 ± 22	367 ± 53	560 ± 106	186 ± 82
	Glh	3.8 ± 1.3	8.0 ± 2.9	9.0 ± 3.5	4.8 ± 1.6	4.3 ± 1.5
	Ants	11.0 ± 3.9	12.0 ± 3.1	2.3 ± 0.6	8.5 ± 1.8	5.3 ± 1.0
	<i>Cyrtorhinus lividipennis</i>	4.0 ± 1.9	15 ± 5.5	8.5 ± 3.2	14 ± 5.1	14 ± 4.7
	Spiders	8.6 ± 3.2	27 ± 6.6	18 ± 5.4	30 ± 7.0	27 ± 5.6
Other predators only	Bph	401 ± 31	168 ± 35	1481 ± 230	7844 ± 299	5583*
	Glh	2.0 ± 1.7	4.8 ± 1.9	9.5 ± 2.4	2.0 ± 0.5	1.7 ± 0.4
	<i>Cyrtorhinus lividipennis</i>	4.8 ± 1.5	16 ± 5.1	22 ± 6.6	82 ± 9.1	206 ± 41
	Spiders	7.4 ± 2.8	18 ± 6.3	38 ± 4.8	42 ± 12	20 ± 6.8
No predators	Bph	288 ± 37	184 ± 30	2016 ± 291	9143 ± 216	3868*

* Some plants dying – hopperburn.

(b)						
Predator exposure	Species	Mean nos/hill for each five-day period				
		Days				
		1–5	6–10	11–15	16–20	21–25
Ants and other predators	Bph	3.4	42	24	0.0	0.0
	Glh	4.6	15	11	2.0	1.7
	Ants	0.6	4.5	3.5	0.5	2.0
	<i>Cyrtorhinus lividipennis</i>	5.4	16	12	0.8	6.6
	Spiders	10	25	19	22	17
Other predators only	Bph	5.2	52	5.0	0.4	0.4
	Glh	6.8	16	7.4	5.0	1.0
	<i>Cyrtorhinus lividipennis</i>	3.0	24	3.4	1.0	1.9
	Spiders	5.4	18	18	15	14
No predators	Bph	6.9	138	194	1890	2010

in the treatment where ‘predators only’ had access only from the cage top. Later observations showed that some *L. pseudoannulata* entered the ‘ant only’ exposed treatment at ground level through holes made for ant access. Other spider species, notably *Atypena formosana* (Oi), made up for the fewer *L. pseudoannulata*, but this species preys mostly on hopper nymphs whereas the latter also preys on adults (Shepard *et al.*, 1987). After ten days, the proportions were restored, 14.3% and 13.8%, respectively ($P < 0.05$). Whilst this problem was mostly solved in experiments with upland rice using an amended technique (Way *et al.*, 2002), it was unfortunate that two well-replicated experiments on wet season irrigated rice crops using the better technique were ruined by leakage from an adjoining field, and by a typhoon.

The numbers of different species were counted visually on individual hills; however, when there were more than about 100 per hill, Bph numbers were estimated (Way *et al.*,

1998). Replicated experiments were analyzed by ANOVA and multiple comparison of means using Duncan’s multiple range test. In general, numbers were no doubt greater than those recorded, partly because all individuals are difficult to find, particularly on the older larger hills, and partly because some spiders and Bph jump or drop from the plants when the plants are disturbed. Nevertheless, the direct counting method is notably more accurate than, for example, suction sampling (Islam *et al.*, 2000) and because destructive methods such as suction sampling are useless for experiments involving sequential counts on particular plants.

The main caging experiment to compare effects of *S. geminata* with and without other predators comprised five replicates of five hills in a wet season crop. Changes in abundance of Bph, ants, spiders and some other predators were recorded throughout the season in one dry season crop. In this experiment, 360 hills were examined individually

Table 3. Estimated total numbers of *S. geminata* workers returning to nests during a 14 h period (06:30–20:30) along six trails directly after partial drainage of a dry season irrigated rice field.

	Trail numbers					
	1	2	3	4	5	6
Total workers	18,430	16,290	8690	3990	3050	2820
Numbers carrying food items	4130	3510	1590	830	510	480
% carrying food items	22.4	21.6	18.3	20.8	16.7	17.0

on a block ten hills wide and extending 36 hills long into the field from a bund. The field was periodically drained for up to four days and then re-flooded.

Results

S. geminata behaviour in periodically drained rice fields

Formation of foraging columns

A dry season crop at the tillering stage was allowed to drain during dry sunny weather. After one day, there was still some standing water, but *S. geminata* workers were already forming foraging trails across the mud. Six trails from a bund length of about ten metres were marked, and the total numbers of workers and those carrying food items crossing a line at the incoming end of each trail were counted for three minutes in every 30 min period from 06.45 to 20.30 h. The total numbers of ants, based on the three-minute counts, were then estimated for the 14 h duration of the study. Those returning varied from totals of 2820 to 18,430 in different trails (table 3) though only 17–22% were carrying food items, including all or parts of hopper adults and nymphs, leafhopper larvae, dipterous detritivore larvae, larval Coleoptera and eggs and young of the golden apple snail, *Pomacea canaliculata* (Lamarck). As an example along one trail, 870 hoppers, including body parts and 226 snail eggs, were among the calculated 4130 food items carried in their mandibles by 18,400 returning workers during the 14 h period.

Ant predation on artificial infestations of Bph

During dry weather in the wet season, two separate pairs of rice hills three metres from a bund were each infested directly after partial drainage with about 900 nymphal and adult Bph. One hour later, there was an *S. geminata* trail to each pair of rice hills from two separate colonies on the adjoining bund. Returning workers were recorded day and night as before although there were gaps in the records during the night of days 2–3. Ants carrying Bph or Bph parts and those carrying other items were counted, and mean numbers per hour were then estimated. Bph and *S. geminata* on each pair of hills were also counted or estimated separately for successive 5–7-h periods. In both pairs of hills and their associated *S. geminata* trails, there were initial peaks of Bph collection by about 10% of the returning workers (figs 1a and 2a). In one trail (fig. 1a), Bph collection continued overnight and into the second day when *S. geminata* numbers on the plants and in the trail again peaked at around

midday. On day 4, no Bph were left on the plants (fig. 1b). In the second trail (fig. 2a), the ants remained active during the first night but were not carrying food items. Moreover, ant numbers peaked around midday on the 3rd day though there were few remaining Bph on the plants. A midnight record on the second night showed that both trails remained active, but neither was carrying food items (figs 1a and 2a). There was one anomaly, namely the estimated numbers of Bph prey taken along the second trail at around 0900 h on day 3 (fig. 2a); this seemed notably greater than the decrease in numbers on the corresponding hills (fig. 2b). Perhaps, ants collected Bph during the night but did not return with them until the next morning.

Estimates of total Bph and their body part numbers carried along trails to each colony during the experimental period were 1006 and 1130 compared with initial infestations of 900 Bph on the hills from which Bph were being taken.

Foraging distance

S. geminata were seen foraging up to about 20 m into a two-day drained field. That the behaviour of different competing colonies varied was demonstrated strikingly in one experiment where six hills 0.2 m apart in a row opposite *S. geminata* colony A (fig. 3) were each infested at 0800 h with about 200 Bph nymphs. The original objective was to determine the speed at which successive infested hills were found and the Bph removed by colony A workers. However, no foragers left colony A. Instead, at 1000 h, a trail of *S. geminata* to the Bph was traced >10 m back to colony B (fig. 3). At first, colony B workers removed all Bph from hills 5 and 6, but by 1700 h they had reached hills 2 to 4. On the following morning, although no trail was seen to hill 1, the numbers of Bph had fallen to seven. Seemingly, workers from one of the ant colonies had removed them. Otherwise, workers from colony B, despite the distance, monopolized hills 2–6, having inhibited foraging from colony A.

Use of selective exclusion techniques

Two experiments were done to compare the roles of ants and other natural enemies, notably spiders, against Bph. Initially, in the dry season, a rice field at the tillering stage was partly drained. The soil was still very muddy when it was re-flooded four days later. Two sets of five hills, each infested with 200 3rd–4th instar Bph, were caged three metres from a bund in three conditions: to permit access of ants and other natural enemies, to exclude ants but not others, and to exclude all natural enemies. These were set up at 0700 h one day after drainage began when the ground was still very muddy with pools of water. Yet, *S. geminata* workers were already making trails in the field, and within about four hours were removing Bph from caged plants to which they had access, leaving only 43 after eight hours and three before the field was re-flooded on day 4 (table 4). Where only other natural enemies had access, the numbers of Bph decreased notably more slowly. Initially the predators were mainly spiders, notably *Lycosa pseudoannulata* and *Atypena formosana*, and latterly also the heteropteran bug *Cyrtorhinus lividipennis* Reuter and predatory Coleoptera. In these circumstances, 27 Bph became adults which reproduced causing a surge of newly hatched nymphs after 18 days when 2050 were recorded on the ten plants, contrasting with none where *S. geminata* had access during field

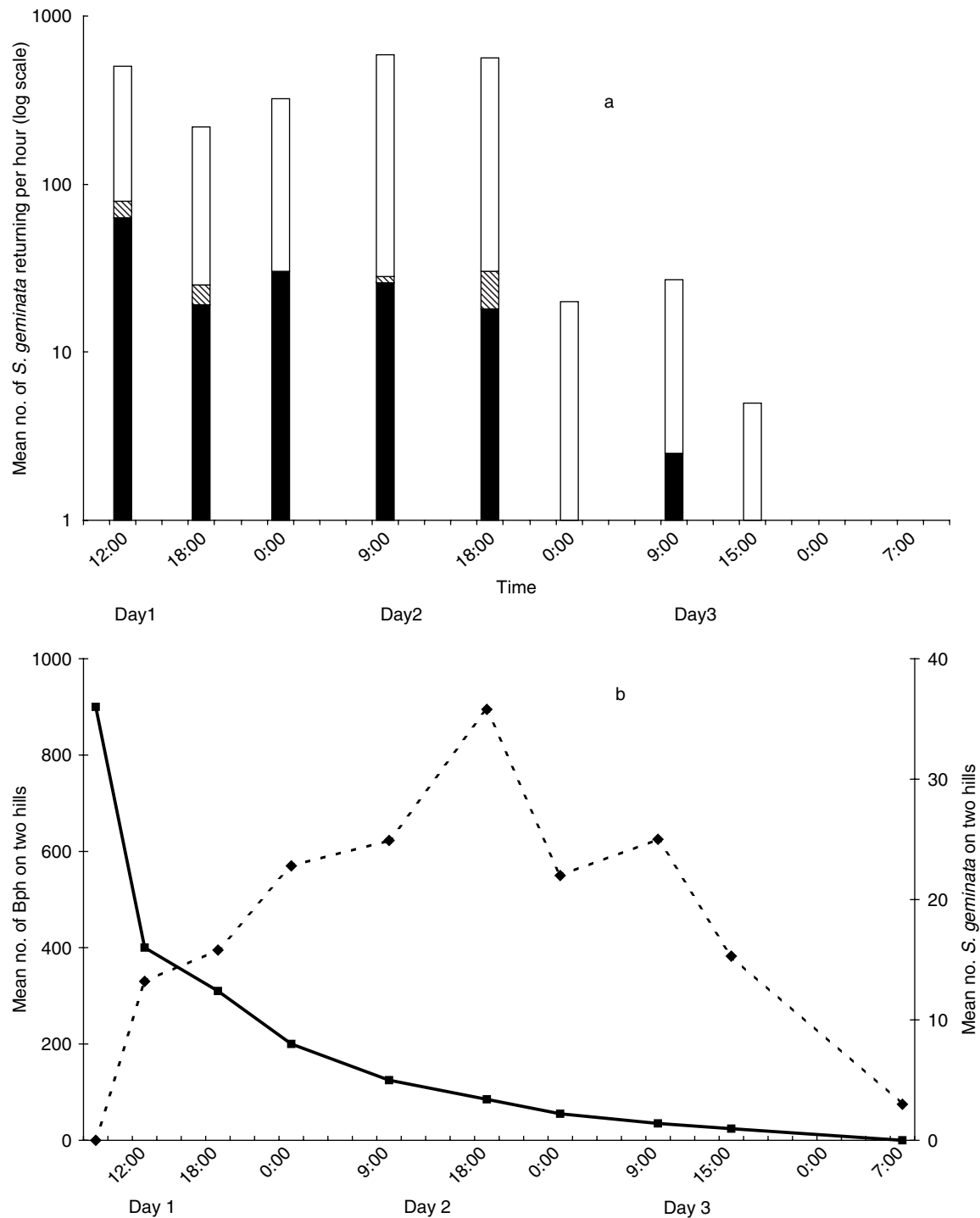


Fig. 1. Predation by *S. geminata* from one colony on 900 Bph nymphs on two rice hills in a drained rice field. (a) calculated numbers of *S. geminata* workers returning per hour to the ant colony with and without transported items (□, totals; ▨, numbers carrying 'other' food items; ■, numbers carrying Bph). (b) changes in numbers of Bph on the infested plants (—■—, Bph; - -◆- -, *S. geminata*).

drainage (table 4). However, where all natural enemies were excluded, the estimate of hatched nymphs reached >21,000 before the experiment was terminated by a typhoon. Dull weather and some rain kept the field muddy during the

period of drainage, but this did not stop *S. geminata* devastating the Bph.

In a wet season experiment, the same caging regimes were used with two densities of Bph, one with five sets of

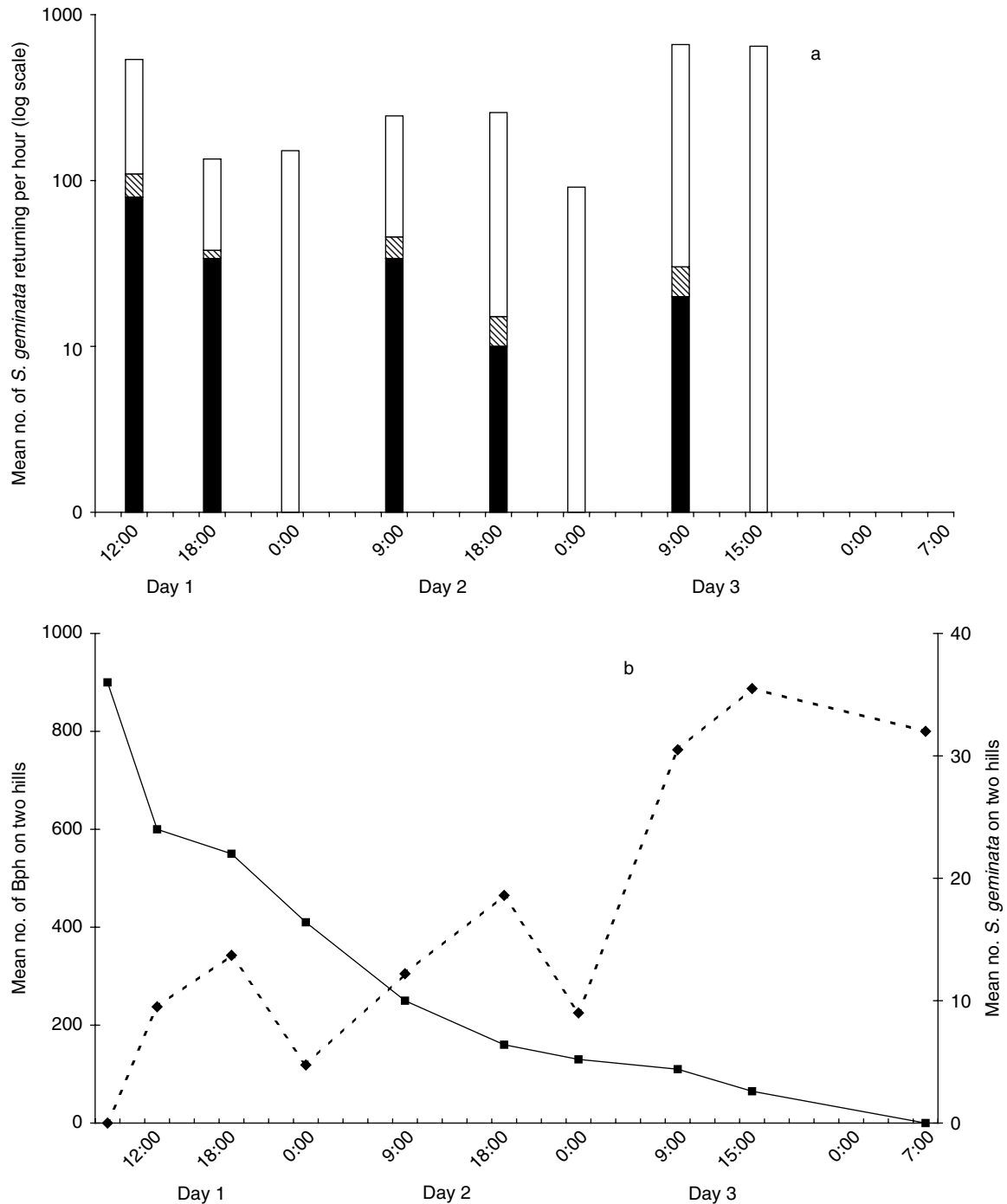


Fig. 2. As in fig. 1 but using a separate *S. geminata* colony in the same rice field.

five caged hills initially infested with 400 3rd instar Bph nymphs and the other with ten adult gravid females, greater than the current level of natural colonization of immigrant adult Bph. Where the 400 nymphs per cage were given access to ants and other natural enemies, the numbers of Bph initially decreased but subsequently increased to up to 500 per five hills during the 25-day experiment (table 2a). In contrast, there was much egg-laying in the 'no-ant other

natural enemy' treatment and in the no-natural enemy controls, creating a surge of newly hatched Bph nymphs. This was followed by a collapse when plants began to die of hopper burn (table 2a), despite an increase to 206 *C. lividipennis* per hill. However, with an initial total of ten adult female Bph, there were no differences between the two natural enemy-exposed treatments (table 2b). In these circumstances, ants were not recruited to the few Bph prey, which,

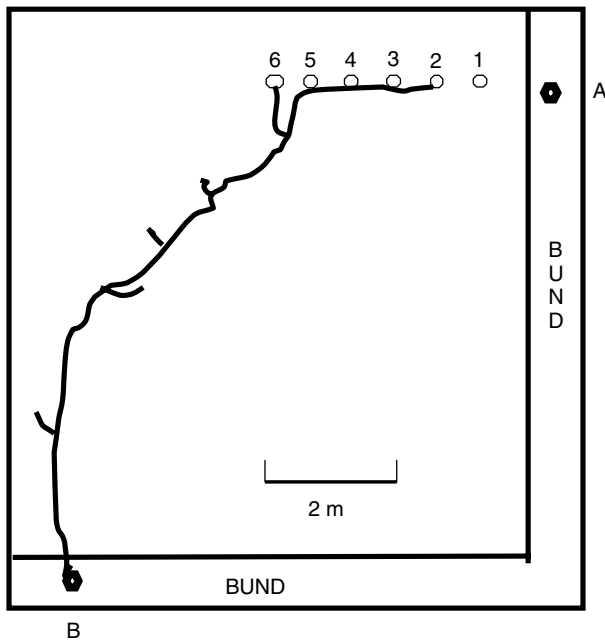


Fig. 3. Approximate line of an *S. geminata* trail across mud to a nest of colony B from a row of rice hills each artificially infested with 200 Bph. Note absence of trail from nest of colony A (—), approx. line of ant trail; ●, *S. geminata* nest).

however, were suppressed successfully by the other predators in the absence of ants, as were naturally occurring immigrants of the green leafhopper (Glh) *Nephotettix virescens* (Distant) (table 2b). This was despite periodic rainfall, which no doubt impaired the rate of predation by *S. geminata* on the large populations of Bph (table 2a).

The next wet season experiment was chosen to show the effect of weather conditions unfavourable to ants when much rainfall caused natural flooding such that artificial re-flooding was only needed once during the first 15 days of the experiment. *S. geminata* and a few *Paratrechina* spp. sporadically entered the crop, yet they were seemingly still sufficient to keep the Bph populations very low in circumstances where there were attractively large hopper populations. However, the inadequate sole effect of other

predators on the large initial Bph populations (table 2a) must be qualified by the evidence (see Methods) that some of one important spider predator species, *L. pseudoannulata*, were initially excluded from the 'non-ant open-top' cage treatment although this species was replaced by more of the other common spiders, notably *A. formosana* and *Tetragnatha* spp. Nevertheless, it is revealing that such non-ant predators still effectively suppressed small adult Bph numbers and also immigrant *N. virescens* equivalent to natural numbers of incoming colonists (table 2b).

In a third wet season experiment in July, the objective was to compare the predatory contribution of *S. geminata* against Bph on hills two metres from the bund and near the middle of a field about 12 m from the bund. Unreplicated groups of five hills were kept either in open cages which allowed access of all predators from the ground as well as from above, or they were entirely uncaged. These were set up one day after field drainage, five including the natural immigrant Bph population and five infested with 400 3rd–4th instar Bph nymphs per hill. One day and four days after drainage (table 1), no *S. geminata* were recorded on hills 12 m from the bund, no doubt because frequent rainfall limited ant foraging except close to the bunds. However, at 12 m, the other predators solely prevented increase of the small natural Bph population. *S. geminata* were still recruited to the artificially infested hills 2 m from the bund where, together with other predators, they greatly decreased the Bph populations in both caged and uncaged conditions (table 1). However, at 12 m distance, with ants absent, the other predators alone had comparatively little effect on the large introduced Bph populations, whether caged or uncaged.

Abundance of S. geminata, spiders and other insects on hills throughout the crop season

In the 360-hill dry season experiment, *S. geminata* moved immediately into the drained field and onto some hills on 1 March. When the field was re-flooded four days later, up to eight *S. geminata* were flushed from the ground per hill but did not affect spider numbers (fig. 4). Subsequently, one day after further drainage on 23 March and 3 April, fewer ants continued foraging on the hills though re-flooding (25 March and 8 April) showed that, overall, there were still many ants in the field (fig. 4). During 20 days continuous

Table 4. Changes in numbers of initially introduced 400 Bph on ten hills given access to *S. geminata* and other predators or to other predators only or with all predators excluded.

Water Regime	Day and time (hrs)	Bph and predators on ten hills.					
		All predators			Other Predators only		No predators
		Bph	<i>S.geminata</i>	Other predators	Bph	Other predators	Bph
Drained (Day 0)	1 (08:00)	400	nr	nr	400	nr	400
	1 (12:00)	102	96	35	305	31	400
	1 (16:00)	43	24	41	286	33	395
	4 (07:30)	3	6	17	150	18	247
Flooded (pm on day 4)	8 (07:30)	1	0	18	27	25	177
	15 (07:30)	4	0	39	1660	38	11,600
	18 (07:30)	0	0	42	2050	48	21,500

nr, not recorded.

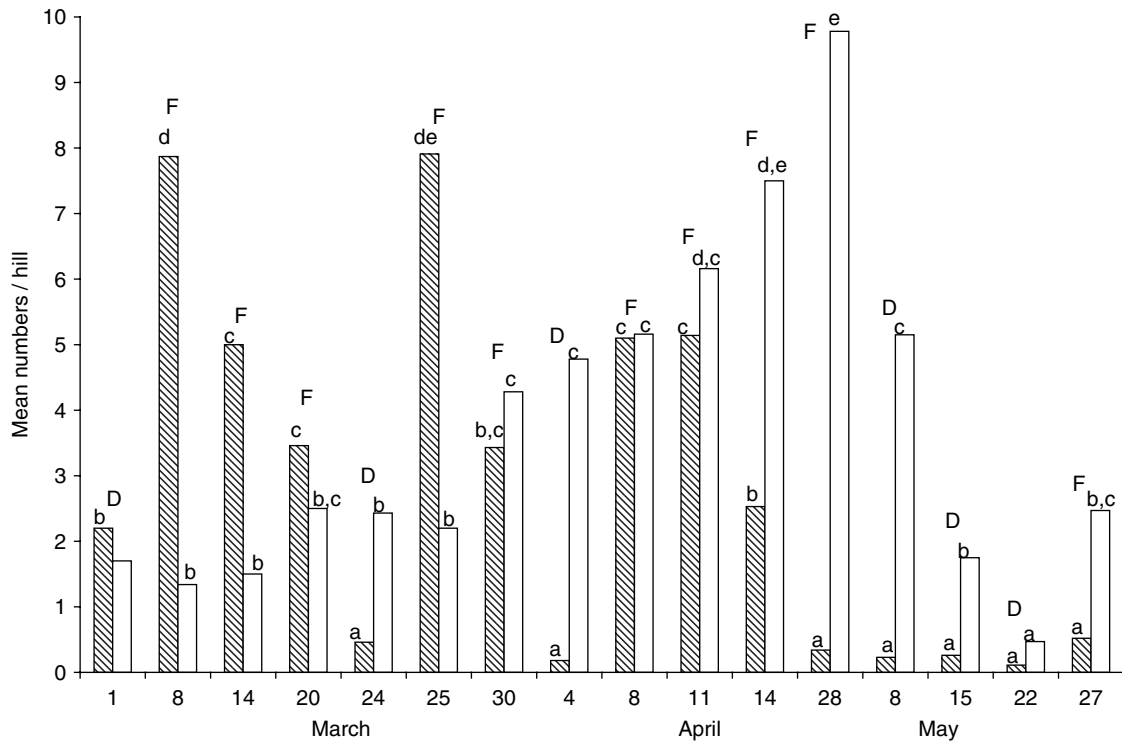


Fig. 4. Mean numbers per hill of *S. geminata* and spiders in a block of 360 rice hills in periodically flooded and drained conditions throughout a dry season rice crop season. F, flooded; D, drained. Histogram numbers with the same letters are not significantly different at $P < 0.05$ (▨, *S. geminata*; □, spiders).

artificial flooding required for crop ripening in April, the numbers of ants stranded on hills notably decreased. Some returned to the bunds across the rice canopy, but others seemingly became dormant and twice were seen being caught by the spider *L. pseudoannulata*. Relatively few ants were counted foraging on the hills after drainage prior to harvesting on 22 May; also few were on the ground and stubble after harvesting, as indicated by a count made on 27 May after they had been flushed onto the stubble by temporary re-flooding (fig. 4). Further counts were made on the stubble until 16 June when, in rainy partly flooded conditions, means of only 1.4 *S. geminata* were stranded per hill.

Regardless of drainage or flooding, spider numbers initially remained at about two per hill in March and then increased to a peak during crop ripening in April when they reached 9.8 per hill on 28 April. This increase was no doubt associated with the great increase in size of territories provided by the growing hills, which also attracted much supplementary prey other than pest species, which remained scarce. Two species of spider predominated – initially about 30% *L. pseudoannulata* decreasing to 10% of the total, and *A. formosana* rising from about 60% to over 80% at the time of peak spider numbers on 28 April. Throughout, the pest population, mainly hoppers, remained very low with Bph at 0.39 per hill on 1 March and between 0.16 and 1.91 from 8 to 28 March. Subsequently, their numbers fluctuated between zero and 0.025 per hill until 28 April, and then remained at zero.

Relationship between *S. geminata* and spider numbers on individual hills

The relative numbers of ants and spiders on individual hills in the 360-hills experiment (fig. 4) were analyzed in order to assess the possible impact of *S. geminata* on the spiders which were chosen as the natural enemies most likely to be interfered with by the ants. Overall, in March and April, the mean numbers of spiders did not differ significantly in relation to increased ant numbers ($P > 0.05$). *S. geminata* were never seen attacking spiders although the latter, like the bug *C. lividipennis* and adult parasitoids, when confronted by an ant crawled aside or moved elsewhere on the hill.

The impact of notably more naturally recruited ants was determined on a total of 33 hills in five drained fields where 500–900 Bph were artificially established on single hills. As already described, aggressively predatory *S. geminata* workers were quickly recruited. Overall, on the first day, the mean numbers of 23 *S. geminata* and 0.4 spiders per hill contrasted with 2.2 ants and 4.8 spiders on 30 randomly examined hills not artificially infested with Bph ($P < 0.01$). As before, spiders were not seen being attacked by the ants, and most moved away to peripheral parts of the hill and to neighbouring hills as the recruited ants arrived. Ten days later, after most ants had departed, there were 5.6 spiders per hill which had returned from adjoining hills or arrived aerially. In these circumstances, the aggression and hyperactivity of the recruited *S. geminata* contrasted sharply with

the behaviour of wandering foragers towards individual Bph prey on naturally infested hills, which they attacked but which did not elicit ant recruitment.

Discussion

Whilst *S. geminata* can undoubtedly be a very effective predator against some pests in upland (dryland) rice (Way *et al.*, 2002), its impact on irrigated rice pests must depend on conditions that enable it to forage into the crop from the very large colonies that can flourish on the bunds. Once the rice canopy is closed and in contact with the bunds, workers can forage across the foliage of flooded fields, though relatively few reach more than a few metres inwards (Way *et al.*, 1998; Islam *et al.*, 2000). Otherwise, this paper shows that they can very quickly spread into fields across the wet mud at times when some farmers regularly practise periodic drainage for about three to four days before re-flooding (S. Masajo, personal communication). In these circumstances, *S. geminata* can forage about 20 m into a field and eliminate large populations of Bph at least 10 m from a nest. However, even in drained conditions, the impact of *S. geminata* is impaired directly by wet season rainfall and indirectly by the semi-flooded conditions that rainfall can create.

We recognize that our experimental caging systems to compare the relative importance of different natural enemies in a pest complex may not accurately represent reality. For example, our experiments did not always distinguish the effect of ants from the full effect of other natural enemies though they nevertheless demonstrated that *S. geminata* can uniquely and rapidly suppress large infestations of Bph. This contrasts with the relative inadequacy of other predators and parasitoids against such infestations. Otherwise, *S. geminata* made no added contribution to the vital early control of the normally few initial immigrant adult Bph and other hoppers in insecticide-untreated fields, as these were still effectively suppressed by the other natural enemies in both drained and flooded conditions. However, it is significant that abundant populations of *S. geminata* flourished in bunds of irrigated fields frequently sprayed with insecticides at IRRI and also in our experiments using broad spectrum cypermethrin and carbofuran (Way & Heong, in prep.). In these circumstances, natural enemies within flooded fields were killed; but, after drainage, *S. geminata* quickly spread into the crops killing incoming Bph and Glh when most other predatory species were still absent or sparse, apart from wind-blown spiderlings, which are too small to attack hopper pests.

As our results confirm, early season mortality of immigrant Bph is crucial because the non-ant natural enemy complex can normally prevent their multiplication to otherwise catastrophically damaging populations (table 2b). Therefore, when drainage permits *S. geminata* to enter a transplanted crop, it is vital that the ant should not impair the impact of early season predators. This is also important in relation to the increasingly used techniques of direct seeding rice, which must remain unflooded for about two weeks after germination. The ant's safety was demonstrated by our experiments, which showed that the normally very few *S. geminata* that in drained fields are regularly seen foraging on a hill do not decrease spider numbers. Exceptionally, more than about 20 *S. geminata* per hill were associated with many fewer spiders. This happened when ant recruits began aggressively preying on initially large populations of Bph. However, this seems irrelevant because

such immediately recruited ants were highly effective against the large Bph populations which are inadequately controlled by the delayed and density responsive predators such as spiders, *C. lividipennis* and also parasitoids (Claridge *et al.*, 2002). Once the ants had departed, spiders re-colonized the hills aerially and from neighbouring plants.

Although Bph was a catastrophic pest of tropical Southeast Asian rice during the 1960–1980 era of excessive insecticide usage and non-resistant rice, it can still be locally severe (Way & Heong, 1994). In these circumstances, drainage would no doubt enable the often huge bund populations of *S. geminata* to make a major impact based not only on the ants' immediately density dependent recruitment but also because such ants can continue predation beyond the immediate needs of a colony (Way & Khoo, 1992). Furthermore, *S. geminata* prey on other pests, notably Lepidoptera including leafrollers (Way *et al.*, 2002) and sometimes stem borers. It is also among the few natural enemies of eggs and young of the golden apple snail *Pomacea canaliculata*, which can be a devastating pest of newly established rice plants in Southeast Asia (Way *et al.*, 1998; Yusa, 2001). In this context, it is noteworthy that early season drainage has been recommended empirically for control of the snail. No doubt predation by *S. geminata* helps explain the value of such drainage.

Until recently, conventional advice has assumed that continuous flooding of irrigated rice is needed to maximize irrigated rice yields. Yet previous evidence had already shown that periodic drainage may not limit yield and indeed can favour it (Singh *et al.*, 1996; Guerra *et al.*, 1998). Moreover, in recent years, there has been disturbing 'yield decline' in some continuously flooded intensive rice monocultures (Dawe *et al.*, 2000), which despite the advent of new higher yielding cultivars has slowed overall rice yield growth in parts of tropical Asia and is confirmed by decreasing yields of the classical Green Revolution IR8 cultivar. Now, the evidence from long term experiments in Southeast Asia shows that continuous flooding is detrimental to soil fertility (Dawe *et al.*, 2000), which can be countered by periodic drainage and lessened volume of irrigation water by as much as 40–70% in southern China, apparently without yield detriment (Guerra *et al.*, 1998). This seems crucially important not only for maintaining soil fertility but also for making better use of declining water for irrigation. Indeed, in view of the 'looming water crisis', 'alternate wetting and drying' practices may become necessary even where it might incur some yield loss (Bouman, 2001; Bouman *et al.*, 2007). The present paper shows that such practices can also confer notable biological pest control benefits from *S. geminata*.

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