

# Egg mortality of the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae) and green leafhoppers, *Nephotettix* spp. (Homoptera: Cicadellidae), on rice in Sri Lanka

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## Abstract

Rice plants, infested with eggs of *Nilaparvata lugens* (Stål) or *Nephotettix* spp. in laboratory cultures, were used to trap egg parasitoids in rice fields at two sites over a period of four days in Sri Lanka. Levels of egg parasitism per plant varied from 0 to 54% in *N. lugens* and 45 to 100% in *Nephotettix* spp. Egg predation was a minor cause of mortality, but attack by a species of *Panstenon* (Hymenoptera: Pteromalidae) killed up to 18% *Nilaparvata lugens* eggs. *N. lugens* eggs were parasitized by *Anagrus* sp. nr *flaveolus* Waterhouse, *A. optabilis* (Perkins) (Hymenoptera: Mymaridae) and *Oligosita* sp. (Hymenoptera: Trichogrammatidae). *Nephotettix* spp. eggs were parasitized by two species of *Gonatocerus* (Hymenoptera: Mymaridae) and one of *Paracentrobia* (Hymenoptera: Trichogrammatidae). There was no overlap in field host range between the two parasitoid assemblages. *Gonatocerus* spp. and *Paracentrobia* spp. seldom attacked the same *Nephotettix* sp. egg batch, suggesting the possibility that these species compete in the field. Overall egg parasitism of *Nilaparvata lugens* was positively related to host egg density at the spatial scale of the rice plant, but unrelated at the tiller or batch scale. *Nephotettix* spp. egg parasitism showed a negative density dependent relationship at the spatial scales of the tiller and plant and no relationship at the batch level. The potential role of these egg parasitoids in preventing outbreaks of hopper pests in Sri Lanka is discussed.

## Introduction

Eggs of planthopper and leafhopper pests of rice are often subjected to high levels of parasitism and predation (see reviews by Chiu, 1979; Greathead, 1983; Otake, 1977). Nevertheless, mortality of hopper nymphs caused

by generalist predators such as lycosid spiders, has been thought to play a more important regulatory role in the population dynamics of these pests (Chiu, 1979; Kenmore, 1980; Kenmore *et al.*, 1985; Kiritani, 1979; Otake, 1977). In a simulation model of *Nilaparvata lugens* populations (Holt *et al.*, 1987), egg mortality was included, but only at a fixed percentage, irrespective of host density. This concentration of work on nymphal predators is due, at least in part, to the comparative ease with

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which they can be sampled from the field and studied in laboratory experiments (Greathead, 1983).

Levels of egg parasitism of rice planthoppers and leafhoppers in the field reported in earlier studies have varied between 10 and 100% (e.g. Chantarasa-ard *et al.*, 1984b; Kiritani *et al.*, 1970; Miura *et al.*, 1979, 1981). Positive density dependence has been reported in one case (Sasaba & Kiritani, 1972) and inverse density dependence in a few cases (e.g. Chantarasa-ard *et al.*, 1984a, 1984b) but most studies indicate levels of parasitism independent of host egg density whether this is explicitly stated or not (e.g. Kenmore, 1980; Miura *et al.*, 1979, 1981; Ooi, 1988; Otake, 1967; Vungsilabutr, 1978). This overall lack of positive density dependence and the variety of scales and methodologies used are subjects we return to in the discussion.

The study of egg parasitoids of rice hoppers in the field is made difficult by the extremely small size of the parasitoids and by the nature of hopper oviposition. The delicate host eggs are inserted inside the plant material and cannot be identified or counted without dissection of the rice plant. This laborious procedure is normally only practicable where host egg density is high. To overcome this problem, in this study we collected egg parasitoids of *N. lugens*, *Nephotettix virescens* (Distant) and *N. nigropictus* (Stål) in the field using 'trap' plants that had been infested with host eggs in laboratory cultures (see Otake, 1968). Complete dissection of the plants allowed us to determine the cause of egg mortality, relationships of levels of attack with host egg density at various spatial scales, the field host specificity of the parasitoid taxa and patterns of attack attributable to parasitoid competition.

### Methods

Ten potted rice plants, variety Bg 94-2, were infested with *Nilaparvata lugens* eggs by placing them in a laboratory culture for four days. A further ten plants were similarly infested with *Nephotettix* eggs (in a mixed culture of *N. virescens* and *N. nigropictus*). All plants used were at the late tillering stage and free from insect attack. On 21 February 1986, five *Nilaparvata lugens* infested plants and five *Nephotettix* infested plants were placed in one rice field at the Central Agricultural Research Institute, Peradeniya (site A). The remaining half of the plants were placed in one rice field at the Central Rice Breeding Station, Batalagoda (site B). At each site the plants were spaced out in single rice fields, avoiding the edges and other irregularities. Both areas of rice were at the milky grain stage (approximately 70 days after transplanting), had low field populations of *Nilaparvata lugens* (<1 adult or nymph per hill) and *Nephotettix* spp. (<1 adult per hill). Neither plot had received any insecticide applications during the current 'Maha' 1985-6, rice season. All of the plants were collected after four days exposure in the field and brought immediately to Cardiff, UK, where host eggs were dissected. Parasitism was determined by egg colour and confirmed subsequently by identification of emerging adult parasitoids. Other causes of mortality were scored and identified as far as possible. Predation by a species of *Panstenon* (Hymenoptera: Pteromalidae) was estimated by multiplying the number of larvae plus pupae of the predator by the average egg batch size of *Nilaparvata lugens* in the samples (5.3), on the assumption

that each *Panstenon* larva destroys one batch. Parasitism was then calculated using the total number of dissected eggs plus the estimated number of eggs killed by *Panstenon* larvae.

Species of *Anagrus* (Hymenoptera: Mymaridae) and *Oligosita* (Hymenoptera: Trichogrammatidae) can be difficult to distinguish at an early stage of development in the host egg and were not adequately distinguished in the site A samples. Total parasitism however, was readily scored. *N. lugens* data from site A were therefore excluded from analyses involving separate egg parasitoid taxa. Several plants were rejected on examination in the UK either because no hopper eggs had been laid on them or because the plants had deteriorated badly in transit. Only 13 of the original 20 plants could eventually be used in the analyses.

Some of the predation we recorded might have occurred while the rice plants were being infested with host eggs in the *N. lugens* and *Nephotettix* cultures. However, no predators were observed in these cultures, so we are confident that little or no egg predation occurred on the rice plants prior to their exposure in the field. The possibility of egg parasitoids attacking the plants prior to field exposure can be excluded because the development of the parasitoid larvae in the host eggs indicated recent parasitism when the plants were dissected: the characteristic egg colour had only partially developed. These colours are strongly developed after four days (Otake, 1968) and our earliest dissections were conducted six days after the removal of the plants from the cultures.

A total of 1369 *Nephotettix* spp. eggs was dissected from 97 egg batches, distributed among 39 tillers. The *Nilaparvata lugens* infested plants yielded 538 eggs in 101 batches, distributed among 31 tillers. Each plant comprised about 25 tillers, but most tillers did not contain hopper eggs.

### Results

#### *General mortality of hopper eggs*

*N. lugens* eggs were attacked by two species of *Anagrus* (*A. nr flaveolus* Waterhouse and *A. optabilis* (Perkins)), one species of *Oligosita*, the predatory pteromalid *Panstenon* sp., and an unidentified predator (suspected to be Coleoptera or Orthoptera on the basis of observed feeding damage) (tables 1 and 2). Eggs of *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae) were found near one batch, but no feeding by this predator on any eggs was noted. Adult *C. lividipennis* were rare in other sampling programmes in these fields (Fowler, 1988).

*Oligosita* sp. was the most abundant *N. lugens* egg parasitoid at both sites (repeated measures analysis of variance on number of adults emerging per plant,  $P < 0.05$ ). *Anagrus nr flaveolus* was more common than *A. optabilis* at site B, but absent from the site A samples, however, this difference was not statistically significant ( $P > 0.1$ ).

*Nephotettix* spp. eggs were attacked by two undetermined species of *Gonatocerus* (designated 'A' and 'B') (Hymenoptera: Mymaridae), one species of *Paracentrobia* (Hymenoptera: Trichogrammatidae), an unidentified

Table 1. Causes of mortality of *Nilaparvata lugens* and *Nephotettix* spp. The mortality figures were calculated from the total numbers of eggs attacked in each category per site and the total number of eggs per site. Further details in text.

Host	Site	Percentage and cause of mortality of host eggs						
		<i>Oligosita</i> sp.	<i>Anagrus</i> spp.	<i>Gonatocerus</i> spp.	<i>Paracentrobia</i> spp.	<i>Panstenon</i> sp.	Unidentified predation	Diptera
<i>Nilaparvata lugens</i>	A	18.0	(A + 0 combined)	0.0	0.0	18.5	0.9	0.0
	B	32.7	10.0	0.0	0.0	6.0	2.0	0.0
<i>Nephotettix</i> spp.	A	0.0	0.0	38.9	10.9	0.0	0.0	0.8
	B	0.0	0.0	43.6	28.2	0.0	0.0	0.0

Table 2. Summed numbers of adult parasitoids emerging from *Nilaparvata lugens* and *Nephotettix* spp. eggs dissected from the plants at each site. Adults can be more accurately identified than parasitized eggs (table 1).

Host	Site	Number of adults emerged					
		<i>Oligosita</i> sp.	<i>Anagrus</i> <i>optabilis</i>	<i>Anagrus</i> nr <i>flaveolus</i>	<i>Gonatocerus</i> sp. 'A'	<i>Gonatocerus</i> sp. 'B'	<i>Paracentrobia</i> sp.
<i>Nilaparvata lugens</i>	A	38	16	0	0	0	0
	B	107	5	12	0	0	0
<i>Nephotettix</i> spp.	A	0	0	0	35	31	33
	B	0	0	0	8	0	0

Diptera larva and a predator causing similar damage to that found in the *Nilaparvata lugens* samples (tables 1 and 2).

*Gonatocerus* spp. were more common than *Paracentrobia* sp. at site A and site B. Both *Gonatocerus* spp. were recorded from site A, and only sp. 'A' from site B, but sample sizes were small because a large percentage of parasitized eggs failed to produce adults (due to water-logging in transit).

#### Interactions between the parasitoid species

The frequencies of egg batches attacked by one, two or neither parasitoid taxa are shown in table 3. Egg colour was used to distinguish parasitoid taxa to the generic level, so comparisons were made between *Anagrus* spp. and *Oligosita* sp. in *N. lugens* eggs, and between *Gonatocerus* spp. and *Paracentrobia* sp. in *Nephotettix* eggs. Calculating the independent probabilities of attack by these parasitoid taxa allows predicted frequency distributions to be tested against the observed distributions, assuming no interaction between the parasitoid taxa.

The frequencies of joint, individual or zero attack by *Oligosita* sp. and *Anagrus* spp. on *Nilaparvata lugens* egg batches (data available only for site B) showed no significant differences from the predicted distribution indicating that the parasitoid genera co-parasitized *N. lugens* egg batches to the extent expected by chance (table 3a). At the tiller scale there was also no evidence of interaction between the parasitoids. In contrast, *Gonatocerus* spp. and *Paracentrobia* sp. occur in the same batch of *Nephotettix* spp. eggs much less commonly than expected by chance (table 3b,  $P < 0.001$ , data summed for site A and site B). At the tiller scale, co-parasitism occurred to the extent expected by chance, but expected values were

less than five so the use of chi squared is inappropriate. Similarly, at the plant level the data sets were too small for analysis, but interactions between the parasitoids are unlikely to be important at these larger scales.

Table 3. Interactions of the parasitoid taxa at the level of host egg batch and plant tiller. Observed figures are the numbers of egg batches, or plant tillers (containing eggs) attacked solely by one taxon of parasitoid, by both taxa or by neither taxon. Further details in text.

#### a) *Nilaparvata lugens*

Category of attack	Numbers of batches attacked		Numbers of tillers attacked	
	Observed	Expected	Observed	Expected
<i>Oligosita</i> sp.	3	4.1	1	1
<i>Anagrus</i> spp.	18	19.1	7	7
<i>Anagrus</i> + <i>Oligosita</i>	9	7.9	7	7
Neither taxon	11	9.9	1	1
$\chi^2$	$P = 0.89$		-	

#### b) *Nephotettix* spp.

Category of attack	Numbers of batches attacked		Numbers of tillers attacked	
	Observed	Expected	Observed	Expected
<i>Gonatocerus</i> spp.	48	39.4	20	17.9
<i>Paracentrobia</i> sp.	19	10.4	6	3.9
<i>Gonatocerus</i> + <i>Paracentrobia</i>	3	11.6	9	11.2
Neither taxon	27	35.5	4	6.1
$\chi^2$	$P < 0.001$		$P = 0.45$	

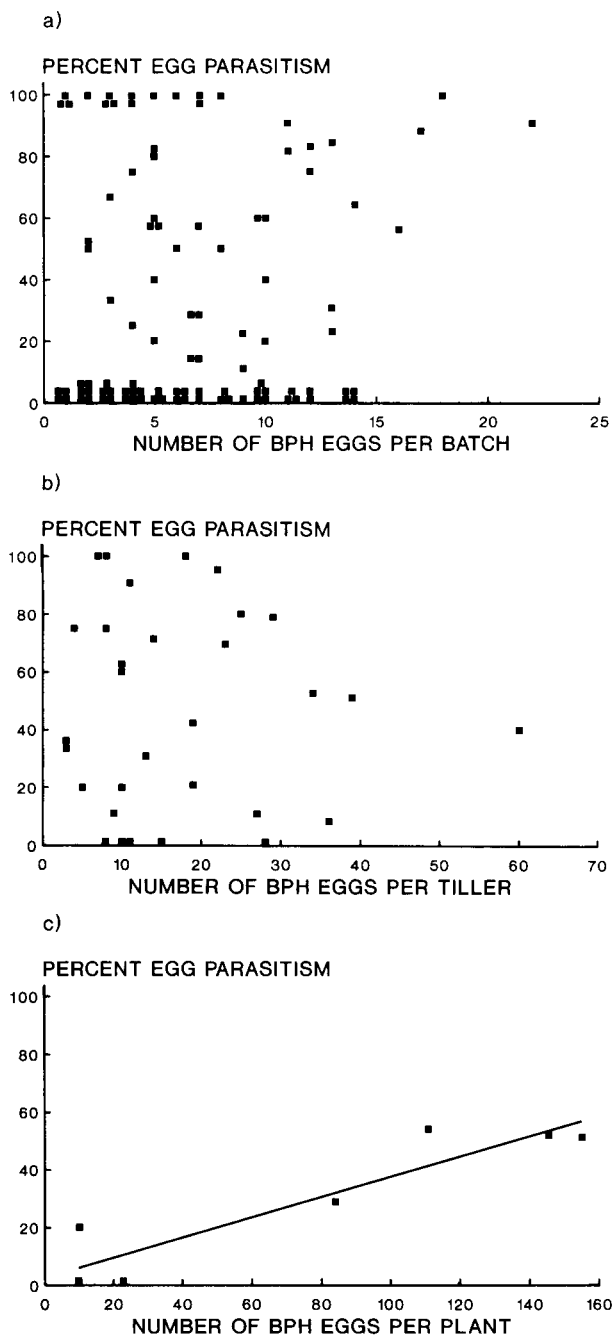


Fig. 1. Egg parasitism of *Nilaparvata lugens* (BPH) by *Anagrus* spp. and *Oligosita* sp., in relation to the numbers of host eggs per batch (a), per tiller (b) and per plant (c). No significant relationships were found in (a) or (b) (both  $P \gg 0.1$ ). Fitted line in (c)  $Y = 0.35 X + 2.56$ ,  $r^2 = 0.84$ ,  $n = 7$ ,  $P < 0.01$ .

*Parasitism in relation to host egg density per batch, per tiller and per plant*

The analyses were conducted on *Oligosita* sp. and *Anagrus* spp., both individually and combined, parasitizing *Nilaparvata lugens*, and similarly on *Gonatocerus* spp. and *Paracentrobia* sp. parasitizing *Nephotettix* spp. Data were summed from site A and site B.

Percentage parasitism was very variable at the batch and tiller level. No parasitoid taxa on *Nilaparvata lugens* or *Nephotettix* spp., individually or combined, showed any significant relationship between percentage parasitism and number of eggs per batch (fig. 1a for *Nilaparvata lugens* and fig. 2a for *Nephotettix* spp.). Percentage parasitism of *Nilaparvata lugens* eggs was also unrelated to host egg density at the tiller level (fig. 1b) but with *Nephotettix* spp., a negative density dependent relationship was apparent at this scale (fig. 2b,  $P < 0.05$ ). Analysing the *Nephotettix* spp. parasitism for site A and site B separately, revealed negative relationships with host egg density per tiller that failed to reach statistical significance ( $P > 0.1$ ). Separate analyses for the two parasitoid genera attacking *Nephotettix* spp. revealed no significant relationships of percentage parasitism with host egg density per tiller, but this is to be expected from the way that the two parasitoid taxa tend to exclude each other from individual egg masses.

Summed parasitism by *Oligosita* sp. and *Anagrus* spp. on *Nilaparvata lugens* was significantly positively related to the number of eggs per plant (fig. 1c,  $P < 0.01$ ). Both parasitoid taxa, analysed separately using the site B data, showed similar relationships at the plant level, but only *Anagrus* spp. reached statistical significance with this reduced data set ( $P < 0.01$ ). By contrast, at the plant level, combined parasitism of *Nephotettix* spp. eggs showed a negative density dependent relationship (fig. 2c,  $P < 0.05$ ).

## Discussion

Many earlier studies of egg parasitism in planthoppers and leafhoppers have examined the relationship between percentage parasitism and host density (Denno & Roderick, 1990). Traditionally, high rates of attack in regions of high host density have been regarded as a stabilizing influence on population fluctuations (Hassell & May, 1973), but recently the role of this spatial density dependence has been questioned (Murdoch & Stewart-Oaten, 1989). Several reviews have shown that the proportion of studies detecting positive density dependent mortality, as opposed to inverse density dependence or density independence, is rather low (Denno & Roderick, 1990; Stiling, 1987; Walde & Murdoch, 1988). However, it has also been argued that a low detection rate of positive spatial density dependence in field studies is to be expected because of problems with choice of spatial scales in experimental work (Heads & Lawton, 1983).

The density independent relationships we found between parasitism rates and egg density per batch (with both hopper taxa) and per tiller (with *Nilaparvata lugens*) support the generalizations made in recent reviews (Denno & Roderick, 1990; Walde & Murdoch, 1988). However, in contrast to the majority of studies they reviewed, we found that increasing the spatial scale revealed relationships between parasitism rates and host egg densities. Mortality from egg parasitism was positively density dependent at the plant level in *Nilaparvata lugens* and inversely density dependent at the tiller and plant levels in *Nephotettix* spp.

Our results with *Nephotettix* spp. contrast with the positive density dependent relationships between egg parasitism and egg density reported for *N. cincticeps*

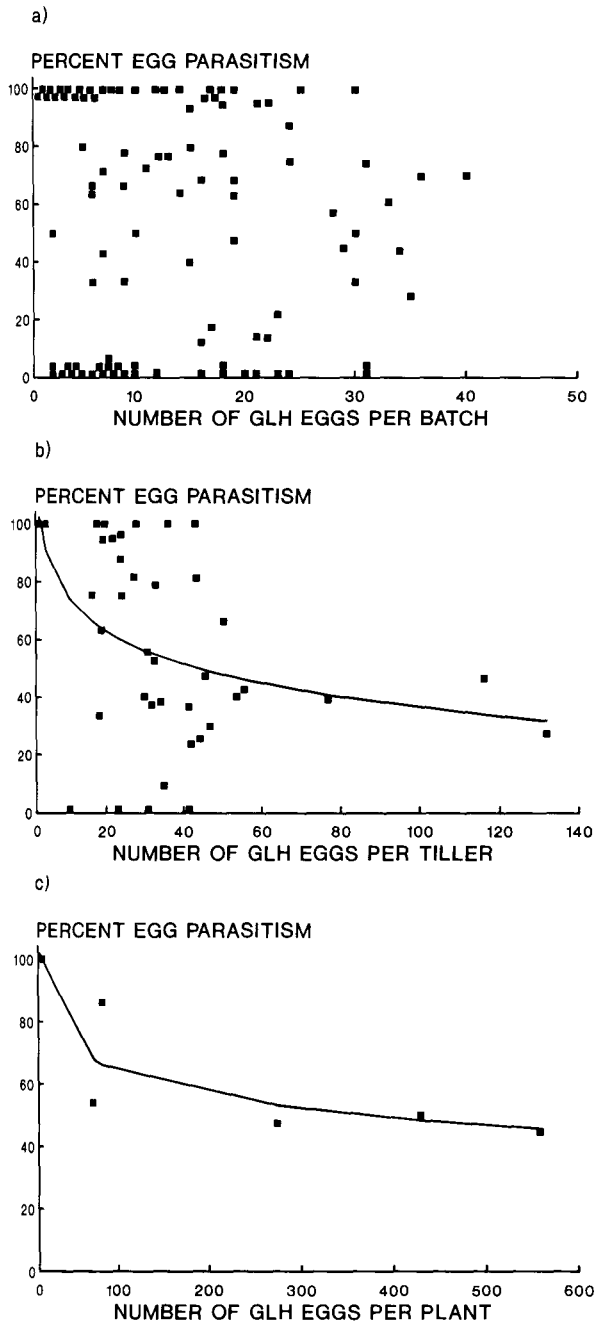


Fig. 2. Egg parasitism of *Nephotettix* spp. (GLH) by *Gonatocerus* spp. and *Paracentrobia* sp., in relation to the numbers of host eggs (a) per batch, (b) per tiller and (c) per plant. No significant relationship was found in (a) ( $P > 0.1$ ). Fitted lines: (b)  $Y = 114 - 38.7 \log(X + 1)$ ,  $r^2 = 0.14$ ,  $n = 39$ ,  $P < 0.05$  (c)  $Y = 117 - 26.1 \log(X + 1)$ ,  $r^2 = 0.78$ ,  $n = 6$ .  $P < 0.05$ .

Uhler in Japan (Sasaba & Kiritani, 1972) and with several studies of cicadellid egg parasitism in other ecosystems (Denno & Roderick, 1990). In our study however, egg densities and percentage egg parasitism reached relatively high levels (fig. 2 b and c) and the number of eggs per tiller reached 132, with few tillers containing less than 20 eggs. In their study of *N. cincticeps*, Sasaba & Kiritani

(1972) used trap plants in a similar way to us, but only achieved a clear-cut result after tillers with numbers of eggs outside the range of 4–14 were excluded (on the grounds that these were outside the measured range of egg densities per tiller in the field over the period when the trap plants were in place). The apparent conflict between the results of Sasaba & Kiritani (1972) and our present study could be due simply to the different host densities being considered. Other things being equal, positive spatial density dependence at relatively low host densities is likely to alter to inverse density dependence at high host densities because of limitations to the fecundity of a given population of parasitoids.

The relatively strong relationship between the rate of egg parasitism and numbers of *Nilaparvata lugens* eggs per plant is more encouraging. Despite the caveats mentioned earlier we consider that positive density dependent mortality in response to patchiness in the spatial distribution of *N. lugens* eggs could be important in tropical rice. *N. lugens* outbreaks in the tropics usually start in small localized patches within rice fields (Dyck *et al.*, 1979; Kuno, 1979) and early concentration of natural enemy impact on these patches could reduce the chance of outbreaks developing. The inconsistency of our result with the apparent absence of such density dependence in many studies of egg parasitism in planthoppers (Denno & Roderick, 1990) could be due to a wide variety of reasons, one of which is our rather small sample size. Rapid population growth of hoppers is cited as a possible reason for inverse relationships of parasitism with host density (Denno & Roderick, 1990) but *N. lugens* population densities in the tropics often remain relatively constant over rice growing seasons compared with those in temperate regions (Otake, 1978). Most existing studies of hopper egg parasitism have been conducted outside the tropics. Very few other studies examine parasitism over a range of spatial scales, particularly those studies in rice. In general, a range of relationships is to be expected because of the inherent variability in rice agroecosystems in such factors as the background levels of host attack, the presence of other major egg predators such as *Cyrtorhinus* spp. (Chiu, 1979), the recent history of pesticide use (Sasaba & Kiritani, 1972) and the local presence of weed reservoirs (Nishida *et al.*, 1976). More careful and comprehensive studies of egg parasitism, such as those on *Anagrus delicatus* Dozier attacking *Prokelisia marginata* Van Duzee (Homoptera: Delphacidae) on saltmarshes in the USA (e.g. Stiling & Strong, 1982), are needed on rice hoppers to examine this problem further.

Despite constraints caused by the poor understanding of the taxonomy of these parasitoids (Claridge *et al.*, 1988), we attempted to study the complete species complex attacking *N. lugens* and *Nephotettix* at our sites. The examination of preserved adults allowed morphologically distinct taxa to be distinguished, revealing three species of egg parasitoids attacking *Nilaparvata lugens* eggs and three species attacking *Nephotettix*. There was no overlap in the parasitoid faunas of *Nilaparvata lugens* and *Nephotettix*. Similar patterns of host specificity have been found where careful dissection of host eggs has been conducted, thereby avoiding possible contamination of samples of eggs of one host with those of another (Claridge *et al.*, 1988). Not surprisingly, the composition of the egg parasitoid fauna varied between sites. We

would also expect the fauna to vary through time, and suggest that the development of the egg parasitoid community on rice hoppers through a rice growing season would be a useful and interesting study. We also know little about any interactions between the parasitoid species in these complexes, but we can make some inferences from the patterns of co-parasitism of individual host batches. *Nilaparvata lugens* egg parasitoids were frequently found co-parasitizing egg batches providing no evidence of any interspecific competition. In contrast, the two taxa of parasitoids attacking *Nephotettix* eggs appeared to exclude each other partially from individual egg batches. Under laboratory conditions, females of *Paracentrobia* sp. aggressively defend egg batches that they have located (J.C. Morgan, unpublished observations).

Predation of hopper eggs was relatively rare in this study, but larvae of *Panstenon* did destroy an estimated 18.5% of *Nilaparvata lugens* eggs at one site. Interactions between egg parasitoids and predators can be expected to be one-sided with predators probably equally capable of consuming parasitized and unparasitized host eggs (Chiu, 1979). The lower level of *N. lugens* egg parasitism (18%) at the site with highest *Panstenon* sp. attack is consistent with this proposal. Competition between egg parasitoids and predators needs further study, particularly in areas where the major egg predator, *Cyrtorhinus lividipennis*, can be abundant.

Previous work on the dynamics of *N. lugens* in Sri Lanka (Otake, 1978; Otake *et al.*, 1976) highlighted the relatively low rate of increase of the populations in the apparent absence of major predators or parasitoids of the nymphs. We suggest that egg parasitoids could play an important role in preventing outbreaks of hopper pests of rice in Sri Lanka. Given the complexity of the natural enemy community found associated with rice in tropical Asia, we would expect the relative importance of different groups of predators and parasitoids to vary both regionally and temporally. Such complexity is daunting, but only by understanding the roles of the natural enemies of rice pests can we hope to maximize the impact of predators and parasitoids within rice pest management strategies.

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