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# Egg dispersion is more important than competition type for herbivores attacked by a parasitoid

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**Abstract** Herbivore fitness can be altered by a combination of interacting organisms, such as its food plant, conspecifics and predators/parasitoids. Here, we tested relative effects of plant species, herbivore's intraspecific competition type, and spatial distribution of the herbivore among plant units on the survival of the herbivore and whether parasitoids modified these effects. We used an endophagous bruchine seed predator, *Callosobruchus maculatus*, for the herbivore and a braconid wasp, *Heterospilus prosopidis*, for the parasitoid. The survival rate of *C. maculatus* was measured for each of 16 combinations of two plants (bean species, *Vigna unguiculata* and *V. radiata*), two competition types of *C. maculatus* larvae (contest and scramble) and two spatial distribution of hosts, sparse (one *C. maculatus* larva per seed over 20 seeds) and dense (two *C. maculatus* larvae per seed over 10 seeds), and with/without a parasitoid pair. In the absence of the parasitoid, the survival rate of *C. maculatus* was lower with *V. radiata* and in the contest type. With the parasitoid, the proportion of hosts parasitised was independent of total host density. Both the proportion of hosts parasitised and the survival rate of hosts were affected neither by the plant species nor by the host strain but by the spatial distribution of hosts. When host distribution was dense, a higher proportion of hosts were parasitised and the survival rate of *C.*

*maculatus* was lower. We discussed the potential of the parasitoid as a selective agent for the sparse within-pod distribution of its hosts in the field.

*Keywords:* Aggregation • Bruchinae • Phytophagous insect • Refuge • Resource • Tritrophic interaction

## Introduction

Intraspecific competition can have significant effects on individual fitness (Smith and Lessells 1985; Thanthianga and Mitchell 1987; Toquenaga and Fujii 1991; Godfray 1994; Tuda and Iwasa 1998; Reeve et al. 1998; Zaviezo and Mills 2000; Agnew et al. 2002; Pexton and Mayhew 2002; Lane and Mills 2003; Vamosi 2005a; Vamosi and Lesack 2007) and population dynamics (Tuda 1998; Tuda and Iwasa 1998). Although a number of studies have investigated various aspects of contest (one individual dominating resource) and scramble (many to all individuals sharing resource) competition strategies, both theoretically (Smith and Lessells 1985; Smith 1990; Toquenaga et al. 1994; Colegrave 1997; Tuda and Iwasa 1998) and empirically (Toquenaga and Fujii 1991; Reeve et al. 1998; Takano et al. 2001; Pexton and Mayhew 2002), the effects of predation by a higher trophic level on the relative fitness of these strategies in consumer populations have received less attention. For example, plant organs that serve as a resource for endophagous herbivores can also serve as a spatial refuge for such herbivores, including gall makers (Weis et al. 1985; Ito and Hijii 2002; Cattell and Stiling 2004) and fruit/seed predators (Biere et al. 2002; Wang et al. 2009). In such situations, contest-type herbivores may benefit more than scramble-type herbivores by monopolising central part of plant organs to escape from predation/parasitism. Additionally, populations with active larvae may be competitively superior in the absence of predators or parasitoids, but increased movements and cues associated with feeding may make such individuals easier to detect, resulting in reduced fitness in the presence of enemies (Carton and Sokolowski 1992). By contrast, endophagous herbivores that display a scramble competition strategy may avoid direct interactions with others by feeding on peripheral tissues of plants (Toquenaga and Fujii 1991) and are typically more willing to superparasitise (i.e., lay more eggs on) previously used resources (Messina and Mitchell 1989). Such behaviours may make the scramble competition strategy more vulnerable to parasitoids. In the only related experiment of which we are aware, the dominant larval competition strategy in a strain of *Callosobruchus maculatus* (F.) shifted from scramble to contest after 20 to 40 generations of being reared with a larval/pupal parasitoid (*Heterospilus prosopidis* Viereck) (Tuda 1998). The aforementioned potential mechanisms, however, have not been explicitly studied in this or other systems.

The effect of spatial distribution of hosts on parasitism is one of the main focuses in behavioural and population ecology. Studies have revealed among-patch distribution of hosts/prey can change the foraging behaviour and functional response of parasitoids/predators (Jones and Turner 1987; Lill 1998; Yasuda and Ishikawa 1999;

Vet 2001; Pitt and Ritchie 2002; Tuda and Shima 2002; Hemerik and Yano 2010) and thus may contribute to the stability of host-parasitoid/prey-predator dynamics (Shimada 1999; Nachman 2006). Within patch distribution of hosts may also determine parasitoid attack efficiency (van Alebeek et al. 1996; Cronin 2009).

Bruchine beetles (Coleoptera: Chrysomelidae: Bruchinae) are an ideal model for investigating possible tritrophic interactions among plant-herbivore-parasitoid. A substantial body of literature has investigated the mechanisms and outcomes of contest vs. scramble larval competition strategies in the absence of parasitoids (Toquenaga and Fujii 1991; Colegrave 1997; Tuda 1998; Takano et al. 2001; Messina and Karren 2003; Messina 2004). However, *C. maculatus* larvae in the wild are potentially exposed not only to intraspecific competition but also to attack by parasitoid wasps (Tuda 1996; van Huis et al. 1998; Schmale et al. 2001; Spitzen and van Huis 2005). Among-patch spatial distribution of hosts is known to affect *H. prosopidis*' parasitism efficiency (Shimada 1999). However, possible effect of within-patch distribution of hosts has not been tested extensively.

Here, we aim to study the relative contribution of plant species, conspecific competitor and parasitoid of an herbivore and spatial distribution of herbivores within a plant to the survival and parasitism of the herbivore, using the seed feeding species *C.*

*maculatus*. We examine the survival of two strains of *C. maculatus* that differ in their larval competition strategy (i.e., contest vs. scramble) and proportion of host, *C. maculatus*, parasitised by *H. prosopidis*. Host density per-seed and number of seeds was controlled, so that within-patch spatial distribution of hosts over seeds was either sparse or less sparse (hereafter, dense).

## Materials and methods

### Organisms

Parasitoids used in this experiment were derived from the 'hpF' strain of *H. prosopidis* (Hymenoptera: Braconidae), originally collected from Hawaii in 1975 (Fujii 1983; Tuda and Shimada 1995). The Hawaiian population had been introduced from Texas, USA in 1910 for the biological control of *Algarobius prosopis* (Beardsley 1961; Clausen 1978). This species is a solitary (i.e., one larva develops successfully from an individual host), weakly synovigenic (i.e., females mostly complete oogenesis prior to eclosion and emerge with many mature eggs; M. Tuda, personal observation) idiobiont ectoparasitoid that does not engage in host feeding (Utida 1944; Schmale et al. 2001). Prior to the experiment, *H. prosopidis* had been reared under laboratory conditions on the ‘jC’ strain of *C. chinensis* (L.), which in turn were reared on adzuki beans (*Vigna angularis* (Willd.) Ohwi & Ohashi) since 1975 (Fujii 1983). The body size of female *H. prosopidis* was 3.92 ± 0.03 mm (mean ± SE, from head to abdomen, *n* = 10).

The experimental hosts were two strains of *C. maculatus*, South India, iQ (hereafter contest strain) and New Zealand, hQ (hereafter scramble strain). The contest strain was established from mung bean (*V. radiata* (L.) Wilczek) and black gram (*V. mungo* (L.) Hepper) in Tirunelveli, India in 1979 (Thanthianga and Mitchell 1987) and has been reared continuously on *V. radiata*. The scramble strain was collected from broad beans (*Vicia faba* L.) imported from New Zealand in 1992, and has since been cultured on adzuki beans (Tuda 1995). The designation of contest and scramble strategies for South India and New Zealand strains, respectively, was based on density-dependent adult emergence patterns (Toquenaga and Fujii 1991; Tuda 1998). There are a number of traits associated with the competition types, including: body size (larger for contest, Credland et al. 1986; Tuda 1998; Vamosi 2005a), superparasitism (lower for contest, Messina and Karren 2003), respiration and per capita consumption rates (both higher for contest, Guedes et al. 2003), natural mortality (higher for contest, Tuda 1998), ability to discriminate among beans based on size (higher for contest, Jones and Vamosi 2010), and development time (longer for contest, Tuda 1998; Takano et al. 2001). In no cases were individual parasitoids or hosts returned to their respective main cultures after being used in these experiments.

The resources used in the experiment were *V. radiata* (small resource) and cowpeas (*V. unguiculata* (L.) Walp.) (large resource). In the absence of parasitoids, the contest strategy is favoured in the former resource type whereas the scramble strategy is predicted to be favoured in the latter (Tuda 1998; Tuda and Iwasa 1998). This outcome is largely driven by differences in size of the two resource types, with the mass of an individual *V. unguiculata* being about 4 × that of *V. radiata* (Jones and Vamosi 2010). Although the contest strain was not naïve to *V. radiata*, we are primarily interested in the relative, not absolute, survival of *C. maculatus* in the presence of parasitoids (to which individuals of all strains were equally naïve) for all resource type × opportunity for competition treatment combinations.

## Experimental design

To obtain *C. maculatus* eggs on seeds, we followed a protocol similar to that used for assaying the effects of intraspecific competition on female fecundity (Vamosi 2005a;

Vamosi and Lesack 2007). A minimum of 200 adult *C. maculatus* was removed from their main cultures within 24 h of survival. These *C. maculatus* were placed in large mason jars that had a thin layer (~250 to 300 seeds) of either fresh *V. radiata* or *V. unguiculata*, and females were allowed to oviposit for 48 h. This period of time allows (i) females ample time to superparasitise individual seeds (i.e., lay an egg on a seed that already has eggs) and (ii) most eggs to harden prior to manipulation, but prevents developing larvae from burrowing into the seed before assigning it to a competition level (Vamosi 2005a). After 48 h, adults were removed from the jars and seeds with one or no eggs were discarded. Discarding seeds with less than two eggs prior to experimental trials ensured that all seeds used are known to be of good quality. To create different larval densities, eggs on approximately two thirds of the seeds were scraped off so that the seeds contained only a single egg, whereas those on the rest were scraped off so that the seeds contained two eggs. After eggs hatched, we reconfirmed the number of hatched eggs on each seed. Seeds were then haphazardly placed into groups of either 20 (with one egg per seed) or 10 (with two eggs per seed) in small Petri dishes (diameter 40 mm, height 10 mm), resulting in two groups that initially contained the same number (i.e., 20) of larvae but distributed over differing numbers of seeds. The small Petri dishes were used to minimize the rolling of seeds and the medium-range foraging that is affected by spatial distribution of hosts (in *H. prosopidis*, Shimada 1999) or their cues (e.g., Ayabe et al. 2008). Because *C. maculatus* larvae may die for other reasons (e.g., competition for resources) prior to exposure to parasitoids, we chose a slightly higher initial number (i.e., 20) of larvae per replicate than the fecundity of *H. prosopidis* females (8-14 offspring, Schmale et al. 2001), so that number of attacks would not be limited by the number of vulnerable hosts. Larvae were reared in an environmental chamber held at standard conditions (28 ± 2°C, 35 ± 5% r.h., and 12h L : 12h D photoperiod).

Sixteen to eighteen days after *C. maculatus* eggs were laid on the seeds the larvae reached a developmental stage (L4, prior to pupation) that is vulnerable to attack from *H. prosopidis.* At this point, we introduced a newly emerged female-male pair of parasitoids to half of the replicates of a given treatment combination. Each resource × host strain × host spatial distribution × parasitoid presence combination was replicated about 22 times (16-28 replicates). Parental parasitoids were removed after they died, to prevent their accidental inclusion in the parasitoid emergence data. We checked dishes once daily beginning 21 days after adult *C. maculatus* had begun to lay eggs, and at least twice daily after the first adult *C. maculatus* was observed to emerge. Adult *C. maculatus* typically commenced emerging 24 or 25 days after adults had begun to lay eggs, and we monitored the emergence of adult *C. maculatus* and parasitoid wasps for a minimum of

14 days (maximum of 21 days) after the first adult *C. maculatus* had been observed to emerge in a given treatment combination.

## Statistical analyses

We analyzed survival rate of *C. maculatus* immature (number of emerging *C. maculatus* adults/(initial number of larvae, i.e., 20)), proportion of *C. maculatus* immatures parasitised by parasitoids (number of emerging parasitoids/sum of *C. maculatus* and parasitoid adults emerging), and survival rate of *C. maculatus* in the presence of parasitoids, in the different treatment combinations. Because the response variables were proportions in all cases, we applied generalized linear models with a logit link and binomial error. Evidence for overdispersion was not found in any of the models. Independent variables were resource, *C. maculatus* strain, and spatial distribution (either sparse or dense) of *C. maculatus* among seeds, and their second- and third-order interaction terms. The main effect of total number of vulnerable hosts (i.e., sum of *C. maculatus* and parasitoid adults emerging) on the proportion of parasitised *C. maculatus* was tested by incorporating it into the full model. In addition to the *C. maculatus* survival rate, to estimate the probability of *C. maculatus* escaping from parasitism, corrected survival rate in the presence of parasitoid was derived by dividing the number of emerging *C. maculatus* adults by the estimated number of emerging *C. maculatus* adults in the absence of parasitoid. This denominator was estimated using a full generalized linear model with log-link and Poisson error family that was fitted to the number of emerging *C. maculatus* in the absence of parasitoid. We conducted all statistical analyses using JMP 8.0.2.2.

## Results

When parasitoids were absent, the survival of *C. maculatus* immatures was unaffected by the spatial distribution of *C. maculatus* hatched eggs (Table 1). The *C. maculatus* survival rate was lower for the contest type and when using *V. radiata* (Table 1, Fig. 1). The effect of spatial distribution of the host was non-significant (Table 1). None of the interaction terms were significant (Table 1).

The proportion of hosts parasitised by the parasitoid, *H. prosopidis*, was affected only by the spatial distribution of the host, *C. maculatus*, among seeds (Table 2). A higher proportion was parasitised when the hosts were sparsely distributed (Fig. 2). The proportion of hosts parasitised was, however, unaffected either by plant species or by host competition type (Table 2), in contrast with the situation without the parasitoid.

None of the interaction terms were significant (Table 2). The proportion parasitised was independent of host density (i.e., sum of *C. maculatus* and *H. prosopidis* adults emerging) ($\chi^2 = 0.34$, $df = 1$, $P = 0.56$).

With the parasitoid, the survival rate of *C. maculatus* was affected significantly by the spatial distribution of *C. maculatus* but not by other main or interaction factors (Table 3). The survival rate was higher when the distribution of *C. maculatus* among seeds was sparse (Fig. 3). Results with the corrected survival rate were the same with regard to significant/non-significant factors (the result not shown).

## Discussion

Our results indicate that under parasitoid (*H. prosopidis*) presence it is more beneficial for its host herbivore, *C. maculatus*, to disperse their eggs among seeds, irrespective of seed traits or host competition type (Table 2, Fig. 2). This contrasts with the situation without the parasitoid: Seed traits and herbivore competition type, not the spatial distribution of herbivore, played a central role in the survival of the herbivore (Table 1, Fig. 1). The lower parasitisation on sparsely-distributed hosts than on densely-distributed hosts may be explained by deceleration of parasitoid searching and parasitisation activity. Alternatively, a higher per-bean density may have led to shallower burrowing by *C. maculatus* larvae, which may have lowered the efficacy of burrowed cavities as a partial spatial refuge against parasitoid attack (K. Kagoshima and M. Tuda, unpublished data). Additionally, increased numbers of larvae feeding close to the surface are expected to provide a stronger cue for female parasitoid wasps as they attempt to locate suitable hosts (see also Thanthianga and Mitchell 1987). We have observed female *H. prosopidis* displaying antennation behaviour prior to oviposition (see also Utida 1944). Experimental evidence shows *H. prosopidis* prefers last-instar larvae to pupae of *C. maculatus* (cf., Tuda 1996) and *C. chinensis* (Shimada and Fujii 1985) for parasitisation. These observations may indicate that this parasitoid species is attracted by feeding sounds made by host larvae. In other braconid parasitoids, there is evidence that substrate vibrations and acoustic cues associated with feeding are used to locate concealed hosts (Lawrence 1981; Sugimoto et al. 1988). Certainly, as in the tephritid fly *Anastrepha suspensa*, which develops within fruit (Lawrence 1981), the scraping/chewing sounds made by *C. maculatus* larvae in large cultures are audible even to the human ear.

The current study highlights the need to incorporate parasitoid attack to understand the fitness of scramble vs. contest competition strategies. Although the combination of plants and herbivore competition types per se was shown to have no effect on parasitism when egg dispersion was controlled as in our experiment, the scramble type tends to lay multiple eggs on a single seed (Messina and Karren 2003). The degree of egg dispersion is variable among different geographical strains (e.g., Horng 1997) and this variation may be associated with different levels of parasitism pressure among the populations of origin. The original primary host of *H. prosopidis* is *A. prosopis* feeding on *Prosopis* seeds both in its introduced and original habitats (Kobayashi and Shimada 2000; M. Shimada, personal communication). *Algarobius prosopis* is a contest type competitor and only one adult can survive in a single seed (Hoffmann et al. 1993). Such sparse distribution in the host populations over seeds may have been selected for under high parasitism rate of *H. prosopidis* on dense hosts.

As reviewed at the outset, the majority of studies to date have measured the relative costs and benefits of the two competition strategies in the absence of parasitoids and other enemies (e.g., Takano et al. 2001; but see Tuda 1998). Further studies will help define the context-dependence of our findings. For example, the relative benefits of the two larval competition strategies may differ when they are exposed to egg parasitoids. High larval densities of *C. maculatus* may facilitate the establishment of an egg parasitoid population (van Huis et al. 1998), although increased host larval competition may result in smaller adults producing smaller eggs (Fox and Savalli 1998;

Yanagi and Tuda 2010), which is likely to reduce fitness of individual parasitoids (Spitzen and van Huis 2005).

Long-term consequences of natural enemies on the fitness of different phenotypes and competition strategies in their victims are now the subjects of considerable attention (e.g., Van Buskirk and Yurewicz 1998; Rundle et al. 2003; Cameron et al. 2005; Eklöv and Svanbäck 2006; Mikolajewski et al. 2006; reviewed by Vamosi 2005b; Hatcher et al. 2006). For example, increased interactions with, and prolonged exposure to, hosts (*Plodia interpunctella*) parasitised by its parasitoid *Venturia canescens* reduced the survivorship of unparasitised hosts (Cameron et al. 2005). Such effects could have destabilizing delay effects on host population dynamics. Although idiobiont *H. prosopidis* may have smaller such effect than koinobiont *V. canescens*, the biology of the host that grows in a limited resource amount/space may exaggerate not only direct but also indirect interaction with conspecifics sharing the same resource unit. These effects of predation may also influence the evolution of traits in the host population (Vamosi 2005b). Together with previous work (e.g., Taper 1990; Tuda 1998; Tuda and Iwasa 1998; a review in Tuda and Shimada 2005), this study highlights the potential for *Callosobruchus* beetles and their parasitoids to be a model system for selection experiments that increase our knowledge of such evolutionary dynamics.

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**Table 1** Generalized linear model on the proportion of hosts, *C. maculatus*, surviving in the absence of the parasitoid, *H. prosopidis*. The *df* for each term was 1. Factors and *P* values in bold show statistical significance.

| | Likelihood ratio $\chi^2$ | *P* |
|---|---|---|
| **resource (R)** | 4.09 | **0.043** |
| **strain (S)** | 16.06 | < **0.0001** |
| distribution (D) | 3.15 | 0.076 |
| R × S | 0.03 | 0.87 |
| R × D | 0.12 | 0.73 |
| S × D | 0.02 | 0.89 |
| R × S × D | 0.15 | 0.70 |

**Table 2** Generalized linear model on the proportion of hosts, *C. maculatus*, parasitised by parasitoid, *H. prosopidis* = number of emerging parasitoids /(number of emerging parasitoids + number of emerging hosts). The *df* for each term was 1. A factor and *P* value in bold show statistical significance.

| | Likelihood ratio $\chi^2$ | *P* |
|---|---|---|
| resource (R) | 0.12 | 0.73 |
| strain (S) | 0.22 | 0.64 |
| **distribution (D)** | 7.39 | **0.0065** |
| R × S | 2.30 | 0.13 |
| R × D | 0.40 | 0.53 |
| S × D | 0.58 | 0.45 |
| R × S × D | 0.26 | 0.61 |

**Table 3** Generalized linear model on the proportion of hosts, *C. maculatus*, surviving in the presence of the parasitoid, *H. prosopidis*. The *df* for each term was 1. A factor and *P* value in bold show statistical significance.

| | Likelihood ratio $\chi^2$ | *P* |
|---|---|---|
| resource (R) | 0.00008 | 0.99 |
| strain (S) | 0.55 | 0.46 |
| **distribution (D)** | 9.02 | **0.0027** |
| R × S | 0.83 | 0.36 |
| R × D | 0.001 | 0.98 |
| S × D | 0.007 | 0.93 |
| R × S × D | 0.11 | 0.74 |

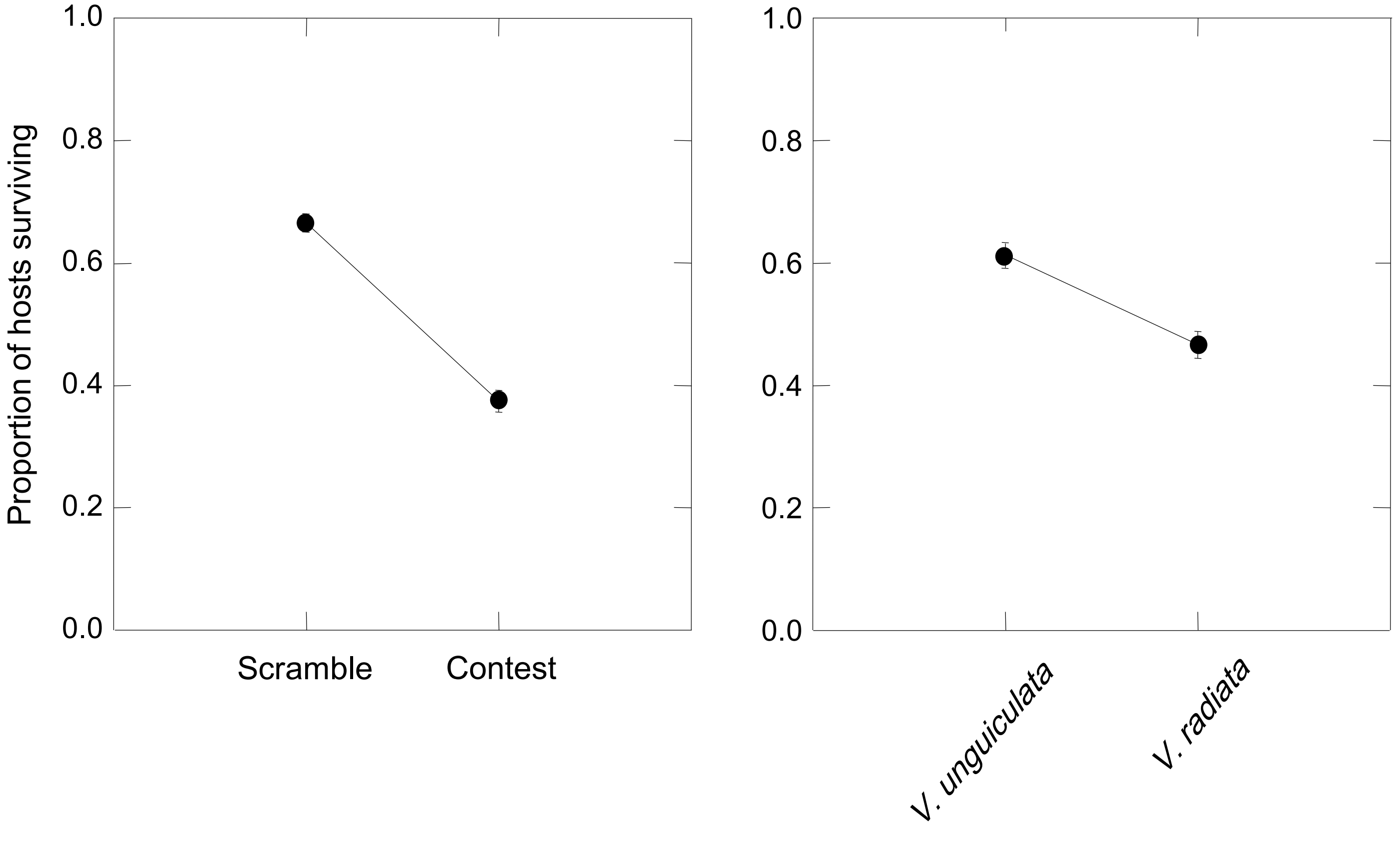
## Figure legends

**Fig. 1** Effect of plant species and host strains on the survival rate of host *C. maculatus* (mean ± SE).

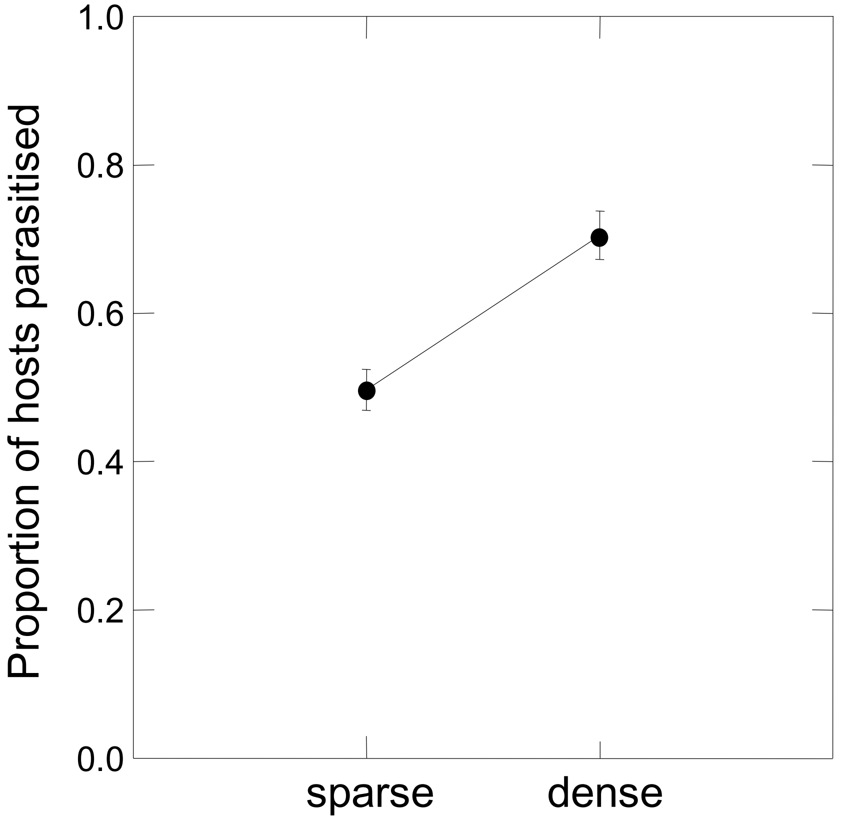
**Fig. 2** Effect of spatial distribution of hosts on the proportion of the host *C. maculatus* parasitised by the parasitoid *Heterospilus prosopidis* (mean ± SE).

**Fig. 3** Effect of spatial distribution of hosts on the survival rate of the host *C. maculatus* in the presence of the parasitoid *Heterospilus prosopidis* (mean ± SE).

(Fig.1)


Proportion of hosts surviving
1.0
0.8
0.6
0.4
0.2
0.0
Scramble
Contest
1.0
0.8
0.6
0.4
0.2
0.0
V. unguiculata
V. radiata

(Fig.2)


Proportion of hosts parasitised
1.0
0.8
0.6
0.4
0.2
0.0
sparse
dense

(Fig.3)