CARFAX

Invasion and Displacement of Experimental Populations of a Conventional Parasitoid by a Heteronomous Hyperparasitoid

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Aphelinid parasitoids have an outstanding record of success in programmes of classical biocontrol against whiteflies and scale insects. Heteronomous hyperparasitoids are aphelinids in which the sexes develop on or in different hosts. The female always develops as a primary endoparasitoid of Homoptera. The male develops as a secondary parasitoid (hyperparasitoid) of his own or another species of homopteran endoparasitoid. Caged experiments were performed with the cabbage whitefly, Aleyrodes proletella, *to examine the invasion of a population of a conventional parasitoid,* Encarsia inaron *(both sexes primary endoparasitoids) by a heteronomous hyperparasitoid,* E. tricolor. *In all cages the heteronomous hyperparasitoid successfully invaded an established population of the conventional parasitoid and the conventional species population declined to very low levels within 8 weeks of the introduction of the heteronomous hyperparasitoid. The patterns of invasion were different in each cage. In two cages, high levels of male production by* E. tricolor *were observed, indicating that hyperparasitism of the conventional species was probably an important factor in causing the decline in the* E. inaron *population. In a reciprocal experiment in which* E. inaron *was introduced to an established population of* E. tricolor *the conventional species failed to invade or persist. A survey of published references to complexes of parasitoids containing a heteronomous hyperparasitoid and one or more conventional species indicated that, in the majority of cases, the heteronomous hyperparasitoid was the most important species in the complex. There are clear implications for the use of these parasitoids in programmes of classical biocontrol. This is because high competitive ability against other parasitoids is not necessarily a good indicator of the ability of a species to maintain high levels of pest control, especially when hyperparasitic behaviour is involved.*

Keywords: Encarsia tricolor, E. inaron, *Aphelinidae*, Aleyrodes protella, *Homoptera autoparasitoid, hyperparasitism, biocontrol*

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INTRODUCTION

The progeny of parasitoid wasps are usually limited to a fairly narrow range of host species which meet their nutritional and physiological requirements. Each host species, however, may be attacked by several, possibly many, different species of parasitoid. For many parasitoids interspecific competition for hosts may be continually or periodically intense. The strength of such competitive interactions may be sufficient to influence the size, structure and stability of parasitoid communities (Askew & Shaw, 1986; Miller & Ehler, 1990).

Heteronomous hyperparasitoids are minute, solitary parasitoids from the family Aphelinidae (Hymenoptera: Chalcidoidea) that attack the immature stages of whitefly and scale insects. Aphelinids have been outstandingly successful agents of classical biocontrol, far more so than any other parasitoid family (Greathead, 1986; Noyes & Hayat, 1994). Heteronomous hyperparasitoids show a remarkable sex-linked divergence in their host relations. Females develop as primary endoparasitoids in the nymphs of whiteflies or scale insects, whereas males develop as secondary parasitoids (hyperparasitoids) of their own or a related hymenopteran species. Such differences in host relations have been used as a basis for the classification of this and related groups of aphelinids (Walter, 1983), although modifications have now been suggested (Williams & Polaszek, 1996). In direct heteronomous hyperparasitoids, the male egg is deposited directly in or on the larva or pupa of a primary homopteran endoparasitoid. For indirect heteronomous hyperparasitoids, the male egg is laid in a primary host (e.g. a whitefly nymph) in anticipation of future primary parasitism; the development of the primary parasitoid permits the development of the hyperparasitic male. The majority of heteronomous hyperparasitoids are direct (Walter, 1983). The production of males as primary endoparasitoids has been reported in *Encarsia pergandiella*, and appears to be due to loss of the paternal genome in a proportion of the diploid (fertilized) eggs (Hunter *et al.*, 1993). The incidence of such sex ratio distorters in other species of heteronomous hyperparasitoids is not known.

Heteronomous hyperparasitoids are often observed in complexes of parasitoids containing conventional primary parasitoids (e.g. Dysart, 1966; Gerling, 1967, 1983; Flanders, 1971; Kuenzel, 1975; Williams, 1977; Viggiani, 1984, 1991; Thompson *et al.*, 1987; Donaldson & Walter, 1991; McAuslane *et al.*, 1993). Consider the most simple situation where one species of heteronomous hyperparasitoid interacts with one conventional parasitoid species of whitefly. This cannot be viewed as a simple two-species, one-resource situation because the conventional parasitoid will suffer from exploitation of the whitefly population and from hyperparasitism. As J. R. Williams (1977) has already noted, heteronomous hyperparasitism may constitute "… an inherent advantage to a species when competing with primary parasitoids that reproduce in the orthodox manner …".

E. tricolor is a direct, heteronomous hyperparasitoid. Both sexes are polyphagous: the female has been reported from 10 species of whitefly and the male from seven species of hymenopteran endoparasitoids, including conspecific females. Compared with many other heteronomous hyperparasitoids, the biology of this species is relatively well studied (Arzone, 1977; Christochowitz *et al.*, 1981; Avilla & Copland, 1987, 1988; Artigues *et al.*, 1992a,b; Williams, 1995). It has been deomonstrated that *E. tricolor* females can discriminate between conspecific primary parasitoids as hosts for the production of males (Avilla *et al.*, 1991; Williams, 1991). In both of these studies, *E. tricolor* showed preferential hyperparasitism of non-conspecific hosts (*E. formosa* or *E. inaron*). This may be a mechanism by which *E. tricolor* females avoid hyperparasitizing their own progeny (Williams, 1991), and may also have benefits in terms of increased size of males emerging from non-conspecific hosts (Avilla & Copland, 1987).

In this study, two questions were addressed concerning the interaction of a heteronomous hyperparasitoid with a conventional parasitoid:

(1) What is the initial trajectory of the two parasitoid populations when in competition for a common host resource?

(2) Is hyperparasitism of the conventional species by the heteronomous hyperparasitoid a significant factor in such competitive interactions?

The species used in this study were the cabbage whitefly, *Aleyrodes proletella*, the heteronomous hyperparasitoid, *E. tricolor* and a conventional bisexual parasitoid, *E. inaron*, in which both sexes are primary endoparasitoids.

MATERIALS AND METHODS

The cabbage whitefly, *A. proletella*, was cultured on Brussels sprout plants (var. winter harvest) grown in a peat-based compost. Plants infested with *A. proletella* were used to maintain cultures of *E. tricolor* and *E. inaron*. All cultures, experimental cages and experimental material were maintained at 25°C, 16:8 h light:dark photoperiod and ambient humidity. Four plants 20–30 cm tall bearing approximately 10 leaves were lightly infested with whitefly of all stages and placed in a muslin-walled cage $40 \times 40 \times 50$ cm tall. Within 48 h of emergence, 50 female and five male *E. inaron* adults were introduced into the cage. Parasitoids emerged *en masse* from individual leaves held in ventilated plastic tubs, so it was assumed that virtually all the females had already mated. After 2 weeks, three leaves were selected at random and removed. For each leaf, the following information was recorded:

(1) the number of apparently healthy scales;
(2) the number of parasitized scales;
(3) the number of parasitoid larvae that pupated in the 10 days following the sample (i.e. the number of scales that initially appeared to be healthy but were actually parasitized).

Parasitoid pupae were allowed to emerge in gelatine capsules with a drop of honey. Adult parasitoids so obtained were returned to the culture cage within 24 h of emergence. Identical samples were taken at weekly intervals thereafter. At 3 weeks, however, 35 mated female *E. tricolor* (< 48 h old) were added to the culture cage. In all subsequent samples, the emerging parasitoids were identified to species. It was thereby possible to observe changes in the level of parasitism due to each species in the cage. Cages sampled for a minimum of 8 weeks, with a final sample 3 weeks after the weekly sampling ceased (11 or 12 weeks after the start of the experiment). New plants lightly infested with all stages of whitefly were added to each cage as necessary to compensate for plant death or defoliation. Thus, through continued 'immigration' of unparasitized whitefly nymphs into experimental cages, the overall percentage parasitism of whitefly by both species combined rarely exceeded 80%. The experiment was repeated three times.

The reciprocal experiment was also performed in which the experimental cage was initially inoculated with 50 mated *E. tricolor* females and five males. After 3 weeks, 35 mated *E. inaron* females were introduced. This experiment was replicated only once.

To complement the result observed in caged experiments, a literature search was performed for articles in which a heteronomous hyperparasitoid species was reported in a complex containing one or more conventional primary parasitoids, and which gave information of the abundance/ importance of each member of the complex. The sources for the search were *Review of Applied Entomology* (1930–89), the International Institute for Biological Control BIOCAT database of biocontrol programmes (up to 1989), *Biological Abstracts* (1989–94), and *Entomology Abstracts* (1989–95). Searches were made for references to genera showing heteronomous host relations. When the abstract suggested that the original paper may offer information on the relative abundance of species within a host–parasitoid complex, the reference was consulted fully. The results of the search were classified according to whether the complex was a natural one or arose as the result of one or more introductions of alien species as part of a biocontrol programme.

RESULTS

The heteronomous hyperparasitoid, *E. tricolor*, was able to reproduce and become the dominant parasitoid species, resulting in a marked reduction in the populations of the conventional parasitoid, *E. inaron*. This result was consistent in all cages, although the patterns of invasion and displacement were rather different for each cage. The results are presented graphically for the addition of *E. tricolor* to cages containing *E. inaron* populations (Figures 1–3) and the reciprocal experiment wherein *E. inaron* was introduced to an *E. tricolor* population (Figure 4). In each case, data are presented for the mean overall percentage parasitism and the mean number of unparasitized hosts/leaf (Figures 1(a), 2(a), 3(a) and 4(a)), the mean number of *E. inaron* that emerged from each sample (Figures 1(b), 2(b), 3(b) and 4(b)) and the mean number of each sex of *E. tricolor* adults/sample that emerged (Figures 1(c), 2(c), 3(c) and 4(c)). A χ^2 test of the overall sex ratio of *E. tricolor* adults emerging from each weekly sample revealed that heteronomous hyperparasitoid sex ratios were significantly biased in favour of one sex or the other in all cages at all time-points with the exception of cage 4 (reciprocal experiment) at weeks 7 and 8.

Cage 1

The *E. inaron* population quickly achieved high levels of parasitism in cage 1 (ca. 70%) (Figure 1(a)). When *E. tricolor* was added to the cage, the *E. tricolor* population grew steadily with a continually female-biased sex ratio (Figure 1(c)). This was concurrent with a steady decline in the *E. inaron* population (Figure 1(b)). The overall percentage parasitism ranged between 76 and 32% during this period (Figure 1(a)). In the final sample (week 11), no *E. inaron* were found in the three-leaf samples.

Cage 2

The *E. inaron* population in cage 2 attained a higher density than that in cage 1 (Figure 2(b)), although the percentage parasitism recorded from leaf samples was less (Figure 2(a)). When *E. tricolor* was added to cage 2, a distinct male-biased sex ratio was produced, and the level of female production did not begin to rise until week 8 (Figure 2(c)). By the final sample the situation had reversed, and the sex ratio of the leaf sample was highly female biased. Fluctuations in the sex ratio of *E. tricolor* tended to follow changes in the overall percentage parasitism in this cage. Despite these differences, the population of *E. inaron* steadily declined, and by the final sample very few *E. inaron* adults emerged.

Cage 3

In cage 3, the *E. inaron* population growth was initially slow, but increased rapidly by week 3 and remained generally high (except for a dip in week 5) (Figure 3(b)). The overall level of parasitism also increased in week 3 and remained relatively stable at 35–40% until week 9 (Figure 3(a)). The sex ratio of *E. tricolor* remained markedly male-biased for the 12 weeks of the study (Figure 3(c)). No appreciable levels of female production were observed for *E. tricolor* until week 8. It was at this point that the *E. inaron* population showed a dramatic crash, and, by week 12, the *E. tricolor* population sex ratio was approaching unity and *E. inaron* individuals were no longer observed in the leaf sample.

Cage 4 (Reciprocal Experiment)

The results of the reciprocal experiment, in which *E. inaron* was introduced to an established population of *E. tricolor*, are strikingly different from the patterns seen in cages 1–3. The population of *E. tricolor* fluctuated by 50–200 individuals/leaf (both sexes combined), but showed a moderate, but consistently male, bias in the population, except at week 7 (Figure 4(c)). The sex ratio of *E. tricolor* did not appear to be sensitive to the overall percentage parasitism in the leaf samples. *E. inaron* was unable to invade this population of *E. tricolor* despite the fact
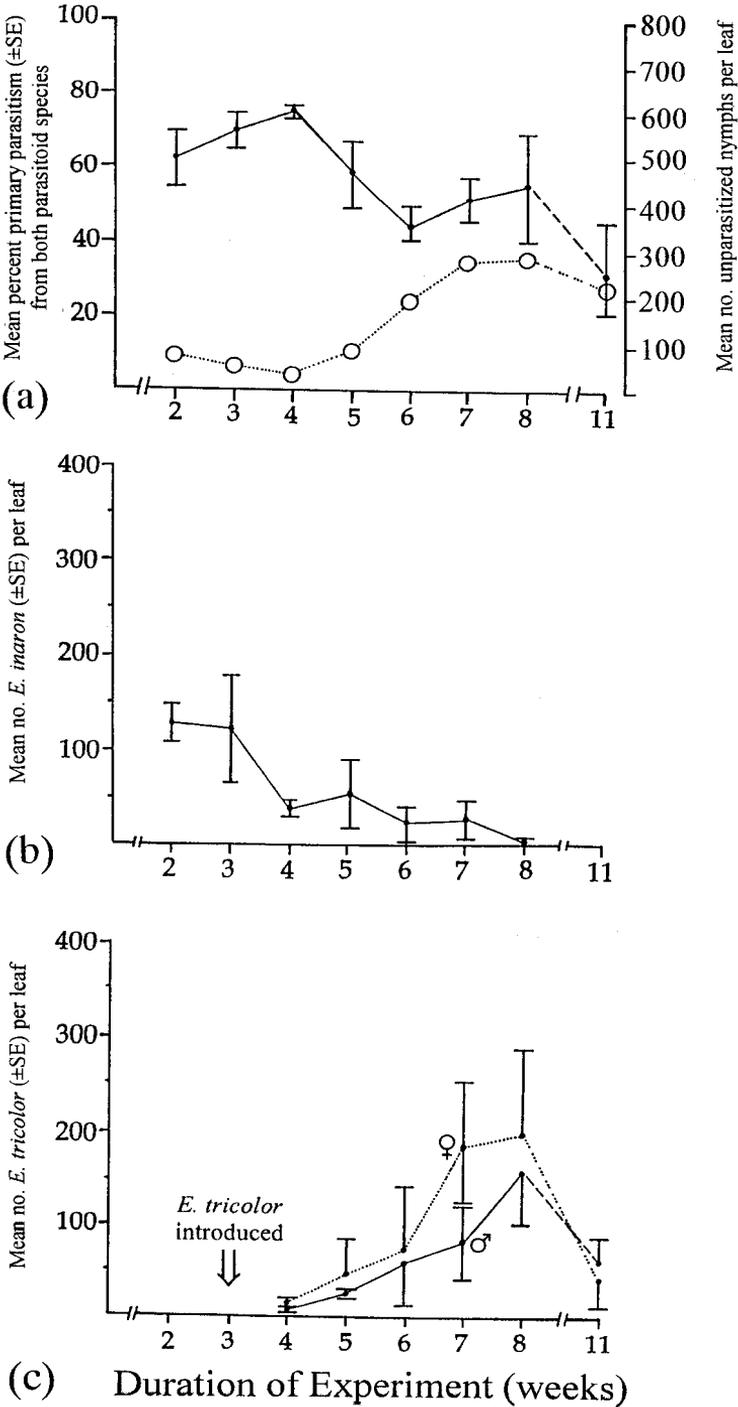
FIGURE 1.   Population dynamics of cage 1 given as: (a) the mean overall percent primary parasitism (●) and the mean number of unparasitized whitefly nymphs per leaf (○); (b) mean number of *E. inaron* adults emerging from leaf samples (both sexes); and (c) the mean number of each sex of *E. tricolor* emerging from leaf samples during the course of the experiment (each sex separately). For improved clarity only half the standard error (SE) bar is shown for some data points.
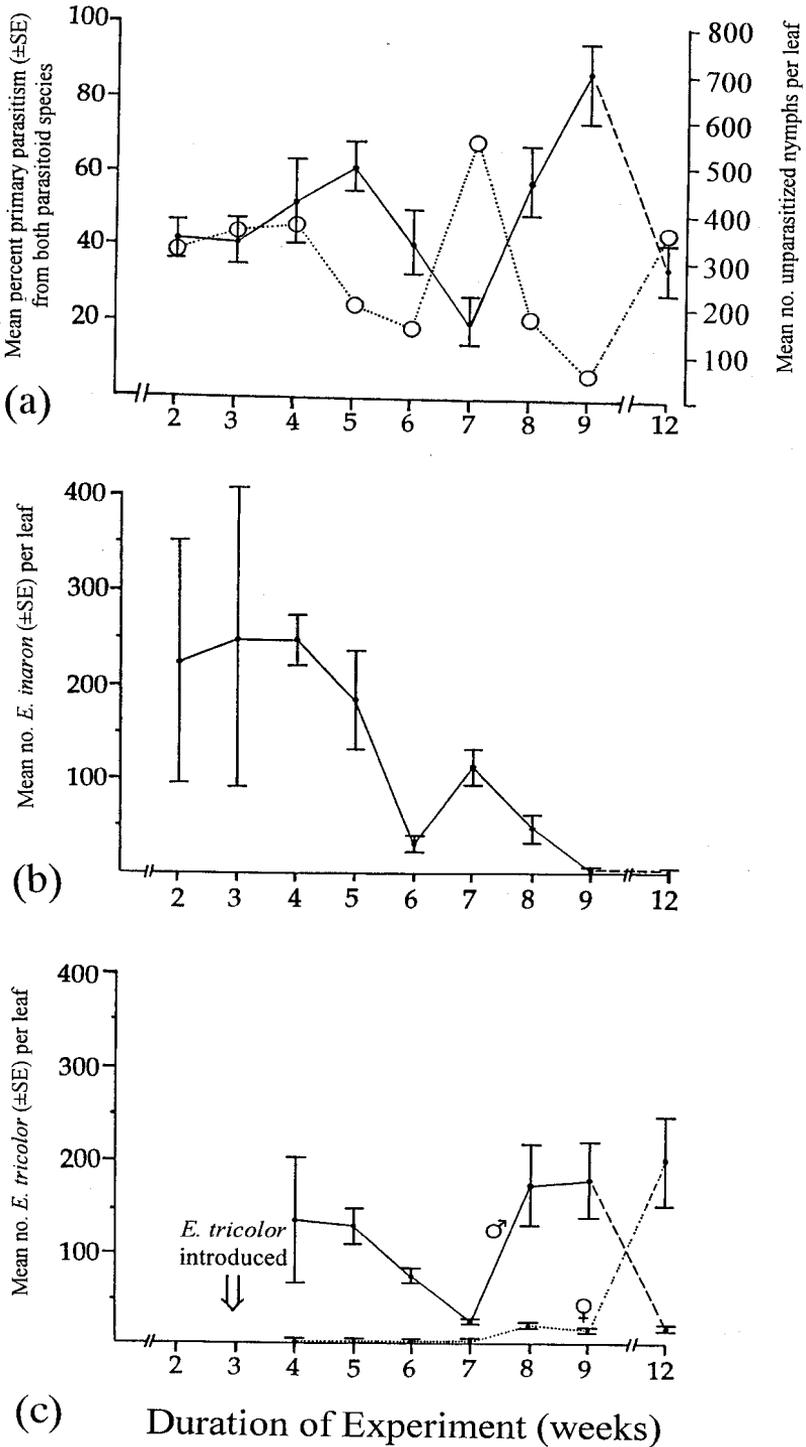
FIGURE 2.   Dynamics of cage 2 given as: (a) the mean overall percent primary parasitism (●) and the mean number of unparasitized whitefly nymphs per leaf (○); (b) mean number of *E. inaron* adults emerging from leaf samples (both sexes); and (c) the mean number of each sex of *E. tricolor* emerging from leaf samples during the course of the experiment (each sex separately). For improved clarity only half the standard error (SE) bar is shown for some data points.
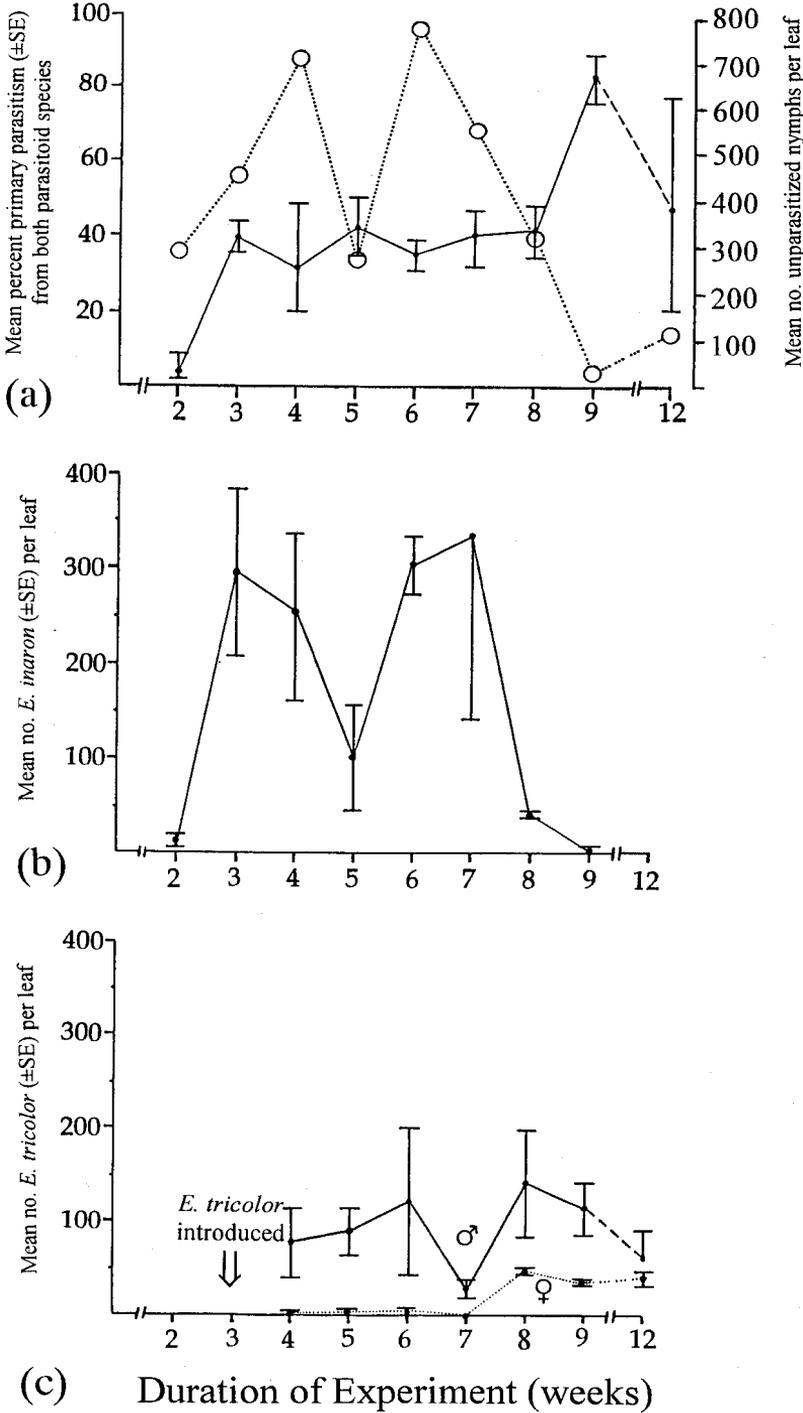
FIGURE 3.   Dynamics of cage 3 given as: (a) the mean overall percent primary parasitism (●) and the mean number of unparasitized whitefly nymphs per leaf (○); (b) mean number of *E. inaron* adults emerging from leaf samples (both sexes); and (c) the mean number of each sex of *E. tricolor* emerging from leaf samples during the course of the experiment (each sex separately). For improved clarity only half the standard error (SE) bar is shown for some data points.
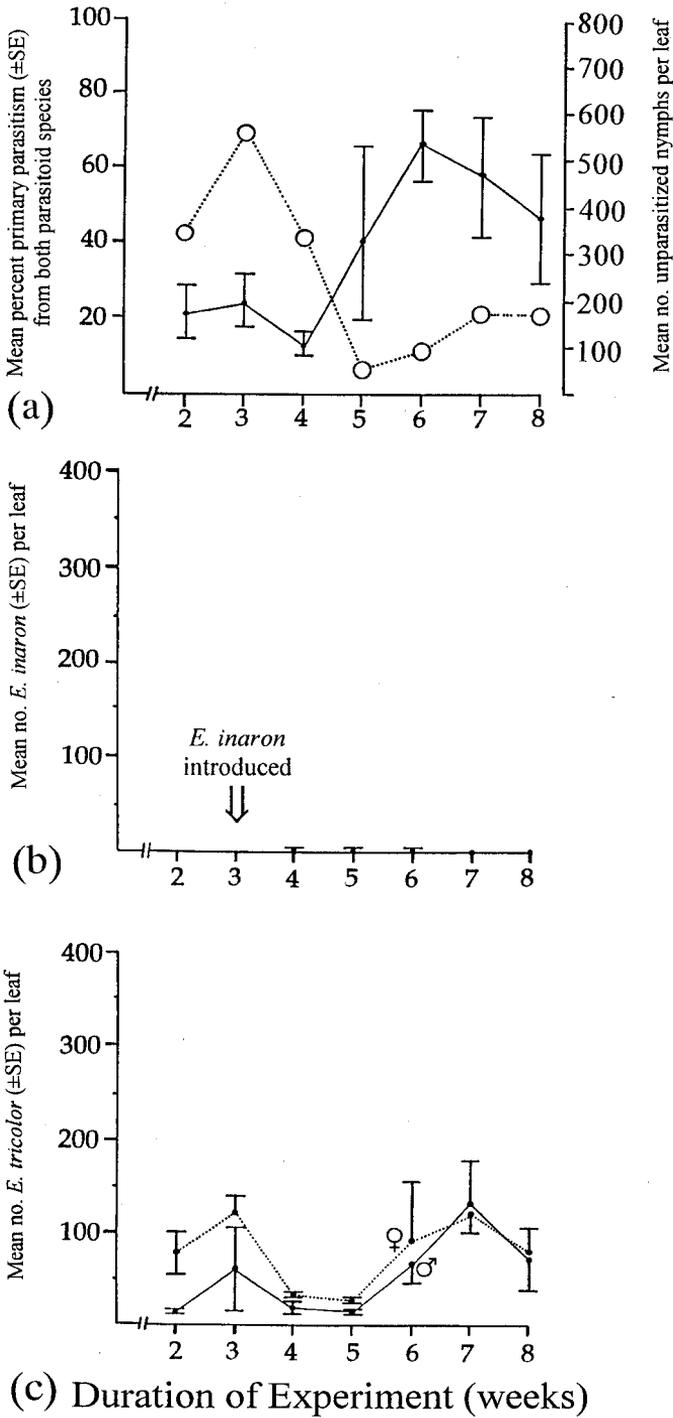
FIGURE 4.   Dynamics of reciprocal experiment where in *E. inaron* was introduced to an established population of
E. tricolor. (a) The mean overall percent primary parasitism (●) and the mean number of unparasitized
whitefly nymphs per leaf (○); (b) mean number of *E. inaron* adults emerging from leaf samples (both
sexes); and (c) the mean number of each sex of *E. tricolor* emerging from leaf samples during the course
of the experiment (each sex separately). For improved clarity only half the standard error (SE) bar is
shown for some data points.

that primary hosts were continually available in substantial numbers, judging from the low to moderate levels of overall parasitism of 14–65% (Figure 4(a) and 4(b)).

Literature Search

The results of the literature search are divided into two parts: references to parasitoid complexes in which the heteronomous hyperparasitoid was dominant (Table 1) or those in which the conventional primary parasitoid was dominant (Table 2). Each table is subdivided into 'natural' complexes and 'artificial' complexes which have arisen from introductions of species in programmes of classical biological control. Due to the variable quality of the literature over the period considered (1930 to present) there is doubt in some cases as to the true host relations of the heteronomous hyperparasitoid. The incidence of such cases is indicated with a footnote. Apparently similar complexes from different locations are listed only when clear differences in the host species or parasitoid species composition of the complex were described. Of the 59 examples where the necessary information was available, 46 came from natural communities and 13 arose from releases made for biological control. In natural communities, 32/46 (70%) of examples showed the heteronomous hyperparasitoid to be the dominant species. In the bio-control complexes, 5/16 examples were found in which a conventional parasitoid was dominant over a heteronomous hyperparasitoid.

DISCUSSION

The patterns of population growth and relative levels of primary and secondary parasitism observed were different in each cage. The method of sampling employed did not show the dynamics of invasion to be a consistent function of the availability of primary or secondary hosts, although some clear general features were apparent. In all cases, the heteronomous hyper-parasitoid successfully invaded established populations of the conventional parasitoid. The conventional parasitoid population declined to very low levels by the end of the sampling period. In the single replicate of the reciprocal experiment, the *E. tricolor* population appeared to be completely resistant to invasion by the conventional species. Given a replicate of one cage, there remains room for doubt regarding the robustness of this finding. The failure of *E. inaron* to invade the heteronomous hyperparasitoid population has marked implications in biocontrol programmes and requires confirmation.

The results of these experiments went beyond what was originally planned regarding the speed and efficacy of the displacement of *E. inaron* by *E. tricolor*. It was supposed that only the initial trajectory of an invading population would be apparent in such experiments, so the speed at which the displacement occurred was unexpected. Clearly, the very male-biased sex ratios observed in populations in cages 2 and 3 reflected the high incidence of hyperparasitism in these cages. Most of this hyperparasitism must have been directed toward *E. inaron*, resulting in the dramatic decline of this species.

It might have been possible to reduce the apparent differences among the cages by employing sampling techniques that accounted for plant age, and by standardizing the supply of primary hosts offered to all cages rather than the *ad lib* system of whitefly supply employed here. The experiment aimed to keep a roughly steady supply of primary hosts on which reproduction of both species could occur. In this respect, the percentage parasitism levels observed in leaf samples (which fluctuated between 20 and 80%) appeared to be reasonable. The number of unparasitized hosts/leaf varied considerably, but maximum and minimum values were maintained within one order of magnitude of each other. Such fluctuations may also be a reflection of the random sampling regimen.

The study did not address the trajectory of single-species populations of either parasitoid, although details of population growth and sex ratio fluctuations in a pure culture of *E. tricolor* have been published (Williams, 1995). In that study, the sex ratio of *E. tricolor* emerging from individual leaves was dependent on the length of time the insects had been exposed to parasitism. Avilla *et al.* (1991) reported that *E. tricolor* produced sex ratios that were more male biased

TABLE 1. Parasitoid complexes in which the heteronomous hyperparasitoid is dominant

Dominant heteronomous hyperparasitoid species	Primary host	Other parasitoid species present	Reference
NATURAL COMMUNITIES			
Coccobius debachi	*Aonidiella aurantii*	"Others in Burma"	Fisher, 1961
Coccobius flavus	*Lepidosaphes beckii*	*Encarsia citrinus* *Aphytis lepidosaphes*	Flanders, 1971
Coccobius testaceous	*Lepidosaphes ficus*	*Pteroptrix* sp. *Aphytis mytilaspidis* Two *Encarsia* spp.	Flanders, 1971
Coccobius testaceous	*Lepidosaphes ulmi*	*Aphytis mytilaspidis* Two *Encarsia* spp.	Flanders, 1971
Coccophagoides similus	*Diaspidiotus viticola* and *Targiona vitis*	*Azotus celsus*	Zinna, 1962
Coccophagus atratus	*Filippia gemina*	*Metaphycus* sp.	Donaldson *et al.,* 1986
Coccophagus basalis and *Coccophagus fallax*	*Saissetia oleae*	*Scutellista cyanea* *Lecaniobus utilis* *Euaphagus* sp. *Coccophagus cardei* Three *Coccophagus* spp.	Flanders *et al.,* 1961
Coccophagus gurneyi	*Pseudococcus gahani*	*Tetracnmemus pretiosus* *Tetracnnemus peregrinus* *Pseudophycus angelicus* *Chrysoplatycerus splendus* *Lepomastidea abnormis*	Bartlett & Lloyd, 1958
Coccophagus insidiator	*Gossyparia spuria*	*Trichomathus cyanifrons*	Flanders, 1952
Coccophagus rusti	*Sassetia oleae*	*Metaphycus hemilecanii*	Flanders, 1965
Coccophagus rusti	*Sassetia oleae*	*Scutellista cyanea*	Flanders, 1965
Encarsia aleurochitonis[a]	*Aleurochiton aceris*	*Encarsia margaritiventris* *Euderomphale secreta*	Huldén, 1986
Encarsia aspidioticola[b]	*Dynaspidiotus britannicus*	*Coccidencyrtus steinbergii* *Encarsia citrina* *Aphytis libanicus*	Battaglia & Viggiani, 1986
Encarsia asterobemisae	*Asterobemisia carpini*	*Encarsia longicornis* *Encarsia coryli*	Viggiani, 1981 Iaccarino & Viggiani, 1983
Encarsia clypealis[c]	*Aleurocanthus woglumi*	*Encarsia opulenta* *Amitus hesperidum* *Eretmocerus serius*	Flanders, 1969
Encarsia clypealis[d]	*Aleurocanthus woglumi*	*Encarsia merceti*	Flanders, 1969
Encarsia elongata	*Lepidosaphes gloverii*	*Encarsia citrinus*	Flanders, 1971
Encarsia lahorensis	*Dialeurodes citri*	"Many others"	Ortu & Prota, 1983
Encarsia lahorensis	*D. citri* and *Aleurocanthus spiniferus*	"Others"	Chen, 1985
Encarsia lutea	*Pseudaulacaspis pentagona*	Twenty other species including *Eretmocerus mundas* *Aphytis* sp. *Pteroptrix orientalis*	Viggiani, 1991
Encarsia lutea	*Bemisia tabaci*	*Eretmocerus mundus*	Gameel, 1969
Encarsia margaritventris	*Aleurotuba jelineki*	*Amitus aleurotubae* *Cales noaki* *Encarsia aleurotubae* *Encarsia tricolor* *Eretmocerus longicornis*	Laudonia & Viggiani, 1984
Encarsia meritoria[a]	*Bemisia tabaci*	*Encarsia formosa* *Encarsia* sp. *Eretmocerus haldemani*	Gerling. 1967
Encarsia moffsi[a]	*Pealius quercus*	*Encarsia borealis* *Eretmocerus zippanguiphagus* *Amitus longicornis*	Huldén, 1986

TABLE 1. *Continued*

Dominant heteronomous hyperparasitoid species	Primary host	Other parasitoid species present	Reference
Encarsia nigricephala	*Bemisia tabaci*	*Encarsia pergandiella* *Encarsia transvena* *Eretmocerus californicus*	McAuslane *et al.*, 1993
Encarsia pergandiella	*Aleyrodes spiraeoides*	*Encarsia coquilletti* *Encarsia meritoria* *Signiphora aleyrodis* *Eretmocerus haldemani* *Euderomphale flavimedia*	Oatman, 1970
Encarsia pergandiella	*Trialeurodes packardi*	*Encarsia quaintancei* *Eretmocerus corni*	Kuenzel, 1975
Encarsia quaintancei	*Trialeurodes abultilonea*	*Encarsia pergandiella* *Amitus aleurodinus* *Eretmocerus haldemani*	Dysart, 1966
Encarsia transvena	Various[e]	Species from six other genera	Viggiani, 1991
Encarsia transvena	*Bemisia tabaci*	*Eretmocerus mundus*	Kapadia & Puri, 1990
Encarsia tricolor	*Aleyrodes proletella*	*Encarsia lutea* *Trichaporus partenopeus*	Dansig, 1964
Encarsia sp. "G"	*Aonidiella citrina*	*Encarsia lounsburyi* *Aphytis* spp. *Comperiella bifasciata*	Flanders, 1971

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Coccobius seminotus	*Anlacaspis tegalensis*	*Adelencrytus miyarai* *Tetrasticlus* sp.	Williams, 1977
Coccophagoides fusiscipennis[a,f,]	*Melanaspis obscura*	*Ablerus clisiocampae* *Coccobius varicornis* *Encarsia berlesei*	Stoetzel & Davidson, 1971 Potter *et al.*, 1989
Coccophagus lycimnia	*Toumeyella pini*	*Coccophagus albicoxa* *Coccophagus* sp. Two *Metaphycus* spp. *Gahaniella saisettiae* *Microterys fuscicornis* *Cheiloneurus* sp.	Clarke *et al.*, 1989
Encarsia clypealis	*Aleurocanthus woglumi*	*Encarsia smithi* *Amitus hesperidum*	Flanders, 1969
Encarsia lingnanensis	*Unaspis citri*	*Encarsia* nr. *funicularis* *Encarsia citrinus* (?) *Encarsia* sp.	DeBach & Rosen, 1976
Encarsia lutea	*Bemisia tabaci*	*Eretmocerus mundus*	Gerling *et al.*, 1980
Encarsia meritoria	*Parabemisia myricae*	*Cales noacki* *Encarsia lutea*	Barbagallo *et al.*, 1992
Encarsia opulenta[g]	*Aleurocanthus woglumi*	*Eretmocerus serius*	Van Whervin, 1968
Encarsia opulenta[h]	*Aleurocanthus woglumi*	*Amitus hesperidum* *Encarsia clypealis* *Eretmocerus serius*	Summy *et al.*, 1983
Encarsia smithi	*Aleurocanthus spiniferus*	*Amitus hesperidum*	Peterson, 1955
Encarsia sublutea	*Bemisia tabaci*	*Eretmocerus mundus*	Gerling, 1985

[a]This species is probably a heteronomous hyperparasitoid.
[b]In the USA.
[c]In Poona and Madras, India.
[d]On lemon, near Assam, India.
[e]Suction trap samples—host spp. not given.
[f]May not be dominant in the presence of *E. aurantii* (see Table 2).
[g]In Jamaica.
[h]Dominant around Portici, rare elsewhere.

TABLE 2. Parasitoid complexes containing a heteronomous hyperparasitoid but in which a conventional parasitoid is dominant

Species of conventional parasitoid dominant	Primary host species	Other parasitoids in complex (*heteronomous hyperparasitoid)	Reference
Natural communities			
Amitus hesperidum	*Aleurocanthus spiniferus*	*Encarsia smithi**	Lin *et al.*, 1975
Anarhopus sydenyensis	*Pseudococcus adonium*	Six other species including *Coccophagus gurneyi**	Bartlett & Lloyd, 1958
Aphytis fusipennis	*Lepidosaphes gloverii*	*Encarsia elongata**	Flanders, 1971
Aphytis lepidosaphes	*Lepidosaphes beckii*	*Encarsia citrinus* *Coccobius fulvius** *Adelencyrtus* sp.	Flanders, 1971
Aphytis spp.	*Aonidiella messengeri*	*Encarsia lounsburyi* *Encarsia* sp. "G"* *Pteroptrix albocinctus*	Flanders, 1971
Blastothrix longipennis	*Lecanium tiliae*	*Coccophagus lycimnia** *Metaphycus kincaidi*	Rumin & Beirne, 1975
Cardiogaster hyalina	*Aleurocybotus* sp.	*Encarsia luteola**	Poinar, 1964
Chrysoplatycerus splendus	*Pseudococcus maritamus*	Five other species including *Coccophagus gurneyi**	Bartlett & Lloyd, 1958
Coccidencyrtus steinbergii	*Dynaspidiotus britannicus*	*Aphytis libanicus* *Encarsia citrina* *Encarsia aspidioticola**	Battaglia & Viggiani, 1968
Compereilla bifasciata	*Aonidiella citrina*	*Aphytis* spp. *Encarsia* sp. "G"* *Pteroptrix wanhsiensis* *Pteroptrix albocinctus*	Flanders, 1971
Encarsia inaron	*Aleyrodes proletella*	*Encarsia tricolor** *Euderomphale chelidonii*	Williams, 1989
Eretmocerus haldemani	*Trialeurodes abutilonea*	*Encarsia* sp. *Encarsia quaintancei** *Encarsia pergandiella**	Watve & Clower, 1976
Euderomphale chelidonii	*Aleyrodes lonicerae*	*Encarsia tricolor**	Williams, 1989
Euderomphale secreta	*Aleurochiton aceris*	*Encarsia margaritiventris** *Encarsia aleurochitonis**[a] *Amitus minervae*	Huldén, 1986
Biocontrol programmes			
Encarsia aurantii	*Melanaspis obscura*	*Coccophagoides fuscipennis**[a,b] *Coccobius varicornis**[b] *Ablerus clisiocampae*	Ehler, 1995
Eretmocerus haldemani	*Bemisia tabaci*	*Encarsia meritoria**[b] *Encarsia formosa* *Encarsia* sp.	Gerling, 1967
Eretmocerus serius	*Aleurocanthus woglumi*	*Encarsia divergens** *Encarsia smithi**	Clausen & Berry, 1932
Metaphycus bartletti	*Saissetia oleae*	Fourteen other spp. including *Coccophagus lycimnia** and *Coccophagus scutellaris**	Daane *et al.*, 1991
Metaphycus lounsburyi	*Saissetia oleae*	Fourteen other native and introduced spp. including *Coccophagus scutellaris**	Paraskakis *et al.*, 1980

[a]Dominant species elsewhere, see Table 1.
[b]This species probably a heteronomous hyperparasitoid.

when *E. formosa* was offered as a secondary host compared with sex ratios produced when conspecific pupae were available. Likewise, simple choice experiments indicated that *E. tricolor* hyperparasitized *E. inaron* much more than conspecific secondary hosts when both species were available in abundance (Williams, 1991). This could be an important refinement to consider in the production of population models which are required to predict the impact of the introduction

of a heteronomous hyperparasitoid in complexes containing conventional parasitoids. There is currently no quantitative evidence that the introduction of a heteronomous hyperparasitoid will offer an improved level of pest control in situations where a level of parasitism from conventional species already exists. The review of the literature gave further support to the notion that heteronomous hyperparasitoids have a high competitive ability; the heteronomous hyperparasitoid was the dominant species in the majority of natural parasitoid complexes considered. The data taken from biological control programmes should be viewed with caution due to the highly selective nature of the introductions.

Clear examples of invasion and displacement of conventional species by a heteronomous hyperparasitoid come from biocontrol release programmes. Parasitoid releases were made against the citrus blackfly, *Aleurocanthus woglumi* in Florida in 1976. The platygastrid *Amitus hesperidum* was released in greatest numbers and brought about a rapid decline in blackfly populations. The direct heteronomous hyperparasitoid, *E. opulenta* subsequently became dominant and displaced *A. hesperidum* throughout the original release area. An indirect heteronomous hyperparasitoid, *E. smithi* was also found established in Florida and was released at several locations. (Males of *E. smithi* are laid in primary hosts in anticipation of subsequent primary parasitism allowing the development of the hyperparasitic *E. smithi* male). In other parts of the state, releases of all three species were made in 1979 (Nguyen *et al.*, 1983). When *A. hesperidum* was released alone or together with *E. opulenta*, control of blackfly outbreaks was achieved in about 6 months. At one site, however, *E. smithi* was also released, and control was delayed by about 12 months. In this case, the *A. hesperidum* population initially peaked but then rapidly declined. *E. smithi* then became dominant briefly, but was quickly overtaken by *E. opulenta*, which remained the dominant species for the remainder of the study. It was reported that both sexes of *E. smithi* may develop as secondary parasitoids (hyperparasitoids) at the expense of *E. opulenta* (Thompson *et al.*, 1987). This observation requires confirmation, but may account for the adverse impact of *E. smithi* on the control programme. In another paper on the biocontrol of *A. woglumi*, Summy *et al.* (1983) described *E. opulenta* as the dominant parasitoid in the Lower Rio Grande Valley of Texas, having competitively displaced *E. clypealis* and reduced *A. hespiridum* populations to the point of several local extinctions. Fortunately, the elimination of competitors in this case did not appear to diminish the degree of blackfly control.

Gerling (1983) reported a negative correlation between the incidence of superparasitism by *E. transvena* (mainly) and the incidence of parasitism by an *Eretmocerus* species (*Eretmocerus* nr. *handemani*) attacking *Trialeurodes vaporariorum* in Hawaii. The reasons behind such levels of superparasitism are not clear, although such observations are consistent with patterns of parasitism switching from mainly primary parasitism at low densities of secondary (male) hosts to increasing levels of hyperparasitism as more male hosts become available in the form of *Eretmocerus* larvae/pupae. The theoretical background to heteronomous hyperparasitoid host selection and sex allocation has been described by Godfray and Waage (1991). Their views have been questioned (Walter & Donaldson, 1994), but good empirical evidence in support of their theory now exists for the heteronomous hyperparasitoid, *E. tricolor* (Hunter & Godfray, 1995).

Hassell *et al.* (1983) found the effect of the unusual reproductive biology of heteronomous hyperparasitoids to be highly stabilizing to host–parasitoid population dynamics. They also considered the dynamics of a host–heteronomous hyperparasitoid–hyperparasitoid three-species system. The key question which the present study highlights concerns the persistence of conventional parasitoids in a host–parasitoid–heteronomous hyperparasitoid system. Until a clear theoretical background to multiple introductions has been established and tested, a high degree of caution is necessary when parasitoids with hyperparasitic male host relations are considered as agents of control. Classical biocontrol programmes tend to focus on species that are dominant in the native habitat, and this may often be a heteronomous hyperparasitoid. However, this may not be the most effective species for host population suppression. Once a heteronomous hyperparasitoid has been introduced, the preliminary observations of this study indicate that further introductions of conventional species may not be possible, and that the level

of parasitism by existing conventional parasitoids may suffer a reduction due to the hyper-parasitic habit of the male.

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