

Host selection and sex ratio in a heteronomous hyperparasitoid

TREVOR WILLIAMS Department of Biology, Imperial College,
Silwood Park, Ascot, Berks.

Abstract. 1. *Encarsia tricolor* Förster is a heteronomous hyperparasitoid: females develop as primary endoparasitoids of Homoptera, whereas males develop hyperparasitically in primary endoparasitoids, including conspecific females.

2. When offered pupae of *Encarsia inaron* (Walker) or conspecific pupae, *E. tricolor* showed a distinct preference to exploit *E. inaron* for male production.

3. Parasitoids were given the opportunity to gain different types of ovipositional experience on male and female hosts and were then offered patches containing mixtures of male and female hosts in various ratios. The mean sex ratio which they laid was not dependent on the relative availability of each type of host, whereas prior ovipositional experience had a significant effect.

4. Adaptive reasons for the observed oviposition strategies are suggested.

Key words. Oviposition strategies, sex ratio, host selection, *Encarsia tricolor*, heteronomous hyperparasitoid, cabbage whitefly.

Introduction

The ovipositional strategies of parasitoid wasps are fundamental in determining the reproductive success of individuals adopting this particular lifestyle. As such, the decisions made by ovipositing parasitoids have almost certainly been subject to rigorous selective pressures.

Having encountered a patch of hosts, the female parasitoid must decide the host species, size or stage of host to attack as well as the number of eggs and sex ratio to lay in each host. The factors which may affect her decisions are of both proximate and ultimate nature. Ultimate (evolutionary) factors relate to optimal solutions in cost/benefits tradeoffs: what is the best strategy to adopt in order to maximize fitness (van

Alphen & Janssen, 1982; Parker & Courtney, 1984; Iwasa *et al.*, 1984; Charnov & Skinner, 1984, 1985; Bakker *et al.*, 1985; Godfray, 1987; Janssen, 1989). Proximate, or immediate factors concern physiological and environmental cues, such as host suitability (physiology, nutrition, size, immunity, etc.), the number of mature eggs a female wasp has to lay, whether or not she has mated, etc. (review by Vinson & Iwantsch, 1980).

Heteronomous hyperparasitoids provide a unique opportunity to test theories of host selection and sex ratio. Heteronomous hyperparasitoids are a remarkable group of solitary aphelinid parasitoids, in which the sexes develop in different hosts. Females always develop as primary endoparasitoids of Homoptera, such as whitefly and scale insects. Males, however, always develop hyperparasitically at the expense of conspecific females (or other species of primary homopteran endoparasitoids). Thus, in heteronomous hyperparasitoids, host species selec-

Correspondence: Dr Trevor Williams, Institute of Virology and Environmental Microbiology, Mansfield Road, Oxford OX1 3SR.

tion is irrevocably linked with the sex of the offspring. Indeed, the ability of heteronomous hyperparasitoids to discriminate between parasitized and unparasitized hosts and lay eggs of the appropriate sex in each type of host, is what determines the classification of this group of parasitoids (Walter, 1983). Once inseminated, a female heteronomous hyperparasitoid, like many other arrhenotokous Hymenoptera, has the ability to lay both male and female eggs by selective fertilization of ova: haploid eggs develop as males and diploid eggs as females (Walter, 1983; Viggiani, 1984).

A number of authors have suggested that heteronomous hyperparasitoids may have relaxed control over their sex ratios and simply lay eggs of each sex according to the availability of parasitized and unparasitized hosts (Flanders, 1939, 1942, 1956, 1967; Zinna, 1961, 1962; Williams, 1977; Hassell *et al.*, 1983; Viggiani, 1984). Such a strategy would clearly result in sex ratios which mirrored the relative abundance of each host type at a particular moment. Heteronomous hyperparasitoid sex ratios which reflect host abundance and which appear to change over time have indeed recorded by Kuenzel (1975) and Donaldson (1985).

Most recently, Godfray & Waage (1991) have presented an argument to explain the reasons why this kind of sex ratio pattern could have evolved as a result of natural selection. Their ideas can be summarized as follows. For most parasitoid species in the field, the time spent searching for hosts will generally be large compared to the time spent ovipositing into victims. If a wasp's reproduction is limited not by the ability to produce eggs, but rather by the ability to locate hosts, it would clearly be maladaptive for the wasps to reject any host discovered providing that such parasitism did not hinder future oviposition opportunities. Thus, when hosts are scarce, the heteronomous hyperparasitoid should lay an egg in each and every host discovered, irrespective of the sex of egg laid (type of host discovered). At the population level, Godfray & Waage predicted that this behaviour would lead to sex ratios reflecting the relative frequencies of the two host types available in the environment.

When hosts are abundant, however, a parasitoid's reproduction is more likely to be limited by her rate of egg production. In such a situation, Godfray & Waage suggested that Fisher's

(1930) rule should apply and the primary sex ratio should show no bias (assuming that the movement and mating of the population is not restricted in space or time and that the cost of producing each sex is equal).

In the case of heteronomous hyperparasitoids, it is also necessary to assume that a female never hyperparasitizes her own daughters, i.e. males never develop hyperparasitically on their female siblings. Colgan & Taylor (1981) considered the effect of males developing at the expense of their sisters. When this became more frequent, male production became increasingly costly and they predicted a sex ratio shift in favour of females. When hyperparasitism of siblings was very rare, however, the predicted sex ratio was dependent only on the relative costs of laying male and female eggs.

Data presented in this paper show ovipositional preferences in the heteronomous hyperparasitoid (facultative autoparasitoid *sensu* Walter, 1983), *Encarsia tricolor* Förster. Both sexes of *E. tricolor* are polyphagous. Females have been recorded as primary endoparasitoids of five species of whiteflies. Males have been shown to be capable of hyperparasitic development on six aphelinid species and one eulophid (Vet & van Lenteren, 1981; Viggiani, 1984; Avila & Copland, 1987; Williams, 1989).

Strategies of oviposition in *E. tricolor* were tested in two experiments. First, the ability of *E. tricolor* to discriminate between *Encarsia inaron* (Walker) pupae and conspecific pupae for hyperparasitism was investigated. This indicated the extent to which preferences for conspecific, or alternative male hosts, could contribute to unequal costs of male and female production, as considered in the model of Colgan & Taylor (1981). *Encarsia inaron* is a native British species and is a normal, bisexual parasitoid in which both sexes develop as primary endoparasitoids of whitefly.

Second, the effect of egg-limitation on sex ratio was investigated given different ratios of male and female hosts. In this situation, Godfray & Waage (1991) predicted equal investment should be allocated to each sex, i.e. sex ratio should not be sensitive to the ratio of male and female hosts offered. *E. tricolor* females were either naive, or had been given prior oviposition experience. The results of the host selection experiment earlier, indicated that host species should also be included as a factor.

Methods

(i) *General*. Throughout this study the Cabbage Whitefly, *Aleyrodes proletella* (Linnaeus) was used as the primary host. Whitefly and parasitoids were cultured in muslin-walled cages at $25 \pm 1^\circ\text{C}$, 16:8 h L:D. The host plant was brussels sprouts var. Winter Harvest. These plants were grown in peat based composed and used when 20–30 cm tall and bearing approximately ten leaves. Both the parasitoid and whitefly cultures were regularly supplemented with field-collected material for the duration of the study.

Clip cages were used to confine parasitoids to a leaf area containing known numbers of parasitized and/or unparasitized hosts. The clip cages were constructed of one half of a Petri dish 35 mm diameter, 5 mm deep, sealed to the leaf by foam draught excluder around the lip of the dish and held in place on the leaf by an elastic band.

All experiments were conducted at 25°C , 16:8 h L:D photoperiod, unless otherwise stated. All sex ratios are quoted as percent male.

(ii) *Host selection experiment*. To generate areas on leaves containing various ratios of pupae of both species of parasitoids, between one and four mated females of both *E.inaron* and *E.tricolor* were offered a patch of third and fourth instar whitefly simultaneously for 24 h. Both sexes of *E.inaron* develop as primary endoparasitoids. Parasitized scales were allowed to develop until the early pupal stage (approximately 10 days), whereupon the leaf was cleared of all unparasitized whitefly nymphs.

Female *E.tricolor* destined for use in experiments emerged individually in gelatin capsules and were always less than 24 h old when initially chosen. An active male was introduced into the capsule and observed to mate the female. Females were then 'experienced' for 24 h by exposure to *E.tricolor* female pupae. After this period of ovipositional experience, individual female *E.tricolor* were transferred to the leaf patch containing whitefly scales parasitized by either *E.tricolor* female larvae or *E.inaron* larvae, which had been generated 10 days previously. Each female *E.tricolor* was confined within this patch using a clip cage for 24 h. During this period she had the choice of laying male eggs in either species of *Encarsia*.

After the experimental period, pupae were transferred individually to gelatin capsules. Hyperparasitic male *E.tricolor* were allowed to develop for 2–3 days, whereupon all scales were dissected to identify the primary parasitoid species and to detect the presence of young male larvae. Those scales which could not be dissected within 3 days were held at $10 \pm 1^\circ\text{C}$ to prevent male larvae destroying the features of the primary parasitoids necessary for identification. The features used to identify the two species were: (1) pigmentation of the abdomen dorso-anteriorly and the thorax dorsally; (2) antennal morphology; (3) sex (*E.inaron* laid both sexes as primary endoparasitoids).

These dissection data gave the ratio of *E.tricolor*:*E.inaron* offered in each replicate and provided information on the decisions made by *E.tricolor* during hyperparasitic oviposition. Data regarding the frequency of encapsulation of eggs was also recorded. There were fifteen successful replicates.

(iii) *Sex ratio experiments*. Leaf areas containing a mixture of parasitized and unparasitized hosts were generated by exposing whitefly-infested leaves to *E.tricolor* females for 24 h after which all the parasitoids were removed. The leaves were left for approximately 10 days, whereupon unwanted whitefly nymphs were removed leaving only a known ratio of parasitoid pupae and unparasitized third and fourth instar whitefly. Each area contained an abundance of parasitized and unparasitized hosts, in various ratios from 12% to 80% parasitized. All the parasitized hosts contained young female *E.tricolor* pupae, laid approximately 10 days previously. The total number of hosts per arena ranged from 25 to 375 (mean [\pm SE] = 99.68 ± 5.96). This was a large number of hosts to offer *E.tricolor* which had a mean fecundity of 7.3 ± 0.3 (\pm SE) eggs per day at 25°C (Williams, 1989).

Individual female *E.tricolor* were given four types of ovipositional experience. In each case, individual females were confined with a young male for 24 h in a standard clip cage. The prior ovipositional experiences offered were: (1) none (access to honey only); (2) female *E.tricolor* pupae; (3) unparasitized late instar whitefly nymphs; (4) *E.inaron* pupae.

After this, both male and female were transferred to the experimental leaf patch and confined using a standard clip cage. Thus, the

female could decide which hosts to attack in the light of her previous experience and given the availability of each host type within the patch offered. After 24 h the adults were removed and the parasitoid pupae placed individually in gelatin capsules. The capsules were checked daily, and parasitoids sexed upon emergence. Those scales which did not emerge were dissected to discover the fate of their contents. Where such dissections gave uncertain results, the data were not included in the analysis. Females which laid only males may not have been successfully inseminated despite having been observed to copulate. Completely male replicates were therefore not included in the analysis.

For those females experienced with *E.inaron* pupae (number 4 above), the same species was offered during the experimental period, i.e. a choice of *E.inaron* pupae or unparasitized whitefly nymphs.

(iv) *Statistical analysis.* Sex ratio data were analysed by fitting a series of generalized linear models, using a GLIM program (Royal Statistical Society, 1985). GLIM fits a model to a response, or 'y' variable in terms of variation in certain explanatory variables specified by the investigator. Data values are compared with model predictions and the point of maximum likelihood determined by adjustment of model parameters. The method of analysis is similar whether the data are of a continuous or discrete nature. Normal, Poisson or binomial error structures can be specified, without the need for prior transformation of data. After fitting an initial null model to give a measure of total variation in the data, the effect of different explanatory variables (parameters) on the deviance between model and data values is assessed by constructing models of increasing complexity. The significance of any reduction in deviance can be calculated by construction of the appropriate F table using GLIM generated values. The results (r) of binomially distributed data are given as a logit function of a linear model (x). Transformation back to the natural state is achieved using the equation:

$$r = \frac{1}{(1 + e^{-x})}$$

For the analysis of the sex ratio data, binomial errors were specified with the y -variable being the number of males laid in each replicate. For

the analysis of egg number, Poisson errors were specified with the y -variate being the total number of hosts parasitized in each replicate. The significance of GLIM answers from binomially distributed data are approximately assessed using Chi-squared statistics with the number of degrees of freedom taken as the overall reduction in degrees of freedom caused by fitting the model specified.

Results

(i) *Host selection.* *E.inaron* pupae suffered over 5 times more hyperparasitism than did conspecific *E.tricolor* pupae (Table 1). The result was highly significant (chi-squared = 30.8, d.f. = 1, $P < 0.005$) and varied little among the fifteen replicates. A total of ten pupae were hyperparasitized but could not be positively identified. Both sexes of *E.inaron* suffered equally from *E.tricolor* attack.

Although more *E.inaron* than *E.tricolor* were offered overall in this experiment, GLIM analysis revealed that the proportion of each species offered as hosts did not affect the degree of hyperparasitism suffered by either species (chi-squared = 0.02, d.f. = 1, N.S.). When the species effect was added, however, model deviance fell from 103.4 to 55.7 (chi-squared = 47.7, d.f. = 1, $P < 0.001$), confirming that *E.tricolor* could distinguish the two host species.

Clearly it was not possible to measure males emerging in this experiment as they were all dissected early in their development. Previous work, however, had shown that male *E.tricolor* which had been laid hyperparasitically in *E.inaron* were not significantly larger than those laid as hyperparasitoids of conspecific females. The mean (\pm SE) width of the head capsule was 0.215 ± 0.007 mm ($n = 39$) for those males from *E.inaron* hosts, and 0.207 ± 0.003 mm ($n = 58$) for males who developed at the expense of *E.tricolor* females ($t = 1.40$, N.S.) (Williams, 1989).

(ii) *Sex ratio.* Parasitoids with no experience and those with experience of laying males in conspecific pupae, laid a mean sex ratio that was not significantly different from 1:1 (Fig. 1 and Table 2). Parasitoids experienced by laying females in healthy whitefly produced a mean sex ratio not significantly different from the above two treatments, but which was signifi-

Table 1. Species discrimination by *E.tricolor* when offered patches containing varying ratios of conspecific female pupae and *E.inaron* pupae as hosts for the hyperparasitic *E.tricolor* males.

	Species of host	
	<i>E.tricolor</i>	<i>E.inaron</i>
Total number of pupae offered	137	213
Total number of male larvae laid	10	82
Percentage of each species attacked	7.2	38.5

Chi-squared = 30.8, d.f. = 1, $P < 0.005$.

cantly female biased (chi-squared = 21.4, d.f. = 1, $P < 0.001$). The *E.inaron*-experienced females which were re-offered *E.inaron* in treatment 4, laid a mean sex ratio which was significantly male biased (chi-squared = 65.0, d.f. = 1, $P < 0.001$) and which was also significantly different from any other treatment.

Wasps with experience of unparasitized whitefly laid significantly more eggs per replicate, on average, than inexperienced wasps or those with experience of conspecific pupae (Fig. 2). This is most likely due to the host feeding opportunities implicit in treatment 3. The number of hosts available in each replicate

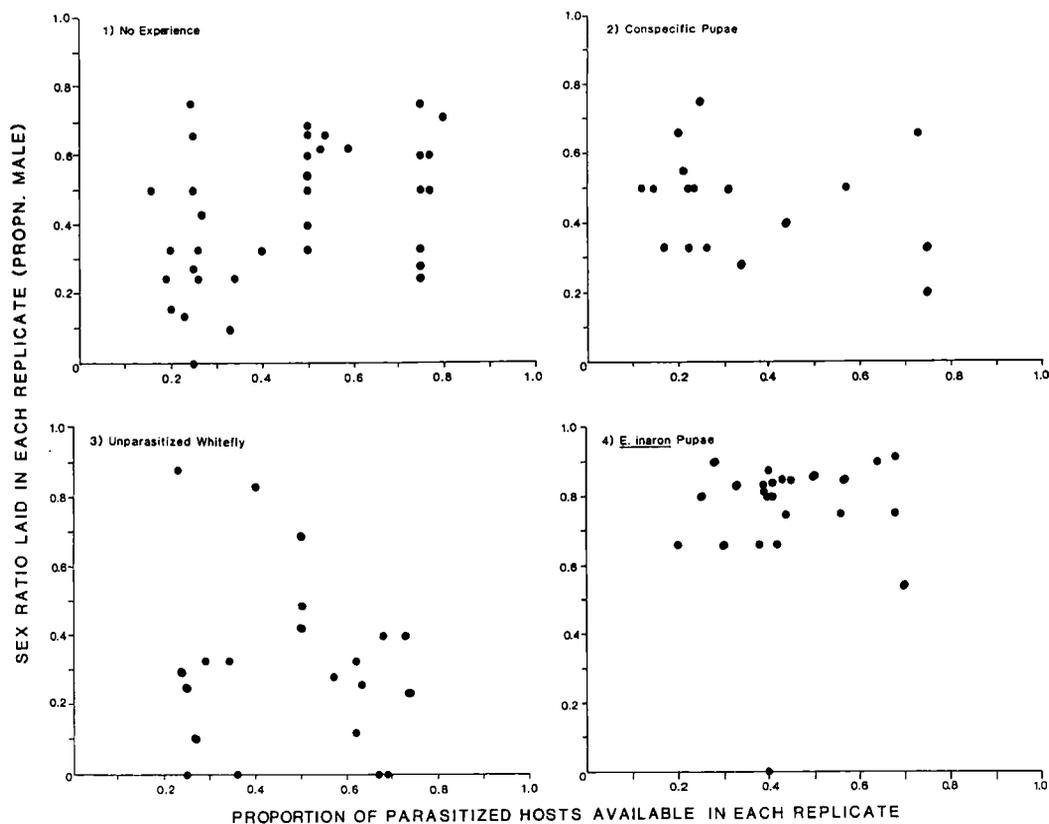


Fig. 1. Per cent egg hatch of *O.brumata* (■---■) and bud burst of Sitka spruce (●—●) in southern Scotland, 1986–90.

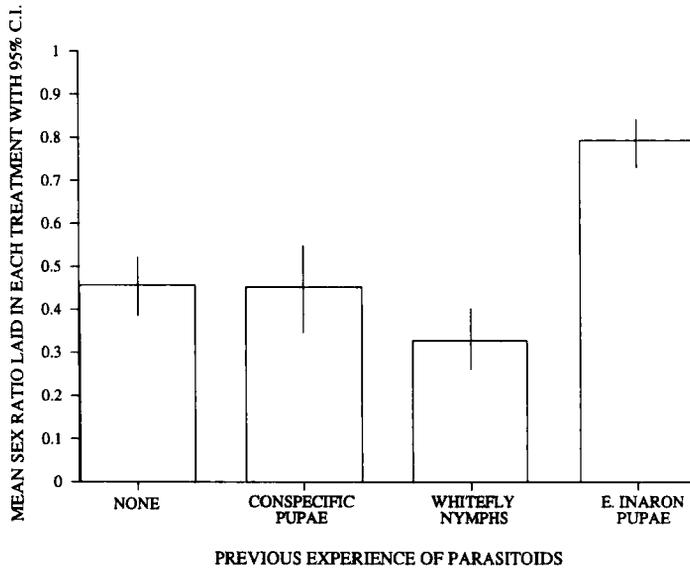


Fig. 2. The effect of prior ovipositional experience on the mean number of male and female eggs laid by *E. tricolor* (with 95% C.I.) when offered an abundance of hosts for both sexes.

had no detectable effect on the number of eggs in any treatment (chi-squared = 0.5, d.f. = 1, N.S.).

The ratio of parasitized to unparasitized hosts did not explain a significant amount of the variation in the data (GLIM model deviance) in any of the four treatments. The total number of hosts present in each experimental arena, the number of parasitized or unparasitized hosts available, or the number of eggs laid in each replicate did not significantly reduce model deviance either singly, together, or in any combination.

However, experience had a marked effect on

explaining variation in the data. When the effect of different treatments was fitted, model deviance fell from 198.22 to 104.82. This change of 93.40 was highly significant (chi-squared = 93.4, d.f. = 3, $P < 0.001$).

Dissection data from the host selection and sex ratio experiments gave information regarding the frequency of male egg encapsulation in *E. tricolor* and *E. inaron* pupae. Dissection of whitefly nymphs in earlier experiments gave the frequency of encapsulation of female eggs (Table 3). As the frequency of encapsulation was consistently low in all hosts, data were not adjusted to compensate. Mechanical damage

Table 2. The effect of different types of ovipositional experience on the mean sex ratio laid by individual *E. tricolor* females when offered large patches of parasitized and unparasitized hosts for male and female production respectively.

Parasitoid experience	No. replicates	Total no. males laid	Total no. females laid	Mean sex ratio (% male)	Range of ± 1 SE
1. No experience	37	101	120	45.6	42.4–49.0
2. Conspecific pupae	17	47	57	45.2	39.4–51.5
3. Unparasitized whitefly	21	59	121	32.8*	28.4–37.5
4. <i>E. inaron</i> pupae	24	150	39	79.4*	75.4–82.8

* Sex ratios significantly different from 0.5 (see text).

Table 3. Frequency of encapsulation of male and female *E. tricolor* eggs in parasitized and unparasitized hosts respectively.

Type of host	No. dissected	No. eggs encapsulated
Third and fourth instar whitefly (female eggs)	40	1
<i>Encarsia tricolor</i> pupae (male eggs)	46	1
<i>Encarsia inaron</i> pupae (male eggs)	82	1*

* Two dead male larvae were also encapsulated.

during manipulation of parasitized scales was more common, but was easily identified.

Discussion

(i) Host selection

E. tricolor females showed a marked preference for hyperparasitism of *E. inaron* over *E. tricolor* female pupae. By avoiding hyperparasitism of conspecifics, a female *E. tricolor* ensures that:

1. A greater number of *E. tricolor* females will emerge from any one patch. This could enhance the frequency of mating opportunities for her sons locally, i.e. mating opportunities for sons prior to their dispersal.

2. She is not exploiting her own progeny for male production. If males are laid in another species, they cannot, by definition, develop at the expense of their sisters.

The latter point has particular relevance to the Colgan & Taylor (1981) model in that it suggests that hyperparasitism of conspecifics (and therefore possibly of relatives) will be low in the presence of other suitable species. Male *E. tricolor* larvae were fully able to exploit conspecific female larvae when the females were still very young: 2–3 days old at 25°C, although exploitation of younger instars prolonged male development time (Williams, 1989). Thus, hyperparasitism of siblings could be a real possibility for these wasps.

E. tricolor males which emerged from *E. inaron* hosts were not significantly larger than when they developed in conspecific females. Avilla & Copland (1987), however, found that *E. tricolor* males laid in *E. formosa* pupae were significantly larger than when they developed at the expense of conspecific female pupae. Pre-

ferential exploitation of *E. formosa* could thus have benefits in terms of the fitness of sons (mating ability, sperm production and longevity) as well as the two advantages mentioned above.

The work of two other groups lend support to these findings. Dowell *et al.* (1981) reported that *Encarsia opulenta* showed a significant preference for citrus blackfly (*Aleurocanthus woglumi*) parasitized by the platygastid, *Amitus hesperidium* when offered mixtures of primary and secondary hosts. Data taken from their paper show the overall sex ratio laid changed from 25.8% male in the presence of conspecific hosts, to 43.1% when *A. hesperidium* was the only species available for male production. Gerling *et al.* (1987) stated that *Encarsia lutea* was incapable of interspecific host discrimination although they present data which show that *E. lutea* laid more eggs in *Bemisia tabaci* parasitized by *Eretmocerus mundus* (35.8% of which were hyperparasitized) than in nymphs previously parasitized by conspecifics (19.4% of which were hyperparasitized).

(ii) Sex ratio

The sex ratio experiments were designed to test the Godfray & Waage (1991) hypothesis that when egg production limits heteronomous hyperparasitoid reproduction, wasps should obey Fisher's rule and invest in the sexes equally. Thus, offering numerous male and female hosts in a spectrum of ratios should not affect the sex ratio produced. The unbiased sex ratios produced by naive wasps and those with experience of conspecific hyperparasitism support this idea. This is not the complete story, however. Clearly, experience can alter the sex

ratio strategies in this parasitoid. Why did the other two treatments yield distinctly biased sex ratios?

First, consider the effect of experience with unparasitized whitefly hosts. This had two effects; an increase in egg production due to host feeding opportunities, and the production of a female biased sex ratio. Why should a female, having already encountered and laid eggs in a patch of unparasitized hosts, continue to lay a high proportion of female eggs in a patch offering opportunities to lay both sexes to a greater or lesser extent? This appears maladaptive from an immediate standpoint.

It may be, however, that in natural populations early female conditioning is important in governing future female oviposition. A female may use the absence of local parasitism as a cue to the presence of a low density of conspecific females in the population, and an even greater scarcity of males. Under such a scenario, female offspring would almost be certainly be mating locally with other members of the natal patch. It would be very unlikely that immigrant males would arrive to exploit the mating opportunities within the patch. A female heteronomous hyperparasitoid would therefore be quite safe in the assumption that her own sons would be major beneficiaries of the female biased sex ratio. By favouring production of females (and sufficient males to mate them) the results of treatment 3 (exposure to whitefly nymphs) could be seen as an adaptation by the female optimizing her lifetime reproductive success: a response to probable local mate competition among her sons (Hamilton, 1967).

Next consider the male biased sex ratio laid when *E.inaron* pupae were offered both prior to the experiment, and within the experimental arena. No *E.tricolor* pupae were available in this experiment, so unlike the species discrimination experiment, the female was not making a choice of which hosts to exploit for male production, but a more fundamental choice of what sex ratio to lay in that patch. It is therefore necessary to explain the adaptive reasons for producing a male biased sex ratio in such a situation. The sex ratio laid in treatment 4 (*E.inaron* experienced) was very different from that of treatment 2 (conspecific experienced). Thus the changes in behaviour must be due to the presence of the competing parasitoid species, rather than purely the response of a

female to experience of parasitized hosts. The marked preference for hyperparasitism of *E.inaron* by *E.tricolor* indicates that there may be strong selective pressures *not* to attack conspecific larvae if non-conspecifics are available. In treatment 4, the advantage to an individual parasitoid comes only from certain avoidance of hyperparasitism of her own daughters. This may be enough to produce the sex ratio shift observed.

This experiment has demonstrated that heteronomous hyperparasitoids do not allocate sex in direct proportion to host availability when they are egg rather than host limited. To test the effects of host limitation it would be necessary to vary the relative proportions of host types *and* their absolute abundance; in the range of typical aphelinid fecundities, i.e. one to twenty hosts per patch. Treatments 1 and 2 lend support to the Godfray & Waage (1991) argument that, given an abundance of hosts and equal reproductive success of the sexes, no bias should be observed in the overall sex ratios. The deviation from equal sex ratios detected in the other two treatments indicates that the factors determining sex allocation decisions in these wasps have yet to be fully explained.

Differences in experimental design and hypothesis-testing means that work published previously cannot be readily compared with the present study. When offered different ratios of conspecific pupae and unparasitized hosts, Hunter (1989) found that inexperienced *Encarsia pergandiella* consistently laid more males than would be predicted by relative host availability. A total of forty hosts were presented in ratios of 25%, 50% and 75% parasitized. The preference for laying a greater proportion of male eggs was significant for all but the 75% treatment. Hunter offered some proximate reasons for this consistent bias.

Donaldson (1985) offered fixed ratios of unparasitized and parasitized (conspecific) hosts at intervals through the life of the heteronomous hyperparasitoid *Coccophagus atratus*. Fifty hosts were presented, a constant proportion of which were parasitized. When the proportion of parasitized hosts was 30%, the mean sex ratio (\pm SE) was $33.1 \pm 3.5\%$. When the proportion of parasitized hosts was 50%, the mean sex ratio was $72.0 \pm 2.4\%$ (figures estimated from graph). Sex ratios were highly variable and did not change significantly over the period of

the experiment (approximately 13 days). Donaldson interpreted these results as 'random' sex ratios with no element of female choice: male and female hosts were parasitized as they were encountered during random searching by *Coccophagus*. Such total relaxation of sex ratio control could only occur if it did not result in the reduction of parasitoid fitness. For example, if both sexes always enjoyed similar reproductive success irrespective of the population sex ratio (unlikely), or if the cost of controlling progeny sex ratio (searching for male and female hosts in the desired proportions) was particularly high, e.g. if hosts were generally rare – which is the Godfray & Waage hypothesis again.

The variation in *E.tricolor* sex ratios were consistent with random production of the sexes, which obeys a binomial frequency distribution. There was no evidence of precise sex ratios in *E.tricolor*. This contrasts with the situation in several gregarious parasitoids which seem to employ clear mechanisms to ensure less than binomial variation in brood sex ratios (Green *et al.*, 1982; Waage, 1982; Waage & Ng, 1984; van Diken & Waage, 1987).

Sampling of whitefly populations from crop and native plants in the grounds of Silwood Park (Ascot, Berks., U.K.) over 3 years revealed that the spatial distribution of parasitism by *E.tricolor* and *E.inaron* in the field was always highly contagious (Williams, 1989). It seems very likely, therefore, that searching females accumulate experience of different patches throughout their lives. The extent to which females respond by changing their ovipositional strategies has only been touched on here, but reveals that knowledge of conspecific and non-conspecific parasitism can indeed affect egg-laying decisions made by this heteronomous hyperparasitoid.

Finally, the data presented here show that *E.tricolor* oviposition strategies broadly agree with one aspect of the model described by Godfray & Waage (1991) who identified egg and host limitation as crucial factors in determining the sex ratio of heteronomous hyperparasitoids. These strategies may not be fixed, however, and may respond to other selective pressures acting to optimize the reproductive success of individuals through decisions made during searching and oviposition. Clearly, further experiments are needed to explicitly test the Godfray & Waage model. These should be

direct observations of parasitoid oviposition strategies under different regimes of host abundance. The results of such work would be of even greater value if collected in the field.

Acknowledgments

I am truly grateful to Jeff Waage and Charles Godfray for their help and advice over the course of this work. The manuscript was much improved by their comments. Andy Polaszek of C.I.E. sorted out my taxonomic problems. Zeyah Metah (Oxford University Statistics Department) and Mark Rees both helped with GLIM. Financial support came from a NERC studentship to J.K.W.

References

- van Alphen, J.J.M. & Janssen, A.R.M. (1982) Host selection by *Asobara tabida* Nees (Braconodae: Alysiinae), a larva parasitoid of fruit inhabiting *Drosophila* species. II. Host species selection. *Netherlands Journal of Zoology*, **32**, 215–231.
- Avilla, J. & Copland, M.J.W. (1987) Effects of host stage on the development of the facultative auto-parasitoid *Encarsia tricolor* (Hymenoptera: Aphelinidae). *Annals of Applied Biology*, **110**, 381–389.
- Bakker, K., van Alphen, J.J.M., van Batenburg, F.H.D., van der Hoeven, N., Nell, H.W., van Strien-van Liempt, W.F.T.H. & Turlings, T.C.J. (1985) The function of host discrimination and superparasitization. *Oecologia*, **67**, 572–576.
- Charnov, E.L. & Skinner, S.W. (1984) Evolution of host selection and clutch size in parasitoid wasps. *Florida Entomologist*, **67**, 5–21.
- Charnov, E.L. & Skinner, S.W. (1985) Complementary approaches to the understanding of parasitoid oviposition decisions. *Environmental Entomology*, **14**, 383–391.
- Colgan, P. & Taylor, P.D. (1981) Sex ratio in auto-parasitic Hymenoptera. *American Naturalist*, **117**, 564–566.
- van Dijken, M.J. & Waage, J.K. (1987) Self and conspecific superparasitism by the egg parasitoid *Trichogramma evanescens*. *Entomologia Experimentalis et Applicata*, **43**, 183–192.
- Donaldson, J.S. (1985) Sex ratios of *Coccophagus atratus* Compere (Hymenoptera: Aphelinidae) in relation to host availability. Unpublished M.Sc. thesis, Rhodes University, South Africa.
- Dowell, R.V., Puckett, D. & Johnson, M. (1981) Searching and ovipositional behaviour of *Amiutus*

- hesperidium* and *Encarsia opulenta*, parasitoids of the citrus blackfly (Homoptera: Aleyrodidae). *Entomophaga*, **26**, 233–239.
- Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, pp. 158–160. Oxford University Press.
- Flanders, S.E. (1939) Environmental control of sex in hymenopterous insects. *Annals of the Entomological Society of America*, **32**, 11–26.
- Flanders, S.E. (1942) The sex ratio in the Hymenoptera: a function of the environment. *Ecology*, **23**, 120–121.
- Flanders, S.E. (1956) The mechanisms of sex ratio regulation in the (parasitic) Hymenoptera. *Insectes Sociaux*, **3**, 325–334.
- Flanders, S.E. (1967) Deviate-ontogenies in the aphelinid male (Hymenoptera) associated with ovipositional behaviour of the parent female. *Entomophaga*, **12**, 415–427.
- Gerling, D., Spivak, D. & Vinson, S.B. (1987) Life history and host discrimination of *Encarsia deserti* (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America*, **80**, 224–229.
- Godfray, H.C.J. (1987) The evolution of clutch size in invertebrates. *Oxford Surveys in Evolutionary Biology*, Volume 4 (ed. by P. H. Harvey and L. Partridge), pp. 117–154.
- Godfray, H.C.J. & Waage, J.K. (1991) Highly skewed sex ratios in Aphelinid wasps can result from equal investment in sons and daughters. *American Naturalist* (in press).
- Green, R.F., Gordh, G.C. & Hawkins, B.A. (1982) Precise sex ratios in highly inbred parasitic wasps. *American Naturalists*, **120**, 653–655.
- Hamilton, W.D. (1967) Extraordinary sex ratios. *Science*, **156**, 477–488.
- Hassell, M.P., Waage, J.K. & May, R.M. (1983) Variable parasitoid sex ratios and their effect on host–parasitoid dynamics. *Journal of Animal Ecology*, **52**, 889–901.
- Hunter, M.S. (1989) Sex allocation and egg distribution of an autoparasitoid, *Encarsia pergandiella* (Hymenoptera: Aphelinidae). *Ecological Entomology*, **14**, 57–67.
- Iwasa, Y., Suzuki, Y. & Matsuda, H. (1984) Theory of oviposition strategy of parasitoids. 1. Effect of mortality and limited egg number. *Theoretical Population Biology*, **26**, 205–227.
- Janssen, A. (1989) Optimal host selection by *Drosophila* parasitoids in the field. *Functional Ecology*, **3**, 469–479.
- Kuenzel, N.T. (1975) Population dynamics of protelean parasites (Hymenoptera: Aphelinidae) attacking natural populations of *Trialeurodes packardi* (Homoptera: Aleyrodidae) and new host records for two species. *Proceedings of the Entomological Society of Washington*, **79**, 400–404.
- Parker, G.A. & Courtney, S.P. (1984) Models of clutch size in insect oviposition. *Theoretical Population Biology*, **26**, 21–48.
- Vet, L.E.M. & van Lenteren, J.C. (1981) The parasite–host relationship between *Encarsia formosa* and *Trialeurodes vaporariorum*. X. A comparison of three *Encarsia* species and one *Eretmocerus* species to estimate their potentialities in controlling whitefly on tomatoes in greenhouses with a low temperature regime. *Zeitschrift für Angewandte Entomologie*, **91**, 327–348.
- Viggiani, G. (1984) Bionomics of the Aphelinidae. *Annual Review of Entomology*, **29**, 257–276.
- Vinson, S.B. & Iwantsch, G.F. (1980) Host suitability in insect parasitoids. *Annual Review of Entomology*, **25**, 397–419.
- Waage, J.K. (1982) Sib-mating and sex ratio strategies in scelionid wasps. *Ecological Entomology*, **7**, 103–112.
- Waage, J.K. & Ng, S.M. (1984) The reproductive strategy of a parasitic wasp. I. Optimal progeny and sex allocation in *Trichogramma evanescens*. *Journal of Animal Ecology*, **53**, 401–415.
- Walter, G.H. (1983) 'Divergent male ontogenies' in Aphelinidae (Hymenoptera: Chalcidoidae): a simplified classification and a suggested evolutionary sequence. *Biological Journal of the Linnean Society*, **19**, 63–82.
- Williams, J.R. (1977) Some features of sex linked hyperparasitism in Aphelinidae. *Entomophaga*, **22**, 345–350.
- Williams, T. (1989) Sex ratio strategies in the facultatively autoparasitic wasp, *Encarsia tricolor* Förster (Hymenoptera: Aphelinidae). Unpublished Ph.D. thesis, University of London.
- Zinna, G. (1961) Ricerche sulgi insectti entomofagi. II. Specializzazione entomoparassitica negli Aphelinidae: Studio morfologico, etologico e fisiologico del *Coccophagus bivittatus* Compere, nuovo parassita del *Coccus hesperidium* L. per l'Italia. *Bolletino Laboratoria Entomologia Agraria Portici*, **19**, 301–358.
- Zinna, G. (1962) Ricerche sulgi insectti entomofagi. III. Specializzazione entomoparassitica negli Aphelinidae: Interdipendeze biocentotiche tra due specie associate. Studio morfologico, etologico e fisiologico del *Coccophagoides similis* (Masi) e *Azotus matritensis* Mercet. *Bolletino Laboratoria Entomologia Agraria Portici*, **20**, 73–182.