

Short communication

## A test of kin recognition in a heteronomous hyperparasitoid

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### Introduction

Female parasitoids which reproduce in the conventional manner have little reason to recognize their own progeny, except during self-superparasitism of previously laid clutches. Self-superparasitism has completely different consequences for female fitness compared to conspecific superparasitism (Waage, 1986; Godfray, 1994).

Heteronomous hyperparasitoids (also known as autoparasitoids or adelphoparasitoids) are a remarkable group of solitary aphelinid parasitoids in which the hosts differ according to the sex of the offspring. Genera containing species with heteronomous host relations include *Coccobius*, *Coccophagus*, *Coccophagoides*, *Encarsia*, and *Lounsburyia*. Females develop as primary endoparasitoids of Homoptera (whiteflies or scale insects) whereas males develop as hyperparasitoids of aphelinids or other homopteran endoparasitoids such as encyrtid or eulophid species (Walter, 1983; Williams & Polaszek, 1996). Hyperparasitic development of males in/on conspecific females is commonplace among many heteronomous hyperparasitoid species (Flanders, 1959; Broodryk & Doutt, 1966; Kennett et al., 1966; Williams, 1972; Keunzel, 1975; Viggiani, 1984; Donaldson & Walter, 1991; Hunter, 1993).

A female heteronomous hyperparasitoid remaining on, or revisiting a patch in which she has previously oviposited may dramatically influence the fitness of both sexes developing locally; especially if she exploits her daughters for the hyperparasitic production of sons. The consequences of such differences in the cost of production of each sex for the optimal sex ratio in these parasitoids has been examined in a simple model (Colgan & Taylor, 1981) based on Fisher's rule of equal investment in the sexes (Fisher, 1930). The

equilibrium sex ratio depended on the probability that males developed at the expense of their sisters. When this probability was high, the sex ratio was strongly female biased, whereas if low, the sex ratio moved in favour of males. However, alternative explanations for adaptive sex ratios in heteronomous hyperparasitoids have since been proposed (Godfray & Waage, 1990). The theory of Godfray & Waage, which focuses on the behaviour of female parasitoids facing egg or time constraints on their reproduction, has received strong support from subsequent empirical studies (Hunter & Godfray, 1995).

In this study I address the question as to whether or not a female heteronomous hyperparasitoid shows discriminative behaviour in the production of males when offered her own progeny or that of an unrelated conspecific.

### Methods

The heteronomous hyperparasitoid, *Encarsia tricolor* Förster was maintained in culture using the Cabbage Whitefly, *Aleurodes proletella* L. as the primary host and Brussels sprout seedlings as the host plant. The basic biology of the parasitoid has been studied previously (Christochowitz et al., 1981; Avilla & Copland, 1987, 1988; Williams, 1995). All material and experimental procedures were conducted at  $25 \pm 1$  °C, L16:D8 unless stated otherwise.

Clip cages were made from the base of a 35 mm diameter Petri dish, 5mm deep and divided in half by a strip of cellulose sponge. Cages were placed over leaves bearing approximately 30 third and fourth instar whitefly nymphs and were sealed to the leaf surface by foam draught excluder around the edge of the dish. Individual mated female *E. tricolor* were placed sim-

ultaneously in each half of the cage. After 24h of oviposition, experimental females were transferred individually to glass vials containing honey and kept at  $20 \pm 1$  °C. Whitefly nymphs were offered occasionally to permit host feeding. Experimental leaves and vials containing *E. tricolor* were labelled to permit later identification. Parasitized whitefly nymphs were allowed to develop until pupation of the primary parasitoid, 10 days later. All unparasitized whitefly nymphs were then removed from the experimental leaf arenas. The divider separating the two halves of the clip cage was removed and one of the females which had previously oviposited on the leaf was replaced and allowed to lay male eggs in the *E. tricolor* pupae over the whole clip cage area, i.e. both on the side of her own progeny and on the side where the conspecific female had oviposited. After 24 h, the female was removed and all parasitoid pupae from each side of the arena were transferred individually to labelled gelatine capsules. Daily checks were made for male emergence. It was thus possible to determine the relative parasitism of daughters and of unrelated females by *E. tricolor*. The experiment was replicated 23 times.

## Results

Female parasitoids were chosen at random for reintroduction onto the leaf. Nevertheless, by chance, slightly more unrelated parasitoid pupae were available on average (total 184; mean  $\pm$  SE  $8.1 \pm 0.66$ ) compared to the test female's own daughters (total 148; mean  $6.4 \pm 0.63$ ). The mean number of males produced in each type of host was, on average,  $1.1 \pm 0.22$  males (total of 26) in sisters compared to  $1.43 \pm 0.29$  males (total of 33) in unrelated female pupae.

It was not possible to detect any preference of *E. tricolor* to avoid laying males in kin. Hyperparasitism appeared to reflect the relative abundance of related and unrelated hosts ( $\chi^2_1 = 0.0$ ; N.S.). This relationship remained non-significant when one assumed that the relative availability of the two host types would not influence parasitism i.e. that equal numbers of each type would be parasitized ( $\chi^2_1 = 0.83$ ; N.S.).

## Discussion

The apparent inability of *E. tricolor* females to recognize their own progeny may suggest that having encountered and laid eggs in a particular patch of hosts

a female has little chance of returning to the patch subsequently. Whether or not a female heteronomous hyperparasitoid in the field could even survive the 10-day interval chosen in this study is a matter of doubt.

There is already some evidence for lack of maternal discrimination against daughters during hyperparasitism in a heteronomous hyperparasitoid. Gerling (1987) mentioned that when *Encarsia lutea* was simultaneously offered unparasitized *Bemisia tabaci*, nymphs parasitized by another female and nymphs previously parasitized by herself, then parasitism of each type of host occurred in much the same frequency as the hosts were offered.

Copland (1976) described the alkaline gland associated with the reproductive system of female Hymenoptera, thought to produce a pheromone important in marking attacked hosts. The gland is well developed in aphelinids. Recently parasitized hosts may thus be distinguished from unparasitized neighbours. Once the primary parasitoid larva hatches, however, it becomes liable to be parasitized by *E. tricolor* (other heteronomous hyperparasitoids may only attack large parasitoid larvae or pupae). Thus, the ovipositional marker need only be detectable for a relatively short duration; much less than the 10 day period in this study. In another system, an individual specific marker chemical released from the Dufour's gland of *Nemeritis canescens* remained detectable for 48 h. This marker was individual-specific and allowed females to discriminate between hosts parasitized by her own progeny or those of conspecifics in order to avoid superparasitism of the former (Hubbard et al., 1987)

Importantly, two studies have detected that *E. tricolor* females prefer to exploit non-conspecific hosts for male production. The production of male *E. tricolor* in *E. formosa* or *E. inaron* was greater than male production in conspecific females (Avilla et al., 1991; Williams, 1991). Preference for heterospecifics may be a mechanism by which *E. tricolor* females ensure that they avoid parasitism of their developing daughters. In the case of *E. tricolor* male production in *E. formosa* there was an additional advantage, in that males from *E. formosa* were larger than their counterparts which developed in conspecifics (Avilla et al., 1991).

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## References

- Avilla, J., J. Anadon, M. J. Sarasua & R. Albajes, 1991. Egg allocation of the autoparasitoid *Encarsia tricolor* at different relative densities of the primary host (*Trialeurodes vaporariorum*) and two secondary hosts (*Encarsia formosa* and *E. tricolor*). *Entomologia Experimentalis et Applicata* 59: 219–227.
- Avilla, J. & M. J. Copland, 1987. Effects of host stage on the development of the facultative autoparasitoid, *Encarsia tricolor* (Hymenoptera: Aphelinidae). *Annals of Applied Biology* 110: 381–389.
- Avilla, J. & M. J. Copland, 1988. Development rate, number of mature oocytes at emergence and adult size of *Encarsia tricolor* at constant and variable temperatures. *Entomophaga* 33: 289–298.
- Broodryk, S.W. & R. L. Doutt, 1966. II The biology of *Coccophagoides utilis* Doutt (Hym., Aphelinidae). *Hilgardia* 37: 233–254.
- Christochowitz, E. E., N. van de Fluit, & J. C. van Lenteren, 1981. Role of development and oviposition frequency of *Trialeurodes vaporariorum*, *Encarsia formosa* (2 species) and *E. tricolor* at low glasshouse temperatures. *Mededelingen van de Faculteit Landbouwetenschappen Rijksuniversiteit (Gent)* 46: 477–485.
- Colgan, P. & P. D. Taylor, 1981. Sex ratio in autoparasitic Hymenoptera. *American Naturalist* 117: 564–566.
- Copland, M. J. W., 1976. Female reproductive system of the Aphelinidae (Hym. Chalcidoidea). *International Journal of Insect Morphology & Embryology* 5: 151–166.
- Donaldson, J. S. & G. H. Walter, 1991. Host population structure affects field sex ratios of the heteronomous hyperparasitoid, *Coccophagus atratus*. *Ecological Entomology* 16: 35–44.
- Fisher, R. A., 1930. *The Genetical Theory of Natural Selection*. Oxford University Press.
- Flanders, S. E., 1959. Differential host relations of the sexes in parasitic Hymenoptera. *Entomologia Experimentalis et Applicata* 2: 125–142.
- Gerling, D., 1987. Evaluation of parasitoids for the control of whiteflies. Unpublished report to CAB International No. I 26481, 77 pp.
- Godfray, H. C. J., 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, NJ.
- Godfray, H. C. J. & J. K. Waage, 1990. The evolution of highly skewed sex ratios in aphelinid wasps. *American Naturalist* 136: 715–721.
- Hunter, M. S., 1993. Sex allocation in a field population of an autoparasitoid. *Oecologia* 93: 421–428.
- Hunter, M. S. & H. C. J. Godfray, 1995. Ecological determinants of sex allocation in an autoparasitoid wasp. *Journal of Animal Ecology* 64: 95–106.
- Hubbard S. F., G. Marris, A. Reynolds & G. W. Rowe, 1987. Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *Journal of Animal Ecology* 56: 387–401.
- Kennett, C. B., C. B. Huffaker & G. L. Finney, 1966. III The role of an autoparasitic aphelinid, *Coccophagoides utilis* Doutt in the control of *Parlatoria oleae* (Colvée). *Hilgardia* 37: 255–282.
- Keunzel, N. T., 1975. Population dynamics of protelean parasites (Hym. Aphel.) attacking a natural population of *Trialeurodes packardii* (Hom. Aley.) and new host record for two species. *Proceedings of the Entomological Society Washington* 79: 400–404.
- Viggiani, G., 1984. Bionomics of the Aphelinidae. *Annual Review of Entomology* 29: 257–276.
- Waage, J., 1986. Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In: J. Waage & D. Greathead (eds) *Insect Parasitoids*. Academic Press, London, pp. 63–96.
- Walter, G. H., 1983. Divergent male ontogenies in Aphelinidae (Hymenoptera: Chalcidoidea): a simplified classification and a suggested evolutionary sequence. *Biological Journal of the Linnean Society* 19: 63–82.
- Williams, J. R., 1972. The biology of *Physcus seminotus* Silv. and *P. subflavus* A&I (Aphelinidae) parasites of the sugar cane scale insect *Aulacaspis tegalensis* (Zhnt) [Diaspididae]. *Bulletin of Entomological Research* 61: 463–484.
- Williams, T., 1991. Host selection and sex ratio in a heteronomous hyperparasitoid. *Ecological Entomology* 16: 377–386.
- Williams, T., 1995. The biology of *Encarsia tricolor*: an autoparasitoid of whitefly. *Biological Control* 5: 209–217.
- Williams, T. & A. Polaszek, 1996. A re-examination of host relations in the Aphelinidae (Hym.: Chalcidoidea). *Biological Journal of the Linnean Society* 57: 35–45. ✓