Biological Journal of the Linnean Society (1996), *57*: 35–45

A re-examination of host relations in the Aphelinidae (Hymenoptera: Chalcidoidea)

TREVOR WILLIAMS

ECOSUR: El Colegio de la Frontera Sur, Aptdo Postal 36, 30700 Tapachula, Chiapas, Mexico

AND

ANDREW POLASZEK

International Institute of Entomology, 56 Queens Gate, London, SW7 5JR

Received 13 September 1994, accepted for publication 20 February 1995

Host relations among the Aphelinidae (Hymenoptera: Chalcidoidea) are highly intriguing from an evolutionary view. Females are usually primary endoparasitoids of whiteflies or scale insects, whereas the development of the male is different and has been used for classification. In heteronomous hyperparasitoids (adelphoparasitoids or autoparasitoids) the male develops as a hyperparasitoid of conspecific females or other endoparasitoid species. We review the consequences of this mode of development which is unique because decisions concerning host selection are inextricably linked with progeny sex ratio. Autoparasitoid field sex ratios can fluctuate dramatically concurrent with changes in the relative availability of male and female hosts. A recent adaptive explanation for these sex ratios involves understanding the reproductive constraints acting on heteronomous parasitoids. Host relations in these parasitoids can show a degree of plasticity. We argue that in many instances autoparasitism may be facultative in nature and should not be used for classification. Heterotrophic parasitism, wherein the male develops as a primary parasitoid of lepidopterous eggs, has been poorly understood in the past due to uncertainties in reports of the biology and taxonomy of heterotrophic parasitoids. The host relations of this group are clarified.

ADDITIONAL KEY WORDS:—divergent host relations – classification – heteronomous hyperparasitoid – autoparasitoid – heterotrophic parasitoid.

CONTENTS

BACKGROUND AND REPRODUCTIVE BIOLOGY

Many species of parasitoids belonging to genera within the family Aphelinidae (Hymenoptera: Chalcidoidea) are remarkable in the sexual asymmetry of their host relations. In most of these species, female parasitoids are primary endoparasitoids of sternorrhynchous Homoptera: whiteflies (Aleyrodidae) and scale insects (Coccoidea). The development of males, however, is quite different from that of the conspecific female. Males may develop as primary ectophagous parasitoids of Homoptera, as hyperparasitoids of chalcid parasitoids of Homoptera, or as primary endoparasitoids of the eggs of Lepidoptera. There are seven genera within the Aphelinidae containing species showing sex-related differences in host relations, namely: *Coccophagoides, Coccophagus, Encarsia, Lounsburyia* and *Coccobius*. Certain species of *Pteroptrix* and *Ablerus* may also belong to this group (Walter, 1983). [The additional genera of *Aneristus, Euxanthellus, Physcus, Prococcophagus*, and *Prospaltella* listed by Walter (1983) have since been synonymized within the seven genera listed here. *Azotus* is now a synonym of *Ablerus*]. The coverall term, heteronomous, meaning subject to different laws or modes of growth, has been used to describe such divergent parasitoid host relations (Walter, 1983).

The sex determination mechanism used by Hymenoptera is haplo-diploidy. Females are diploid and arise from fertilized eggs whereas males are haploid and develop parthenogenetically from unfertilized eggs. Consequently, virgin females have the ability to lay male eggs prior to mating, and can facultatively control the sex of their offspring by selective fertilization of eggs following insemination. This phenomenon is termed arrhenotoky. This is the key practice which allows the sex-related differences in host relations to exist; ovipositing females can precisely determine progeny sex according to the type of host encountered. Some aphelinid species also show thelytoky (the parthenogenetic production of solely female offspring) and amphitoky (parthenogenetic production of both sexes).

Aphelinid parasitoids have been by far the most successful agents of biological control against whitefly and scale insect pests. Since their economic potential was recognized in the first half of this century they have been released for classical biological control on more than 150 occasions (Greathead, 1986; Noyes & Hayat, 1993). However, their small size and the divergent nature of the host relations have often meant that detailed studies on the reproductive biology of these species have been neglected. The remarkable modes of male development in heteronomous parasitoids were first recognized by Flanders (1936a,b,c). He also proposed the first attempt at classification, based on ovipositional behaviour pre- and post-mating (Flanders, 1959). Alternative, but incomplete schemes followed based upon the host relations of the male (Zinna, 1961, 1962; Ferrière, 1965). The nomenclature in both of these systems was awkward and uninformative. Two decades later, Walter (1983) produced the most viable and complete system to date. The group was classified by Walter under three main headings according the development of the male: (1) diphagous parasitoids; (2) heteronomous hyperparasitoids; and (3) heterotrophic parasitoids.

Both male and female diphagous parasitoids use the same, or a closely related species of homopteran host for development. However, the site of feeding differs; female larvae are endoparasitic whereas male larvae are ectoparasitic. Such differences in the type of primary parasitism between the sexes does not have particularly interesting consequences for strategies of host selection or sex ratio in these parasitoids and we shall not consider them further.

Heteronomous hyperparasitoids, on the other hand, present a fascinating problem in host selection and sex ratio decision making. Males of this group develop hyperparasitically on other endoparasitoids, in particular, aphelinids, encyrtids, and eulophids; records of Aphelinidae hyperparasitic on platygastrids require confirmation. Male exploitation of conspecific females is a common phenomenon in this group. Walter (1983) proposed that the group be subdivided into *obligate autoparasitoids*, in which the male always develops on a conspecific, *facultative autoparasitoids*, in which males develop on other chalcid species as well as conspecifics, and *alloparasitoids* in which males never develop on conspecifics. Two strategies of male hyperparasitism can also be distinguished: direct, when the male egg is laid in/on the primary endoparasitoid host, or indirect, when a male egg is laid in a primary host (whitefly/scale) in anticipation of future parasitism by a suitable primary endoparasitoid. Direct heteronomous hyperparasitoids may be endophagous or ectophagous in their behaviour, whereas indirect heteronomous hyperparasitoids are strictly ectophagous (Walter, 1983). We will consider the heteronomous hyperparasitoids in some detail in terms of the ovipositional decisions they face, and the plasticity of their host relations.

Heterotrophic parasitoids lay males as primary endoparasitoids in the eggs of Lepidoptera. This means that mated females may have to search for two completely different host types, which may occupy different (micro)habitats, in contrast with heteronomous hyperparasitoids which only search for one host type (e.g. scale insects) which may be already parasitized (male hosts) or unparasitized (female hosts).

HOST SELECTION AND SEX RATIO IN HETERONOMOUS PARASITOIDS

As males and females develop in different hosts, the ovipositional decisions faced by direct heteronomous hyperparasitoids initially seem highly complicated. A mated female must decide which of the available hosts to select for parasitism, and in doing so, she is simultaneously deciding what local sex ratio to produce. Godfray & Waage (1991) made the key observation that the optimal reproductive strategy will depend on the type of constraints acting on heteronomous hyperparasitoid reproduction at any one time. They reasoned that when both types of hosts, parasitized and unparasitized, are numerous, a direct female heteronomous hyperparasitoid will be reproductively constrained by her rate of egg production. This is usually low in aphelinids, often < 10 eggs per day (Williams, 1972; Vet & van Lenteren, 1981; Viggiani, 1984). In the absence of complicating issues, then Fisher's rule should apply and ovipositing females should invest equally in production of each sex leading to an unbiased sex ratio (assuming the costs of producing each sex is the same and that each sex experiences equal reproductive success) (Fisher, 1930).

When both types of host are rare, the direct heteronomous hyperparasitoid will be constrained by her rate of host finding. In this case, it would be maladaptive to reject any host encountered. Therefore, each and every host discovered should be parasitized irrespective of the consequent sex of the offspring, (Fisher's rule does not apply because there is no longer a tradeoff between male and female production). As a result, the population sex ratio would be a direct reflection of the rate of finding each host type, i.e. the relative abundance of primary (unparasitized) and secondary (parasitized) hosts.

Godfray & Waage (1991) also addressed the problems facing heterotrophic parasitoids in which males are laid as primary endoparasitoids of lepidopterous eggs. They reasoned that, following Fisher's rule, a heterotrophic parasitoid should invest equal searching time in (micro)habitats containing each host type (lepidopterous eggs and homopteran nymphs). However, when the two hosts occurred together, the strategy would be the same as for a direct heteronomous hyperparasitoid, i.e. parasitize all hosts encountered, irrespective of type, when host limited, and lay equal numbers of each sex when egg limited. Due to the paucity of information on the biology of heterotrophic parasitoids (reviewed later), no empirical evidence is available to endorse their hypothesis for this group.

Support for the predictions of Godfray & Waage (1991) came from laboratory studies and field observations of heteronomous hyperparasitoid secondary sex ratios. In *Encarsia tricolor*, unbiased secondary sex ratios have been detected under conditions of egg limitation (Williams, 1991) whereas sex ratios were strongly influenced by the relative abundance of secondary (male) hosts under conditions of host limitation (Avilla *et al.*, 1991). Heteronomous hyperparasitoid field sex ratios often reflect, and fluctuate in response to, the relative abundance of each host type, as indicated by the overall percentage parasitism of the primary host (Keunzel, 1975; Williams, 1977; Donaldson & Walter, 1991b; Hunter, 1993). This is consistent with parasitoids which are constrained by searching time (host encounter rate) in the field.

The most compelling support for these predictions comes from a recent study by Hunter & Godfray (1995). At low rates of host discovery (low host densities), *E. tricolor* sex ratios mirrored the relative abundance of male and female hosts. As the density of hosts was increased, sex ratios clearly shifted towards equality (unbiased), as was predicted for a gradual change from host to egg limitation.

The ideas of Godfray & Waage (1991) are not universally accepted. Donaldson & Walter (1991a,b) reported population and brood sex ratios which were influenced by the relative availability of each type of host for the direct heteronomous hyperparasitoid, *Coccophagus atratus*. They suggested that sex ratio in heteronomous hyperparasitoids is not adaptive. Walter & Donaldson (1994) argue that the Godfray & Waage model is not applicable to heteronomous hyperparasitoids because pure egg limitation or pure time limitation may not be common and may change during the lifetime of a parasitoid, and because a female wasp cannot predict her future rate of encounter with hosts of either type and so will not have complete knowledge of the reproductive opportunities available during her lifetime. They have also suggested that selection pressures acting on heteronomous hyperparasitoid sex ratios have become uncoupled from those acting on host selection due to the unusual host relations which involve recognition of each type of host to elicit the correct egg laying response. This explanation has been criticized as inappropriate (Godfray & Hunter, 1992, 1994). Godfray & Hunter (1994) argue that sex ratio is one facet of the overall reproductive strategy of heteronomous hyperparasitoids upon which selection forces act, and should not be considered as a separate entity by merit of the inherent dichotomy in host relations. One might expect a flexible response in heteronomous hyperparasitoids encountering changing situations of host availability such that wasps would not reject any host at low encounter rates and gradually switch to producing even sex ratios as the encounter rate increased, in a similar manner to the study reported by Hunter & Godfray (1995) using *Encarsia tricolor*.

Hassell, Waage & May (1983) considered the effect of the unusual host relations of heteronomous hyperparasitoids on the populations dynamics of systems containing these parasitoids. By modification of existing models they found that heteronomous hyperparasitoid populations exhibited very high levels of stability. These species also displayed stabilizing properties when introduced into host-heteronomous hyperparasitoid-hyperparasitoid systems. They attributed the marked success of biocontrol programs using heteronomous hyperparasitoids to the stabilizing nature of the population dynamics arising from their differential host relations.

Complicating factors

There are a number of factors which act to complicate issues of sex ratio and host selection in heteronomous hyperparasitoids which are not considered by the simple adaptive model of Godfray & Waage (1991). One of them is local mate competition (Hamilton, 1967), wherein a wasp biases her progeny sex ratio in favour of daughters in order to minimize competition for mates among her sons mating locally. However, most aphelinids are good fliers and seem likely to have good dispersal abilities. Consequently, males may enter and leave patches containing potential mates such that mating tends to be independent of the spatial structure of the population. Under such conditions local mate competition is no longer important (see for example Donaldson & Walter, 1991a).

Differences in the cost of producing each sex may also affect the Godfray & Waage model. Such differences could arise by hyperparasitism of siblings wherein a male develops at the expense of one of his sisters (Colgan & Taylor, 1981), or marked differences in the handling times for each host type because laying a male egg in a parasitized host can take several times longer than laying a female egg (e.g. Williams, 1972; Donaldson *et al.*, 1986). Recent studies have highlighted two other relevant factors: first, preferential hyperparasitism of non-conspecifics, and second, the presence of sex ratio distorters in aphelinids.

Several studies have detected heteronomous hyperparasitoid ovipositional preferences in favour of secondary parasitism. Avilla *et al.* (1991) reported that *Encarsia tricolor* produced sex ratios which were more male biased when *E. formosa* was offered as a secondary host compared to sex ratios produced when conspecific pupae were available. Similarly, Williams (1991) observed a strong preference for hyperparasitism of *E. inaron* rather than conspecifics by *E. tricolor*. This preference also influenced the sex ratios of individual female *E. tricolor*. When simultaneously offered primary and secondary hosts, *E. tricolor* sex ratios were unbiased in the presence of conspecifics, but showed a significant male bias in the presence of *E. inaron*. Given an alternative host species for male production, there are selective advantages to preferential hyperparasitism of the non-conspecific host. In particular, this could be a mechanism through which a female avoids hyperparasitizing her own progeny. It may also reflect differences in the size (and therefore potential fitness) of males emerging from non-conspecific hosts. Size differences have been observed in the predicted direction for *E. tricolor* males emerging from *E. formosa* (Avilla & Copland, 1987), but not for *E. tricolor* males parasitizing *E. inaron* (Williams, 1991).

In the field, Hunter (1993) has noted that *Encarsia pergandiella* females laid more males than expected given the availability of secondary hosts. This was not due to differential rates of encounter with primary and secondary hosts, or due to unmatedness constraining female production. The reason for such bias is uncertain but this may be indicative of a higher mating success of male compared to female offspring of *E. pergandiella.*

Recently, two sex ratio disorders have been reported in heteronomous hyperparasitoids. The loss of the paternal genome in female (diploid) eggs of *Encarsia pergandiella* resulted in the production of functional males (Hunter, Nur & Werren, 1993). The effect of this is that up to 39% of *E. pergandiella* males develop in primary (whitefly) hosts. The transmission or expression of the causative factor (possibly a paternally inherited transposon or virus) was low and variable, with only half of the primary male matings resulting in any primary male offspring. Another species, *Encarsia formosa,* is usually thelytokous, but primary males are produced in large numbers following antibiotic treatment (Zchori-Fein, Roush & Hunter, 1992). Males produced in this way carried sperm but failed to inseminate successfully.

A RE-EXAMINATION OF HETERONOMOUS PARASITOID CLASSIFICATION

A system of heteronomous parasitoid classification proposed by Walter (1983) has been valuable in clarifying a rather complicated and diverse set of parasitoid host relations. The evidence for diphagous parasitism seems clear (Walter, 1993), and we will not consider this further. However, his system of nomenclature and classification for heteronomous hyperparasitoids and heterotrophic parasitoids may not be ecologically realistic, and the need for certain modifications has already been recognized (Williams, 1989; Polaszek, 1991).

Do obligate autoparasitoids exist?

First, let us consider the so-called 'obligate autoparasitoids' in which males only develop as hyperparasitoids of conspecific females. There are no selective advantages, however, which we can envisage for obligate autoparasitism. That is not to say that certain species may show preferences to parasitize conspecific hosts, due to host-size effects for example, as described above in the counter situation of *Encarsia tricolor* preferentially attacking *E. formosa.* Notwithstanding that, we see no adaptive reasons why this highly restrictive type of reproduction could have evolved, except in situations when a heteronomous hyperparasitoid species became geographically, temporally or otherwise isolated from non-conspecific primary endoparasitoid species (alternative male hosts). Detailed examination of the references cited by Walter (1983) in support of his scheme has revealed that there are no verified cases of true obligate autoparasitism, and very few of alloparasitism.

Walter (1983) listed 11 species of obligate autoparasitoids, namely: *Coccophagoides abnormicornis* Girault, *Coccophagoides kuwanae* (Silvestri), *Coccophagoides utilis* Doutt, *Coccophagus insidiator* (Dalman) (as *C. gossypariae* Gahan), *Coccophagus semicircularis* (Förster), *Encarsia formosa* Gahan, *Coccobius fulvus* (Compere & Annecke), *Coccobius intermedius* (Gahan), *Coccobius* sp. nr. *varicornis* (Howard), *Encarsia lahorensis* (Howard), and *Encarsia perniciosi* (Tower) (San José scale race, bisexual form). Of these 11, *Coccophagoides kuwanae, Coccophagus semicircularis* and *Coccobius* sp. nr. *varicornis,* all have footnotes to the effect that their actual host relations are uncertain. *Encarsia lahorensis* has subsequently been shown to be a facultative autoparasitoid (Viggiani & Mazzone, 1978; Rue & Sailer, 1979; Rose & DeBach, 1981; Hudson & Williams, 1986). *Encarsia formosa* is thelytokous. Gerling (1966, 1983) stated that *E. formosa* was a facultative autoparasitoid although this was not demonstrated explicitly and other studies have shown that *E. formosa* males develop as primary parasitoids of whiteflies (Vet & van Lenteren, 1981; Zchori-Fein, Roush & Hunter, 1992). Male production by *E. formosa* only occurs under specific conditions (reviewed by Stouthamer & Luck, 1991). *E. formosa* also appears to harbour a sex ratio distorting infection, as described previously. For five of the six remaining species, the nature of the male conspecific dependency is stated solely as fact, with no references made to experimental or field data in the presence of alternative secondary hosts. The ability to develop in conspecifics is stated, but never the necessity to do so. The exception to this lies in the papers by Broodryk & Doutt (1966) and Kennett, Huffaker & Finney (1966), who clearly state that *Coccophagoides utilis* does not exploit its competitor, *Aphytis paramaculicornis* for male production. However, both of these species are exotic introductions to the US for control of the olive scale and moreover *A. paramaculicornis*, like all *Aphytis*, develops ectoparasitically and so may not be suitable for hyperparasitism by *C. utilis.*

Do alloparasitoids exist?

Next, let us consider the alloparasitoids, in which males utilize only non-conspecific hosts for development. There seem to be some genuine cases of alloparasitism, although it will be shown that these are usually a result of female ovipositional preferences. Walter (1983) lists five species, namely: *Coccophagus basalis* Compere, *Coccophagus ceroplastae* (Howard), *Coccophagus malthusi, Coccophagus pulvinariae* Compere, and *Lousburyia trifasciata* (Compere). Of these, *C. ceroplastae* and *C. pulvinariae* lack statements relating to obligate alloparasitoid development. The remaining species are all indirect heteronomous hyperparasitoids of non-conspecifics. Apparently, in *Coccophagus malthusi,* female eggs are laid in waxy scales of the genus *Ceroplastes*, whereas male eggs are laid in various lecaniine coccids other than those used for female production (Annecke, 1964; Annecke & Insley, 1974). Male *C. malthusi* can only develop in the presence of a primary endoparasitoid of the lecaniine scales, which, by definition, will not be a conspecific female. Such ovipositional behaviour on the part of the female has the same selective advantages as preferential hyperparasitism of competitors in that a female avoids hyperparasitism of her own daughters.

For *Coccophagus basalis* and *Lounsburyia trifasciata* a physiological mechanism prevents conspecific hyperparasitism. Conspecific female larvae fail to consume sufficient primary host body fluids to stimulate hatching of the quiescent male hyperparasitoid larva previously laid in the primary host (indirect hyperparasitism). Species of *Metaphycus*, however, totally consume the primary host internally and thereby stimulate hatching of the fluid-sensitive male (Flanders, 1936c; Flanders, Bartlett & Fisher, 1961).

It now seems more appropriate to view both "obligate" (habitual) autoparasitism and alloparasitism as the extremes of a range of facultative responses determined by the physiological and behavioural constraints on an heteronomous parasitoid given a range of opportunities available for male production.

Do heterotrophic parasitoids exist?

Let us now consider heterotrophic parasitoids. In a recent examination of egg parasitism by aphelinids, Polaszek (1991) critically reviewed the published evidence for heterotrophic development, wherein males develop as primary endoparasitoids of lepidopterous eggs. In particular, he drew upon those references cited by Walter (1983). In a similar vein to the present study, he argued that the majority of such reports may concern facultative parasitism and that the evidence was weak in support of a distinct grouping for heterotrophic parasitoids.

There is limited evidence that certain species of heterotrophic parasitoids can be facultative in their host relations (Beingolea, 1959). He observed that two unidentified species of *Encarsia* were both facultative endoparasitoids of eggs of the noctuid, *Anomis texana*. Males of species A were commonly recorded from these eggs, and occasionally as homopteran hyperparasitoids, whereas males of species B were frequently recorded as hyperparasitoids and infrequently developed as primary endoparasitoids of lepidopterous eggs. However, the data in support of these assertions are not conclusive: the evidence for heteronomous hyperparasitism by species A rests on the observation of three males (which may have been contaminants of the culture by species B), whereas the evidence presented for heterotrophic parasitism by species B is purely anecdotal. Moreover, the male of *Encarsia lutea* is well known as a heteronomous hyperparasitoid of whiteflies (e.g. Viggiani, 1984) but has also been recorded from the eggs of the moths *Helicoverpa zea* and *Trichoplusia ni* (Stoner & Butler, 1965). *E. lutea* was therefore listed as an heterotrophic parasitoid by Walter (1983). The fact that *E. lutea* males also develop as heteronomous hyperparasitoids supported Polaszek's (1991) conclusion that obligate heterotrophic parasitoids may not exist. However, recently we were able to examine specimens of male *Encarsia* reared from eggs of *H. zea* and *T. ni* from the same locality as Stoner & Butler's study (Arizona) including voucher specimens from both their study and that of Davies *et al.*, (1933) who mentioned an *Encarsia* (*Prospaltella*) sp. reared from *H. zea* and *Diatraea grandiosella* eggs. These specimens are not *E. lutea*, but belong to a species very close to, but different from, *Encarsia porteri* (Mercet). Until now, *E. porteri* is the only *Encarsia* species in which development of males in lepidopterous eggs has been reported with any frequency (Arretz, Lamborot & Guerroro 1985, Rojas, 1968). The obligate nature of male development in lepidopterous eggs has now been demonstrated convincingly for *E. porteri* and for the North American species (Polaszek, *et al.*, 1995; M.S. Hunter pers. comm.). In this respect they stand alone as the sole heterotrophic parasitoids known to date. We conclude that the five species of *Encarsia* listed by Walter (1983) probably represent two species: *E. porteri* and the (probably undescribed) North American species.

Among the material in the United States National Museum, Washington studied by the second author is another *Encarsia* species, belonging to the *E. inaron* group, in which both sexes appear to be capable of developing in Lepidoptera eggs. It may eventually be necessary to erect a new biological category for this species. Interestingly, *E. inaron* and *E. porteri* belong to widely different species groups and in some species of the *E. inaron* group both males and females develop as primary parasitoids

CONCLUSIONS

Although certain problems with the classification of Walter (1983) have been identified, it is undeniable that Walter has done much to clarify a confused situation and has provided a system with a structured biological basis. Much of Walter's system is valid and should be retained. However, we suggest that future studies involving the classification of heteronomous parasitoids according to their mode of development should consider the possibility that host relations may be labile and cannot be accurately assessed without the appropriate evidence. In particular, the sub-divisions within the heteronomous hyperparasitoids (obligate autoparasitoids and alloparasitoids) are not realistic or particularly useful. We recommend heteronomous hyperparasitoids be viewed as a unified group defined by the hyperparasitic male development. A sub-set of the group is capable of heterotrophic parasitism. We now know that heterotrophic parasitism certainly occurs in an undescribed North American species and in *Encarsia porteri* (wherein the host relationship appears to be obligate). Without doubt, this group of parasitoids merits greater attention in studies of basic biology and ecology than it has received to date and such work is currently being undertaken.

We believe this approach to be biologically more realistic and will permit greater flexibility in aphelinid classification while retaining the description powers and user-friendliness of Walter's original system. Greater realism in describing autoparasitoid ovipositional behaviour and host relations of both sexes should enhance the accuracy and value of future work on these most intriguing and valuable insects. Studies testing the predictions made by Godfray & Waage (1991) are revealing that simple adaptive explanations related to reproductive constraints on heteronomous hyperparasitoids are sufficient to explain the sometimes dramatic fluctuations observed in field sex ratios in autoparasitoid populations. Field studies on the rate of host encounter and female reproductive status would give even greater support to their adaptive model, which is currently a subject of dispute.

ACKNOWLEDGEMENTS

We thank M. Schauff (USDA) and the Office of Fellowships and Grants of the Smithsonian Institution, Washington DC; S. Ovruski and E. Frias of CIRPON (Tucuman, Argentina); and S.P. Rojas of Subestacion Experimental de Control Biologico (La Cruz, Chile), for their assistance. We acknowledge with gratitude the constructive comments on various aspects of this work offered by John Donaldson, Charles Godfray, Molly Hunter, John LaSalle, Richard Stouthamer, Jeff Waage and Gimme Walter. John Noyes kindly gave unlimited access to his unique catalogue of world Chalcidoidea.

REFERENCES

Annecke DP. 1964. The encyrtid and aphelinid parasites (Hymenoptera: Chalcidoidea) of soft brown scale, *Coccus hesperidum* L. (Hemiptera: Coccidae) in South Africa. *Entomology Memoirs* **7:** 1–74.

Annecke DP, Insley HP. 1974. The species of *Coccophagus* Westwood, 1833 from the Ethiopian region (Hymenoptera: Aphelinidae). *Entomology Memoirs* **37:** 1–62.

Arretez VP, Lamborot CL, Guerroro MA. 1985. Evaluacion del parasitismo sobre ios estados immaduros de la cuncunilla verde del frijol *Rachiplusia nu* Guenée en praderas de alfalfa. *Revista Chileana de Entomologia* **12:** 209–215.

Avilla J, Anadon J, Sarasua MJ, Albajes R. 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, Copland MJ. 1987. Effects of host stage on the development of the facultative autoparasitoid, *Encarsia tricolor* (Hymenoptera: Aphelinidae). *Annals of Applied Biology* **110:** 381–389.

Beingolea O. 1959. Nota sobre *Encarsia* spp. (Hymenoptera: Aphelinidae) parasito de los heuvos de *Anomis texana* (Lepidoptera: Noctuidae). *Revista Peruana de Entomología Agrícola* **2:** 59–64.

Broodryk SW, Doutt RL. 1966. II The biology of *Coccophagoides utilis* Doutt (Hym., Aphelinidae). *Hilgardia* **37:** 233–254.

Colgan P, Taylor PD. 1981. Sex ratio in autoparasitic Hymenoptera. *American Naturalist* **117:** 564–566.

Davies EG, Horton JR, Gable CH, Walter EV, Blanchard RA, Heinrich C. 1933. The southwestern corn borer. *Technical Bulletin United States Department of Agriculture* **388:** 1–49.

Donaldson JS, Clark MM, Walter GH. 1986. Biology of the heteronomous hyperparasitoid *Coccophagus atratus* Compere (Hymenoptera: Aphelinidae): adult behaviour and larval development. *Journal of the Entomological Society of Southern Africa* **49:** 349–357.

Donaldson JS, Walter GH. 1991a. Brood sex ratios of the solitary parasitoid wasp, *Coccophagus atratus*. *Ecological Entomology* **16:** 25–33.

Donaldson JS, Walter GH. 1991b. Host population structure effects field sex ratios of the heteronomous hyperparasitoid, *Coccophagus atratus*. *Ecological Entomology* **16:** 35–44.

Ferrière C. 1965. *Hymenoptera Aphelinidae d'Europe et du bassin Méditeranéen.* Paris: Masson, 1–206.

Fisher RA. 1930. *The genetical theory of natural selection.* Oxford: Oxford University Press, 158–160.

Flanders SE. 1936a. A reproduction phenomenon. *Science* **83:** 499.

Flanders SE. 1936b. Remarkable phenomenon of reproduction in the parasitic Hymenoptera. *Journal of Economic Entomology* **29:** 468.

Flanders SE. 1936c. A biological phenomenon affecting the establishment of Aphelinidae as parasites. *Annals of the Entomological Society of America* **29:** 251–255.

Flanders SE. 1959. Differential host relations of the sexes in parasitic Hymenoptera. *Entomologia experimentalis et applicata* **2:** 125–142.

Flanders SE, Bartlett BR, Fisher TW. 1961. *Coccophagus basalis* (Hymenoptera: Aphelinidae): its introduction into California with studies of its biology. *Annals of the Entomological Society of America* **57:** 227–236.

Gerling D. 1966. Biological studies on *Encarsia formosa* (Hymenoptera: Aphelinidae). *Annals of the Entomological Society of America* **59:** 142–143.

Gerling D. 1983. Observations of the biologies and interrelationships of parasites attacking the greenhouse whitefly, *Trialeurodes vaporariorum* (West.) in Hawaii. *Proceedings of the Hawaiian Entomological Society* **24:** 217–225.

Godfray HCJ, Waage JK. 1991. The evolution of highly skewed sex ratios in aphelinid wasps. *American Naturalist* **136:** 715–721.

Godfray HCJ, Hunter MS. 1992. Sex ratios of heteronomous hyperparasitoids: adaptive of non-adaptive? *Ecological Entomology* **17:** 89–90.

Godfray HCJ, Hunter MS. 1994. Heteronomous hyperparasitoids, sex ratios and adaptations: a reply. *Ecological Entomology* **19:** 93–95.

Greathead DJ. 1986. Parasitoids in classical biological control. In: Waage JK, Greathead DJ, eds. *Insect Parasitoids* 13th Symposium Royal Entomological Society. London: Academic Press, 290–318.

Hamilton WD. 1967. Extraordinary sex ratios. *Science* **156:** 477–488.

Hassell MP, Waage JK, May RM. 1983. Variable parasitoid sex ratios and their effect on host parasitoid dynamics. *Journal of Animal Ecology* **52:** 889–904.

Hudson WG, Williams ML. 1986. Release of the parasitic wasp, *Encarsia lahorensis* (Hymenoptera: Aphelinidae) for control of citrus whitefly (Homoptera: Aleyrodidae) on Gardenia in Alabama. *Environmental Entomology* **15:** 585–589.

Hunter MS. 1993. Sex allocation in a field population of an autoparasitoid. *Oecologia* **93:** 421–428.

Hunter MS, Nur U, Werren JH. 1993. Origin of males by genome loss in an autoparasitoid wasp. *Heredity* **70:** 162–171.

Hunter MS, Godfray HCJ. 1995 Ecological determinants of sex allocation in an autoparasitoid wasp. *Journal of Animal Ecology* **64:** 95–106.

Kennett CB, Huffaker CB, Finney GL. 1966. III The role of an autoparasitic aphelinid, *Coccophagoides utilis* Doutt in the control of *Parlatoria oleae* (Colvée). *Hilgardia* **37:** 255–282.

Keunzel NT. 1975. Population dynamics of protelean parasites (Hym. Aphel.) attacking a natural population of *Trialeurodes packardi* (Hom. Aley.) and new host record for two species. *Proceedings of the Entomological Society Washington* **79:** 400–404.

Noyes JS, Hayat M. 1994. *Oriental mealybug parasitoids of the Anagyrini (Hymenoptera: Encrytidae).* CAB International, Wallingford, U.K. pp 554.

Polaszek A. 1991. Egg parasitism in Aphelinidae (Hymenoptera: Chalcidoidea) with special reference to *Centrodora* and *Encarsia* species. *Bulletin of Entomological Research* **81:** 97–106.

Polaszek A, Stouthamer R, Hunter MS, Rose M, Ovruski SM, Frias E, Rojas SP. 1995. Heterotrophic parasitoids revisited: Preliminary observations on Encarsia porteri (Mercet) (Hymenoptera: Aphelinidae). *Trichogramma and Other Egg Parasitoids, Cairo (Egypt), 4-7 October 1994. Les Colloques de l'INRA* **73:** 31–32.

Rojas SP. 1968. Nota sobre *Prospaltella porteri* Mercet (Hym.: Aphelinidae) un nuevo parasito de huevos de lepidopteros. *Revista Chileana de Entomologia* **6:** 123–125.

Rose M, DeBach P. 1981. Citrus whitefly parasites established in California. *California Agriculture* **35:** 21–23.

Ru N, Sailer RI. 1979. Colonization of a citrus whitefly parasite, *Prospaltella lahorensis*, in Gainesville Florida. *Florida Entomologist* **62:** 59–65.

Stoner A, Butler GD. 1965. *Encarsia lutea* as an egg parasite of the bollworm and cabbage looper in Arizona cotton. *Journal of Economic Entomology* **58:** 1148–1150.

Stouthamer R, Luck RF. 1991. Transition from bisexual to unisexual cultures in *Encarsia perniciosi* (hymenoptera: Aphelinidae): new data and a reinterpretation. *Annals of the Entomological Society of America* **84:** 150–157.

Vet LEM, van Lenteren JC. 1981. The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). X. A comparison of 3 *Encarsia* spp. and one *Eretmocerus* sp. to estimate their potentialities in controlling whitefly on tomatoes in glasshouses 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.

Vigginai G, Mazzone P. 1978. Morfologia, biologia, e utilizzazione di *Prospaltella lahorensis* How. (Hymenoptera: Aphelinidae), parassita esotico introdotto in Italia per la lotta biologica al *Dialuerodes citri* (Ashm.). *Bolletino del Laboratorio di entomologia agraria 'Filippo Silvestri' Portici* **35:** 99–161.

Walter GH. 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.

Walter GH. 1993. Oviposition behaviour of diphagous parasitoids (Hymenoptera, Aphelinidae): A case of intersexual resource partitioning? *Behaviour* **124:** 73–87.

Walter GH, Donaldson JS. 1994. Heteronomous hyperparasitoids, sex ratios and adaptations. *Ecological Entomology*, **19:** 89–92.

Williams JR. 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 JR. 1977. Some features of sex linked hyperparasitism in *Aphelinidae* (Hymenoptera). *Entomophaga* **22:** 345–350.

Williams T. 1989. Sex ratio strategies in the facultatively autoparasitic wasp, *Encarsia tricolor*Förster. PhD thesis, University of London.

Williams T. 1991. Host selection and sex ratio in a heteronomous hyperparasitoid. *Ecological Entomology* **16:** 377–386.

Zinna G. 1961. Ricerche sugli insetti entomofagi. II Specializzione entomoparassitica negli Aphelinidae: Studio morfologico, etologico e fisiologico del *Coccophagus bivittatus* Compere, nuevo parassita del *Coccus hesperidium* L. per l'Italia. *Bolletino del Laboratorio di entomologia agraria 'Filippo Silvestri' Portici* **19:** 301–358.

Zinna G. 1962. Ricerche sugli insetti entomofagi. III Specializzione entomoparassitica negli Aphelinidae: Interdependenze biocenotiche tra due specie associate. Sudio morphologico, etologico e fisiologico del *Coccophagoides similis* (Masi) e *Azotus matritensis* Mercet. *Bolletino del Laboratorio di entomologia agraria 'Filippo Silvestri' Portici* **20:** 73–182.

Zchori-Fein E, Roush RT, Hunter MS. 1992. Male production induced by antibiotic treatment in *Encarsia formosa* (Hymenoptera Aphelinidae), an asexual species. *Experientia* **48:** 102–:105.