

An analysis of the superparasitic behaviour and host discrimination of chalcid wasps (Hymenoptera: Chalcidoidea)

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Abstract. Superparasitism is frequently met with in chalcids. The actual mechanism of suppression of the supernumerary individuals is by mutual combat though exceptions to this general rule may also be seen rarely. Many chalcids are known to discriminate between parasitised and healthy hosts. It is an interesting phenomenon that superparasitism occurs even when a female is capable of discriminating parasitised and unparasitised hosts. Several factors play prominent roles in causing superparasitism and the avoidance of superparasitism by a chalcid is the result of maximisation of its reproductive success.

Keywords. Superparasitism; host discrimination; analysis; chalcids.

1. Introduction

The chalcid wasps are well known for various salient features of their ethology. The majority of chalcids are solitary, developing singly upon their hosts. Superparasitic behaviour is frequently exhibited by many species of chalcids. Superparasitism is the parasitisation of an individual host by more larvae of a single parasitic species than can mature in that host. In superparasitism usually a single parasite individual survives or all may die or the brood may produce undersized weaker adults. When a parasite superparasitises a host it usually condemns its own progeny to death thus resulting in a wastage of its own eggs. To avoid such a contingency it must be able to discriminate between parasitised hosts and unparasitised hosts. Such avoidance of superparasitism is an interesting aspect of insect behaviour. This paper presents an analysis of some of these interesting aspects of the ethology of chalcids.

2. Ethology and analysis

Supernumerary individuals are usually suppressed by destruction by mutual combat between the first instar larvae. They attack each other with their mandibles and finally only one survives. However if an egg is laid in a host that already contained an advanced larva then the younger of the two dies due to oxygen starvation and apparently no fighting occurs in most cases, though autoparasitism and hyperparasitism are occasionally met with in chalcids. A different method of suppression of supernumeraries is seen in an *Elachertus* species (Eulophidae) which is a solitary ectoparasite of caterpillars of *Artona*. In this case when more than one egg is laid on a host, the eclosion of one egg causes immediate cessation of development of the remaining ones (Clausen 1940).

When a chalcid finds a host a sequence of behavioural patterns follow (figure 1).

where $e = 2.72$ (natural logarithm base), and

$$Z = \frac{\text{total number of parasites}}{\text{total number of hosts}}$$

If the actual distribution of parasite eggs differs significantly from the calculated random distribution in the direction of more hosts than expected supporting only one parasite, and fewer than expected remaining unparasitised then it can be said that the parasite exercises discrimination." There are several reports which show that many chalcids have the ability to discriminate parasitised and healthy hosts. *Melittobia acasta* Walker (Eulophidae) will not oviposit in puparia of Diptera which contain either their own larvae or pupae or those of *Pteromalus* (Pteromalidae) or *Dibrachys* (Pteromalidae) (Thompson and Parker 1927). The female *Trichogramma evanescens* Westwood (Eulophidae) is capable of discriminating parasitised hosts from unparasitised hosts (Salt 1934, 1937; Flanders 1937). With her antennae the female can recognise the residual odour of the tarsal gland's secretion left on the eggs that have been walked on by another female of the same species. This was subsequently termed by Flanders (1951) as the 'spoor effect'. Parasitised hosts may be thus detected by the female *Trichogramma evanescens* initially by the antennal 'drumming' on the surface of the host. If this initial examination of the host with the antennae fails to indicate parasitism due to the washing away of the odour by rain or by other means, the female tested the hosts by inserting its ovipositor into the host and withdrawing it immediately (Salt 1934, 1937). The present author in his observations has noted that several species of *Brachymeria* (Chalcididae) were unable to discriminate between parasitised hosts and healthy hosts in the beginning stages and superparasitism was a common occurrence. However the females were found taking a longer time than usual for 'drumming' if they happened to meet hosts which were parasitised for the first time by another female of the same species or by the same female, 4 to 6 days earlier. In such instances the female either abandoned the hosts after a thorough antennal 'drumming' or pierced the host with its ovipositor just to withdraw it immediately and then left the host. It is suggested that changes in the physical or chemical condition of the parasitised hosts might be responsible for providing the stimuli for discrimination between potential hosts (Salt 1938; Wylie 1965; Fisher 1971; Narendran 1975; Narendran and Joseph 1977). In those cases where a parasitised host is detected only after the penetration of the ovipositor, it is evidently the sense organs of the ovipositor that are believed to be responsible for detecting the hosts. Such sense organs especially chemosensory "pores" are seen in several species of chalcids such as *Eurytoma tibialis* Boheman (Eurytomidae), *Brachymeria lasus* Walker (Chalcididae), *Tetrastichus rapo* (Walker) (Eulophidae), *Nasonia vitripennis* (Walker) (Pteromalidae), *Microterys flavus* (Howard) (Encyrtidae), *Aphytis* sp. (Aphelinidae) and in several other species of chalcids (Fulton 1933; Varley 1941; Copland and King 1971a, b, 1972a, b, c; Fisher 1971; King and Rafai 1970; Jackson 1966, 1969; Edwards 1954; Wylie 1958; King and Fordy 1970; Bartlett and Lagace 1961; Quendnau and Hubsch 1964; Weseloh 1969; Narendran 1975; Askew 1971). It is suggested by Fisher (1971) that biochemical changes of the host's haemolymph are likely to act as sign stimuli for discrimination between parasitised and unparasitised hosts. Mouthparts and tarsi are also reported to play a role (probably a minor one when compared to antenna and ovipositor) in the host detection behaviour of certain chalcids of the family Aphelinidae (Viggiani 1984).

In *Spalangia drosophilae* Ashmead, either the smell of the host's haemolymph clotted around the oviposition puncture or the odour of the fluid left by the ovipositor provided the stimulus for the detection of parasitised hosts from healthy hosts (Simmonds 1954). The discharge of a 'venom' presumably from the poison apparatus of the ovipositing female was suggested (Jackson 1966) to be responsible for providing the stimulus for discrimination between parasitised and unparasitised hosts by *Caraphractus cinctus* Walker (Mymaridae). The vibrations produced by the palpation of the host provided the stimulus for discrimination between parasitised host and healthy host in the case of *Microplectron fuscipennis* Zett (Eulophidae) (Ullyett 1936). Similarly movement or lack of movement by the host might contribute part of the stimulus for detecting healthy and parasitised hosts by *Spalangia drosophilae*, and *Nasonia vitripennis* (Simmonds 1954; Wylie 1965). In certain chalcids like *Lasiochalcidia igiliensis* Steffan, (Chalcididae), active movement of the host is an essential requisite for oviposition. This interesting chalcid parasitises the larvae of antlion. The female provokes its host to come out from its burrow and to seize the leg of the chalcid whereupon the chalcid inserts its ovipositor into the membrane between the head and thorax of the host. Among the chalcid parasites of the knapweed (*Centaurea nigra* L.) gall fly (*Urophora jaceana* Hering) only the endoparasitic *Eurytoma tibialis* is able to discriminate parasitised and healthy hosts by avoiding superparasitism whilst the four ectoparasitic chalcids species either distribute their eggs randomly or even in an aggregated manner (Varley 1941). In perilampids and eucharitids the planidium or the first instar larva upon emergence undergoes a freelifing period during which it must find its hosts. In these cases this is "more exactly a waiting period rather than a searching period; for relatively little movement takes place and the greater portion of the time is passed in the erect position awaiting the arrival of a host or carrier" (Clausen 1940). In these cases, the instincts of the planidium are not sufficiently developed to enable it to discriminate parasitised and unparasitised hosts and in several instances the planidium responds to virtually any moving object that approaches its immediate vicinity.

In chalcids, superparasitism is not always caused by the failure of the discriminative ability. In *Trichogramma evanescens*, *Encarsia formosa* Gahan (Aphelinidae), *Pachycrepoides vindemmiae* Rondani (Pteromalidae) and in several other species, superparasitism occurs although the females were capable of discriminating parasitised and unparasitised hosts. One of the possible reasons for this is the breakdown of the 'restraint' of the ovipositing females when there is a scarcity of healthy hosts. Another possible suggested explanation is that the female has to learn to discriminate between parasitised and unparasitised hosts if it is an inexperienced one (Salt 1934; Van Lenteren and Bakker 1975; Van Lenteren *et al* 1978). It is known that the 'restraint' exercised by the chalcid *Caraphractus cinctus* Walker in avoiding superparasitism of water-beetle eggs was best developed in old females and inexperienced young females would superparasitise the hosts (Jackson 1966). In the case of *Ooencyrtus kuwanae* (Howard) (Encyrtidae) the female tends to retain her eggs rather than deposit them if she finds only parasitised hosts and the exercise of this 'restraint' in this case is shown to be related to the developmental stage of the parasite in the parasitised hosts, the age and condition of the ovary of the female and the number and nature of the hosts available (Lloyd 1940). There are several other possible causes for superparasitisation such as, when a female lays more than one egg after the first oviposition within the period which is needed for building up the factor which causes avoidance of superparasitisation and

when two or more females oviposit simultaneously in one host (Van Lenteren and Bakker 1975).

Gregarious parasitism and polyembryonic parasitism are also met with in the case of some chalcids. In these cases two or more individuals can develop in one host but the number is often limited so that the danger of superparasitism is present. Hence in such cases the parasite would have to distinguish not only parasitised hosts from unparasitised hosts but also hosts already bearing a full compliment of parasites from those not yet fully supplied (Salt 1934). This capacity to discriminate parasitised hosts with different number of eggs is found in some species of parasitic hymenopterans including chalcids especially when there is a failure of the 'restraint' to oviposit due to scarcity of healthy hosts. However it is not undoubtedly established how exactly the parasite recognise the hosts with different number of eggs and the only fact so far known clearly is that such an ability does exist atleast in some species. Hence the avoidance of superparasitism in a sense is not only by discriminating parasitised hosts from unparasitised hosts but also by discriminating hosts with different number of eggs.

3. Conclusion

Superparasitism and avoidance of superparasitism are commonly found among chalcids. The stimuli for the discrimination of parasitised and healthy hosts varied from species to species. It may be based on the changes of the physical and chemical properties of the hosts due to parasitisation or based on the odour of the fluid left by the ovipositor or tarsal glands. It can be based on the odour of the haemolymph clotted around the oviposition puncture or based on any other causes. Whatever may be the stimulus, the primary and final detection of hosts are done by chalcids mainly by using antennae and ovipositor respectively, though occasionally either of the two alone is used by certain species.

In chalcids superparasitism is not always caused by the lack of ability to discriminate parasitised hosts and unparasitised hosts. Breakdown of the 'restraint' due to scarcity of healthy hosts, inability to learn to discriminate between parasitised and unparasitised hosts by inexperienced parasites, simultaneous oviposition by more than one or two females on a host, laying more than one egg at an act of oviposition etc, are some of the main possible causes for superparasitism. Avoidance of superparasitism by chalcids, in *sensu lato*, is not only by distinguishing parasitised hosts from unparasitised hosts but also by discriminating hosts with different number of eggs. The avoidance of superparasitism by a chalcid shows the maximisation of its reproductive success and this trait is one of the important attributes of an effective biological control agent.

Acknowledgements

The author thanks Dr R R Askew of University of Manchester for permission to quote from one of his books.

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