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A brief note on unusually high superparasitism in some sawfly parasitoids (Hym., Ichneumonidae: Euryproctini)

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Several cases of unusually high superparasitism in some endoparasitoids of sawfly larvae are described and discussed. All observations refer to members of the tribe Euryproctini of the ichneumonid subfamily Ctenopelmatinae which are also characterized by the possession of a protracted trophamnion stage. The peculiar, heavily armoured first instar larva of *Phobetes atomator* (MÜLLER), a parasitoid of *Selandria sixii* VOLLENHOVEN, is also described.

Keywords: superparasitism, Euryproctini, sawfly parasitoids.

INTRODUCTION

Superparasitism in a solitary parasitoid occurs when 2 or more larvae of the same parasitoid species are found in (or on) a single host individual, but only one parasitoid larva can develop successfully, whereas the others usually perish. The occurrence of supernumerary parasitoid eggs or larvae may be the consequence of a host being attacked more than once by a single parasitoid female ("self superparasitism" sensu VAN DIJKEN & WAAGE, 1987); or it may be the result of several parasitoids of the same species ovipositing in (or on) a single host ("conspecific superparasitism"). Usually, superparasitism leads to the death of the supernumerary parasitoids, frequently due to aggressive interference between the larvae, and may thus be seen as a special form of intraspecific competition common among insect parasitoids.

Whilst formerly superparasitism has generally been interpreted as a wastage of progeny (e.g. HUFFAKER, 1971, VAN LENTEREN, 1981) and therefore as maladaptive, a number of recent studies have challenged this traditional view (e.g. VAN ALPHEN & NELL, 1982, WAAGE, 1986). Several theoretical arguments based upon optimal foraging theory and the theory of sex allocation have been put forward, and examined in laboratory and field studies, asserting that there might be conditions under which superparasitism is adaptive (summarized in VAN ALPHEN & VISSER, 1990). For instance, several parasitoid larvae per host may be more effective in overcoming the defense reaction of the host's immune system, or they may have a better chance to survive in interspecific competition, i.e. when the host is simultaneously attacked by another parasitoid species.

Here we report some scattered observations upon the unusually frequent occurrence of superparasitism in several larval parasitoids of sawflies which may be of interest to those engaged in an experimental analysis of these phenomena. Interestingly, all relevant cases observed by us concern members of the tribe Euryproctini, subfamily Ctenopelmatinae, in the family Ichneumonidae.

The majority of Ctenopelmatinae species is restricted to sawflies as hosts and has possibly undergone a certain degree of parallel evolution with them (PSCHORN-WALCHER 1969). In contrast to the ectoparasitic Tryphoninae, representing another dominant ichneumonid group of specialized sawfly parasites, the Ctenopelmatinae are koinobiotic endoparasitoids of sawfly larvae (GAULD & BOLTON, 1988). Although the eggs are usually laid into the larva of the host, parasitoid development occurs largely at the expense of the cocooned prepupa and is always solitary. Most species show a very high degree of host specificity. All Euryproctini species observed by us were moreover characterized by the existence of a trophamnion in which the embryo and young larva developed and by the fact that this trophamnion stage was often of unusually long duration.

RECORDED OCCURRENCES OF UNUSUAL SUPERPARASITISM

Synomelix scutulatus (HARTIG)

This species (formerly known as *Zemphorus scutulatus*) is a regular larval parasitoid of Diprionid sawflies such as *Diprion pini* (L.), *Microdiprion palipes* (FALLÉN) and *Neodiprion sertifer* (GEOFFR.). Superparasitism has been of common occurrence on *N. sertifer* and 2 or more *Synomelix* larvae per host have been more frequently found than expected by chance, even at very low host densities, i.e. in isolated larval colonies with very low rates of parasitism (PSCHORN-WALCHER, 1967). However, a detailed analysis of the data has not been made.

Mesoleptidea prosoleuca (GRAV.)

This species was reared by RÄTHER (1987) from larvae of *Tenthredo scrophulariae* L. feeding on common figwort (*Scrophularia*) in beech woods. Based upon dissections, overall larval parasitism by this specific ichneumonid was 56 ± 5 per cent. However, up to 6 eggs per host larva have been found, with an average of nearly 2 parasitoids per host individual. Superparasitism was much more frequent than expected by chance.

Euryproctus sinister BRISCHKE

This is a typical larval parasitoid of sawflies of the genus *Caliroa*. An unusually high degree of superparasitism was observed by SCHÖNROGGE (1991) in *C. cinxia* (KLUG), a sawfly monophagous on oaks. A comparison with the Poisson distribution showed that hosts with 3 or more parasitoid eggs per host larva were nearly 3 times more common than expected ($p < 0.001$). In the maximum, 10 eggs of *E. sinister* have been found in a single host larva. The occurrence of high numbers of parasitoid eggs per host was independent of host density and of the degree of parasitism observed. Obviously the same species, tentatively referred to as *Synomelix* sp., has already been reared earlier by CARL (1976) from the common pear slug, *Caliroa cerasi* (L.). However, in this case superparasitism, although of frequent occurrence, conformed well to the Poisson series (comp. Tab. 8 in CARL, 1976). Up to 7 eggs per host were found in the maximum. CARL stated that no more than one egg was laid during a single attack which agreed with the findings in laboratory experiments, but that ovipositing females were unable to distinguish hosts that were already parasitized.

Hypamblys albopictus (GRAV.)

This species is a common parasitoid of various Nematinae sawflies. It is possible that a complex of closely related, host-specific species is involved as e.g. individuals reared from the alder sawfly *Hemichroa crocea* (GEOFFR.) differ in colouration from those associated with the larch sawfly, *Pristiphora erichsonii* (HARTIG). Heavy superparasitism has already been reported to occur in the latter host (PSCHORN-WALCHER & ZINNERT, 1971).

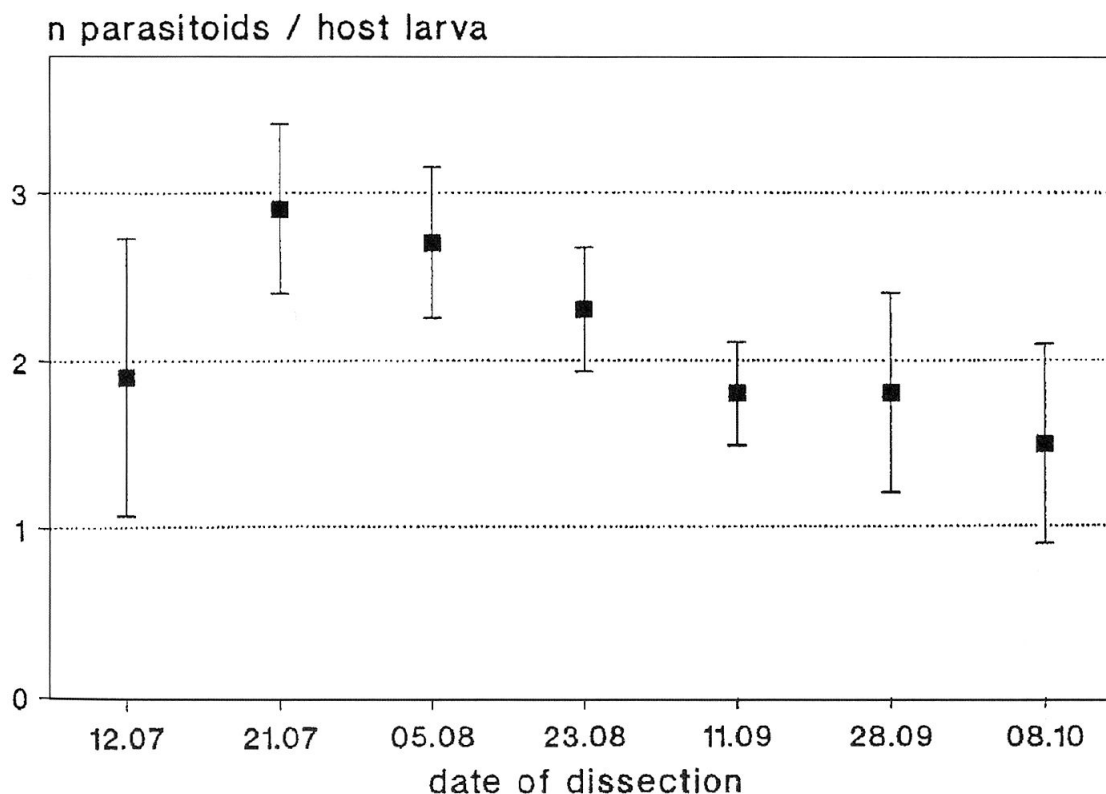


Fig. 1. Number of eggs and/or trophamnions of *Hypamblys albopictus* per parasitized host larva during the season of 1987 (near Kiel). (Mean and 95 % C.L.).

Recently, unusually high superparasitism has been recorded by one of us (W.H.) in the larvae of *Platycampus luridiventris* (FALLÉN), a sawfly common on *Alnus* spp. Fig. 1 shows the average number of parasitoid eggs and trophamnions observed per parasitized host larva during the season of 1987 on road-side trees near Kiel. Oviposition by the parasitoid into very young host larvae occurred during the first half of July and was completed by about mid-July. On July 21, as many as 2.9 parasitoid eggs per parasitized host larva have been found on average. Due to encapsulation and natural mortality this number decreased steadily during the season. On October 8, an average of 1.5 trophamnions per parasitized host were still present in the dissected host material, this stage lasting well into the hibernation period.

Comparing the parasitoid distribution with the Poisson series, highly significant differences ($p < 0,001$) were observed in 1987 and 1990, and a significant deviation ($p < 0,05$) was also found in 1986. In all three years the number of hosts

with one parasitoid per host larva was always considerably lower than expected, whereas superparasitized hosts, especially those with 3 or more parasitoids, were clearly more common than expected assuming a random distribution of progeny. In 1988 and 1989 the differences were not significant, probably due to the limited data available for these years. The maximum number of eggs per host was 14. Laboratory observations indicated that both, self superparasitism and conspecific superparasitism were involved.

DISCUSSION

Admittedly, the fragmentary data presented here are quite "weak", excepting perhaps those on *Hypamblys albopictus*. In addition, only field data are available the interpretation of which is often doubtful (VAN LENTEREN, 1981). However, the unusually frequent appearance of superparasitism in species of the ichneumonid tribe Euryproctini, independent of host density and rate of parasitism, contrasts strongly with the many other sawfly parasitoids of the other tribes of the subfamily Ctenopelmatinae forming the major component of typical endoparasitoids of sawfly larvae. In these species superparasitism was usually density dependent and conforming to the Poisson distribution indicating that its occurrence was mainly due to chance, and thus high only when total parasitism was high. Typical examples from our own working group are: e.g. *Lophyroleptus oblongopunctatus* (HARTIG), a specific larval parasitoid of *Neodiprion sertifer* (GEOFFR.) (PSCHORN-WALCHER, 1967), *Lathrolestes nigricollis* THOMS., parasitizing larvae of the leaf-mining sawfly *Fenusa pusilla* (LEPEL.) (EICHORN & PSCHORN-WALCHER 1973) or *Lathrolestes luteolator* (GRAV.), a common larval parasitoid of *Caliroa cerasi* and of other sawfly species (CARL, 1976). These parasitoid species belong to the tribe Perilissini of the subfamily Ctenopelmatinae and lack a trophamnion during early development.

If we accept the possibility that superparasitism is a regular phenomenon in at least several members of the tribe Euryproctini, then the question arises how it originated and what advantages are involved. As no laboratory experiments have been made it cannot be decided whether Euryproctini females are unable to distinguish between unparasitized and parasitized hosts. It is also unknown whether the parasitoid species recorded lay frequently more than one egg per oviposition (self superparasitism) or whether the same host individual is more or less regularly attacked by 2 or more parasitoid females (conspecific superparasitism). The latter could arise e.g. because some host larvae are more "apparent" than others and thus more easily found, or because parasitized host individuals are more "attractive" for conspecific parasitoid females.

It also remains to be seen whether there exists a correlation between the unusual degree of superparasitism and the existence of a protracted trophamnion stage in the Euryproctini species involved. Species with a long trophamnion period might be especially vulnerable to multiple parasitism, as their young larvae enveloped in a sac are not able to actively defend themselves against aggressive larvae of a competing parasitoid species. Recently, a very strange and large first instar larva of the caudate type has been found with larvae of the grass-feeding sawfly *Selandria sixii* VOLLENH. which turned out to belong to the Euryproctini species *Phobetes atomator* (MÜLL.) (C. PUSCH, pers. comm.). Whereas all other endoparasitic ichneumonid larvae hitherto dissected out of sawfly larvae are rather weakly segmented and sclerotized, whitish or transparent (except the head-capsule), the young larvae of *P. atomator* are very distinctly articulated, heavily sclerotized and of brownish colour,

only the base of the "tail" and the tail itself being of "fleshy" appearance. The meal-worm-like sclerotization and colouration of these larvae is so conspicuous that they can easily be seen from the outside within the large, greencoloured host larvae. The development of this protective "armour" might be an alternative strategy to survive in cases of intrinsic competition. If this assumption is correct, then superparasitism should be of little advantage to the well defended larvae of *P. atomator*. Unfortunately, detailed data on the level of parasitism are not yet available.

As incomplete as the observations reported here may be, as interesting might they be if they could be confirmed by more data upon more species of Euryproctini ichneumonids. The aim of this brief article is to draw the attention of other researchers to this interesting group of sawfly parasitoids, a more detailed examination of which may help to provide new insights into the complex phenomenon of superparasitism in insect parasitoids.

ZUSAMMENFASSUNG

Es werden mehrere Fälle von ungewöhnlich hoher Superparasitierung bei Endoparasiten von Blattwespenlarven diskutiert. Alle diesbezüglichen Befunde beziehen sich auf Schlupfwespen der Tribus Euryproctini der Ichneumoniden-Unterfamilie Ctenopelmatinae, die außerdem durch das regelmäßige Auftreten eines verlängerten Trophamnion-Stadiums gekennzeichnet sind. Zusätzlich wird ein ungewöhnlich stark gepanzerter Junglarventyp für die in *Selandria*-Larven schmarotzende Schlupfwespe *Phobetes atomator* (MÜLLER) (Euryproctini) beschrieben.

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