

Precocious larvae in the polyembryonic parasitoid *Copidosoma sosares* (Hymenoptera: Encyrtidae)

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Abstract: In polyembryonic Hymenoptera, many larvae develop clonally from a single egg. Some species exhibit within-clone dimorphism: most larvae eventually develop into adult parasitoids, but a minority of precociously developing larvae differ in form and die before pupation. Precocious larvae in some (and possibly all) species defend their genetically identical siblings from competition by other parasitoids. In this paper I document, for the first time, the occurrence and prevalence of precocious larvae in *Copidosoma sosares* (Hymenoptera: Encyrtidae) and discuss their possible function.

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Introduction

Polyembryony, defined as the production of multiple embryos from a single egg, has evolved in four families of parasitoid Hymenoptera: Braconidae, Platygasteridae, Dryinidae and the Encyrtidae (Ivanova-Kasas, 1972). Polyembryony is the most extreme in the copidosomatine encyrtids where up to 3000 larvae can be produced from just one egg (Ode & Strand, 1995). In some encyrtid species, genetically identical larvae are dimorphic. The majority, termed 'reproductive' larvae, eventually pupate and develop into adult parasitoids. A minority of larvae develop precociously into 'asexuals' which die before pupation.

Such precocious larvae were first described in *Copidosoma truncatellum* (Dalman) (probably a misidentification of *Copidosoma floridanum* (Ashmead) (Noyes, 1988)) by Silvestri (1906) who suggested that their function is to macerate host tissues to assist their siblings in feeding. This explanation for their reproductive altruism has, however, been supplanted by subsequent observations of larval behaviour which suggest that precocious larvae protect their genetically identical siblings from both inter- and intraspecific resource competition. Precocious larvae of both *Copidosoma tanytmemus* Caltagirone and *C. floridanum* have been observed attacking larvae of

competing endoparasitic species (Cruz, 1981, 1986a; Grbić & Strand, 1991) offering a compelling explanation for the observed success of polyembryonic species faced with interspecific competition (Browning & Oatman, 1984; Cruz, 1986a; Strand et al., 1990). Furthermore, precocious larvae developing from female *C. floridanum* eggs attack their male siblings when male and female eggs are laid in the same host (Grbić et al., 1992). Intersexual attack is probably explained by the differing sex ratio optima of males and females due to the details of adult mating behaviour; the sex ratio conflict is apparently settled in favour of females (Grbić et al., 1992; see also Godfray, 1992; Hardy, 1994).

There is a large interspecific, intersexual and intrasexual variation in the production of precocious larvae, the causes and consequences of which are not fully understood. For instance, *C. floridanum* and *C. tanytmemus*, respectively produce up to about 50 and 20 precocious larvae in each host (Cruz, 1986b; Grbić et al., 1992), while some polyembryonic species may lack precocious larvae altogether (references in Cruz, 1986a). In *C. koehleri* Blanchard (probably a misidentification of *Copidosoma desantisi* Annecke and Mynhardt (Annecke & Mynhardt, 1974)) precocious larvae are found in female but not male broods (Doutt, 1947). In *C. floridanum*, broods of

both sexes produce precocious larvae, but they are usually more numerous in female broods, and are also produced earlier during brood development in females (Grbić & Strand, 1991; Grbić et al., 1992). The age of the host-egg in which the female *C. floridanum* oviposits has also been shown to influence the production of precocious larvae by the subsequently developing brood (Ode & Strand 1995).

In this paper, which forms part of an investigation into the reproductive biology of the polyembryonic encyrtid *Copidosoma sosares* (Walker), I report that precocious larvae are produced and investigate the between-brood variation in their numbers.

Biology of *C. sosares* and its host

Like all known polyembryonic encyrtids, *C. sosares* is an egg-larval parasitoid of Lepidoptera. Its life history appears to be quite similar to that of other polyembryonic encyrtids (e.g. Cruz, 1986b; and see Godfray (1994, pp 10-12) for the most recent summary). *Copidosoma sosares* females parasitize the eggs of *Depressaria pastinacella* Duponchel (Lepidoptera: Oecophoridae) in the spring. The parasitized host eggs hatch into larvae which feed and develop until the end of their larval stage, whereupon the host body contents become completely consumed by the parasitoid brood and the host forms a stiff 'mummy', inside which the parasitoids pupate. Adult parasitoids emerge several weeks later (late August to early September, personal observations). Like its host (Gorder & Mertins, 1984), *C. sosares* appears to be univoltine and to overwinter in the adult stage. Brood sizes at emergence range from less than 10 to more than 300 individuals, and may contain only males, only females or both sexes (I. Hardy, unpublished data). Mixed sex broods almost certainly arise from the oviposition of more than one parasitoid egg into the host.

Depressaria pastinacella females oviposit onto the leaves and flower stalks of various members of three genera of Umbelliferae: *Heracleum*, *Angelica* and *Pastinaca* (e.g. Gorder & Mertins, 1984; Nitao & Berenbaum,

1988; Hendrix & Trapp, 1989; Berenbaum, 1991). On hatching, *D. pastinacella* larvae move to the floral structures, feeding inside the umbel petiole sheaths and also on more mature flowers and fruits. Larvae typically bore into the plant stem before pupation, emerging several weeks later to overwinter as adults (Gorder & Mertins, 1984; I. Hardy, personal observations). In The Netherlands, I have found *D. pastinacella* (and *C. sosares*) most commonly on *Heracleum sphondylium* L. but also on *H. mantegazzianum* Sommier and Levier and *Pastinaca sativa* L. However, I have not found *D. pastinacella* on *Angelica sylvestris* L. or (in concord with the literature) on other Umbelliferae such as *Anthriscus sylvestris* (L.) Hoffm. or *Aegopodium podagraria* L., despite year round entomological field work involving these plant species.

Methods

Depressaria pastinacella larvae were collected from *H. sphondylium* growing in a patch of partially wooded wasteland next to a railway line, a canal and near urban dwellings in Leiden, The Netherlands at the end of July 1995. *Heracleum sphondylium* plants which hosted *D. pastinacella* larvae were obvious due to the webbed-up and damaged appearance of their umbels and by the holes in their stems made by larvae entering the hollow stem prior to pupation. Some larvae were collected from the umbels on which they were feeding, but most were collected from inside the stems by slicing these open longitudinally. A total of 171 motile larvae was collected. Twenty mummified *D. pastinacella* larvae found inside the stems were also collected, but pupae were not (because they were not parasitized by egg-larval parasitoids).

Motile and mummified *D. pastinacella* larvae were brought back to the laboratory and individually dissected under a binocular microscope using fine needles. Following decapitation the body contents of motile larvae were squeezed out into a drop of water. The remains of the larvae were then ripped open to expose remaining tissue. The contents of the larvae



Figure 1. Well developed reproductive larvae.

were examined for the presence of parasitoid larvae or developing parasitoid tissue. When parasitoid broods or tissue were found, they conformed closely to published descriptions of immature polyembryonic encyrtids. In previous collections from the same field site (I. Hardy, unpublished data) almost all parasitized *D. pastinacella* larvae contained *C. sosares* (identified by J.S. Noyes, British Museum, Natural History, London [where voucher material is lodged]), and no other *Copidosoma* species were found. Thus all parasitoid broods were assumed to be *C. sosares*. In each host, *C. sosares* broods were scored as present or absent and the number of precocious larvae in each host counted. Mummified hosts were also dissected and any precocious larvae found were counted.

Results

Thirty of the 171 motile larvae contained 'reproductive' parasitoid larvae or developing tissue. Developing tissue could be distinguished from that of the host (such as white fatty tissue) by its slightly brown colour and lobed appearance. Parasitoid tissue was found in a range of developmental stages. As development advances, the volume of tissue increases and the lobes become more defined until they form distinct embryos which then become separate larvae. Reproductive larvae are initially transparent, but larger, more developed, larvae take on a light yellow colour. On dissection of the host, larvae are very obvious, not least due

to their large numbers (fig. 1). Larvae develop to virtually fill the host, by which time host fatty tissue is absent, presumably consumed by the parasitoid brood. When hosts were dissected, parasitoid larvae could clearly be observed ingesting particles floating in the water around them. However, larvae were not obviously associated with any particular host tissue or part of the host's anatomy. Hosts which were mummified but not stiff were found to contain parasitoid larvae. Stiff mummified hosts contained parasitoid pupae which are, initially, white. There was an approximately twofold variation in size among the collected motile hosts. Although parasitoids were found in both small and large hosts, large *D. pastinacella* larvae very frequently contained *C. sosares*. Mummified hosts were large and bloated in comparison to active larvae. These observations suggest that parasitized *D. pastinacella* may undergo a supernumerary larval instar, as reported for hosts of another *Copidosoma* species (Jones et al., 1982).

Precocious larvae were found in 27 of the 30 motile hosts and also in 3 of the 20 mummies (in these 3 cases the mummified larvae were not stiff and contained reproductive larvae rather than pupae). Precocious larvae occurred singly, with one exception in which six precocious larvae were found in a motile host. Precocious larvae were approximately 1.7-3.4 mm long and were clearly different from reproductive larvae (figs 2-3). All precocious larvae had yellow coloured intestines and a clear integument. Mandibles could not be clearly observed.

Precocious larvae were motile but, at least when the hosts were dissected, did not appear to differ greatly in motility from large reproductive larvae. Precocious larvae were normally found 'free' in the host haemocoel, among the reproductive brood and not associated with any particular host tissue or part of the host's anatomy. There were no obvious differences in morphology or mobility between precocious larvae found in hosts containing reproductive brood tissue, small larvae, large larvae or in mummies. Clearly, precocious larvae do indeed have very ad-



Figure 2. Precocious larva.

vanced development as they are already fully formed when the reproductive brood consists of yet undifferentiated tissue.

Discussion

To my knowledge, this is the first record of precocious larvae in *C. sosares*. There can be little doubt that the observed serpentine larvae are indeed precocious 'asexual' larvae: the resemblance to published drawings and photographs of precocious larvae of other polyembryonic encyrtids is striking (e.g. Silvestri, 1906; Cruz, 1981, 1986b; Grbić et al., 1992). In addition, they were never found in hosts which did not contain reproductive larvae or developing tissue, making extremely unlikely the possibility that they belong to another species.

Precocious larvae are present in most *C. sosares* broods. Although it is unlikely that I did not find intact precocious larvae in a motile host once dissected, it remains possible that precocious larvae may have been inadvertently destroyed during the dissection process. It is thus not possible to determine whether the recorded absence of precocious larvae from three motile but parasitized hosts is a biological phenomenon or an experimental artifact. Studies on other polyembryonic encyrtids indicate that precocious larvae die once the reproductive larvae pupate (e.g. Cruz, 1986b; Strand, 1989). It is thus not surprising that precocious larvae were found only in newly mummified hosts in which the brood was yet

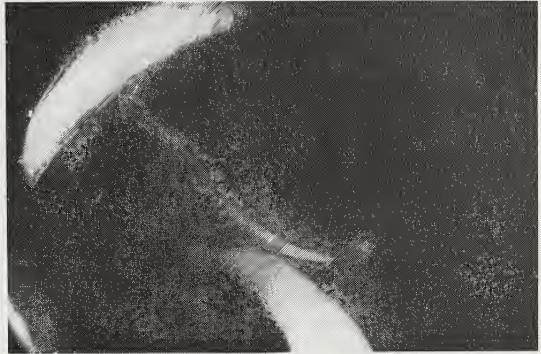


Figure 3. Precocious larva between two reproductive larvae from the same brood.

to pupate and not in stiff mummies containing *C. sosares* pupae.

The production of precocious larvae in *C. sosares* is low in comparison with some other polyembryonic species (e.g. Cruz, 1986b; Grbić & Strand, 1991). Most broods contain just one precocious larva, although there is a small degree of variation (even if recorded absences are artifacts) since six precocious larvae were found in one of the hosts. The importance of this finding is unclear, but it is possible that multiple precocious larvae arise due to superparasitism (multiple females parasitizing one host). However, five of the six precocious larvae found in this host were in close association with each other and displayed none of the aggressive behaviour which might be expected if they were not genetically identical. Furthermore, the reproductive larvae in this particular brood were well developed, implying that the precocious larvae had coexisted in the host for several weeks. Although in this study I was unable to determine the sexual composition of immature broods, it seems unlikely that there is much inter-sexual variation in precocious larval production in *C. sosares*, in contrast to some other *Copidosoma* species (Doutt, 1947; Grbić & Strand, 1991).

The role of precocious larvae in *C. sosares* is unknown, although there are several plausible possibilities. *Copidosoma sosares* broods are occasionally hyperparasitized by *Tyndarichus scaurus* (Walker) (Hymenoptera: Encyrtidae) and either multi- or hyperparasi-

tized by *Dibrachys* sp. (Hymenoptera: Pteromalidae) (the latter trophic relationship is not clear, I. Hardy, unpublished data). Further, three unidentified species of Ichneumonidae, and possibly one Braconid species, are also parasitoids of *D. pastinacella* (I. Hardy, unpublished data, E. Dijkstra, personal communication). These observations suggest that precocious larvae may defend the reproductive brood against interspecific competition. The prevalence of superparasitism in *C. sosares* is unknown, but precocious larvae could also function to defend against conspecific competitors. A role in influencing the sex ratio of mixed sex broods (Grbić et al., 1992) is also possible as about 12% of *C. sosares* broods contain both sexes (I. Hardy, unpublished data). Although it currently seems unlikely that precocious larva production differs between the sexes, among mixed sex broods females tend to predominate on adult emergence (I. Hardy, unpublished data). Future investigations will examine these possibilities further.

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