

COTESIA (APANTELES) POPULARIS L. PARASITOIDS
DO NOT ALWAYS KILL THEIR HOST

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According to the generally accepted definition, parasitoids are natural enemies of which the larvae feed upon a host and eventually kill it. We report on an exceptional case in which two full-grown hymenopteran parasitoid larvae left their lepidopteran host without killing it and successfully produced cocoons. The host larva successfully pupated. Observations of survival of both parasitoids and lepidopteran hosts are extremely rare and only reported for tachinid flies as parasitoids (Richards & Waloff, 1948; DeVries, 1984; English-Loeb *et al.*, 1990). In the latter study 6 out of 22 caterpillars of the Arctiid moth *Platyprepia virginialis* Bdv, from which the tachinid parasitoid *Thelairia bryanti* Curran emerged, survived and produced offspring. Quicke (1997) gives some examples of lepidopteran larvae that carried on moving and feeding for up to two weeks following emergence of braconid parasitoids; he explicitly states "but they always die without pupating". There are a few observations on other host groups (Quicke, 1997), but we know of no other reports on lepidopteran hosts surviving hymenopteran parasitism.

C. popularis (Braconidae, Microgastrinae) (fig. 1) is a specialist gregarious parasitoid of the cinnabar moth, *Tyria jacobaeae* L. (Arctiidae). Both host and parasitoid have a single generation per year. Adult hosts can be observed between the end of April and the beginning of July, caterpillars between May and August. We once observed a fresh cinnabar moth flying in the second half of October; but we do not know of other observations of a second generation. The life cycle of *C. popularis* is similar to that of most other Microgastrinae (Shaw & Huddleston, 1991): after leaving the host larva, it hibernates as a larva and only pupates late in the next season, before emerging as an adult (Cameron, 1935). Experimentally provided with first to fourth instar larvae of *T. jacobaeae*, we found *C. popularis* to parasitize only first and second instar larvae of its host. Up to 15 parasitoid larvae were found to emerge from a single host larva (van der Meijden, 1980). Dempster (1971) calculated mean values of 5 to 6 *Cotesia* larvae per host in Weeting Heath (U.K.). From fully fed *Tyria* caterpillars in Meijndel (the Netherlands) 5 to 9 *Cotesia* larvae were raised (van der Meijden, 1980). The number of successfully developing larvae strongly depends on the amount of food consumed by their host. The host, *T. jacobaeae*, completely defoliates its food plant *Senecio jacobaea* (ragwort) once every two or three years (Dempster, 1982; Crawley & Gillman, 1989; van der Meijden *et al.*, 1998). Especially late-season larvae may be faced with food shortage and starvation. This has probably selected for a relatively early phenology of the parasitoid, compared to its host (Soldaat, 1991). Both in years of total defoliation of

S. jacobaea and in years without food shortage the percentage parasitism is high among early-season caterpillars of *T. jacobaeae* and drops sharply among later developing caterpillars (van der Meijden *et al.*, in prep.). This time pattern of parasitization enables the host to increase in numbers in years without defoliation and starvation. This is one of the reasons why the parasitoid *C. popularis* is not able to regulate its host population and thus prevent total defoliation of its host's food resource. Dempster (1982) even found an inverse density-dependent relationship between percentage parasitism and host population density. The poor dispersal ability of the parasitoid compared to its host is probably another important reason. The food plant of *T. jacobaeae*, ragwort, is very patchily distributed. In coastal dunes we can distinguish a metapopulation consisting of small local populations (van der Meijden & van der Veen-van Wijk, 1997). The host, *T. jacobaeae*, seems to be much more successful in colonizing new food-plant patches than the parasitoid (van der Meijden, 1980; van der Meijden & van der Veen-van Wijk, 1997).

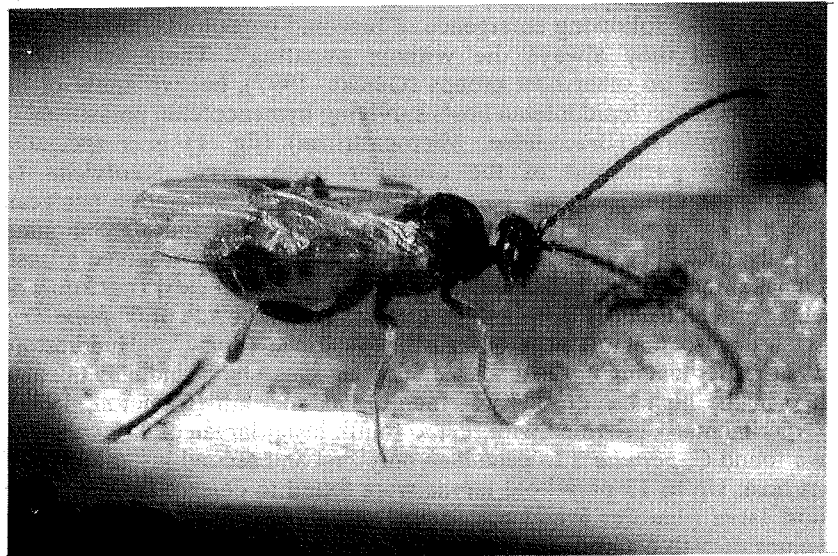


Fig. 1. — *Cotesia popularis* female. (Photograph by Kees Kofker.)

During the last 8 years we have collected information on parasitism by sampling 5 different sampling sites (local populations) within the metapopulation, at three different sampling dates during the season. Sampled caterpillars were placed singly in glass vials and their fate, either survival as a pupa, death as an unparasitized larva or death as a parasitized larva was recorded (Table 1). In 1998 it was found that one of the (499) sampled caterpillars was parasitized but nevertheless able to pupate

successfully. Only two parasitoid larvae emerged from the host larva and produced cocoons.

TABLE 1. — PARASITISM OF *TYRIA JACOBABAEAE* BY *COTESIA POPULARIS*.

Year	sample size	percentage parasitism
1991	785	0.3
1992	852	0.8
1993	787	4.7
1994	740	8.8
1995	677	7.4
1996	786	10.3
1997	831	3.2
1998	499	7.8

In order to find out whether we were dealing with a living pupa or simply a case of delayed death NMR measurements were performed on a Bruker MSL400 spectrometer (magnetic field strength 9.4 T). For the spectral references a creatine phosphate solution in H₂O was used. By comparing living with dead pupae we found differences in the spectra of both ¹H and ³¹P. It is most likely sugar phosphates that were (almost) absent in dead pupae. We could not find any differences between the pattern of the spectra of the pupa of the parasitized larvae and the pattern of living pupae and conclude that the first mentioned pupa was still alive in December 1998. This was confirmed in June 1999 when the (female) moth successfully hatched from the pupa.

Lepidopteran hosts of braconids may remain alive for a few days after the parasitoid larva has emerged. As mentioned earlier there are even some examples of lepidopteran larvae that continued to move and feed for some time following emergence of braconid parasitoids. Shaw & Huddleston (1991) explain this temporary survival by the feeding behaviour of these parasitoids. They are essentially haemolymph and fat-body feeders that leave the host incompletely consumed. The successful pupation that we described can probably be explained by the combination of a low number of *Cotesia popularis* larvae in combination with this feeding habit.

The extraordinary interaction between parasitoid and host described fits the definition of parasitism instead of parasitoidism. It is interesting to consider the possibility of evolution of life histories derived from parasitoids (see Godfray, 1994). The three players in this evolutionary game are the host, the parasitoid and finally its offspring. Without any doubt a host will gain in fitness when it evolves some form of tolerance to parasitoids leading to true parasitism. It might, however, gain more by evolving a defence mechanism, like encapsulation of eggs. We do not know anything about the relative importance of these two mechanisms, and about possible trade offs. By laying eggs in batches, resulting in coherent groups of first and second instar larvae, the host is able to reduce

mortality among its early instar offspring (Dempster, 1971; van der Meijden, 1979). Disturbed early-instar larvae demonstrate an escape reaction by dropping themselves from the leaf that they were feeding on, but nevertheless keep contact through a life line (a silk thread). We think that this life line is also effective in reducing parasitism. Once an adult *Cotesia* parasitoid has successfully selected a host for oviposition, it 'pumps' several eggs in that host.

Parasitoids may reduce their host numbers considerably, and consequently reduce survival chances of their own offspring. Nevertheless, in general, there is no evolutionary advantage in evolving mutualistic relationships with hosts leading to survival of individual hosts. Leaving individual hosts alive will also benefit the offspring of other parents. The evolution of gregariousness in parasitoid wasps (Mayhew, 1998), leading to optimal clutch size should be viewed in this context. Clutch sizes smaller than the optimal value, however, may occasionally lead to individual host survival. Such small clutch sizes may be the result of a variety of processes:

- a, defensive behaviour of host larvae leading to early leaving of adult parasitoids;
- b, running out of eggs of parasitoids;
- c, errors in estimating optimal clutch size by the parasitoid.

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