

Apparent competition between parasitoids mediated by a shared hyperparasitoid

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Abstract

Cocoons of the specialist parasitoid *Cotesia melitaeorum*, which attacks the Glanville fritillary butterfly in the Åland islands of SW Finland, are parasitized by the generalist hyperparasitoid *Gelis agilis*. We added experimentally to the system a second host species for *G. agilis*, *C. glomerata*, with which *C. melitaeorum* does not compete for resources. After the one-time addition of the second parasitoid the natural populations of *C. melitaeorum* declined in the treatment, as predicted by the apparent competition theory.

Keywords

Apparent competition, *Cotesia*, indirect interactions, parasitoid, population dynamics, species assemblages.

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INTRODUCTION

Apparent competition refers to an indirect relationship between species at the same trophic level that do not share resources. The mutually negative interaction, which therefore may appear like competition, is the consequence of shared enemies rather than shared resources (Holt 1977; Bonsall & Hassell 1998; Hudson & Greenman 1998). Apparent competition may have significant consequences for the structure and persistence of species assemblages and it may even lead to the elimination of one of the apparent competitors (Holt 1977; Begon *et al.* 1996; Rott *et al.* 1998; Bonsall & Hassell 1999; Crooks & Soulé 1999). Most empirical evidence for apparent competition concerns herbivores with a shared generalist parasitoid (Bonsall & Hassell 1998; Müller *et al.* 1999) or pathogens (Schraggs & Wiener 1995). In this paper we present the result of a manipulative field experiment in which we find evidence for short-term apparent competition between two primary parasitoids mediated by a shared secondary parasitoid (hyperparasitoid).

MATERIALS AND METHODS

The host-parasitoid system

The parasitoid wasp *Cotesia melitaeorum* (Wilkinson) (Hymenoptera: Braconidae) parasitizes the Glanville fritillary butterfly, *Melitaea cinxia* (L.) (Lepidoptera: Nymphalidae), in the Åland islands in SW Finland (Lei *et al.* 1997; Hanski 1999). The host butterfly lives in small

local populations (Hanski *et al.* 1995), some of which are inhabited by the parasitoid, which has no other hosts in the study area (Lei 1997; van Nouhuys, personal observation). There is a lot of turnover both in the host (Hanski 1999) and in the parasitoid populations (Lei & Hanski 1997; van Nouhuys & Hanski 1999). The host butterfly lays eggs in clusters of 100–200 in June, and caterpillars live gregariously in a communal web until just before pupation in the following May (Kuussaari 1998). The parasitoid *C. melitaeorum* has two to three generations during each host generation and overwinters within the host larva (Lei *et al.* 1997; van Nouhuys, personal observation).

The wingless generalist parasitoid *Gelis agilis* (Hymenoptera: Ichneumonidae) parasitizes the cocoons of *C. melitaeorum* (Lei *et al.* 1997). This secondary parasitoid has been shown to strongly aggregate in response to a high local density of *C. melitaeorum* cocoons (Lei & Camara 1999). Because *G. agilis* is wingless, spatial aggregation to host cocoons in a small area is likely to lead to a high level of hyperparasitism in the next host generation at that spot.

Experimental design

In the spring of 1998 three pairs of host butterfly populations inhabited by *C. melitaeorum* were chosen. The two populations in each pair were 300–800 m apart and of similar host food and nonhost food plant density. Our intention was to pair populations that were the most similar ecologically given the great variation in the host and parasitoid population sizes, and the limited number of suitable parasitoid populations in the spring of 1998. The

pairs differed from each other in habitat and host plant composition and were separated by 20–30 km.

One population from each pair was chosen randomly to receive *Cotesia glomerata* (Hymenoptera: Braconidae) cocoons. *Cotesia glomerata* does not compete for resources with *C. melitaearum*, as the former species parasitizes butterflies in the genus *Pieris*, which feed primarily on plants in the mustard family. There are no hosts or even host food plants for *C. glomerata* within the *M. cinxia* habitat patches. Nonetheless, *C. glomerata* is known to be a suitable alternative host for the generalist secondary parasitoid *G. agilis* (Lei 1997).

Cotesia glomerata was reared in the laboratory from *Pieris brassicae* caterpillars fed on cabbage. In mid-May 1998 30 fresh cocoon clusters were gathered and the number of cocoons per cluster counted (or estimated in some cases to avoid destroying the cluster). Ten clusters were distributed in each of the treatment populations, giving a total of 250–300 cocoons per population. Each cluster was placed within 20 cm of a *M. cinxia* larval nest to attract hyperparasitoids close to the host larval of *C. melitaearum*. The addition of *C. glomerata* cocoons represents a several fold increase in the number of hosts available for parasitism by *Gelis agilis* in the early spring.

In the spring of 1998 and 1999 we counted the number of *M. cinxia* larval nests, the number of larvae per nest, and the number of *C. melitaearum* cocoons in each population. In the autumn of 1998 and 1999 we counted the *M. cinxia* larval nests. On three days during the flight season in 1999 we counted the numbers of adult butterflies. The length of time spent searching for adult butterflies was proportional to the area of the habitat patch.

RESULTS

All three populations of the target parasitoid *C. melitaearum* in host populations receiving cocoons of the second parasitoid (*C. glomerata*) declined, two of them declining in fact to extinction (Fig. 1). Meanwhile, all untreated populations increased or remained the same (Fig. 1). As we do not have independent data to estimate the probability of decline, or increase, in the populations of *C. melitaearum*, we condition the analysis with the observed number of declines. Thus, taking the observed number of declines (three out of six) as given, the probability of all three declines occurring in the treatment populations is $(3/6)(2/5)(1/4) = 0.05$.

CONCLUSION

The most likely mechanism for this result is apparent competition via the generalist secondary parasitoid, *Gelis agilis*. These parasitoids are known to aggregate within

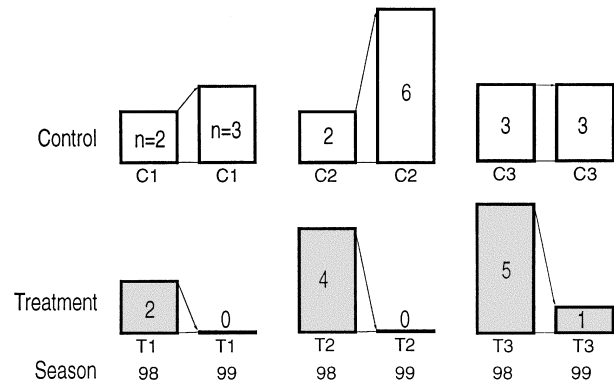


Figure 1 The number of *M. cinxia* nests parasitized by the target parasitoid *C. melitaearum* before (1998) and after (1999) addition of the second parasitoid to the treatment populations (T1, T2, T3).

one generation where their host density is high (Lei & Camara 1999) and their progeny are not likely to leave the patch quickly because they are small and wingless. Thus, addition of *C. glomerata* in the spring probably increased the local hyperparasitoid density so that an exceptionally large fraction of the summer generation of *C. melitaearum* was parasitized.

A predicted consequence of the decrease in *C. melitaearum* in the autumn of 1998 is an increase in the host butterfly population size in the summer of 1999. In one of the three pairs of populations, the summer of 1999 butterfly density relative to the number of larvae in the spring, was indeed twice as high in the treatment than in the control population, but in the other two pairs the result was opposite (Table 1). Lack of consistent response in the butterfly is perhaps not very surprising considering the many other factors apart from parasitism that are known to influence population change in *M. cinxia* (Hanski 1999). All of the *C. melitaearum* populations included in this study were small and it has been shown previously that *C. melitaearum* only has a strongly negative impact on *M. cinxia* populations under certain circumstances (Lei & Hanski 1997; van Nouhuys & Hanski 1999). Thus our results demonstrate apparent competition among the primary parasitoids mediated by the shared hyperparasitoid, but the consequences do not, in this case, extend to the next lower trophic level.

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Table 1 The number of *M. cinxia* and *C. melitaeorum* in the treatment (T) and control (C) paired populations in 1998 and 1999

Population	<i>M. cinxia</i> nests Spring 98	Parasitized <i>M. cinxia</i> nests Spring 98	<i>M. cinxia</i> nests Fall 98	<i>M. cinxia</i> larvae Spring 99	Parasitized nests Spring 99	<i>M. cinxia</i> 99 adults per Spring 99 larvae	<i>M. cinxia</i> nests Fall 99
C1	16	2	11	253	3	0.03	2
T1	24	2	20	508	0	0.02	17
C2	7	2	35	291	6	0.13	29
T2	7	4	12	59	0	0.25	6
C3	11	3	9	246	3	0.04	10
T3	13	5	20	603	1	0.01	14

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BIOSKETCH

Saskya van Nouhuys has worked mostly on the influence of habitat on the ecology and evolution of parasitoid wasps. Currently she is working on parasitoid population ecology at the University of Helsinki in Finland.

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