Res. Popul. Ecol. 38(2), 1996, pp. 265–273.

Researches on
POPULATION ECOLOGY Original paper

Inter- and Intraspecific Interactions among Larvae of Specialist and Generalist Parasitoids

Keisuke IWAO[1] and Naota OHSAKI

Laboratory of Entomology, Faculty of Agriculture, Kyoto University, Kyoto 606-01, Japan

Abstract. Intra- and interspecific larval interactions that take place in a host body were investigated for two tachinid flies *Epicampocera succincta* and *Compsilura concinnata* (Diptera: Tachinidae) parasitizing *Pieris* butterfly larvae. *E. succincta*, a specialist on *Pieris* butterflies, showed contest-type intraspecific competition, eliminating all the other conspecific larvae. On the other hand, an extreme generalist parasitoid *C. concinnata* exhibited scramble-type competition, sharing the host with other conspecifics and suffering reduced body size as a result. However, when these two species occurred together in a single host, *C. concinnata* had a much higher chance of survival. Moreover, *C. concinnata* could often survive in the presence of a parasitoid wasp *Cotesia glomerata* (Hymenoptera: Braconidae) while *E. succincta* could not. The high tolerance of *C. concinnata* could be attributable to its being an extreme generalist: To attack and survive on many different hosts, one has to be able to deal with various competitors. The competitive inferiority of the specialist *E. succincta*, on the other hand, may be a result of relatively recent encounter with those competitors.

Key words: Tachinidae, specialization, competition, host range, *Epicampocera succincta*, *Compsilura concinnata*.

Introduction

Most organisms are adapted to relatively narrow ranges of some resources, both biotic and abiotic. Specialization on particular resources is a key component of the organismal diversity which we observe in the world (MacArthur 1972). However, our understanding of the process of specialization is surprisingly minimal. In particular, the presence of generalist species in nature is intriguing, as it illuminates that generalization is possible, nevertheless specialization is the norm.

Although the terms "specialist" and "generalist" are meaningful only in an appropriate relative scale along an appropriate axis, there are nevertheless undeniable generalists among organisms. For example, the Egyptian cotton leaf worm *Spodoptera littoralis* feeds on more than 100 plant species from 49 families (Bernays and Chapman 1994), and the tachinid fly *Compsilura concinnata* attacks more than 200 insect species (Shima 1973). If such an extreme generalism is physiologically ever attainable, why are not more organisms generalists?

An important question is under what conditions either specialization or generalization are favored. In theory, since having more usable resource is a strong advantage for generalists, specialized genotypes cannot spread in a generalist population evolutionarily unless there is some advantage in being specialized. In reality, most organisms are specialized to a limited range of resources. It has thus been customary to assume that specialization accompanies an increase in efficiency in using the resource (MacArthur 1972). Tests of this assumption revealed that some more specialized organisms had higher foraging efficiency, such as solitary bees (Strickler 1979), stinkbugs (Evans 1982), and jackdaws (Partridge and Green 1987). On the other hand, a physiological advantage of specialization has not been confirmed in most of the empirical studies on herbivorous insects (e.g., Scriber and Feeny 1979; Futuyma and Wasserman 1981; Rausher 1984; Futuyma and Philippi 1987).

Considerable effort has been given to find the determinants of parasitoid host range. A simplistic but well accepted view is that endoparasitic koinobionts (parasitoids that grow in a host which is alive and growing) tend to have a narrower host range than ectoparasitic idiobionts

---

[1] *Present address: Division of Entomology, National Institute of Agro-Environmental Sciences, Tsukuba, Ibaraki 305, Japan. E-mail: iwao@niaes.affrc.go.jp*

(parasitoids that attach themselves outside a paralyzed host) because the former requires more elaborate adaptation to the host species physiologically (Askew and Shaw 1986). Other factors such as host taxonomy and shared ecology of the hosts seem to affect parasitoid host range (Askew and Shaw 1986). Also suggested are the structure of food plants of the host (Askew 1994) and hostility of the host (Shaw 1994), though these factors may be specific to the system studied. Finding a correlation between host range variation and some traits of the parasitoids can yield further clues to understand the evolution of specialism and generalism.

In this paper, we compared ecological responses of larvae of a specialist and a generalist parasitoid to confrontations with other parasitoid larvae inside a shared host. *Epicampocera succincta* (Diptera: Tachinidae) is a specialist species that attacks mainly larvae of the genus *Pieris* (Lepidoptera: Pieridae), while *Compsilura concinnata* (Diptera: Tachinidae) is a generalist that is one of the most polyphagous parasitoids in the world (Shima 1973). Both of these parasitoid flies are endoparasitic koinobionts and are found naturally parasitizing the white butterflies *Pieris rapae* and *P. melete* in Kyoto, Japan (Sato 1976; Iwao et al. 1989; Ohsaki and Sato 1994). In addition, when these flies parasitize *P. rapae*, they frequently encounter larvae of the parasitoid wasp *Cotesia glomerata* (formerly *Apanteles glomeratus*) (Hymenoptera: Braconidae), which is a common parasitoid of *P. rapae*. Using this parasitoid guild, we investigated how larvae of the two tachinid flies respond in the host to other larvae of their own species, of the other tachinid species, and of the parasitoid wasp.

Materials and methods

Study organisms

Epicampocera succincta is recorded as a parasitoid of *Pieris rapae* in Europe (Bisset 1938; Richards 1940; Dempster 1967) and of both *P. rapae* and *P. melete* in Japan (Yasumatsu and Watanabe 1964; Sato 1976; Iwao et al. 1989). Although a few other species are recorded as its host, *E. succincta* is apparently an oligophagous parasitoid of *Pieris*. In the northern part of Kyoto City, *E. succincta* inhabits primarily mountainous area (600-m altitude) where hosts are present continuously over four to six generations from spring to fall (Iwao et al. 1989). As it is a specialist of *Pieris*, it cannot inhabit lowland areas (100-m altitude) where hosts disappear in summer.

In contrast, *Compsilura concinnata* is, without question, one of the most polyphagous parasitoids. Arnaud (1978) lists more than 150 species in three orders as hosts in North America alone, where this tachinid was introduced as a natural enemy of the gypsy moth (Culver 1919). Worldwide, more than 200 species, including five orders in two classes (Insecta and Chelicerata), have been recorded as its hosts (Shima 1973). This species inhabits both mountainous and lowland regions in Kyoto (Fig. 1, Iwao et al. 1989). Since it attacks *Pieris* primarily in fall, it must parasitize other hosts during the other seasons.

E. succincta lays mature eggs on host larvae (K. Iwao, personal observation), while *C. concinnata* deposits larvae into hosts through a hole made with a piercing apparatus at the tip of its abdomen (Culver 1919; Weseloh 1983). Both species primarily attack the last (fifth) instar of their larval hosts and occasionally attack the fourth instars. In both species, hatched larvae remain in the first instar until the host starts pupating, after which parasitoid growth becomes rapid (K. Iwao, personal observation). A few days after the host finishes pupating, the third instar maggot emerges and pupates outside the host.

The parasitoid wasp *Cotesia glomerata* (Hymenoptera: Braconidae) is a major parasitoid of *P. rapae*. The female wasp lays about 10–30 eggs in the first- and second-instar larvae of the host (Matsuzawa 1958). The parasitoid larvae emerge from the host at the end of the fifth instar of the host larva. Parasitism rate of *P. rapae* by this parasitoid ranges from 10% to nearly 100% in the study area (Ohsaki and Sato 1990). Multiple parasitism is thus almost inevitable for the tachinid flies that attack *P. rapae*. On the other hand, *P. melete* is usually not parasitized by this parasitoid wasp as its eggs are encapsulated in the host hemolymph (Sato 1976).

Census method

Data in this study was obtained from host larvae collected in the field for the study described in Iwao et al. (1989) and from some additional collections. Effects of larval interactions were evaluated solely from observations of naturally occurring superparasitisms (two or more larvae of the same species in a single host) and multiple parasitisms (larvae of two or more species in a single host). Although the study is purely observational, we could reconstruct, with little ambiguity, the events that had occurred in a host after one or more parasitoids had emerged from the host (see below).

Fifth-instar larvae of *P. rapae* and *P. melete* were collected in the northern part of Kyoto City, Kyoto, Japan, from 1985 to 1988 on cruciferous crops (e.g., cabbage, Chinese cabbage, broccoli, radish, turnip) and wild crucifers (the yellow cress *Rorippa indica*, the bitter cress *Cardamine appendiculata*). Collections were made at regular intervals in 1985 and 1986 (described in Iwao et al. 1989) and sporadically in 1987 and 1988 at the sites and times where/when high parasitism rate was expected.

Larvae collected were reared in the laboratory at 25°C under 16L:8D photoperiod until either parasitoids or adult butterflies emerged. Tachinid larvae that emerged from the hosts were allowed to pupate in a small amount of sand. When eclosed, adult flies were anesthetized and weighed immediately. No measurement of body mass was made for emerged *Cotesia*.

Except for the experiment described below, the hosts were dissected immediately after one or more parasitoids emerged to see whether there were other parasitoids in the host. When superparasitism or multiple parasitism was detected, the species, developmental stage, and whether it was dead or alive were recorded for the parasitoid left in the host. Immature larvae of tachinid flies have a characteristic mouth hook that can be used to distinguish species and developmental stages (Bisset 1938).

Data collected was summarized as follows. First, to illustrate the distribution of the three parasitoids in the study area, their parasitism rates were summarized according to the location (the mountainous, openland, and intermediate areas according to the altitude; see Iwao et al. 1989 for detail) to the food plant of the host larvae (cruciferous crops, *Rorippa indica*, and *Cardamine appendiculata*) and to the host species (*P. rapae* and *P. melete*). The parasitism rate was determined as the percentage of hosts that contained each of the parasitoid species, many of which were discovered upon dissection. Thus the same host could be counted twice or three times in cases of multiple parasitism. This summary of parasitism distribution was intended to show under which environment in the field super- and multiple parasitisms tended to occur. Frequencies and outcomes (survival and body weight) of superparasitism and multiple parasitisms then follow. Host preference and a possible avoidance between parasitoids at the oviposition step will be examined in another paper.

Experiment: survival of tachinids after Cotesia *emergence*

The *Cotesia* parasitoid wasp larvae emerge from the final instar larvae of the host and thus kill the host before its pupation when the tachinid larvae are still immature. Although direct interference between larvae of *Cotesia* and of the flies was never observed or suspected (see Results), tachinids may be unable to complete their development and may suffer high mortality when multiple parasitism by tachinids and *Cotesia* occurs. To compare the effects of the co-occurring *Cotesia* on the two tachinid species, an additional experiment was conducted.

A separate set of fifth-instar larvae of *P. rapae* were collected in 1988 from a small crop field in Muramatsu, at the northern edge of a residential area of Kyoto City. Each larva was kept individually in a plastic container covered with a piece of gauze to maintain low humidity. The containers were kept at 25°C rearing room, where the relative humidity inside the containers was approximately 30%. Low humidity was necessary to prevent the host bodies from decaying too quickly after *Cotesia* emergence.

Hosts that produced *Cotesia* were kept in the container to see if any more parasitoids would emerge. When tachinid larvae emerged from hosts parasitized by *Cotesia* or from those not parasitized by *Cotesia*, they were weighed one day after they pupated. One-week after *Cotesia* emergence, all hosts were dissected to determine the presence of any more parasitoids. The effects of *Cotesia* on survival rate and pupal weight between the two tachinid species were compared. Mean survival rates of *Cotesia* larvae were compared between hosts that did and did not contain tachinid flies to see whether the tachinid larvae had any effect on the parasitoid wasps.

Results

Distribution of parasitoids

Figure 1 summarizes the parasitism rates by the two tachinids, *E. succincta* and *C. concinnata*, and by the braconid wasp, *Cotesia*. The composition of the parasitoid guild varied depending on the area where the hosts were collected and on the food plant on which the hosts were feeding, as well as on the host species. For example, the parasitism rate of *P. melete* by the specialist tachinid *E. succincta* was extremely high (85%) on bitter cress *Cardamine appendiculata* growing only in the mountain area, and consequently superparasitism was almost always observed in those hosts. On the other hand, parasitism by the generalist tachinid *C. concinnata* were mostly confined to *P. rapae* larvae feeding on crucifer crops in all of the census areas. Because those *P. rapae* were also the target of heavy parasitism by the parasitoid wasp *Cotesia*, multiple parasitism by *C. concinnata* and *Cotesia* was frequently observed in those hosts. As noted above, parasitism by *Cotesia* was limited to *P. rapae*, as *P. melete* is not a suitable host for the wasp larvae. The probability of different interactions among parasitoid larvae was thus not homogeneous across host species, feeding plants of the host, and locations. In the following sections, however, we focus only on the outcomes of encounters between parasitoid larvae within hosts.

Superparasitisms

Although the tachinid flies usually deposit only one egg or larva at a time, superparasitism often occurred in the field (Fig. 2a). Up to twelve *E. succincta* larvae were observed in a single host, as were up to four *C. concinnata*.

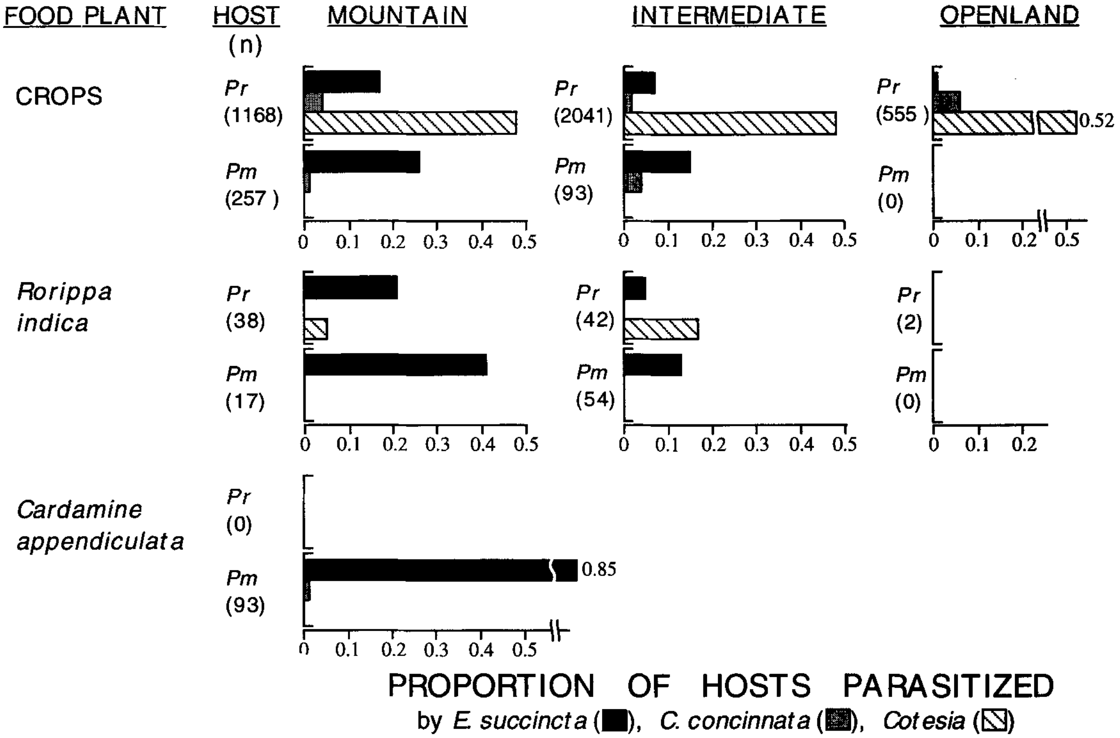


Fig. 1. Distribution of the two tachinid flies, *E. succincta* and *C. concinnata*, and the braconid wasp *Cotesia*. Fifth-instar larvae of *P. rapae* (*Pr*) and *P. melete* (*Pm*) were collected on cruciferous crops and wild crucifers, *R. indica* and *C. appendiculata*, in three regions: mountain (600-m altitude), openland (100-m), and an intermediate area (300-m) in 1985 and 1986. All the census data was pooled to yield the proportions parasitized. Both successful parasitisms and those detected upon dissection were included. Figures in parentheses under host species names are the number of host larvae examined. See Iwao et al. (1989) for more details of the census method.

For the specialist species *E. succincta*, no matter how many larvae were in a host, only one individual grew up and emerged from the host without a single exception regardless of the host species (Fig. 2b). Upon dissection of the hosts, all larvae remaining in hosts were found dead at a very early stage of the first instar, as indicated by undeveloped, very thin mouth hooks. Therefore the death of these larvae had occurred shortly after their entrance into the host. Many of the dead carried melanized wound marks on their body, indicating that physical attacks from other larvae were a cause of their death. Such attacks could be made by the sharp mouth hooks of first-instar larvae. Adult flies which had developed in hosts containing more than one *E. succincta* weighed no less than normal adults (Fig. 2c). The effect of the number of parasites, averaged over two sexes, was not significant (ANCOVA with sex, the number of parasites and the interaction as effects, $P=0.444$).

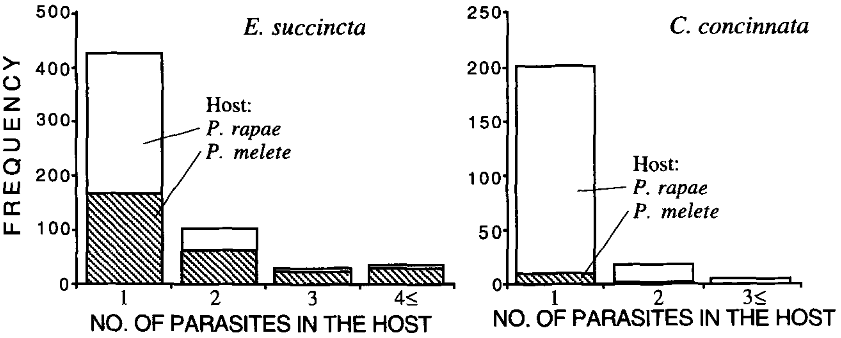
In contrast, emergence of more than one individual was frequently observed for the generalist, *C. concinnata* (Fig. 2b). When three or less individuals parasitized a single host, all larvae were able to emerge. When four larvae shared a host, occasionally only three emerged to pupate. The cost of sharing a host was reflected in the body weight of adult flies. Adults that had experienced superparasitism weighed significantly less than those that had occupied a host alone (Fig. 2c). The slope of linear regression of adult weight on the number of parasites, averaged over two sexes, was significantly negative (ANCOVA, $P=0.006$).

In summary, when more than one *E. succincta* occupied a host, one larva eliminated all the other co-occurring larvae to monopolize the host. The body size of the survivor was unaffected by this intraspecific battle. By contrast, when more than one *C. concinnata* occurred in a host, most of them survived, suffering a reduction of body size.

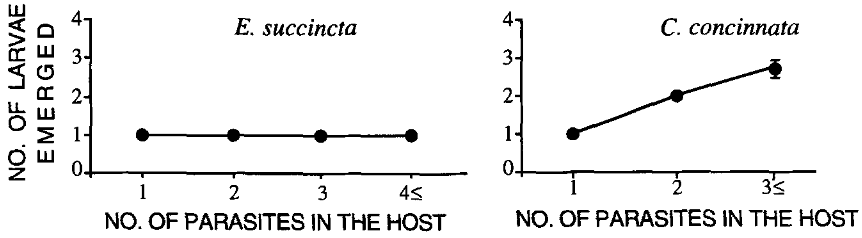
Multiple parasitisms between the two tachinid species

Multiple parasitism by *E. succincta* and *C. concinnata* was very rare: only 24 hosts were parasitized by both flies from about 5,500 hosts collected between 1985 and 1988. This is not a surprisingly low number according to the observed parasitism rates of the two tachinid flies. Both flies had rather low parasitism rates on average, and their spatial

(a) Frequencies of single and superparasitism



(b) The number of larvae which emerged from a single host



(c) Adult body weight

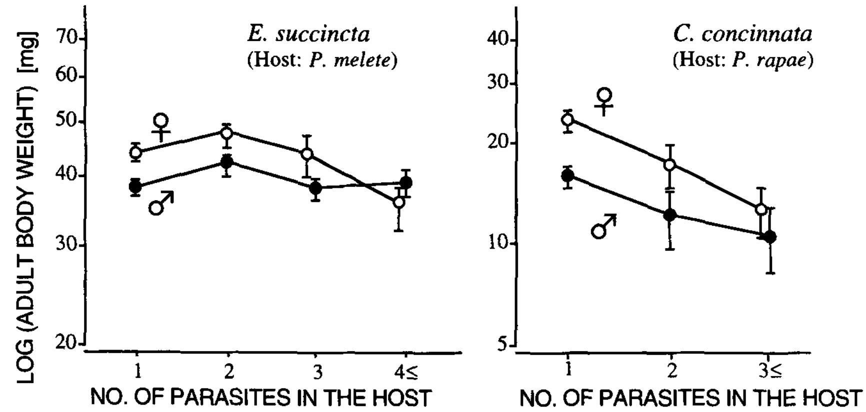


Fig. 2. The frequencies and outcomes of superparasitism by the two tachinid flies. (a) Frequency distributions of single- and superparasitism. (b) The mean number of larvae which survived in a single host. Vertical line indicates standard error. Data points without vertical lines indicate no variation in the output number. (c) Adult body weight as a function of the number of conspecific larvae in the host. Vertical lines indicate standard error. Open circles represent females, closed circles males. Only *E. succincta* that emerged from *P. melete* and *C. concinnata* emerged from *P. rapae* were used due to lack of data for the other combinations.

and temporal distributions were different as noted above (Fig. 1).

Among the 24 multiple parasitisms, emergence of parasitoids was observed for seven host individuals. From six of them, the generalist *C. concinnata* emerged from hosts in which the specialist *E. succincta* larvae were found dead (Table 1). Four of the dead specialists were at the third instar. There was only one case in which *E. succincta* emerged and a dead *C. concinnata* was found in the host. Emergence of both flies from a host was never observed. The remaining 17 hosts were found to be parasitized by the two species upon dissection. When one species was eliminated in a host, it was almost always an *E. succincta* larvae (Table 1). When both species were alive, their larvae were at early developmental stages. Dead *E. succincta* were observed in any of the three larval instars, while the single dead *C. concinnata* was a first instar. Only the dead *C. concinnata* had melanized

Table 1. Frequencies and outcomes of multiple parasitism by the specialist *E. succincta* and the generalist *C. concinnata*. A total of 21 *P. rapae* and 3 *P. melete* were parasitized by both tachinids. Numbers in parentheses indicate the incidence in *P. melete*.

Parasitoid emerged:

E. succincta emerged, *C. concinnata* dead	*E. succincta* dead, *C. concinnata* emerged	Both spp. emerged	Total
1	6(2)	0	7

Host dissected before parasitoid emergence:

E. succincta alive, *C. concinnata* dead	*E. succincta* dead, *C. concinnata* alive	Both spp. alive	Both spp. dead	Total
1(1)	7	9	0	17

wound marks on its body, indicating a physical injury as the cause of death.

In summary, of 24 hosts parasitized by both species, there were 13 cases of *E. succincta* being eliminated, 2 cases of *C. concinnata* being eliminated, and 9 of coexistence of young larvae. Under the null hypothesis that the two species have an equal probability of survival, the probability of getting a survival ratio of 13:2 or more extreme is 0.0037, assuming a binomial distribution. The observations thus suggest that the generalist *C. concinnata* had a significant advantage over *E. succincta* in a confrontation between them.

Multiple parasitisms between the parasitoid wasp and the flies

Throughout the census periods, the parasitoid wasp *Cotesia* exhibited a high parasitism rate of *P. rapae*. Multiple parasitisms between the wasp and each of the fly species were consequently quite frequent. In 1985 and 1986, about one third of all the hosts parasitized by *E. succincta* also contained *Cotesia* larvae, as did nearly half or more of the hosts parasitized by *C. concinnata* (Fig. 3).

When hosts collected from Muramatsu in 1988 were kept at low humidity in the lab, *C. concinnata*, the generalist species, frequently emerged from hosts from which *Cotesia* larvae had emerged earlier. Survival rate of *C. concinnata* was 77.1% (Table 2), and the mean pupal weight of survivors was significantly lower than that of normal pupae ($P<0.001$ by Wilcoxon two-sample test, Table 2). These small pupae subsequently produced very small, but apparently still intact, adult flies. The smallest pupa weighed only 5.4 mg, which is 13% of the average weight of normal pupae in the same collection. By contrast, the specialist *E. succincta* did not survive multiple parasitisms with *Cotesia*. Only in one case out of 12 did a larva emerge from the host, but this failed to pupate (Table 2). The survival rate of *E. succincta* was significantly lower than that of *C. concinnata* ($P<0.001$ by Fisher's exact probability test). On the other hand, no detrimental effect of tachinid flies was detected on the survival rate of *Cotesia* larvae (Table 3).

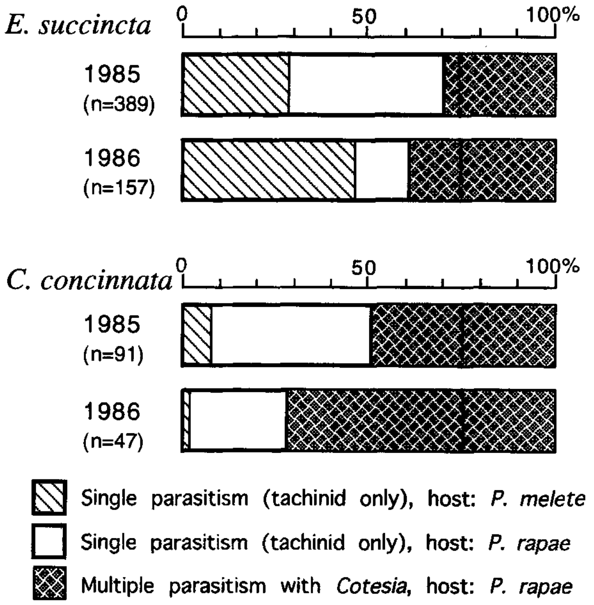


Fig. 3. Frequencies of multiple parasitism by the braconid wasp *Cotesia* and each of the two tachinid flies in 1985 and 1986. Of all the hosts parasitized by each of the tachinid flies, the proportions are shown for *P. melete*, for *P. rapae* that was attacked only by the tachinid fly (single parasitism), and for *P. rapae* that was attacked by both the tachinid and the braconid wasp (multiple parasitism).

In summary, although both tachinid flies had no effect on the survival of *Cotesia*, the presence of *Cotesia* in the same host severely affected the tachinid larvae. The specialist *E. succincta* never survived to adult in the presence of *Cotesia*, while the generalist *C. concinnata* did survive to some extent, but suffered a reduction of body size.

Discussion

The purpose of this paper was to compare a specialist and a generalist parasitoid in terms of their response to confrontations with other parasitoid larvae, and to elucidate characteristics associated with the differing degrees of host specialization. The results indicated that the generalist parasitoid *C. concinnata* may have a far superior ability to handle confronting species than the specialist *E. succincta*. *C. concinnata* had an advantage when faced with *E. succincta* larvae, and it could also tolerate the presence of the braconid wasp *Cotesia* in the same host which *E. succincta*

Table 2. Survival rate of tachinid fly larvae when they co-occurred with the parasitoid wasp *Cotesia glomerata*, and the survivors' pupal weight compared to normal flies. Hosts were collected from Muramatsu in 1988 and kept at 25°C and 20–40%RH. The normal flies were those obtained from the same set of hosts.

	Multiple parasitism with *Cotesia*				Normal	
Tachinid species	*n*	Died in host (%)	Emerged (%)	Pupal weight (SE)	*n*	Pupal weight (SE)
E. succincta	12	11 (91.7)	1[a] (8.3)	— (—)	5	71.0 (5.8)
C. concinnata	35	8 (22.9)	27 (77.1)	14.4 (0.9)	9	44.7 (3.0)

[a] Died before pupation.

could not. Below we discuss how these differences could occur.

Multiple parasitism between flies

The outcome of contests between the two tachinid flies was 13 to 2 in favor of *C. concinnata* (Table 1). There were also nine cases in which young larvae of both species were found together in the host. Although there is no way to know the final outcomes of these cases, we speculate that *C. concinnata* larvae were at an advantage over *E. succincta* based on the following reason. When superparasitism occurred, two live *E. succincta* together in a host were never observed. This implies that the mechanism of intraspecific battle in *E. succincta* is quite efficient for finding and eliminating the opponent. Given that mechanism, the simple fact that both species were still alive upon dissection therefore indicates a failure of this mechanism against *C. concinnata*. Once this elimination mechanism fails, *E. succincta* may be susceptible to whatever effects *C. concinnata* imposes.

Such a dominance of *C. concinnata* was counterintuitive based on the type of intraspecific competition that each species exhibited. The specialist *E. succincta* showed a contest-type competition, eliminating conspecific larvae in the host apparently by physical attack (Fig. 2). By contrast, the generalist *C. concinnata* showed no direct conflict among larvae, resulting only in the reduction of individual body mass (Fig. 2). Nevertheless in most cases *E. succincta* could not eliminate *C. concinnata*.

Table 3. Effect of co-occurrence with tachinid flies on the survival rate of *Cotesia* larvae. Larvae that successfully pupated and those that did not were both counted to obtain a survival rate for each parasitized host. Hosts were collected from Muramatsu in 1988. Each set of survival rates under multiple parasitism was compared to that of single parasitism using a Wilcoxon signed-rank test.

	n	Mean survival rate	*P*-value
Normal (alone)	84	0.989	
with *E. succincta*	12	0.994	0.604
with *C. concinnata*	35	0.997	0.304

A similar result was reported for multiple parasitism between *C. concinnata* and a solitary parasitoid *Apanteles melanoscelus* (Hymenoptera: Braconidae) (Weseloh 1983). *C. concinnata* often survived and emerged from the host a few days after the emergence of *A. melanoscelus*, which is likely to have the ability to eliminate conspecific larvae. A probable cause for *C. concinnata* being able to evade aggressive competitors is by hiding in the host's intestine. Larvae of this species are known to enter the host midgut soon after being oviposited and stay there until they reach the third instar (Culver 1919; Weseloh 1983). Once inside the host midgut, larvae probably have little chance of being found by competitors, and thus can wait until the situation improves. The same behavior might be at work in evading the aggressive larvae of *E. succincta*.

However, this does not explain why *E. succincta* died in the presence of *C. concinnata*. It may be that, even without a direct influence, *E. succincta* simply cannot tolerate the presence of other parasitoids, possibly due to lack of enough nutrients or oxygen, or to changes in the chemistry of the host body (Salt 1961; Fisher 1963).

Multiple parasitisms with Cotesia

Cotesia is a gregarious parasitoid whose larvae do not possess aggressive behavior toward other parasitoid larvae. Thus the cause of death of tachinid larvae in multiple parasitisms with the wasp was not due to a fight with the wasp larvae but in how they tolerate the environment in the host. The generalist *C. concinnata* showed relatively good ability to tolerate this and survived well (Table 2). Although, under field conditions, survival after wasp emergence will depend on how quickly the host body is destroyed (by predators, bacteria, etc.), *C. concinnata* has a good chance to survive against this type of parasitoid.

By contrast, the specialist *E. succincta* again showed little tolerance for the presence of wasp larvae in the same host. Questions as to both why *E. succincta* had to die and why *E. succincta* did not fight with the wasp larvae using the mouth hook cannot be answered without further detailed study.

Host range and the characteristics of parasitoid larvae

This study involves only two species, one of which is a specialist and the other a generalist. With only one sample of species in each category of the host range, any association between species characteristics and the degree of host range could be fortuitous. Nevertheless, we attempt, based on logical plausibility, to interpret some of the traits observed in this study as characteristics associated with the differing degree of specialization, hoping to build a basis for future research of parasitoid host range.

As noted above, the generalist *C. concinnata* had a remarkable ability to tolerate the presence of other parasitoid larvae. It could tolerate both benign larvae of gregarious parasitoids and hostile larvae of solitary parasitoids by hiding in the host midgut. The peculiar behavior of first-instar larva entering the host midgut was also observed in another tachinid species *Lydella nigripes*, which is, interestingly, also extremely polyphagous (Dowden 1933). It is conceivable that such a high tolerance is associated with the wide host range. When parasitizing many different host species, *C. concinnata* will probably have to face as many competitors as the number of host species, if not more. High tolerance for the presence of other parasitoids would then be quite effective for increasing survival without directly confronting each competitor.

Compsilura concinnata also showed a tremendous plasticity in body size. The smallest individual weighed only 13% of the average of normal ones, yet they seemed to be perfectly capable of reproducing (K. Iwao, personal observation). Such size plasticity is certainly useful in tolerating competition for limited nutrients of a host, and may be necessary to parasitize host species of various sizes.

Examination of these hypotheses would require a full knowledge of *C. concinnata* biology: a list of host species which a population (not the whole species) of *C. concinnata* attacks over a year, the probability and consequences of multiple parasitism with other parasitoids, etc. In addition, whether these traits are the causes or the results of being an extreme generalist would have to be determined using phylogenetic analyses.

The poor performance of the larvae of the specialist *E. succincta* is more difficult to interpret. This species could not survive in the presence of either *C. concinnata* or the parasitoid wasp *Cotesia*. What could possibly contribute to such inferior competitive ability?

One possibility is that it is a manifestation of its mode of intraspecific competition and has nothing to do with its being a specialist. *E. succincta* eliminates conspecific larvae when more than one individual occupy a single host, which suggests that this species may be adapted to occupy the entire host-body alone. This in turn may explain why this species cannot share a host with other parasitoids. Even without any direct confrontation, *E. succincta* may be simply unable to tolerate the presence of others due to physiological reasons (Salt 1961; Fisher 1963).

On the other hand, it is intuitively puzzling to see a specialist being so powerless in larval conflict with other species. How can it evade extinction when it is outperformed by every competitor in its own arena? There are several possible explanations.

First, the specialist may have an advantage in other stages of life history, which offsets the disadvantage in the larval stage. For example, *E. succincta* has been shown to be attracted by the odor of the bittercress *Cardamine appendiculata*, which is an exclusive feeding plant for *P. melete* (S. Nakamura, personal communication). Such ability for host-habitat location would certainly increase the efficiency of host finding.

Second, larval competition may have an insignificant effect on population dynamics. This may be the case for competition with *C. concinnata*. The occurrence of these two species together in a single host was an extremely rare event due to their distributional difference and low average parasitism rate. That fact alone can explain why there is no pressure for *E. succincta* to perform better against the generalist. Both populations might be regulated, for example, by predators of adult flies, well below the level at which larval competition would have significant consequences on the persistence of populations.

Third, the specialist may have a "refuge" which no competitors can reach. Indeed this may be the case for *E. succincta* vs. the parasitoid wasp *Cotesia*. In the area where this study was done, *E. succincta* attacks both *P. rapae* and *P. melete*, while *Cotesia* can survive only on *P. rapae*. Therefore, no matter how severe the competition in *P. rapae* may be, *P. melete* larvae are always available to *E. succincta*. As noted above, *E. succincta* is attracted to the odor of an exclusive feeding plant of *P. melete*. Locating these "refuge" hosts may efficiently offset the disadvantage in using *P. rapae*.

Indeed *P. melete* feeding on plants in the genus *Cardamine* may historically be the original host for *E. succincta* (Ohsaki and Sato 1994). Before crucifer crops started being cultivated, there would have been little contact between *E. succincta* and the wasp *Cotesia*: *E. succincta* was confined to forest regions to which *P. melete* was also confined, while the parasitoid wasp *Cotesia* inhabited open-habitats where *P. rapae* dominated (Fig. 1, see Ohsaki 1982 for habitat preference of *Pieris* butterflies). Only when people started to cultivate crops on the edge of forest, *E. succincta* may have started attacking *P. rapae*, in which the parasitoid wasp often resided. Although many generations must have passed since the spread of crucifer cultivation in Japan, the time may not have been enough for *E. succincta* larvae to evolve an effective countermeasure against the newly encountered competitors.

Acknowledgments: We thank Profs. E. Kuno, A. Takafuji, H. Shima, Drs. Y. Sato, T. Nishida, N. Osawa, T. Kakutani, K. Nagasaka and T. Itioka for their assistance during the research. We also thank the following people for their valuable comments on earlier versions of the manuscript: Profs. E. Kuno, A. Takafuji, M. D. Rausher, B. Rathcke, Drs. J. Fry, F. J. Odendaal, J. Yoshimura, the corresponding editor and two anonymous reviewers.

References

Arnaud, P. H. (1978) A host-parasite catalog of North American Tachinidae (Diptera). *U.S.D.A. Miscellaneous Publication* **1319:** 1–860.

Askew, R. R. (1994) Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? pp. 177–202. *In* B. A. Hawkins and W. Sheehan (eds.) *Parasitoid community ecology*. Oxford University Press, Oxford.

Askew, R. R. and M. R. Shaw (1986) Parasitoid communities: their size, structure and development. pp. 225–264. *In* J. Waage and D. Greathead (eds.) *Insect parasitoids*. Academic Press, London.

Bernays, E. A. and R. F. Chapman (1994) *Host-plant selection by phytophagous insects*. Chapman & Hall, New York.

Bisset, G. A. (1938) Larvae and pupae of tachinids parasitizing *Pieris rapae* L. and *P. brassicae* L. *Parasitology* **30:** 111–122.

Culver, J. J. (1919) A study of *Compsilura concinnata*, an imported tachinid parasite of the gipsy moth and the brown-tail moth. *USDA Bulletin* **766:** 1–27.

Dempster, J. P. (1967) The control of *Pieris rapae* with DDT. I. The natural mortality of the young stages of *Pieris*. *Journal of Applied Ecology* **4:** 485–500.

Dowden, P. B. (1933) *Lydella nigripes* and *L. piniariae*, fly parasites of certain tree-defoliating caterpillars. *Journal of Agricultural Research* **46:** 963–995.

Evans, E. W. (1982) Timing of reproduction by predatory stinkbugs (Hemiptera: Pentatomidae): patterns and consequences for a generalist and a specialist. *Ecology* **63:** 147–158.

Fisher, R. C. (1963) Oxygen requirements and the physiological suppression of supernumerary insect parasitoids. *Journal of Experimental Biology* **40:** 531–540.

Futuyma, D. J. and T. E. Philippi (1987) Genetic variation and covariation in responses to host plants by *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution* **41:** 269–279.

Futuyma, D. J. and S. S. Wasserman (1981) Food plant specialization and feeding efficiency in the tent caterpillars *Malacosoma disstria* and *M. americanum*. *Entomologia Experimentalis et Applicata* **30:** 106–110.

Iwao, K., Y. Sato and N. Ohsaki (1989) Spatio-temporal distribution patterns of two tachinid flies, *Epicampocera succincta* and *Compsilura concinnata* parasitizing *Pieris*. *Researches on Population Ecology* **31:** 105–112.

MacArthur, R. H. (1972) *Geographical ecology*. Harper & Row, New York.

Matsuzawa, H. (1958) Ecological studies on the braconid wasp, *Apanteles glomeratus*. *Memoirs of Faculty of Agriculture, Kagawa University* **3:** 1–125.

Ohsaki, N. (1982) Comparative population studies of three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi*, living in the same area. III. Difference in the annual generation numbers in relation to habitat selection by adults. *Researches on Population Ecology* **24:** 193–210.

Ohsaki, N. and Y. Sato (1990) Avoidance mechanisms of three *Pieris* butterfly species against the parasitoid wasp *Apanteles glomeratus*. *Ecological Entomology* **15:** 169–176.

Ohsaki, N. and Y. Sato (1994) Food plant choice of *Pieris* butterflies as a trade-off between parasitoid avoidance and quality of plants. *Ecology* **75:** 59–68.

Partridge, L. and P. Green (1987) An advantage for specialist feeding in jackdaws, *Corvus monedula*. *Animal Behavior* **35:** 982–990.

Rausher, M. D. (1984) Tradeoffs in performance on different hosts: evidence from within- and between-site variation in the beetle *Deloyala guttata*. *Evolution* **38:** 582-595.

Richards, O. W. (1940) The biology of the small white butterfly (*Pieris rapae*), with special reference to the factors controlling its abundance. *Journal of Animal Ecology* **9:** 243–288.

Salt, G. (1961) Competition among insect parasitoids. *Symposium of the Society for Experimental Biology* **15:** 96–119.

Sato, Y. (1976) Experimental studies on parasitization by *Apanteles glomeratus* L. (Hymenoptera: Braconidae). I. Parasitization of different species of genus *Pieris*. *Applied Entomology and Zoology* **11:** 165–175.

Scriber, J. M. and P. Feeny (1979) Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their food plants. *Ecology* **60:** 829–850.

Shaw, M. R. (1994) Parasitoid host ranges. pp. 111–144. *In* B. A. Hawkins and W. Sheehan (eds.) *Parasitoid community ecology*. Oxford University Press, Oxford.

Shima, H. (1973) New host records of Japanese Tachinidae (Diptera: Calyptrata). *Sieboldia* **4:** 153–160.

Strickler, K. (1979) Specialization and foraging efficiency of solitary bees. *Ecology* **60:** 998–1009.

Weseloh, R. M. (1983) Effects of multiple parasitism on the gypsy moth parasites *Apanteles melanoscelus* (Hymenoptera: Braconidae) and *Compsilura concinnata* (Diptera: Tachinidae). *Environmental Entomology* **12:** 599–602.

Yasumatsu, K. and C. Watanabe (1964) *A tentative catalogue of insect natural enemies of injurious insects in Japan. Part 1. Parasite-predator host catalogue*. Entomology Lab., Faculty of Agriculture, Kyushu University, Fukuoka.

Received 19 June 1996; Accepted 1 November 1996