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Interactions Between Searching Strategies of *Drosophila* Parasitoids and the Polymorphic Behavior of Their Hosts

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Two strains of Drosophila melanogaster, *"rover" and "sitter," differing in locomotion while foraging were simultaneously exposed to females of either* Leptopilina boulardi *or* Ganaspis xanthopoda *(parasitic Hymenoptera). These two parasitoids show different modes of host-searching behavior, ovipositor searching, or vibrotaxis, respectively.* L. boulardi *parasitized the sitter host strain significantly more than the rover. In contrast,* G. xanthopoda *parasitized the rover strain more than the sitter. In one case,* L. boulardi *selected far more sitters than rovers in population cage experiments. We also describe the frequencies of rovers and sitters in three natural populations where the local parasitoid community may have partially contributed to the differences in rover and sitter frequencies.*

KEY WORDS: rover/sitter; larval behavior; genetics; *Drosophila melanogaster*; parasitoid success; field population.

INTRODUCTION

The success of parasitization of insect larvae by a parasitoid depends on the outcome of a conflicting process between the host and the parasitic wasp (Carton and Nappi, 1991). There are several steps in these counter strategies during the process of parasitization (Doutt, 1964; Vinson, 1975). After having found an

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appropriate host habitat, the female wasp must locate the host within it. During this step, ethological characters of both the host and the parasitoid influence the probability of successful parasitization. In other words, there is a conflict between the infestation capacity of the wasp and the host's ability to escape.

Our purpose was to investigate if the searching behavior of the parasitic wasp can influence the genetic structure of the host population by studying some ethological characters that may be linked to the probability of infestation.

Vet and van Alphen (1985) have previously studied the searching modes of larval parasitoids used to detect *Drosophila* larvae within a food patch. The infestation capacity of the female wasp depends on its ability to locate the host in the food medium. These authors recognized three main modes of searching:

(1) *Vibrotaxis:* Vibrations caused by host movements are utilized as the host detection stimulus. The female shows a walk–stop–walk locomotor pattern, spending most of her time standing still to facilitate host detection.
(2) *Ovipositor searching:* The female continuously walks over the substrate while randomly probing the medium for host larvae.
(3) *Antennal searching:* The female rhythmically drums the substrate with her antennal tips.

We hypothesize that the efficiency of parasitoid searching behavior will vary with parasitoid searching strategy and host behavior. Parasitoids which use the vibrotaxis searching mode should more easily detect larvae with high activity levels by reacting to the host vibration. On the contrary, a motionless larva would cause little vibration and would therefore be difficult to localize. Alternatively, in the case of a parasitoid with ovipositor searching behavior, high larval activity may facilitate escape from parasitization by the wasp ovipositor. In this case, a slow-moving larvae should be parasitized more often.

Differences in the locomotory activity of foraging larvae of *D. melanogaster* has a genetic basis (Sokolowski, 1980; Sokolowski *et al.*, 1986; de Belle and Sokolowski, 1987, 1989; de Belle *et al.*, 1989). This behavior depends on a major gene, *for* (foraging), localized on the left arm of the second chromosome, with two alleles, for^R and for^S. The phenotype is measured as the distance (path length) a larva travels while foraging in the food medium. Rovers (for^R/for^R) have significantly longer paths than sitters (for^S/for^S); this corresponds to a higher velocity of rover phenotypes. This polymorphism is present in natural populations with an appreciable frequency of both phenotypes [for example, 30% sitters: 70% rovers in a Toronto population (Sokolowski, 1982)]. Some natural populations (for example, in Tunisia), however, show a lower frequency of sitter phenotypes (Sokolowski and Carton, 1989).

Carton and David (1985) observed a difference in parasitization rates of *Leptopilina boulardi*. This parasitoid uses an ovipositor searching mode. In this

case, nondigger (those that did not dig into the food) larvae were more infested than digger larvae of *D. melanogaster*. In addition, digger larvae showed a rover phenotype, whereas nondigger larvae had a sitter phenotype. Sokolowski and Turlings (1987) showed that larval movement has a strong effect on host detection by *Asobara tabida*, which uses a vibrotaxis strategy. They used a temperature-sensitive paralytic mutant (sh^{TS}) of *Drosophila melanogaster* which is motionless at 29°C but moves as a rover at 20°C. Wasps were given a choice between an equal numbers of sh^{TS} larvae and rovers at the two temperatures. At the control temperature (20°C) both strains were parasitized equally. However, at 29°C the moving larvae were located for parasitization. This study provided conclusive evidence that *A. tabida* uses larval movement to detect its host.

We wanted to test the hypothesis that the degree of parasitization will be influenced by the foraging phenotype of the larvae. For this purpose, we utilize two parasitoids with different modes of host searching behavior: vibrotaxis and ovipositor searching. In the second part, we examine whether the selective pressure exerted by the parasitoid can modify the frequencies of rovers and sitters in the host population using population cage experiments. In the third part of this work, we analyze the rover–sitter phenotypic frequencies of several natural populations where the parasitoid guild is well-known (Carton *et al.*, 1986).

MATERIALS AND METHODS

Parasitoids

Ganaspis xanthopoda (strain G 302-1) and *Leptopilina boulardi* (strain G 301-1) were initiated with 20–30 inseminated females collected in banana-baited traps in the dry season (January 1975) on the island of Guadeloupe (French West Indies). Rearing methods are explained by Carton and Kitano (1981).

Infestation Tests

Strains of Flies

Two laboratory strains of *D. melanogaster* were utilized for infestation tests: E_2E_3 and B15B15 stocks. The E_2E_3 strain (Sokolowski, 1980) is isogenic for the second and third pair of chromosomes. Larvae of this strain have a "sitter" (short path length) foraging behavior (de Belle and Sokolowski, 1987). This strain also has the ebony e^{11} (3-35.5) mutation (Lindsley and Grell, 1968), which blackens the anterior spiracles of larvae. This marker made it possible to distinguish E_2E_3 larvae from B15B15 wild-type larvae. The B15B15 strain,

isogenic for the second and third pair of chromosomes, was derived from an isofemale line (Bauer and Sokolowski, 1985).

Experimental Conditions

Infestation experiments were performed in a petri dish (8.5 × 1.4 cm). A thick layer of agar (2% solution) was coated with a thin homogeneous layer of aquaeous live yeast suspension (22 g of Alsa's dry yeast in 100 ml of distilled water) applied with a brush. Under these conditions, larvae did not dig into the agar; they forage on the surface. Twenty second-instar larvae (48 h posthatching) of each strain (E_2E_3 and B15B15) were placed together on the surface of the yeast coated agar petri dish. The second instar is the stage preferred by the cynipid wasps (Carton and Kitano, 1981). One female wasp of one of the two species was introduced with a paintbrush into the petri dish for 6 h. Twenty-four hours prior to this test, all wasps were given oviposition experience with 48 h posthatching sitter and rover larvae at a 1:1 ratio. Experienced females start to oviposit immediately and simultaneously after introduction to the hosts and are able to avoid superparasitism (van Lenteren, 1976). Under our experimental conditions, the two host strains are mixed together so that in each replicate, an individual female searches and infests larvae of the two host strains. In this way the effect of intraspecific variability between wasps on the infestation of the two strains are comparable. After 6 h larvae were then removed from the medium and identified as to their ebony (sitter strain) or wild-type (rover strain) phenotype after which they were dissected. This experimental procedure was repeated 20 times for each wasp species (*L. boulardi* or *G. xanthopoda*). The level of infestation (percentage) of each strain was defined as the recovered larvae that were parasitized. All the experiments were performed at 25°C.

Population Cage Experiments

Due to previous studies (de Belle and Sokolowski, 1989), we were able to use compound strains (described below) of flies where rovers and sitters were associated with morphological markers with no crossing-over. This enabled us to evaluate the frequency of rover and sitter by measuring the frequency of morphological markers in mixed populations housed in population cages. We monitored the weekly frequency of morphological markers in cages with and without *L. boulardi* for at least 45 weeks.

Strains of Flies

Compound second-chromosome lines had been constructed (de Belle and Sokolowski, 1989) using the two *D. melanogaster* strains (see above): E_2E_3 (expressing a sitter phenotype) and B15B15 (expressing a rover phenotype),

with morphological mutant markers [*j* (*jaunty*) and *px* (*plexus*) described by Lindsley and Grell (1968)]. These two lines have the following constitution: *C(2L) j* "R"; *C(2R)* and *C(2L)* "S"; *C(2R) px*, respectively, for the second chromosome (de Belle and Sokolowski, 1989).

Compound left and right autosomes are physically unattached and segregate at random, resulting in two viable types of gametes (Grell, 1970). Viable progeny are produced from the union of gametes, giving four genotypes in offspring:

C(2L) j "R"; *C(2R)* with a *jaunty* wing phenotype,
C(2L) j "R"; *C(2R) px* with *jaunty* and *plexus* wing phenotypes,
C(2L) "S"; *C(2R) px* with a *plexus* wing phenotype, and
C(2L) "S"; *C(2R)* with a wild-type phenotype.

The percentage of *j* and *j/px* flies enabled us to determine the frequency of rovers, whereas the percentage of *px* and wild flies gave the frequency of sitters.

Experimental Conditions

One hundred females and one hundred males belonging to the two compound chromosome strains *C(2L) j* "R"; *C(2R)* and *C(2L)* "S"; *C(2R) px* were placed in each of four population cages. Two weeks later 50 females of the parasitoid species, *L. boulardi*, were introduced into two of these cages; these were the treatment cages. The other two cages did not contain parasitoids and were controls. Each week, we collected dead flies and determined their phenotypes (*j*, *px*, *j/px*, or +/+). We collected dead flies as opposed to live ones to minimize disturbance to the population cages. The adult life span of parasites in these conditions is no more than 10 days.

Field Population Studies

Samples of *Drosophila* larvae were obtained from two laboratory strains initiated with flies collected in Guadeloupe (Lesser Antilles) and Nasrallah oasis (Tunisia). These strains were established 3 months prior to the test. One hundred early third-instar larvae (72 h post hatching) per strain were tested by measuring path length over a 5-min period [for more detail on this test, see Sokolowski and Carton (1989)]. We also include results previously obtained on a Canadian population (Sokolowski, 1982) investigated as midthird-instar larvae (96 h post-hatching).

Statistical Tests

Student's *t* tests were used on arcsine square root-transformed proportions to compare the number of parasitized larvae of the sitter (E_2E_3) and rover (B15B15) strains. An estimation of the standard deviation of the coefficient of

variation (CV) is possible when the sample size is not too large. In this case it is equal to $CV/\sqrt{2n}$ (David *et al.*, 1978). The regression line of sitter percentage as a function of time (in population cage experiments) was calculated using the SAS general linear model procedure (SAS Institute Inc., 1987). The regression coefficient with a value around 0 determined the week after which equilibrium is obtained.

RESULTS

Experimental Infestation of Sitter and Rover Larvae

Data in Table I were obtained with *L. boulardi*. This parasitoid has ovipositor host searching behavior. In 16 of 20 replicates, sitter larvae were infested more than rovers. The mean level of infestation was 61.6% on sitter larvae and 49.7% on rovers (Student's $t = 2.98$, $P < 0.01$, df = 19).

Results obtained on *Ganaspis xanthopoda* are strikingly different (Table

Table I. Results of Infestation of Sitter and Rover Larvae with *Leptopilina boulardi*[a]

	Sitter infestation		Rover infestation	
Replicate No.	No. larvae recovered	% rate	No. larvae recovered	% rate
1	20	80.0	19	73.7
2	20	75.0	17	82.3
3	17	70.6	17	52.9
4	19	73.7	20	65.0
5	17	82.3	15	60.0
6	18	94.4	17	52.6
7	15	66.7	19	52.6
8	18	83.3	18	61.1
9	18	44.4	18	50.0
10	18	44.4	18	36.8
11	20	70.0	20	45.0
12	18	44.4	19	39.9
13	20	55.0	20	66.7
14	17	41.2	17	52.9
15	20	20.0	17	17.6
16	19	31.6	19	15.8
17	18	33.3	20	10.0
18	19	57.9	19	36.8
19	17	88.2	19	57.9
20	17	76.5	17	64.7

[a]The larvae of both types are placed together on a yeast agar substrate with one female wasp for 6 h.

II). This parasitoid detects its host by vibrotaxis. In this case, the rover strain is attacked in 14 of 20 replicates. The mean level of infestation was 39.6% on the rover larvae and 29.9% on the sitters ($t = 2.51$, $P < 0.01$, df = 19).

Population Cage Studies

Two series of cage experiments were conducted. In each series, two cages were started with a frequency of 50% sitters and 50% rovers. One cage contained parasitoids (treatment), while the other cage did not (control) (Fig. 1).

We calculated the slope of the regression line using the percentage sitter frequency as a function of time. A stable equilibrium was reached in series 1 by the ninth week (Table III). We then calculated the percentage sitters averaged over the 9th to the 48th week. In series 1, the average percentage of sitters was less in the treatment with the parasite (75.4%) than in the control (86.5%). These results were not found for the second series. In series 2, an equilibrium was reached by week 21, but only in the treatment cage. The mean percentages of sitters in the treatment (91.5%) and control (89.7%) in series 2 did not differ

Table II. Results on Infestation of Sitter and Rover Larvae with *banaspis xanthopoda*[a]

	Sitter infestation		Rover infestation	
Replicate No.	No. larvae recovered	% rate	No. larvae recovered	% rate
1	18	16.6	18	66.7
2	18	16.6	15	20.0
3	19	31.6	19	47.4
4	17	29.4	20	55.0
5	18	22.2	17	23.5
6	18	27.8	18	55.6
7	16	50.0	18	55.6
8	17	29.4	14	57.1
9	16	18.7	15	13.3
10	20	20.0	19	10.5
11	18	50.0	19	31.6
12	19	36.8	17	52.9
13	19	42.1	20	60.0
14	18	61.1	19	31.6
15	19	26.3	18	27.8
16	19	26.3	20	56.0
17	19	5.5	18	0.0
18	18	11.1	19	21.1
19	19	31.6	19	36.8
20	20	45.0	20	70.0

[a]The larvae of both types are placed together on a yeast agar substrate with one female wasp for 6 h.

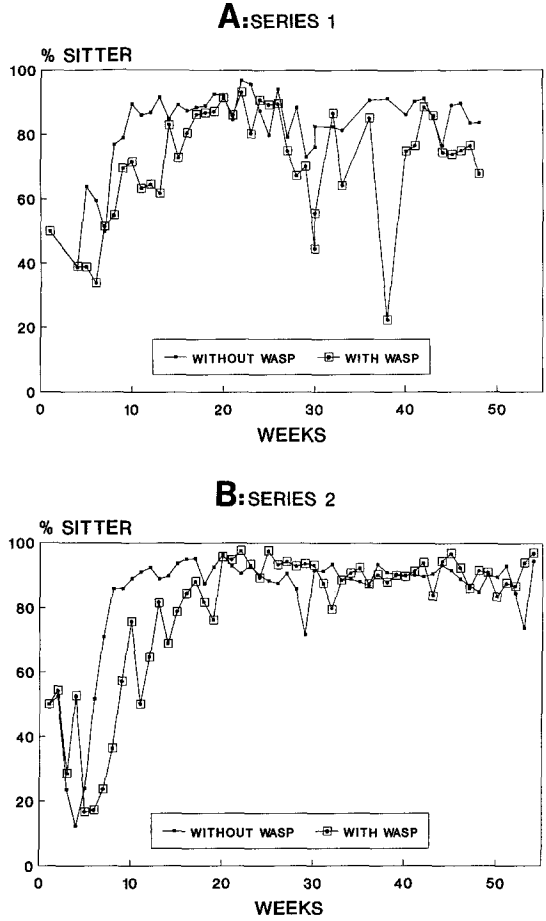


Fig. 1. (A,B) Evolution of the sitter frequencies in population cages with *L. boulardi* (treatment) and without it (control). Two sets of experiments (series 1 and 2) were performed at different times.

significantly. However, during the first half of series 2 (from week 1 to week 19), the sitter percentage was, on average, lower in treatment (57.2%) than in the control (73.3%).

Interestingly, the parasitoid does not damp the fluctuations in the percentages of sitters. Comparisons of the coefficient of variation indicate that the sitter oscillations are greater in population cages with the parasitoids compared to those without: 19.1 $\pm$ 4.4 and 11.7 $\pm$ 2.8 in the treatment, compared to 6.4 $\pm$ 1.5 and 5.1 $\pm$ 4.0 in the control cages (Table III).

Table III. Evolution of the Sitter Gene Frequency in Population Cages Started from a *D. melanogaster* Population with Equal Frequencies (0.5) of for^R and for^S Alleles

	Series 1		Series 2	
	Cage with parasitoid	Cage without parasitoid	Cage with parasitoid	Cage without parasitoid
Estimated regression line (after the 9th week)	$Y = -0.11X + 78.5$	$Y = -0.06X + 88.3$	$Y = -0.11X + 95.3$	$Y = -0.07X + 91.9$
Mean percentage of sitter (after the 9th week)	75.4%	86.5%	91.5% (after the 20th week)	89.7%
t-test comparison	$t = 6.3$ ($t_{0.01} = 2.63$, df = 70)		$t = 1.52$ ($t_{0.01} = 2.61$, df = 79)	
Coefficient of variation ± SE	19.1 ± 4.4	6.4 ± 1.5	11.7 ± 2.8	5.1 ± 4.0

The overall proportion of sitters was high (75–90%) in the cages. This does not reflect superior competitive ability of sitter relative to rover. Rather it arises from differential selection on the morphological mutant markers. As you recall the rover allele is marked with *jaunty* or *jaunty* and *plexus*, whereas the sitter allele is marked with *plexus* or with wild-type wing phenotypes. As expected, the wild-type phenotypes are more fit than the mutant ones (Bouletreau *et al.*, 1984; Bouletreau, 1986). Since the sitter allele was linked to the wild-type phenotype, its frequencies in the cages were high. Thus the absolute frequencies of rovers and sitters in these experiments would differ if morphological mutant markers were not used.

Rover/Sitter Frequencies in the Field Situation

Here we present some very preliminary evidence for a correlation between larval behavior and the parasitoid community. Three natural populations of *D. melanogaster* were analyzed for the frequency distributions of path length in the third-instar larvae (Fig. 2). These three populations were used for investigations because their parasitoid guilds were well characterized and differed between each other.

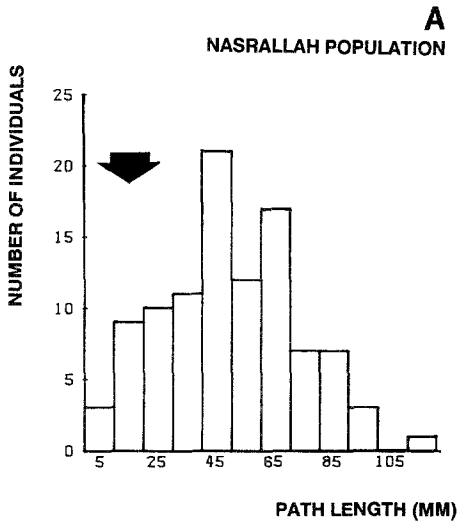
In the oasis of Nasrallah (Tunisia, North Africa), we observed a unimodal distribution of path lengths with no obvious sitter mode (as did Sokolowski and Carton (1989). In this locality, *D. melanogaster* larvae are attacked by only two closely related wasp species: *Leptopilina boulardi* and *L. heterotoma* (Carton *et al.*, 1987, 1991). These two parasites have been shown to have typical ovipositor searching behavior, likely resulting in a higher infestation of sitter larvae, which has had consequences on the distribution.

In Guadeloupe we find a different pattern than in Nasrallah, with the possibility of several modes in the path length distribution of rover/sitter phenotypes. In this tropical site, more than 14 wasp species are present (Carton *et al.*, 1986). Most of them showed ovipositor searching or vibrotaxis modes; only one has an antennal searching mode (Vet and van Alphen, 1985). Five of them at least have the capacity to infest *D. melanogaster* larvae, especially *L. boulardi* and *G. xanthopoda*.

In a Canadian site (a pear tree orchard near Toronto), the larval path length at third instar has been studied previously (Sokolowski, 1982). Here we find a clear sitter mode. *Asobara tabida* is the only larval parasitoid found in this orchard and it uses vibrotaxis to find its host presumably selecting against rovers.

DISCUSSION AND CONCLUSION

In the field conditions, *L. boulardi* females spend most of their searching time randomly probing the substrate with their ovipositor. They parasitize sitter behaving larvae which show less locomotion during foraging. On the contrary,



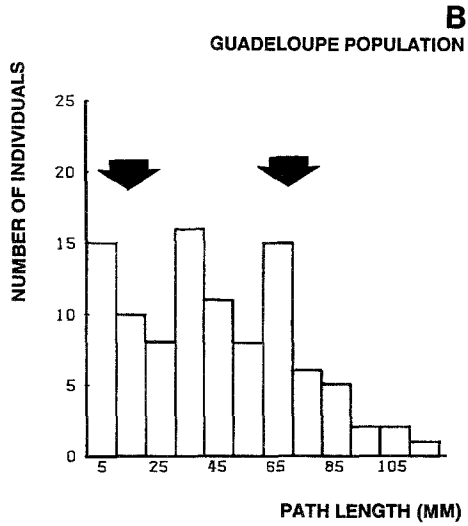


Fig. 2. The frequency distributions of path lengths in early third-instar larvae of *Drosophila melanogaster* sampled from different field populations (arrows represent potential selection pressure from the parasitoid community of the locality). (A) Tunisian population; (B) Caribbean island population; (C) Canadian population (from Sokolowski, 1982).

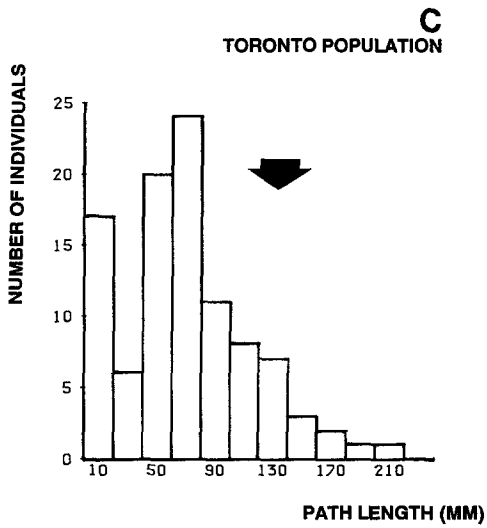


Fig. 2. Continued

G. xanthopoda females spend most of their time standing still and detect vibrations produced by the more active rover larvae.

The results of this work have permitted us to correlate the searching mode of parasitoids used for host detection and the behavior of the attacked larval host. The observed parasitization differences are likely due to differences in host movements. Even though host movement differences are subtle, we found significant differences in parasitization frequencies in the two wasp species for the two types of hosts, rover and sitter.

Experimental populations started in cages with *L. boulardi* and a *D. melanogaster* population (initiated with a for^S allelic frequency of 0.5) allowed us to show that the parasitoid displayed weak selection against sitters in one set of cage populations. In fact, host larvae can dig more or less deeply in the artificial medium deposited in the cups. In these cages, the sitter frequency was lower than in the noninfested cages (control). This difference may correspond to a higher vulnerability of sitter genotypes to parasitism. This result could explain the observations of Bouletreau (1985) in experiments conducted over 87 weeks on *D. melanogaster–L. boulardi* cage interactions. After 50 weeks of selection with *L. boulardi*, the host population was less susceptible to parasitoid attack than the control population, which was maintained in cages without parasitoids. This difference may have resulted from a change in the rover/sitter frequencies in these cages.

Our field observations were restricted to localities for which data on parasitoid guilds are available. These data are limited (Carton *et al.*, 1986) and

should be interpreted with caution. The more typical and perhaps demonstrative situation is obtained from the Tunisian oasis locality. The scarcity of sitter phenotypes could be correlated with the high rate of parasitoid attack on the *Drosophila* population. In Tunisia, larvae collected in their unique natural breeding site (the *Opuntia* prickly pear) can be infested by only two species of *Leptopilina*. Infestation frequencies at this locality vary from 50% (Carton *et al.*, 1987) to 85% (Rouault, 1979). This high selective pressure may explain, along with other ecological factors (Sokolowski *et al.*, 1986), the rover/sitter genetic structure of the larval population in Tunisia. We observed polymorphism in the two other sites studied. For the Guadeloupe tropical site, the high diversity of parasitoids present and their different searching modes could explain the existence of polymorphism in this locality. The Toronto population is characterized by a poorly diversified fauna of parasitoids and also a low level of attack, which seem to be the characteristics of north temperate regions (Carton *et al.*, 1986). The results of a field study near Oxford (Great Britain) by Baker (1979), who studied the parasitoid complex of fruit inhabiting *Drosophila*, suggested that the percentage of parasitism by *A. tabida* is very low. Similar results were obtained by Janssen *et al.* (1988) on natural populations of woodland *Drosophila* in Netherlands. The presence of only one larval parasitoid (*Asobara tabida*) which parasitizes rovers more frequently than sitters may explain the existence of the sitter morph in the Toronto locality.

Whether the rover/sitter genetic polymorphism in larval behavior can be explained by the different host searching modes in parasitoids is still an unresolved question. It is certain, however, that interactions between host and parasitoid modify the host population at the physiological level (Carton and Nappi, 1991) and the ethological level (van Alphen and Vet, 1986). From an evolutionary perspective, variability in parasitoid searching modes may have evolved to optimize the exploitation of polymorphic host populations (rover/sitter polymorphism, for example). This in turn may minimize interspecific competition between parasitoids. The interaction between a parasitoid and its host can be thought of as a conflict where the host is being selected for parasitoid avoidance and escape while the parasitoid is being selected for more efficient host finding and capture (Price, 1980).

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