

## Egg-Laying Experience and Acceptance of Parasitized Hosts by the Parasitoid, *Leptopilina heterotoma* (Hymenoptera: Eucoilidae)

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*The influence of egg-laying experience on the response of females of the eucoilid parasitoid, Leptopilina heterotoma, to parasitized and unparasitized Drosophila melanogaster host larvae was examined under more controlled conditions than those used in past studies. In laboratory assays, we precisely manipulated both the number of eggs laid by females and the kind of larvae (parasitized versus unparasitized) in which the eggs were laid. We found that the tendency to avoid laying eggs in parasitized hosts depended markedly on whether or not eggs had been laid previously, but depended little on whether those eggs had been laid in parasitized or unparasitized hosts. The observed effect of general egg-laying experience on avoidance of parasitized hosts may reflect responses to either changes in the wasp's internal state (perhaps, changes in egg load) or changes in the wasp's neural representation of the external environment (such as those presumed to occur during learning). In light of these results, we offer a tentative reinterpretation of several earlier studies.*

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**KEY WORDS:** parasitoid; superparasitism; learning; motivation; egg load; *Drosophila*.

### INTRODUCTION

Females of many species of parasitoids avoid depositing eggs in previously parasitized hosts, at least when it is functional to do so (reviewed by van Lenteren, 1981; van Alphen and Visser, 1990). Females of many species also learn

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aspects of microhabitats associated with host presence, behavior which may also be functional (reviewed by Turlings *et al.*, 1993). Given the interest in the use of parasitized hosts, on one hand, and learning, on the other, it is natural to ask if female parasitoids learn to avoid parasitized hosts. In fact, this issue has been examined several times by past investigators with conflicting results. van Lenteren and Bakker (1975) and Klomp *et al.* (1980), for example, concluded that selective avoidance of parasitized hosts must be acquired through experience with unparasitized hosts. In contrast, van Alphen *et al.* (1987) maintained that the ability to discriminate between parasitized and unparasitized hosts need not be learned. Visser *et al.* (1992) found that parasitoids having prepatch experience with parasitized hosts parasitized a significantly greater proportion of the already parasitized host larvae placed in a test patch than did wasps having prepatch experience with unparasitized hosts. The latter authors explained their result in functional terms: wasps that encounter only parasitized hosts estimate the fitness value of a parasitized host to be relatively higher than do wasps that encounter only unparasitized hosts. In terms of mechanism, this pattern in behavior is reminiscent of discrimination learning—experience with a specific host type increases the relative tendency of a wasp to accept that host type. Learning, including discrimination learning, is thought to involve a change in an animal's neural representation of some aspect of the external environment (Edelman, 1987; Putters and Vonk, 1990; Mangel, 1993), e.g., representation of the quality and abundance of hosts in the habitat.

The possible reasons for the contrasting sentiments expressed by these investigators are many, including differences in experimental methods. Above all, it is important to note that none of the previous studies was intended (and, consequently, none was designed) to distinguish learning from other possible mechanisms of behavioral change. van Alphen (1993) identifies a suite of factors affecting parasitoid foraging behavior within a patch of hosts, some of which cannot be easily separated experimentally. Most of these factors apply generally to foraging insects. Recent studies, for example, indicate that host acceptance behavior is highly sensitive to the number of mature eggs that an insect has available to lay (i.e., the insect's egg load) (reviewed by Minkenberg *et al.*, 1992). Frequently in such studies, insects with higher egg load are more likely to accept hosts of lower quality (such as parasitized hosts) than are insects with lower egg load. Rosenheim (1993) points out that it can be very difficult in practice to distinguish learning from effects of changes in egg load on behavior. In the following study we made our task a somewhat easier one. We attempted simply to define more precisely how egg-laying experience modifies acceptance of parasitized and unparasitized hosts.

Using *Leptopilina heterotoma*, the eucoilid parasitoid studied in common by van Lenteren and Bakker (1975), van Alphen *et al.* (1987), and Visser *et*

*al.* (1992), we systematically manipulated the number of eggs (if any) laid by same-age females as well as the type of hosts (parasitized versus unparasitized) in which eggs were laid. We then asked a somewhat different question from that of previous authors: if oviposition behavior changes as a result of egg-laying experience, which influences host acceptance behavior more—laying an egg in a host of a particular type (parasitized or unparasitized) or simply laying an egg in a host regardless of type? If wasps were sensitive only to the quality of hosts previously experienced, host acceptance should depend on the type of host experienced in the following way. Wasps encountering only parasitized larvae ought to adopt a “bad world” view and show a greater propensity to accept a parasitized host than naive wasps, since it is (based on their experience) the only type of host available to them. Wasps encountering only unparasitized hosts, by contrast, ought to adopt a “good world” view and show a lower propensity than naive wasps to accept a parasitized host.

Alternatively, if wasps were sensitive only to past opportunity to lay eggs, then according to predictions of dynamical foraging theory (Mangel, 1993), wasps with prior egg-laying experience should show a lower propensity to accept hosts of any type than would naive wasps. We might also expect that acceptance of parasitized hosts should be reduced more by egg-laying experience than should acceptance of unparasitized hosts.

## MATERIALS AND METHODS

### Study Organism

*Leptopilina heterotoma* is a eucoilid parasitoid which attacks larvae of a variety of *Drosophila* species that inhabit fermenting fruits and sap fluxes as well as decaying mushrooms and plant material. A number of characteristics make this parasitoid ideal for studies on both learning and avoidance of parasitized hosts. First, it is a solitary parasitoid (meaning that a single egg is laid in a host), thus facilitating experimental manipulation of the number of eggs laid by an individual wasp as well as the kind of host in which those eggs are laid. Second, both learning and avoidance of parasitized hosts are particularly well studied in this insect (Tumlinson *et al.*, 1993; Visser, 1992 and 1993; Visser *et al.*, 1992; Vet and Dicke, 1992; van Alphen and Visser, 1990, and references therein).

We used for our experiment a laboratory-cultured strain established with wasps collected from *Drosophila phalerata* in mushrooms in 1985 and reared since on this host in commercially grown mushrooms. Reproductively mature females between 2 and 3 weeks old were used. Females were maintained in clean agar vials supplied with water and honey at ca. 25°C.

### Experimental Protocol

Groups of naive females (i.e., females with no previous oviposition experience) were allocated to one of three treatments: five ovipositions in once-parasitized *Drosophila melanogaster* larvae only (PPPPP), five ovipositions in unparasitized larvae only (UUUUU), or no experience (NONE). Larvae observed to have been parasitized once were obtained using wasps different from the experimental wasps. Females in the two experience treatments were permitted to forage individually for larvae in a petri dish lined with moist filter paper coated thinly with a suspension of bakers' yeast. Ten to 20 larvae, either parasitized only or unparasitized only, were placed in a roughly circular area 5 cm in diameter in the center of the dish. Each female was allowed to parasitize five larvae, a task which usually required 10–15 min to complete. Females generally oviposited in five larvae in succession; however, females presented with parasitized larvae occasionally rejected one or several of the larvae that they encountered. To avoid selecting for wasps with particular behavioral responses, we used all females in our assays regardless of whether or not they had rejected hosts during the prepatch experience.

Following experience (if any), wasps were isolated individually for ca. 1 h, after which they were placed individually on a test patch and their response to parasitized and unparasitized larvae assayed. The test patch consisted of a circle of yeast suspension 1 cm in diameter located in the center of a petri dish lined with moist filter paper. In the test, wasps were presented successively with a parasitized and unparasitized larva placed in the yeast patch and their response to each larva (accept versus reject) noted. The order in which unparasitized versus parasitized larvae were presented was altered systematically for wasps within a given treatment. Assay of an individual's responses required 5–10 min to complete. Data for 5 wasps (of a total of over 150) whose responses were tested on only one test larva were omitted. All prepatch experience manipulations and all patch assays were conducted at room temperature (ca. 25°C) under a stereoscope fitted with fiber-optic illumination.

### Statistical Methods

Incorporated in our experimental design are two independent variables. The first variable, prior experience, has three levels: experienced with parasitized hosts (P-TRAIN), experienced with unparasitized host (U-TRAIN), and naive (NAIVE). The second variable, type of test larva presented, has two levels: parasitized (P) and unparasitized (U). Our single dependent variable, the behavioral response to test larva, has two possible and mutually exclusive outcomes: acceptance (ACC) or rejection of the larva.

Although categorical repeated-measures analyses would be appropriate to

our experimental design, such analyses are notorious for problems caused by singularities in the variance matrix, problems which are not easily overcome (Stanek *et al.*, 1987). We instead performed discriminant analyses using UniMult (Gorsuch, 1990). A univariate discriminant analysis is the equivalent of a multiple regression on a categorical dependent variable. One advantage of this test is that, unlike more conventional log-linear repeated measures analyses, it does not assume a logarithmic relationship among independent variables. For a dichotomous dependent variable such as ACC, discriminant analysis uses  $\chi^2$  values instead of  $F$  ratios to test each independent variable for statistical significance. The model is hierarchical in order to control for correlations between the independent variables; thus, the order in which the independent variables are tested is critically important. The amount of variation due to each variable in turn is given by  $\eta^2$  values. We tested the independent variables in reverse chronological order, from current host type, to most recent host experience, to least recent host experiences. This was done under the presumption that it is most parsimonious to hypothesize that the behavior of a wasp is affected most by its most recent experience.

In order to examine effects of oviposition experience in general, we contrasted ALL TRAINED wasps (=P-TRAIN + U-TRAIN) with NAIVE wasps. To examine effects of specific host type experience we contrasted P-TRAIN with U-TRAIN. Because experience with the first test host could affect the acceptance of the second test host, we considered the effects on the acceptance of each test host separately and included the acceptance of the first test host (ACC 1ST HOST) as a variable in the analysis of acceptance of the second host.

## RESULTS

Overall, the majority of test hosts were accepted regardless of type (Fig. 1; acceptance of first test hosts,  $\chi^2 = 33.86$ ,  $df = 5$ ,  $P < 0.0001$ ; acceptance of second test host,  $\chi^2 = 70.12$ ,  $df = 7$ ,  $P < 0.0001$ ). However, acceptance depended on both the type of host with which females were presented and the degree of prior egg-laying experience. The most important factor in the acceptance of both the first and the second test hosts was host type (Table I; 1ST HOST  $P \eta^2 = 0.12$ ): while unparasitized hosts were usually accepted under any condition, the acceptance of parasitized hosts was more variable (Fig. 1).

Acceptance of all hosts depended on whether or not the wasp had any prior experience at all (ALL TRAIN versus NAIVE; Table I). The specific training that the experienced wasps received (P-TRAIN versus U-TRAIN) did not affect their host choice in the test presentations.

There is a nonsignificant trend of lower acceptance of parasitized larvae by

pre-patch experience	order of test larvae presentation	
PPPPP	P → U 58%      96%    (26)	
	U → P 89%      30%    (27)	
UUUUU	P → U 43%      96%    (28)	
	U → P 86%      21%    (28)	
None	P → U 90%      95%    (20)	
	U → P 100%     65%    (20)	

Fig. 1. Schematic diagram and results of experiment. U, unparasitized larva; P, parasitized larva. Shown are percentages of wasps within a given prepatch treatment presented with a test larva of a given type that laid an egg in that larva. Sample sizes are shown in parentheses.

U-TRAIN wasps versus P-TRAIN wasps. A power analysis of selected  $\eta^2$  values reveals the following probabilities ( $\beta$ ) of failing to reject a false null hypothesis, i.e., failing to find that  $\eta^2$  is different from 0 when in fact it is (type II error):  $\beta = 0.01$  for  $\eta^2 = 0.25$ , 0.04 for  $\eta^2 = 0.09$ , and 0.31 for  $\eta^2 = 0.04$ . The values of  $\eta^2$  for each P-TRAIN versus U-TRAIN comparison are 0.008 and 0.001 (Table I), indicating that if a true difference exists between these groups, we would need a much larger sample size to detect it. However, even if the use of a higher sample size yielded a significant difference between P-TRAIN and U-TRAIN, the fact remains that the ALL TRAIN versus NAIVE difference is much greater than that of P-TRAIN versus U-TRAIN. Thus, regardless of sample size limits on our statistical power to resolve small differences, it is clear that the effect of laying an egg on subsequent acceptance of parasitized larvae is far stronger than the effect of what type of larva that egg is laid in.

Whether or not the first test host had been accepted (ACC 1ST HOST) also did not affect acceptance of the second test host. However, the type (P versus U) of the second host (2ND HOST P  $\eta^2 = 0.40$ ) explains more of the variation in the wasps' behavior than the type of the first host (1ST HOST P  $\eta^2 = 0.12$ ). This is not surprising because wasps that received a parasitized larva in the

**Table I.** Hierarchical Discriminant Analysis: Summary Table for Acceptance of First Host and Acceptance of Second Host

Variable	$\eta^2$ <sup>a</sup>	df	$\chi^2$	P
Acceptance of first test host				
1ST HOST P	0.12	1	18.12	<0.0005
ALL TRAIN vs NAIVE	0.073	1	11.07	<0.005
ALL TRAIN vs NAIVE * 1ST HOST P	0.020	1	2.97	0.08
P-TRAIN vs U-TRAIN	0.0081	1	1.19	0.3
P-TRAIN vs U-TRAIN * 1ST HOST P	0.0036	1	0.51	n.s.
Acceptance of second test host				
2ND HOST P	0.40	1	59.46	<0.0001
ACC 1ST HOST	0.0001	1	0.02	n.s.
ACC 1ST HOST * 2ND HOST P	0.0009	1	0.18	n.s.
ALL TRAIN vs NAIVE	0.032	1	5.05	0.02
ALL TRAIN vs NAIVE * 2ND HOST P	0.032	1	4.99	0.02
P-TRAIN vs U-TRAIN	0.0016	1	0.21	n.s.
P-TRAIN vs U-TRAIN * 2ND HOST P	0.0016	1	0.22	n.s.

<sup>a</sup> $\eta^2$  represents the amount of variation due to each variable after all prior variable(s), if any, have been partialled out.  $N = 149$ .

second test position had more oviposition experience (since most wasps accepted the unparasitized larva presented first) than wasps that received a parasitized larva in the first position.

The interaction between the two variables affecting host acceptance (ALL TRAIN versus NAIVE \* 1ST HOST P or ALL TRAIN versus NAIVE \* 2ND HOST P) describes how the training of a wasp affects her decision to accept parasitized larvae only. This variable was marginally not significant in the case of the first host, and significant in the case of the second host (Table I). However, in both cases, the variable accounts for little of the overall effect ( $\eta^2 = 0.020$  and  $0.032$ , respectively). The statistical effects taken all together indicate that prepatch experience affected acceptance of both parasitized and unparasitized hosts in the same direction, with a tendency for acceptance of parasitized hosts to be affected more than acceptance of unparasitized hosts.

## DISCUSSION

### Absence of Discrimination Learning

Our wasps' behavior was affected not so much by whether they had previously laid eggs in parasitized or unparasitized hosts, but by whether or not they had laid eggs at all. Females with any kind of egg-laying experience (including previously naive females which had laid a single egg in an unpar-

asitized test larva) were significantly less likely to accept a test larva (especially a parasitized test larva) than were females with no egg-laying experience. In short, we failed to find compelling evidence of discrimination learning, but instead found that the general experience of laying an egg profoundly influenced *L. heterotoma*'s tendency to accept hosts, especially parasitized ones.

### Is It Learning?

While little evidence for one type of learning, discrimination learning, was found in our study, the observed effect of egg-laying experience on host acceptance is nonetheless consistent with some general definitions of learning [e.g., learning as "a change in behavior with experience" (Papaj and Prokopy, 1989)]. At the same time, the effect is also consistent with current ideas about how a change in egg load influences host acceptance by insects (Odendaal and Rausher, 1990; Rosenheim and Rosen, 1991; Minkenberg *et al.*, 1992; Drost and Cardé, 1992; Rosenheim, 1993), a phenomenon more akin to the concept of motivation than to learning (Mangel, 1989; Mangel, 1993). As noted in the Introduction, distinguishing learning from effects of changes in egg load on behavior is difficult. Rosenheim (1993) in particular emphasizes that both comparisons of naive females with females exposed to hosts and comparisons between females exposed to different host types will confound the two kinds of effects. In separate attempts to manipulate egg load independently of experience, Rosenheim and Rosen (1991) reared wasps under different temperatures, and Prokopy *et al.* (1994) reared flies under different protein regimes. Both procedures generated insects whose egg loads varied, but which uniformly lacked host experience. In both cases, behavior varied with egg load in predictable ways.

Such experiments have their own problems of interpretation. First, besides altering egg load, both procedures may generate physiological changes other than changes in egg load (perhaps even neural changes) that could influence behavior in the manner observed. Second, while such techniques inform us as to how individuals that differ in egg load differ in behavior, they do not necessarily inform us as to how a change in a given individual's egg load causes a change in that same individual's behavior. Nevertheless, such experiments are clearly a step beyond what has been done in the past. It would be useful to conduct analogous experiments with respect to acceptance of parasitized hosts in *L. heterotoma*. Based on the present results, it is certainly conceivable that changes in egg load account entirely for the observed patterns in acceptance of parasitized hosts. Given that *L. heterotoma* females are carrying as many as 300 mature eggs at any given time (Jenni, 1951), it may seem surprising that reducing egg load by just a single egg could influence a wasp's behavior so profoundly. Possibly, the effect, while initially strong, wanes over time. In this regard, it would be interesting to manipulate the time prior to presentation of test larvae.

Physiological mechanisms other than egg load change itself are possible explanations as well. The action of an egg moving through the ovipositor or sensory input from the ovipositor itself might trigger the observed response. Because *L. heterotoma* is a solitary parasitoid, such mechanisms are inextricably confounded. In a gregarious parasitoid, however, the effects of attacking a host versus those of a change in egg load can be separated. Figueredo (1989) showed that in the pteromalid *Nasonia vitripennis*, the number of unparasitized hosts attacked was the important factor affecting subsequent behavior, while the number of eggs laid itself did not have an effect. This suggests that a mechanism other than change in egg load explains the observed changes in behavior.

Whatever the underlying mechanism, the strong and immediate effect of laying an egg on acceptance of parasitized larvae generated an unfortunate but unavoidable confound in our experimental design. Because P-TRAINED wasps rejected more larvae during their prepatch experience than did U-TRAINED wasps, P-TRAINED and U-TRAINED wasps differed with respect not only to the larval type presented but also to the total number of larvae encountered and possibly the total time over which eggs were laid. One might argue that, had the two groups of wasps been given experience different only with respect to larval type, we would have observed a significant effect of larval type on host acceptance.

### Is Discrimination Against Parasitized Hosts Even Partly Innate?

Contrary to van Lenteren and Bakker (1975), discrimination against parasitized hosts did not require prior experience with unparasitized hosts; in our experiment, laying eggs in parasitized hosts had largely the same effect as laying eggs in unparasitized ones. In this respect, our results are at variance with theirs. Yet contrary to the sense of van Alphen *et al.* (1987), neither can we conclude from our results that recognition of parasitized hosts is even partly innate. In statistical terms at least, truly naive wasps were equally likely to accept parasitized and unparasitized hosts (90 versus 100%, respectively; Fig. 1).

Based on our present results, we are unwilling to state unequivocally that discrimination against parasitized hosts is not partly innate. First, owing to the labor-intensive nature of our design, our sample size was limited. Second, we suspect that younger wasps or wasps bearing fewer eggs than those used in our experiments might well discriminate against parasitized hosts.

On this point, the existing literature on parasitoid behavior is of little help because wasps deemed "inexperienced" in various studies were rarely truly naive. In van Alphen *et al.* (1987), for example, host acceptance by "inexperienced" females was measured in terms of the response to all hosts encountered by a previously naive female in a test patch. In such a circumstance, egg load is changing and the female is gaining experience *while she is foraging in the test patch itself*. The female's host acceptance profile at test's end could partly

reflect innate tendencies, changes in egg load, accumulation of experience or all of these. The same point can be made of van Lenteren and Bakker's (1975) assays. In Visser *et al.*'s (1992) study (which was not intended to measure naive responses precisely), host acceptance by a group of previously naive females (Treatment AL 5/1/E in that study) was inferred from the distribution of eggs among larvae in a test patch in which the females had been permitted to forage freely among a mixture of parasitized and unparasitized larvae. Clearly, the inferred level of acceptance of parasitized and unparasitized test larvae by apparently naive females could have been a function in part of changes in egg load, experience with larvae, or both.

Given the scarcity of data on truly naive wasps, it seems especially significant that Klomp *et al.* (1980) found (exactly as we did using *L. heterotoma*) that truly naive *Trichogramma embryophagum* wasps accepted unparasitized and parasitized hosts at high and virtually equal frequencies. Although few individuals were used in the experiments, a similar result is presented in *L. heterotoma* data presented by van Lenteren (1976). It would be useful to have more data on more species for which naive responses are measured directly in an elemental way (i.e., no more than one test per host type per individual insect with appropriate controls for test sequence effects).

### **Recasting Earlier Results as Possible Effects of Changes in Egg Load**

We believe that earlier results are as likely to reflect changes in egg load as learning. In van Alphen *et al.*'s (1987) study, for instance, previously naive wasps laid eggs in parasitized larvae in the test patch. The fact that they accepted a lower proportion of hosts overall than did previously naive wasps foraging for unparasitized hosts could reflect a selective effect of changes in egg load on acceptance of parasitized hosts. In Visser *et al.*'s (1992) assays, too, wasps experienced with parasitized hosts presumably deposited fewer eggs during the prepatch experience than did those experienced with unparasitized hosts. The former wasps might have been more likely, given their relatively higher egg load, to lay eggs in parasitized hosts than were the latter wasps. Exactly this pattern was observed.

In closing, we reiterate that our results do not allow us to distinguish unambiguously between learning and effects of physiological changes such as in egg load. Nevertheless, it is intriguing that a mechanism which resembles motivation could even potentially account for results that appear on the surface to be explained only by learning and which have been interpreted as such in several instances. Thus, although learning is sometimes defined as the generation of an internal representation of an animal's external environment (Edelman, 1987; Mangel, 1993), changes in egg load may actually serve the function of internal representation for foraging parasitoids. It is tempting to speculate that

the mechanism used by parasitoids to adjust their level of avoidance of parasitized hosts is more economical in a cognitive sense than one involving learning, while achieving a similar result.

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