

# Learning by the parasitoid wasp, *Aphidius ervi* (Hymenoptera: Braconidae), alters individual fixed preferences for pea aphid color morphs

Shaun A. Langley · Kelley J. Tilmon ·  
Bradley J. Cardinale · Anthony R. Ives

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**Abstract** Learning, defined as changes in behavior that occur due to past experience, has been well documented for nearly 20 species of hymenopterous parasitoids. Few studies, however, have explored the influence of learning on population-level patterns of host use by parasitoids in field populations. Our study explores learning in the parasitoid *Aphidius ervi* Haliday that attacks pea aphids, *Acyrtosiphon pisum* (Harris). We used a sequence of laboratory experiments to investigate whether there is a learned component in the selection of red or green aphid color morphs. We then used the results of these experiments to parameterize a model that examines whether learned behaviors can explain the changes in the rates of parasitism observed in field populations in South-central Wisconsin, USA. In the first of two experi-

ments, we measured the sequence of host choice by *A. ervi* on pea aphid color morphs and analyzed this sequence for patterns in biased host selection. Parasitoids exhibited an inherent preference for green aphid morphs, but this preference was malleable; initial encounters with red aphids led to a greater chance of subsequent orientation towards red aphids than predicted by chance. In a second experiment, we found no evidence that parasitoids specialize on red or green morphs; for the same parasitoids tested in trials separated by 2 h, color preference in the first trial did not predict color preference in the second, as would be expected if they differed in fixed preferences or exhibited long-term (> 2 h) learning. Using data from the two experiments, we parameterized a population dynamics model and found that learning of the magnitude observed in our experiments leads to biased parasitism towards the most common color morph. This bias is sufficient to explain changes in the ratio of aphid color morphs observed in field sites over multiple years. Our study suggests that for even relatively simple organisms, learned behaviors may be important for explaining the population dynamics of their hosts.

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S. A. Langley · K. J. Tilmon · B. J. Cardinale · A. R. Ives  
Department of Zoology, University of Wisconsin,  
Madison, WI 53706, USA

*Present Address:*

S. A. Langley (✉)  
Department of Entomology, Michigan State University,  
243 Natural Science, East Lansing, MI 48824, USA  
e-mail: shaunlangley@gmail.com

*Present Address:*

K. J. Tilmon  
Plant Science Department, South Dakota State University,  
Box 2207A AGH 219, Brookings, SD 57007-1096, USA

*Present Address:*

B. J. Cardinale  
Department of Ecology, Evolution and Marine Biology,  
University of California, Santa Barbara, CA 93106, USA

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## Introduction

Foraging parasitoids are ideal organisms for studies on the role of experience in modulating behavioral decisions, because their behaviors can easily be quantified through visual observations in a controlled

environment. Learning has been well documented for nearly 20 species of hymenopterous parasitoids (Chow and Mackauer 1992; Dukas and Duan 2000; Godfray and Waage 1988; Guerrieri et al. 1997; Kaiser and Jong 1993; Lewis and Tumlinson 1988; Papaj and Vet 1990; Sheehan and Shelton 1989; Turlings et al. 1993; Vet et al. 1991; Wäckers and Lewis 1991). Learning can lead to a number of changes in the behavioral repertoire of individuals, including an increase in the number of stimuli eliciting a response, development of a preference, and a decrease in the variability of a parasitoid's response to a stimulus (Turlings et al. 1993; Vet et al. 1990). Parasitoids regularly encounter a broad range of insects throughout their environment, only some of which are appropriate hosts (Battaglia et al. 1995; Powell et al. 1998). Therefore, it is vital that they be able to identify and select appropriate individuals to parasitize in a manner that is efficient and reliable. Learning from prior foraging experience is one of several ways that parasitoids might improve their searching efficiency for suitable hosts.

Despite numerous examples of parasitoid learning, few studies have explored how learning might influence population-level patterns of host use by parasitoids in the field. Our study explores the learning behavior of the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae) attacking pea aphids, *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae), which occur as two color morphs, green and red. Populations in southern Wisconsin (the location of our study) have historically been of the green morph. It was not until the early 1990s that the red morph was first detected in alfalfa crops (A. R. Ives, unpublished data). Over the subsequent 10 years, relative frequencies of the green and red color morphs equilibrated, reaching roughly 1:1 by 2001. At the same time, the relative percent parasitism on green and red morphs changed; in 1996 the percent parasitism on red morphs averaged 0.64 times the percent parasitism on green morphs (Losey et al. 1997), compared to 1.16 times that on green morphs in 2001 (see below). This change in the relative parasitism rates on red versus green morphs occurred despite the well-documented innate preference of *A. ervi* for green pea aphid morphs over red morphs (but see Henter and Via 1995 for an exception; Losey et al. 1997; Michaud and Mackauer 1994; Powell et al. 1998).

Here, we investigate whether there is a learned component in the preference of *A. ervi* for red versus green color morphs, and whether this learned behavior can explain the change in relative parasitism rates on color morphs observed in the field. Our

hypothesis that learned behaviors could explain changes in patterns of parasitism in the field is derived heuristically as follows. When red morphs were initially rare, *A. ervi* would encounter them rarely; the resulting lack of experience would limit learning that red morph pea aphids were suitable hosts. Thus, percent parasitism on red morphs would be low relative to the more common green morph. However, once red and green morphs had reached similar densities, encounters with red morphs would become more common. With more frequent encounters, learned behavior would no longer favor the green morph, thereby leading to similar percent parasitism rates between morphs.

Our study consists of experiments and a model. First, we used two laboratory experiments to quantify the learning component of *A. ervi* preference for color morphs. This allowed us to determine if the sequence of attacks by a parasitoid is consistent with learning behavior. Second, we used the data from the laboratory experiments to parameterize a model of *A. ervi* foraging behavior and quantify the change in relative percent parasitism on the different color morphs that would be expected with changes in the relative densities of the morphs. This allowed us to ask whether the behavior observed in the laboratory experiments could explain the change in relative parasitism of red versus green morphs observed in the field.

## Materials and methods

### Aphids and parasitoids

Pea aphids, *Acyrtosiphon pisum*, were accidentally introduced to North America in the 1800s (Mackauer 1968) and have since spread as pests of peas, alfalfa, red clover, and other agricultural crops across North America. Pea aphids commonly occur as two color morphs, green and red. This dimorphism is maintained by a single locus with red as the dominant color morph (J. E. Losey, personal communication). The parasitic wasp *Aphidius ervi* was first introduced to the United States between 1961 and 1963 from populations in Europe for biological control of pea aphids in alfalfa (Angalet and Fuester 1977; Halfhill et al. 1972; Mackauer and Campbell 1972). It is currently the dominant parasitoid of pea aphids in alfalfa in southern Wisconsin, USA.

Parasitoid and pea aphid cultures used for this experiment originated from field populations at our study site, the Arlington Agricultural Research Station

of the University of Wisconsin, Columbia County, Wisconsin. Parasitoids were reared on pea aphids (red and green morphs) feeding on fava bean plants at  $23 \pm 5^\circ\text{C}$ , light:dark 16:8 h.

To determine the relative frequency and parasitism of the red versus green morphs in field sites, we sampled between four and nine alfalfa fields using sweep nets in 1996, 2001, 2002, and 2004 from May to September. Up to 50 adult or fourth instar aphids were collected in each field on each sampling date, with smaller samples taken from fields containing low pea aphid densities. Aphids were scored for color and dissected to determine parasitism, and sample sizes are given in Table 1.

#### Experiment 1: effect of experience on foraging behavior

The objective of the first experiment was to determine if successful parasitism on a green or red morph affect subsequent color preferences for green or red morphs? We performed a choice experiment in which we placed a naïve, mated female parasitoid (3 days after emergence) with ten green and ten red, 5-day-old aphids in a  $100 \times 15$ -mm plastic Petri dish (Fisher-brand). Although we did not randomly distribute aphids, we allowed sufficient time for them to distribute themselves; preliminary trials demonstrated that the distribution of aphids was independent of color morphs (results not reported). We observed the foraging behavior of each parasitoid for 20 min, classifying female behavior as follows. As a parasitoid forages, she typically orients towards an aphid and palpates it with her antennae. We classified each of

these contacts as a discrete event, an “encounter.” We further categorized each “encounter” as an “attack” (ovipositor inserted into the aphid host) or a “rejection” (encounter without oviposition). Thus, an “encounter” represents an orientation behavior towards a potential host, which further leads to either a host acceptance or rejection. Note that our category “attack” includes both oviposition and insertion of the ovipositor without oviposition (pseudoparasitism), two possibilities that we cannot distinguish in this study. Previous studies (Ives et al. 1999) show that 25% of *A. ervi* attacks are pseudoparasitisms. In observing the foraging behavior, we collected information on the order of encounters and attacks, and the corresponding color morph the behavior was directed towards. We performed these choice tests for 92 parasitoids resulting in more than 30 h of observation time.

#### Experiment 2: persistence of fixed preferences

In a complementary experiment, we examined whether parasitoids exhibit a fixed preference for green or red morphs. We performed choice tests like those in experiment 1, giving each of 31 parasitoids a choice of ten green and ten red aphids. For each parasitoid, we then repeated the choice test using new aphids after the parasitoid had been given a 2-h resting period. We observed the parasitoid for 20 min and recorded the number of attacks on green and red morphs. Since the purpose of this experiment was to determine overall preference (proportion of each color morph attacked), it was not necessary for us to record the order of events.

**Table 1** Field samples to determine the proportion of red morph pea aphids in the population and the percent parasitism on green and red morphs

Year	Number of fields	Number of samples	Total aphids	Proportion red morphs <sup>a</sup>	Difference between morphs <sup>b</sup>	Parasitism on green morphs <sup>a</sup> (%)	Parasitism on red morphs <sup>a</sup> (%)	Difference between parasitism <sup>b</sup>
1996	9	39	1,521	0.197	$P < 0.001$ $df = 8^c$	$46.6 \pm 4.7$	$29.7 \pm 7.5$	$P < 0.02$ $df = 8^c$
2001	9	226	9,594	0.498	$P > 0.1$ $df = 225$	$15.7 \pm 1.4$	$18.3 \pm 1.4$	$P < 0.01$ $df = 225$
2002	5	37	1,793	0.405	$P < 0.001$ $df = 36$	$19.7 \pm 3.1$	$24.2 \pm 3.7$	$P > 0.1$ $df = 34^d$
2004	4	25	674	0.442	$P < 0.05$ $df = 24$	$18.2 \pm 2.9$	$15.8 \pm 3.1$	$P > 0.1$ $df = 24$

<sup>a</sup>Data reported are averages among samples

<sup>b</sup>Paired two-tailed *t*-test on arcsine-square root-transformed data

<sup>c</sup>Samples pooled within fields due to low red morph counts in samples

<sup>d</sup>Samples with no red or green morphs excluded

## Statistical analysis

We performed analyses of the data from experiment 1 to determine:

1. Whether attacks were more likely to be followed by attacks than rejections.
2. Whether encounters (regardless of whether the aphid was attacked or rejected) with green (red) color morphs were more likely to be followed by another encounter with a green (red) morph.
3. Whether attacks on green (red) morphs were more likely to be followed by another attack on a green (red) morph.
4. What the most likely event (attack vs. rejection of green vs. red morph) was following attacks on green vs. red morphs.

We used the same general statistical procedure to address each of these questions. To illustrate this procedure, suppose we were to analyze whether attacks on green morphs were more likely to be followed by attacks on green or red morphs. If the continuous observation on a single parasitoid gave the sequence G–G–R–G (where G = attack on green, R = attack on red), we would decompose this sequence into three event pairs: G–G, G–R, and R–G. By combining data from all parasitoids, the numbers of each of the four possible event pairs (G–G, G–R, R–G, and R–R) can be arranged in a contingency table with elements  $x_{i,j}$  ( $i, j = G$  or  $R$ ) giving the number of observed event pairs with the first event  $i$  and second event  $j$ . A test statistic can be derived in the standard way for a contingency table with the “expected” number of event pairs calculated as:

$$\hat{x}_{i,j} = \frac{\sum_i x_{i,j} \sum_j x_{i,j}}{\sum_{i,j} x_{i,j}},$$

and the test statistic

$$X^2 = \sum_{i,j} \frac{(x_{i,j} - \hat{x}_{i,j})^2}{\hat{x}_{i,j}}.$$

If all values in the contingency table were independent, the test statistic  $X^2$  would follow a  $\chi^2$  distribution. However, the event pairs in our study were not independent, because multiple event pairs were observed for the same parasitoid. Therefore, we performed a bootstrap analysis in which replicate bootstrap data sets were created by randomly permuting the sequence of events observed for each parasitoid. Because permutations were performed for each parasitoid

separately, the bootstrapping procedure accounts for non-independence due to repeated observations on the same parasitoid. For each bootstrap data set, we calculated the value of the test statistic  $X^2$ . We repeated this procedure for 5,000 bootstrap replication data sets and used the resulting distribution of 5,000 values of  $X^2$  as the approximate distribution of  $X^2$  under the assumption that the sequence of attacks on morphs was random within sequences observed for each parasitoid. Note that because we randomized the events within sequences for individual parasitoids, we preserved any overall bias for green morphs that might be caused if some parasitoids had inherent preferences for green morphs. In other words, the bootstrapped test targeted only the order of encounters and attacks on the color morphs for individual parasitoids, factoring out any differences among parasitoids.

We used the data from experiment 2 to test directly for consistent differences among parasitoids in possible fixed preferences for color morphs. Specifically, we calculated the correlation between the proportion of red morphs attacked by a parasitoid in the first trial and the proportion of red morphs attacked in the second trial using Kendall’s rank correlation test. A strong correlation would suggest that a preference for green or red morphs is fixed for individual parasitoids over the 2-h period between trials.

## Results

### Field data

Table 1 presents data on the distribution of color morphs in field collections between 1996 and 2004. The proportion of red morphs increased from 0.197 in 1996 to a maximum of 0.498 in 2001, and then dropped slightly in 2002 and 2004. The ratio of parasitism rates on red to green morphs increased from 0.64 to 1.16 from 1996 to 2001, and were then statistically equal in 2002 and 2004.

### Experiment 1

Of the 1,703 encounters (antennal palpitations followed by either attack or rejection) we observed, 54% were directed towards green morphs. We documented 598 attacks, of which 62% were on green morphs.

Tables 2, 3, and 4 present matrices comparing event pairs drawn from the strings of encounters of individual parasitoids (see [Materials and methods: Statistical analysis](#)). Table 2 compares 1,611 event pairs in terms of attacks and rejections, regardless of aphid color;

**Table 2** Attack and rejection event pairs from observations of 92 parasitoids. Numbers in parentheses are expected values calculated from the bootstrapped analysis (see Statistical analysis). Attacks frequently follow attacks (353/565 = 61%), whereas rejections rarely follow attacks (206/1046 = 20%)

Second event	First event	
	Attack	Rejection
Attack	353*** (334)	206 (235)
Rejection	212 (230)	840*** (813)

\*\*\* $P < 0.001$  (observations greater than expected)

note that the number of event pairs is 92 less than the number of events, because there is one less event pair than event for each of the 92 parasitoids. Attacks were most often followed by additional attacks, 353/565 = 62%, whereas rejections were rarely followed by attacks, 206/1,046 = 20%; if attacks were completely independent of previous experience, then these percentages would be equal, 559/1,611 = 35%. This strong contrast is potentially misleading, however, because it does not account for correlations caused by multiple observations made on the same parasitoid; it could arise from variation among parasitoids in the frequency of attacks on aphids. Correcting for this individual variation using the bootstrap procedure (see Materials and methods), the expected proportion of attacks following attacks is 334/565 = 59% and the expected proportion of attacks following rejections is 235/1,046 = 22%. Even though these values are closer to the observed values of 62 and 20% than those predicted under the assumption that attacks are completely independent of previous actions (both 35%), the observed values are still significantly different from those predicted if parasitoids attacked or rejected aphids in random sequence (bootstrap  $P < 0.001$ ).

Table 3 compares the 1,611 event pairs in terms of encounters with green or red aphids, regardless of the outcome of the encounter (attacks or rejections). An encounter with a red morph was followed by another

**Table 3** Event pairs of encounters with green/red morphs<sup>a</sup> (see Table 2 for details)

Second encounter	First encounter	
	Green	Red
Green	522*** (490)	344 (378)
Red	346 (374)	399*** (369)

\*\*\* $P < 0.001$

<sup>a</sup>Encounters with red morphs were more frequently followed by encounters with the red versus green morph (399/743 = 54% vs. 344/743 = 46%)

encounter with a red morph 399/743 = 54% of the time, whereas an encounter with a red morph was followed by an encounter with a green morph 344/743 = 46% of the time (bootstrap  $P < 0.001$ ). This means that parasitoids that encountered a red aphid were more likely to encounter another red aphid in the subsequent encounter.

Table 4 compares just the 541 encounters in which parasitoids were observed attacking aphids. After a parasitoid attacked a green morph, the proportion of the following attacks that were on a green morph was 244/345 = 71%, whereas after attacking a red morph, the proportion of the following attacks on a green morph was 98/196 = 50% (bootstrap  $P < 0.001$ ).

Finally, Fig. 1 shows the relationship between an initial attack on either green or red morph, and the proportion of subsequent events that were attacks or encounters with red morphs. An encounter with a red morph is correlated with the color morph previously attacked (135/355 = 38% vs. 109/204 = 53.4% for the parasitoids initially attacking green and red morphs, respectively)—a difference of 15.4%. Similarly, an attack on a red morph is correlated with a previous attack (57/355 = 16% vs. 64/204 = 31.3% for parasitoids initially attacking green and red morphs, respectively)—a difference of 15.3%.

## Experiment 2

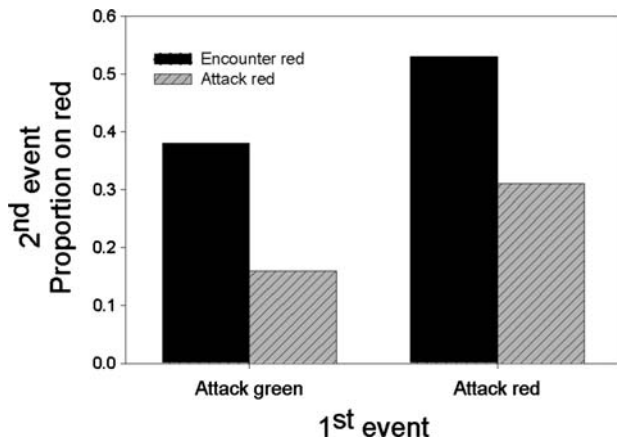
Experiment 2 complements experiment 1 by investigating whether parasitoids exhibit a fixed preference for either green or red morphs. We found no significant correlation between a parasitoid's host preference in the first trial and second trial at least 2 h later (Kendall's rank correlation = -0.0077;  $P > 0.9$ ) (Fig. 2). The lack of any association between the first and second trials shows that any apparent color preference within the first trial does not persist predictably for more than 2 h.

**Table 4** Event pairs of attacks on green/red morphs<sup>a</sup> (see Table 2 for details)

Second attack	First attack	
	Green	Red
Green	244*** (230)	98 (111)
Red	101 (118)	98*** (82)

\*\*\* $P < 0.001$

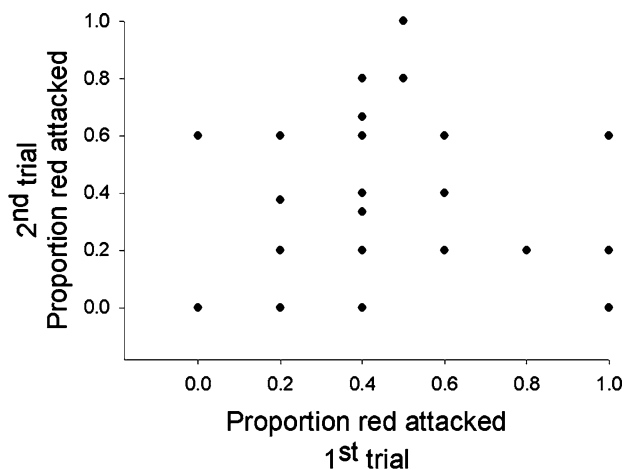
<sup>a</sup>Attacks on the green morph were frequently followed by attacks on green (244/345 = 71%); however, there was no discrimination in attacks on green versus red morphs following an attack on the red morph (98/196 = 50%)



**Fig. 1** Proportion of encounters (palpitation of aphid with antennae; black bars) and attacks (parasitism or pseudoparasitism; patterned bars) on red morph pea aphids (*Acyrtosiphon pisum*) that follow an initial attack on green or red morphs (first event). Data from experiment 1 using 92 individual parasitoids (bootstrap  $P < 0.001$ )

Model

We constructed a model parameterized by data from the laboratory experiments to assess whether learned color preferences can potentially explain patterns of parasitism in the field. Specifically, how does the relative density of red vs. green morphs affect the percent parasitism of red vs. green morphs when color preference has a learned component similar in magnitude to that documented in our laboratory experiment? Intuitively, learned color preferences



**Fig. 2** From experiment 2, the proportion of red morph pea aphids attacked during the second trial versus the first trial. Each dot represents the preference for red aphids expressed by a single parasitoid. There is no significant correlation between the preference expressed in the first and second trials (Kendall’s rank correlation =  $-0.0077$ )

might be expected to increase percent parasitism on the most common morph because foraging parasitoids will experience the most common morph more frequently, which should then lead to a learned preference and increased parasitism on the most common morph.

To construct the model, we let  $p_{G|G}$  denote the probability that a parasitoid, after attacking a green morph, attacks another green morph, and let  $p_{R|G}$  ( $= 1 - p_{G|G}$ ) denote the probability that her second attack is on a red morph. Similarly, we let  $p_{G|R}$  and  $p_{R|R}$  ( $= 1 - p_{G|R}$ ) denote similar probabilities for a parasitoid that initially attacks a red morph. These probabilities can be calculated from Table 3 as  $p_{G|G} = 0.71$  ( $= 244/345$ ) and  $p_{G|R} = 0.50$  ( $= 98/196$ ). While our experiments were performed with equal numbers of red and green morphs in the experimental arenas, we want to use the data to ask how parasitism changes with different relative densities of red and green morphs in the field. If the two morphs have different densities, let  $q$  be the proportion of the morphs that are green morphs and  $1 - q$  be the proportion that are red. We assume that, for a parasitoid having just attacked a green morph, the probability she will next attack a green morph is proportional to the relative density of green morphs multiplied by the preference for green morphs,  $q p_{G|G}$ , while the probability she will next attack a red morph is proportional to  $(1 - q) p_{R|G}$ . Similar quantities can be derived for parasitoids that initially attack a red morph. These assumptions produce a transition probability matrix  $\mathbf{M}$  whose elements  $m_{i,j}$  ( $i, j = G, R$ ) give the probability that a parasitoid having just attacked morph  $j$  subsequently attacks morph  $i$ :

$$\mathbf{M} = \begin{pmatrix} \frac{q p_{G|G}}{q p_{G|G} + (1-q) p_{R|G}} & \frac{q p_{G|R}}{q p_{G|R} + (1-q) p_{R|R}} \\ \frac{(1-q) p_{R|G}}{q p_{G|G} + (1-q) p_{R|G}} & \frac{(1-q) p_{R|R}}{q p_{G|R} + (1-q) p_{R|R}} \end{pmatrix} \quad (1)$$

This transition probability matrix defines a stochastic Markov process for the sequence of attacks made on green vs. red morphs (Caswell 1989). The long-term (stationary) proportion of attacks on green and red morphs is given by the eigenvector of  $\mathbf{M}$  corresponding to the dominant eigenvalue (which equals one).

This model assumes that all parasitoids behave in the same way, showing the same learned and fixed components of color preference. Therefore, it is not suitable for the case in which some parasitoids have fixed preferences for red and others have fixed preferences for green morphs. However, our statistical analyses of experiment 1 explicitly allowed for differences in fixed preferences among parasitoids, and

experiment 2 showed no consistent variation in fixed preferences among parasitoids. These results justify this assumption of the model.

In addition to the model given in Eq. 1, we considered two variants. Equation 1 contains two components of preferences. First, there is a fixed preference for green over red morphs; because both  $p_{G|G} = 0.71$  and  $p_{G|R} = 0.50$  are  $\geq 1/2$ , green morphs are at least as preferred as red morphs regardless of whether a parasitoid has initially attacked a green or red morph. Second, there is a learned component, since parasitoids initially attacking green morphs are more likely to attack green morphs than parasitoids initially attacking red morphs. In the first variant of the base model, we removed the fixed preference for green morphs but retained the learned preference by letting  $p_{G|G} = 0.605$  and  $p_{G|R} = 0.395$ ; here, the relative increase in preference for green morphs expressed by parasitoids initially attacking green morphs is the same as in the base model, but on average there is no preference for green or red morphs,  $(p_{G|G} + p_{G|R})/2 = 0.5$ . In the second variant, we remove the learned preference but retain the fixed preference by letting  $p_{G|G} = p_{G|R} = (0.71 + 0.50)/2 = 0.605$ .

Figure 3 shows the relative percent parasitism on red vs. green morphs against the relative density of red morphs in the population,  $1 - q$ . For the base model the predicted relative parasitism rate on red morphs increases with the relative density of red morphs, yet the relative parasitism rate is lower than that observed in the field. However, when the fixed preference for green morphs is removed from the model and we consider the effect of learning alone, there is a close match between the predicted percent parasitism on red morphs and that which we have observed in the field. According to the fixed preference alone, the percent parasitism on red morphs should only be 60% of percent parasitism on green morphs, which is clearly much lower than observed in the field.

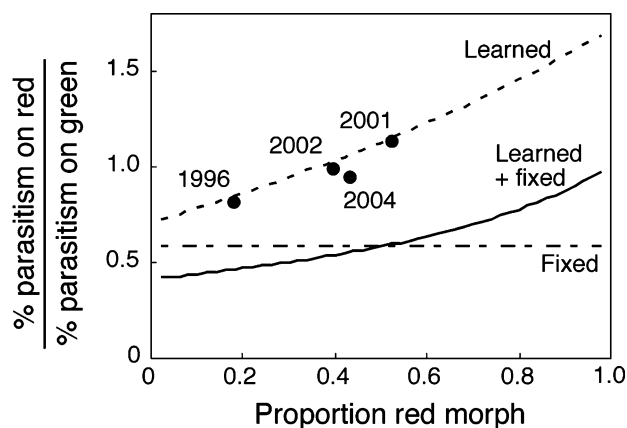
## Discussion

Our experiments revealed both a fixed and a learned component to *A. ervi* host preference. Parasitoids had a fixed preference for green pea aphids. In addition, however, parasitoids were more likely to orient towards and attack the color morph they had encountered immediately before. Therefore, parasitoids showed a learned behavior.

Our finding of a fixed preference for green morphs is consistent with studies by Powell et al. (1998) who showed an overall preference by *A. ervi* for green over

red morphs. Our results differ, however, from observation by Henter and Via (1995) of higher parasitism on red pea aphids, a difference we cannot explain. Furthermore, the fixed preference for green morphs in our laboratory experiments was not consistent with the pattern of percent parasitism in the field; the model assuming only learned and no fixed color preference fits the field data best. One explanation for this apparent inconsistency is that we (and others) used naïve parasitoids in the laboratory experiments, while older, experienced parasitoids dominate in the field. This experience may quickly override any initial preference of newly emerged parasitoids. Alternatively, the fixed preference for green in our laboratory experiments may be an artifact of our experimental design. Parasitoids were given the opportunity to select between green and red aphids, while in the field parasitoids encounter aphids more or less sequentially. Sequential encounters with hosts in the field might accentuate the role of learned cues for detecting hosts over any fixed preferences.

Learned preferences were demonstrated in the laboratory experiments, as parasitoids were more likely to orient towards and attack morphs of the same color as those they most recently experienced. Not only attacks (Table 4) but also encounters (Table 3) elicited a change in preference; therefore, learning did not



**Fig. 3** Model predictions (Eq. 1) for the relative percent parasitism on red versus green morphs against the relative density of red morphs in the population. Results are of the base model parameterized directly from experiment 1 ( $P_{G|G} = 0.71$  and  $P_{R|G} = 0.50$ ; solid line, *Learned + fixed*), the model variant with learned but not fixed preferences ( $P_{G|G} = 0.605$  and  $P_{R|G} = 0.39$ ; dashed line, *Learned*), and the model variant with fixed preferences ( $P_{G|G} = 0.605$  and  $P_{R|G} = 0.605$ ; dashed and dotted line, *Fixed*). Circles give the data from the field in 1996, 2001, 2002, and 2004 (labeled) for the total numbers of aphids dissected (i.e., aggregating the data from all samples within a year). Sample sizes for the field observations are provided in Table 1

depend on the outcome of prior experiences. Furthermore, the main effect of learning appeared to be to increase encounter rates with the same colored morph; once an aphid was encountered, the probability of attack was not strongly dependent on the color of the morph initially attacked (Fig. 1). This suggests that color is used as a long-distance, pre-contact cue.

Finally, the model showed that the learned behavior documented in the laboratory experiments could explain the increase in percent parasitism on red morphs relative to green morphs observed in the field. Although the field data are not consistent with the fixed preference observed in the laboratory for naïve females, the magnitude of increase in percent parasitism with increasing proportion of red morphs is consistent with the learned preference in the laboratory (Fig. 3). Therefore, our work demonstrates that it may be possible for learned behavior to affect population-level patterns of parasitism in the field.

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