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LETTER

Adaptive learning of host preference in a herbivorous arthropod

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Abstract

Although many publications deal with the effects of experience on behaviour, adaptive learning (i.e. behavioural change with experience resulting in improved reproductive success) is poorly documented. We present direct evidence that learning of host preference improves fitness in the herbivorous mite, *Tetranychus urticae*. Individual mites from two strains were repeatedly given a choice between two host plants, tomato and cucumber, and then subjected to a performance test on each. For both strains, food experience affected the subsequent choice: individual mites learned to prefer cucumber over tomato. The performance test showed this effect to be adaptive, as the food plant the mites learned to prefer (cucumber) allowed for increased oviposition, survival and development. These findings have important implications for the interpretation of the preference–performance relationship among herbivorous arthropods. The frequently reported absence of such a relationship may be due to experience-dependent preference and/or performance.

Keywords

Adaptive learning, experience, *Tetranychus urticae*, preference–performance relationship, tomato, cucumber, phytophagous arthropod, evolution of specialization, host race formation.

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INTRODUCTION

Herbivorous arthropods are excellent objects for studying the ecology and evolution of learning (Papaj & Prokopy 1989). The fitness consequences of learning are poorly studied (Maynard Smith 1987; Papaj & Lewis 1993; Dukas 1998), and this also holds for herbivorous arthropods (Papaj & Prokopy 1989; Szentesi & Jermy 1990; Bernays 1995). In studies on food aversion learning (where insects learn to avoid food which causes nausea or other nuisances), fitness effects were never quantified (Bernays 1993). This also applies to studies on induction of food preference (Szentesi & Jermy 1990). However, grasshopper nymphs can enhance their growth rate by associative learning (Dukas & Bernays 2000) and parasitic wasps enhance offspring survival by learning to avoid superparasitism (Van Alphen & Visser 1990). Hence, the few studies that do connect learning and fitness, show positive effects (but see Parmesan *et al.* 1995). However, the performance measures (larval growth rate and offspring survival) may be partial or even weak fitness correlates.

In this paper we test whether behaviour changes with experience such that reproductive performance is im-

proved. Although we refer to this process as adaptive learning (Papaj 1993), we are not concerned with mechanisms underlying the change in behaviour with experience (e.g. associative learning, habituation, etc.). Hence, throughout this paper we use the term learning in a general sense.

We used the herbivorous mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), to investigate (a) whether experience affects food choice and (b) whether such changes in food choice result in fitness benefits. We measure fitness effects of learning over the entire life cycle.

MATERIALS AND METHODS

Mites and plants

Tetranychus urticae is a polyphagous herbivore recorded from over 900 plant species (Bolland *et al.* 1998) and a well-known pest of many crops (Helle & Sabelis 1985). Mites were collected from tomato (*Lycopersicon esculentum*) and cucumber (*Cucumis sativa*) from two separate greenhouses in the Netherlands (Gotoh *et al.* 1993). The cucumber variety used is susceptible to mite attack, but

tomato is known as a hostile host due to secondary compounds in leaves and sticky exudates of glandular hairs (Fry 1990, 1999; Chatzivassileiadis & Sabelis 1997, 1998; Chatzivassileiadis *et al.* 1999). The two lines of mites, further referred to as Tomato and Cucumber strain, were maintained on detached bean leaves (*Phaseolus vulgaris*) for over two years prior to experiments. Adult females of equal age were used, obtained from eggs laid within one hour by many females on fresh bean leaves.

Tomato (cv. 'Moneymaker') and cucumber plants (cv. 'Corona F1') were grown in a climate-controlled greenhouse and leaf material was collected from four-week-old plants. Experiments were performed in a climate room, at 23 °C, 65% RH, and 16 : 8 h light: dark period.

Experimental setup

Choice arenas consisted of two flanking leaf disk halves (one of each host plant; < diameter > 1.5 cm), with a pin in the centre. To prevent desiccation, the arenas were placed on wet cotton-wool covered sponges. One adult female was put on top of each pin with a fine brush. Generally, mites descend the pin, probe both disk halves, settle after approximately one hour and do not change position for the next 24 h. This is because they produce a web where they feed and reproduce (Helle & Sabelis 1985).

After 24 h, the position of the mites and egg numbers per disk half were scored. Although in virtually all trials eggs were seen on one disk half, occasionally both contained eggs, indicating a change of food. In that case, the food chosen was defined as the host with most eggs. Each mite was then transferred to a fresh arena for a second and third choice test. The few females (< 5%) that made no choice on one or more days were excluded from further analysis.

Next, females were transferred to leaf disks (< diameter > 1.5 cm) of cucumber or tomato. Females of similar choice history were equally distributed over the two food plants. Every 24 h, leaf disks were replaced and eggs counted, until females had died or oviposited for six days. Over this period, the average number of eggs per day was calculated.

Each day, after replacing the leaf disk, the eggs of each individual female were equally distributed over a tomato disk and a cucumber disk (< diameter > 1.5 cm) to measure offspring mortality and development rate. After 11 days the developmental stage of offspring was recorded and assigned an index. Adults were assigned the number 11, teleiochrysales 10, deutonymphs 9, deutochrysales 8, protonymphs 7, protochrysales 6 and larvae 5. The index reflects the number of days it takes to reach this stage on bean under our climate conditions. Dead individuals and

eggs not hatched after 11 days were discarded from analysis. Average offspring development indices on each food plant were calculated for each mother.

RESULTS

Multiple-choice test

Sequential choices showed increasingly more mites of both the Tomato and the Cucumber strains preferring cucumber over tomato (Fig. 1). The preferences for cucumber in the second and third choice tests were significantly higher than in the first [3-D contingency table χ^2 (Zar 1999); Tomato strain: $G_4 = 22.82$, $P < 0.001$; Cucumber strain: $G_4 = 66.60$, $P < 0.001$]. The strains differed only in their first choice: the Cucumber strain showed no preference, whereas the Tomato strain preferred cucumber. This was contrary to our expectation that the strains would prefer their original host.

To investigate how feeding experience affected the subsequent choice, we calculated the fraction of mites changing food choice from one test to the next. For both the second and the third choice test, this yields a fraction of mites that first preferred tomato and then cucumber (T→K), and a fraction of mites that first preferred cucumber and then tomato (K→T).

For both strains, the fraction of K→T mites was very low, and lower than expected from the preference in the first choice test (Fig. 2, left panels; goodness-of-fit test; Cucumber strain: second choice $G_1 = 6.86$, $P < 0.01$, third choice $G_1 = 35.9$, $P < 0.001$; Tomato strain: second choice $G_1 = 1.44$, n.s., third choice $G_1 = 11.1$,

Fig. 1 The fraction of mites choosing cucumber in the three subsequent choice tests (white bars: Tomato strain; hatched bars: Cucumber strain; for both strains $n = 46$).

$P < 0.001$). Hence, mites that had chosen cucumber before were more likely to choose cucumber again. The fractions of T→K mites show a different trend for the two strains. In the Tomato strain, fewer mites than expected from the first choice test switched to cucumber (although not significant due to low numbers; goodness-of-fit test; second choice $G_1 = 0.35$, n.s., third choice $G_1 = 0.99$, n.s.), whereas in the Cucumber strain the switching frequency was higher than expected (almost all mites coming from tomato chose cucumber next; Fig. 2, left panels; goodness-of-fit test; second choice $G_1 = 22.1$, $P < 0.001$, third choice $G_1 = 7.20$, $P < 0.01$).

Fig. 2 Fractions of mites switching host plant in subsequent choices. (a) Tomato strain, (b) Cucumber strain. In the left panels, the fractions making different choices in two subsequent choice tests are shown. White bars: mites switching food plant in the second choice test; grey bars: mites switching food plant in the third choice test (T→K: first choosing tomato, then cucumber; K→T: vice versa). In the right panels, the fractions of individuals switching in the third choice test are shown for all combinations of the previous two choices (e.g. TT→K is the fraction switching to cucumber after choosing tomato twice). Numbers of individuals are indicated above the bars, above the graph; for both strains $n = 46$.

Comparing the fractions switching in the third test with those in the second is only justified if the third choice is independent of the first choice. For the Cucumber strain this holds (3-D contingency table χ^2 ; $G_3 = 3.14$, $P > 0.25$), but not for the Tomato strain ($G_3 = 13.40$, $P < 0.01$). In the right panels of Fig. 2, the fractions of mites switching in the third choice test are given for all combinations of the previous two choices (e.g. TT→K is the fraction switching to cucumber after choosing tomato twice). Comparing TT→K with KT→K, and TK→T with KK→T, shows that these fractions are indeed equal for the Cucumber strain. In the Tomato strain, however, TT→K and KT→K differ extremely. This causes the overall dependence of the third choice on the first, even though this stems from only three individuals choosing tomato consistently (i.e. TT→T = 1, thus TT→K = 0).

Performance test

For both the Cucumber and the Tomato strain, all fitness measures—oviposition rate of the females, mortality and development rates of their offspring—were independent of choice history (Kruskal–Wallis tests for both strains yielded $P > 0.20$ in all cases). Therefore, all performance results were pooled with respect to choice history.

Females of both strains had higher oviposition rates on cucumber than on tomato (Fig. 3; Kruskal–Wallis test, Tomato strain: $H_1 = 324.5$, $P > 0.001$; Cucumber strain: $H_1 = 441$, $P > 0.0001$). Tomato strain females laid many more eggs on tomato than Cucumber strain females;

Fig. 3 Average oviposition rates (± 1 SE) of the Tomato strain and the Cucumber strain on cucumber (white bars) or tomato (grey bars). For both strains $n = 46$.

however, on cucumber oviposition rates were comparable (Fig. 3). For both strains, female mortality rate was higher on tomato than on cucumber (Table 1).

For both strains, mortality rate of the offspring was significantly lower on cucumber than on tomato (Fig. 4a,b; clusters of points lie above the diagonal; Table 2a,b). The ANOVA for the Tomato strain (Table 2a) shows that the interaction between the effects of the mothers' host plants and that of their offspring was bordering significance. This could not be tested for the Cucumber strain due to high mortality of mothers on tomato. Offspring development rate was significantly higher on cucumber than on tomato (Fig. 4c,d; clusters of points lie below the diagonal; Table 2c,d). However, for the

Tomato strain this difference was small. The ANOVA for the Tomato strain (Table 2c) shows that the effect of host plant on which the mother had oviposited was bordering significance: offspring of females ovipositing on tomato developed slightly faster. This effect could not be tested for the Cucumber strain because too few offspring survived on tomato.

DISCUSSION

Adaptive learning

In the first choice test, the Cucumber strain exhibited no preference (Fig. 1). In the second and third choice test, preference shifted towards cucumber, as manifested by (1) a larger than expected T→K fraction and (2) a smaller than expected K→T fraction. This provides compelling evidence for a learned preference. In contrast, the Tomato strain preferred cucumber from the first choice onwards. Yet, again there is a learned preference, as evidenced by a decreasing K→T fraction. Thus, experience with cucum-

Table 1 Mortality rate of adult females on tomato or cucumber during the oviposition test (for both strains $n = 46$)

	Tomato strain	Cucumber strain
On tomato	0.53	0.22
On cucumber	0	0.045

Fig. 4 Average offspring mortality rate (top graphs) and development index (bottom graphs) on tomato and cucumber. Each point represents offspring of one female (open circles: mothers ovipositing on tomato; filled circles: mothers ovipositing on cucumber). The diagonal indicates equal mortality rate (or developmental rate) on cucumber and on tomato. (a, c) Tomato strain; (b, d) Cucumber strain.

Table 2 Analysis of variance for the average offspring mortality rate and development index. Mortality rate was angularly transformed ($= \arcsin [\sqrt{\cdot}]$). Note that for the Cucumber strain the effect of the host plant of the mother could not be incorporated due to lack of data

Source	d.f.	SS	<i>F</i>	<i>p</i>
(a) Tomato strain, mortality rate				
Block (mother)	37	5.811		
Host-mother (A)	1	0.103	0.649	n.s.
Error a	36	5.708		
Host-offspring (B)	1	0.744	7.480	< 0.01
Interaction (A × B)	1	0.399	4.010	0.054
Error b	35	4.625		
(b) Cucumber strain, mortality rate				
Host-offspring	1	0.661	10.9	< 0.01
Block (mother)	20	0.445		
Error	20	1.21		
(c) Tomato strain, development rate				
Block (mother)	33	25.88		
Host-mother (A)	1	2.937	4.097	0.052
Error a	32	22.94		
Host-offspring (B)	1	19.03	54.56	< 0.001
Interaction (A × B)	1	0.063	0.180	n.s.
Error b	31	10.82		
(d) Cucumber strain, development rate				
Host-offspring	1	146	506	< 0.001
Block (mother)	20	8.88		
Error	20	5.78		

ber induced a strong preference for cucumber in both strains, whereas experience with tomato induced a strong aversion for tomato in the Cucumber strain (due to insufficient data this cannot be inferred for the Tomato strain). The altered preferences cannot be due to induction of plant defences, because each test was done with fresh leaf disks.

Because both mite strains learn to prefer cucumber over tomato and yield higher reproductive output on cucumber than on tomato, learning is adaptive. Evidently, the mites do not immediately perceive plant quality, but need feeding experience on the plants to adjust their preference. Such learned responses are by no means self-evident. First, previous tests of adaptive learning in herbivorous arthropods yielded positive (Dukas & Bernays 2000) and negative results (Parmesan *et al.* 1995). Second, learning is not the best response to every type of variable environment (Stephens 1987, 1993).

Preference–performance relationship

Preference–performance relations are not easy to assess, because experience may change preference as well as performance. In our experiments, however, performance was independent of the choices made. In particular, mites with rigid plant preferences (i.e. always choosing

tomato or always choosing cucumber) did not achieve higher reproductive success than mites with changing preferences. This facilitates the interpretation of our results in terms of a preference–performance relationship. Thus, given enough opportunity, herbivorous mites may learn to adjust their preference to the host that yields the better performance.

Preference of adult females and the performance of their offspring do not always correlate (Thompson 1988; Jaenike 1990; Via 1990; Thompson & Pellmyr 1991). However, studies investigating the preference–performance relation are typically based on a single preference test, thus assuming preference and performance are not changed by experience. If we would have measured the first choice only, we would have concluded that preference in females of the Cucumber strain has no relation to performance of their offspring. By allowing the mites to gain experience, we recovered a positive relationship. Therefore, lack of a positive correlation between preference and performance, as often reported in the literature, may have been observed because ovipositing females were deprived of the opportunity to learn. This claim is supported by studies demonstrating experience-based changes in host preference in herbivorous arthropods (Jermy 1987; Papaj & Prokopy 1989; Bernays 1995).

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BIOSKETCH

Martijn Egas is a PhD-student, working on the evolution of specialization in phytophagous arthropods and its implications for host race formation and sympatric speciation

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