

Direct and indirect responses of parasitoids to plants: sex ratio, plant quality and herbivore diet breadth

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Introduction

Parasitoid behavior may be influenced directly by the plants on which their hosts feed (Vet & Dicke, 1992), but it is usually assumed that aspects of parasitoid demography (e.g., growth, survival and sex ratio) only respond indirectly to plants, via changes in properties of their hosts (Godfray, 1994). A large body of literature shows that sex ratios of parasitoids respond directly to such host properties as body size or population density, and to environmental factors such as temperature (King, 1993; Godfray, 1994). In this paper, we demonstrate that demographic responses, particularly sex ratios of parasitoids, are properties that may be affected directly by their hosts' foodplants. We assessed the direct effects of plant properties on sex allocation in two different herbivore-parasitoid systems, and explored indirect effects of plants on wasp fecundity and survival.

We used two systems: (1) the diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera, Plutellidae), and its parasitoid, *Diadegma insulare* Cress. (Hymenoptera, Ichneumonidae), and (2) the cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera, Noctuidae), and its parasitoid, *Patrocloides montanus* (Cresson) (Hymenoptera, Ichneumonidae). These systems are similar in that both parasitoids are ichneumonids native to North America, solitary, and parasitize larvae of only a few closely related herbivore species that are important pests of crucifer crops. The major difference

between these systems is in the diet breadth of their herbivore hosts: DBM is a specialist on plants within the family Brassicaceae, while *T. ni* is a generalist on plants from many families. Comparing these systems allowed us to ask whether the breadths of the herbivores' diets affected parasitoid demographic responses to food plants.

In the field, sex ratios of *D. insulare* change with the nutritional quality of the foodplants consumed by its hosts: more female wasps emerged from DBM larvae on well-fertilized plants (Fox *et al.*, 1990). In both field and laboratory experiments, DBM preferred to lay eggs on low quality (low fertilizer) plants, while *D. insulare* preferred to search high quality plants (Fox & Eisenbach, 1992). Field experiments to assess whether wasps use host cues and/or plant cues to determine sex allocation were hard to interpret, but suggested that wasps respond directly to both the herbivores and their foodplants. The experiments reported here assess the mechanisms that could generate the patterns observed in the field.

Materials and methods

Plutella xylostella – *Diadegma insulare*. To test whether sex allocation in the wasp, *D. insulare*, responded directly to the foodplants eaten by DBM caterpillars, we used two short-term, laboratory oviposition experiments. Each lasted two hours. These trials

were run in cubic cages (44 cm each side), in each of which three female wasps were offered a choice between ten larval hosts placed on High-fertilizer collard leaves (*Brassica oleracea* var. *acephala* L.) and ten hosts on Low-fertilizer leaves; larvae were mid-third instars, matched visually for size. In the first experiment, the larvae had been reared from hatching on the test plants, but they were transferred to High-fertilizer collards after parasitization to maximize survival. The second experiment specifically tested whether the females' sex allocation was affected directly by their hosts' foodplant. Larvae were reared on a 'neutral' plant (rape, *Brassica napus* L.), but during the two hour parasitization period they were placed on either High- or Low-fertilizer collard leaves. They were fed on High-fertilizer collards afterwards.

Trichoplusia ni – *Patrocloides montanus*. Four 5th instar *T. ni* larvae were offered on either High-fertilizer or Low-fertilizer collard leaves to individual *P. montanus* wasps for two hours, in petri dishes (9 cm diameter) containing pieces of one of the test leaves. The larvae had been reared since hatching on artificial diet (pinto beans) and were returned to the artificial diet to complete their development after the parasitization period. This experiment was done twice; since there were no significant block effects, the data were combined for analysis.

A second experiment with this system assessed both direct effects of plants on wasp parasitism and indirect effects on the performance of the subsequent F1 generation of wasps. We used three species of *Brassica* that had elicited different responses in the herbivore and parasitoid in our previous experiments: collards, green cabbage (*B. oleracea* var. *capitata* L.) and black mustard (*B. nigra* (L.) Koch). For two hours, individual wasps in the Parental generation were offered four young 5th instar larvae that had been reared on one of the three test-plant species. All hosts were the same age in days, but larvae reared on black mustard were smaller than the others because of differences in growth rates (L. R. Fox & K. M. Kester, pers. obs). There were 15 initial replicates per plant but not every female produced viable offspring. The wasps of the F1 generation were paired immediately after emergence. When they were 1–2 weeks old, each female was offered 20 larvae from the 5th instar (from a pinto bean diet) for 24 h; this was repeated three times, 48 h apart. Larvae were given pinto bean diet during parasitization. Adult F1 females were kept individually in plastic box-

es (10 × 19 × 32 cm) with sugar water, pollen, honey and water until they died.

Results

D. insulare sex ratios responded to both host quality and plant quality. More than 10 times as many female wasps emerged from hosts reared and offered on High-fertilizer plants, compared to larvae reared and offered on Low-fertilizer plants (Table 1A). Even when potential hosts had identical, neutral, feeding histories (Table 1B), ca. 4 times as many female wasps emerged from larvae that had been on the High-fertilizer plants during the choice experiments. In addition, in both experiments, all *D. insulare* wasps produced female offspring on the High-fertilizer plants, significantly higher proportions than on the Low-fertilizer plants, although more wasps in total emerged from Low-fertilizer plants.

By contrast to the DBM-*D. insulare* system, food-plant quality did not affect the sex ratio of emerging wasps in the *T. ni* – *P. montanus* system, although parasitism rates were higher on Low-fertilizer plants (Table 1C). Similarly, neither parasitism rates nor sex allocation were sensitive to three different plants in the Parental generation of *P. montanus* (Table 2A), but the interpretation of these results is complicated by the small number of wasps that emerged from black mustard plants. However, fecundity and longevity of F1 generation wasps were affected significantly by the foodplants on which their hosts developed (Table 2B), with highest fecundity on collards and longest survival on green cabbage. While sex ratios of their offspring (F2) were marginally not significant ($P=0.055$), the number of females produced per day was higher on collards than on the other two plants.

Discussion

Sex ratio variation in wasps is usually attributed either to differences in host quality, local mate competition or environmental conditions such as temperature, light and humidity (Godfray & Hardy, 1993; King, 1993; Godfray, 1994). The role of plants in sex allocation is commonly assumed to be indirect: differences in plant quality (nutrients or secondary chemicals) first influence properties of the herbivore (e.g., size, growth or survival), and the parasitoids then respond to those properties in their herbivorous hosts (Lawton

Table 1. Parasitoid performance (means \pm SE) on hosts parasitized while on High- or Low-fertilizer collards. The choice tests used with the DBM-D. insulare system (A,B) were analyzed by paired sample t-tests (number of wasps produced and % females [arcsine square root transformation]) and by G-tests (% replicates producing females). The nonchoice tests used with the *T. ni*-*P. montanus* system (C) were analyzed by 1-way ANOVA and by a G-test (% replicates producing females)

A. DBM-D. insulare: Hosts reared and offered on similar test plants			
Test plants:			
	High-fertilizer	Low-fertilizer	P-value
Number of replicates	10	10	
Wasps emerging per replicate	2.2 \pm 0.4	4.9 \pm 0.5	<0.01
% Replicates with females	100 %	20 %	<0.001
Sex Ratio (% females)	78 \pm 8 %	7 \pm 5 %	<0.001
B. DBM-D. insulare: Hosts reared on a 'neutral' plant, then offered on test plants			
	N=8	N=8	P-value
Wasps emerging per replicate	3.6 \pm 0.8	4.2 \pm 0.6	ns
% Replicates with females	100 %	50 %	<0.01
Sex Ratio (% females)	57 \pm 8 %	13 \pm 5 %	<0.01
C. <i>T. ni</i> - <i>P. montanus</i> : Hosts reared on artificial diet, then offered on test plants			
	N=24	N=19	P-value
Wasps emerging per replicate	2.2 \pm 0.2	2.8 \pm 0.2	<0.05
% parasitized	56 \pm 5 %	71 \pm 5 %	<0.05
% Replicates with females	72 %	70 %	ns
Sex Ratio (% females)	54 \pm 9 %	47 \pm 8 %	ns

Table 2. Performance (means + SE) of (A) Parental and (B) F1 generation *P. montanus*. Wasps in the parental generation parasitized hosts reared on one of three different foodplants (N is the number of wasps per treatment (out of 15) that successfully produced any F1 wasps). Each F1 wasp was offered 20 host caterpillars reared on artificial diet on three separate days; data are the means of the three trials for each wasp. Number of F1 females is the number emerging and surviving to reproduce. Data were analyzed by 1-way ANOVAs and G-tests (% replicates with females). Different superscript letters within a line indicates significant differences among means ($P < 0.05$)

A. Parental generation:				
Food plants of parental generation hosts:	Black Mustard	Collards	Green Cabbage	P-value
Number producing F1 wasps	6	12	11	
F1 wasps emerging per host	1.3 \pm 0.2	1.9 \pm 0.3	2.0 \pm 1.9	ns
% parasitized	33 \pm 5 %	48 \pm 7 %	50 \pm 5 %	ns
% Replicates with females	50 %	58 %	64 %	ns
F1 Sex Ratio (% females)	50 \pm 7 %	46 \pm 13 %	58 \pm 15 %	ns
B. F1 Generation:				
Number of F1 females	2	8	10	P-value
Fecundity	6.8 \pm 0.8 ^a	11.4 \pm 0.4 ^b	7.0 \pm 0.6 ^a	<0.0001
% Replicates with females	50 %	87 %	50 %	ns
F2 Sex Ratio (% females)	32 \pm 3 % ^{ab}	42 \pm 10 ^a	13 \pm 5 % ^b	0.055
F2 females/day	1.8 \pm 1.8 ^a	4.7 \pm 1.2 ^b	0.9 \pm 0.4 ^a	0.016
Days surviving	21 \pm 6 ^{ac}	56 \pm 11 ^{ab}	67 \pm 6 ^b	<0.05

& McNeill, 1979; Godfray, 1994). We know of very few demonstrations that wasp sex ratios can respond directly to plants in the field (Fox *et al.*, 1990) or in the laboratory (Shulka & Tripathi, 1993).

Our work clearly shows that *D. insulare* females can respond directly to plants when making sex allocation decisions. The sex ratios of emerging *D. insulare* were heavily and consistently biased towards females when they oviposited on hosts on the High-fertilizer plants and towards males on hosts on the Low-fertilizer plants, even when they were offered identical, 'neutral' host larvae on each type of plant. In the field, *D. insulare* probably uses cues from both the foodplants and their DBM hosts for these decisions. The differences in sex ratio (% female) were approximately the same as the differences between offspring of females experiencing large vs small instars of DBM hosts offered in other experiments (Fox *et al.*, 1990). We suggest that *D. insulare* females use plant cues as a surrogate as well as a supplement to clues about host quality.

In contrast to the DBM-*D. insulare* system, sex ratios of emerging *P. montanus* wasps were not affected directly by fertilizer level of plants or by plant type. But subsequent effects of host foodplants were expressed in fecundity, longevity and some measurements of sex allocation by F1 wasps. By most criteria, *P. montanus* performed best in hosts that fed on collards. Low survival of both Parental generation and F1 wasps on black mustard may have been a response to the smaller sizes of hosts on that species, and of the wasps that subsequently emerged from them, rather than to the plant *per se*. Intergenerational effects of plant species have not been examined in the DBM-*D. insulare* system.

Explanations of many properties of parasitoids are often linked to level of specificity of the wasps themselves (Godfray, 1994). As an alternative, we suggest that the different sensitivities of the parasitoids to similar arrays of plants is related to the diet breadth of their herbivorous hosts. Selection to recognize a broad array of plants in many families as harboring potential host larvae may reduce the ability of those parasitoids (e.g. *P. montanus* on the generalized herbivore, *T. ni*) to recognize and respond to qualitative differences among the plants. When their hosts use a narrow array of plants, with greater similarities in secondary chemistry (e.g., *D. insulare* on the family specialist, *P. xylostella*), finer discrimination for the parasitoids may be possible.

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