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The Importance of Behavioral Plasticity for Maximizing Foraging Efficiency in Frugivorous Lepidopteran Larvae

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In this study, we present evidence that the larvae of Acrobasis vaccinii *(Lepidoptera: Pyralidae), a species that feeds on cranberry fruit, are able to take into account at least three cues (fruit size, fruit color, and the distance between fruits) when searching for food. In laboratory experiments, the relative impact of each cue depended on which cues were presented in a given bioassay. Fruit color was the dominant cue in some contexts (e.g., larvae showed a significant perference for green fruit over red ones regardless of fruit size when fruits were equidistant from the larvae) but not in others (e.g., when given a choice between a large red fruit placed close to the larvae and a small green fruit placed farther away, a significantly higher proportion of larvae chose the former). This plasticity in foraging behavior allows larvae to maximize foraging efficiency under conditions of differing fruit and larval densities, which this species experiences in nature.*

KEY WORDS: *Acrobasis vaccinii*; foraging; fruit size; fruit color; distance; behavioral plasticity.

INTRODUCTION

Insect larvae are faced with risks of predation (Cohen *et al.*, 1988; Wratten *et al.*, 1988; Bell, 1991), and expend large amounts of energy (even to the

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point of death; Damman, 1991) when searching for food resources. Thus, individuals that reduce their travel time among food patches should increase their fitness. Foraging behaviors usually reflect a trade-off between optimizing food acquisition (i.e., maximizing the net rate of energy intake) and avoiding dangers such as predation (Sih, 1980; Sih and McCarthy, 2002) or competition (Bell, 1991, and references therein). In insect larvae, such trade-offs may force individuals to eat food of lower nutritional quality (in order to avoid a higher risk of predation in food patches of higher quality; Damman, 1987; Stamp and Bowers, 1991; Ohsaki and Sato, 1994), to leave food patches prematurely (e.g., where leaf damage is a cue for visually oriented predators; Heinrich, 1979; Heinrich and Collins, 1983), or, for insect herbivores, to avoid hosts that have already been attacked (since herbivore-induced emissions of plant volatiles may attract natural enemies; Turlings and Benrey, 1998).

For larvae that feed inside fruit, the risk of predation and levels of energy expenditure are relatively low when larvae are inside a host (Serrano *et al.*, 2001). Therefore, larvae requiring several hosts should show a preference for large fruits with high nutritional value since this strategy would reduce the number of fruits required to complete development and consequently reduce the risk of mortality associated with moving between fruits. However, in the field, fruits are usually not homogeneously distributed, and a trade-off between increasing food intake and lowering mortality risks or energy expenditure may occur when larvae move between fruits.

Choosing a particular habitat in order to reduce predation risk may lead to increased intraspecific competition for food resources within these habitats (e.g., Persson, 1993; Lima, 1998). For grazer larvae (i.e., larvae that must feed on several hosts to complete their development; Thompson, 1982) that feed inside fruit, entering a fruit that already contains another larva may result in contest (i.e., where only one competitor wins) or exploitation (i.e., the sharing of resources; see Price, 1997) competition. Competition may force individuals to move from a fruit thereby increasing the risk of predation for the larvae when searching for a new fruit. Therefore, a trade-off may also be expected between searching for the best food resource available and reducing intraspecific competition by avoiding occupied fruits.

To test if such trade-offs (fruit size vs. foraging distance, and fruit size vs. intraspecific competition) occur in fruit-eating grazer larvae, we studied the behavior of the cranberry fruitworm, *Acrobasis vaccinii* (Lepidoptera: Pyralidae). The cranberry fruitworm is a univoltine fruit-eating grazer species, and we had several reasons to expect that these parameters may affect larval foraging behavior in this species. Firstly, to complete its development, each larva has to eat several cranberry (*Vaccinium oxycoccos*) fruits (Lasota, 1990) in an environment where fruits of different sizes are distributed in patches of varying densities. Secondly, the incidence of predation on lepidopteran larvae by spiders in cranberry bogs may be high (Bardwell and Averill, 1996). Thirdly, larvae within a fruit exhibit aggressive behavior (turning their heads toward the entry hole and biting) when fruit is manipulated (personal observation). Finally, as opposed to other lepidopteran larvae which forage randomly until touching a food source (e.g., Rausher, 1979; Dethier, 1988), laboratory experiments suggest that *A. vaccinii* larvae use visual cues to move toward and make choices among fruit (Marchand and McNeil, 2004). Attacks by *A. vaccinii* larvae induce a premature reddening of fruit, similar to the reddening observed during normal maturation at the end of August/beginning of September (long after *A. vaccinii* larvae have completed their development), and we postulated that color may be an important cue used by larvae to help avoid intraspecific competition. When given the choice between similarly sized red and green fruit or plastic colored beads in the laboratory, a significantly higher proportion of larvae approach and remain on the green fruit/bead (Marchand and McNeil, 2004).

The present study was undertaken to test whether (i) fruit size affects the number of fruits *A. vaccinii* larvae need to complete their development, (ii) larvae choose fruit based on their size, and (iii), if so, whether distance and/or color (green vs. red) of the fruit affects this preference.

METHODS

Insect Rearing

Acrobasis vaccinii larvae were obtained from infested fruits collected in the field near Notre Dame de Lourdes, Quebec. The resulting cocoons, containing diapausing prepupae, were held over the winter in plastic boxes under moss in natural bogs. In May, the cocoons were moved to growth chambers and the temperature was gradually increased to mimic spring and summer conditions (15 days at 10°C, 15 days at 15°C, and then at 25°C) until adult emergence. Adults were held at 20 ± 0.5°C, 16L:8D, 80 ± 5% R.H., the standard conditions for all subsequent experiments. Once-mated females were provided with cranberries, obtained from a natural bog, as oviposition sites. Fruits with eggs were maintained in individual plastic cups, and each larva had continuous access to fruit to complete its development.

Laboratory Experiments

To determine the number of fruits a larva needs to complete its development, fruits with eggs ($n = 317$) were maintained on sand in individual plastic cups, together with two additional fruits (one large and one small). Larval movement between fruits was recorded every 2 days. When a larva entered a new host fruit, the other one was removed and two new ones added, so that the foraging larvae always had the choice between a large and a small unattacked fruit. The size of small and large fruits offered to larvae varied with time in order to take into account normal fruit growth occurring in the field. Fruit choice by larvae was expressed as the ratio of large fruits eaten to the total number of fruits eaten for each larval development period.

Six different treatments were set up to test for any interaction between fruit size (small (4–5 mm diameter) vs. large (8–9 mm diameter) fruit) and color on larval foraging behavior. Individual 3rd–4th instar larvae, used only once, were placed on sand in a plastic cup (10 cm in diameter), 8 cm in front of, and equidistant from, two fruits that were 4 cm apart in all treatments. Green and red fruits used in this experiment were collected in the field but none had been attacked. The early maturing red fruit are generally found in sheltered areas where temperatures are probably somewhat warmer than in the rest of the bog. Treatments 1 (small green vs. large green fruit) and 2 (small red vs. large red fruit) were set up to test for any effect of host size on fruit choice by larvae, irrespective of fruit color. Treatments 3 (large green vs. large red fruit) and 4 (small green vs. small red fruit) were used to test for any influence of host color, independent of fruit size. The two final treatments 5 (a large green vs. a small red fruit) and 6 (a small green vs. a large red fruit) were set up to test for any interaction between fruit size and fruit color. Larvae were considered to have chosen a fruit once they entered it.

We used a similar experimental setup to test the effect of fruit size (4–5 mm and 8–9 mm in diameter), foraging distance to the fruit and any interaction between these parameters on larval foraging behavior. Larvae were tested, using only green fruit, in one of the four following treatments. In treatment 1, one small and one large fruit were placed 4 cm apart and equidistant (either 4 or 8 cm) from the larva. In treatment 2, larvae were given a choice between two similarly sized fruits (between 4 and 8 mm in diameter), one placed at 4 cm and the other at 8 cm from the release point. In treatment 3, larvae were given a choice between a large fruit at 4 cm and a small fruit at 8 cm from the larva while in treatment 4, the relative position of the two fruits was reversed. In treatments 2, 3, and 4, the two fruit were placed about 2 cm on either side of the axis of the larvae release point, and not one directly behind the other.

Field Observations

To test if there was a larval preference for the largest fruits available, we conducted experiments in two natural bogs, near Notre Dame de Lourdes, Quebec. Cranberry fruit were randomly picked from plants on four occasions between 4th and 14th August 2000, brought back to the laboratory, and examined for the presence of *A. vaccinii* larvae inside the fruits. The diameter of all attacked fruits (varying from 3 to 29 per "site × day" combination; $\bar{\chi} \pm$ S.E. $= 13.6 \pm 2.7$) and 50 randomly chosen unattacked fruits was measured for each "site × day" combination.

Statistical Analysis

Statistical comparisons of the mean diameter of attacked and unattacked fruits in field observations were conducted with ANOVA for Randomized Complete Block Design with Subsampling (SAS GLM procedure; SAS Institute, 1999). Differences in the number of fruits eaten as a function of the ratio Large Fruits/Total Fruits chosen by larvae were compared with ANOVA (Genmod procedure on SAS 8.01; SAS Institute, 1999). Data on host choice were analyzed using a chi-square goodness of fit test.

RESULTS

Laboratory Experiments

There was an inverse relationship between the size of fruit exploited by larvae and the total number of fruits required to complete larval development (Fig. 1; $\chi^2_1 = 30.69$, $p < 0.0001$). If larvae chose only small fruits (which was never the case) they would require 11.3 ± 1.1 fruits ($\bar{\chi} \pm$ SE, extrapolated from the model) to complete their development, approximately twice as many fruits as those larvae that always chose large fruits (5.4 ± 0.2 fruits).

When given a choice between a large and a small fruit equidistant away from the larvae, significantly more larvae chose the larger fruit when both

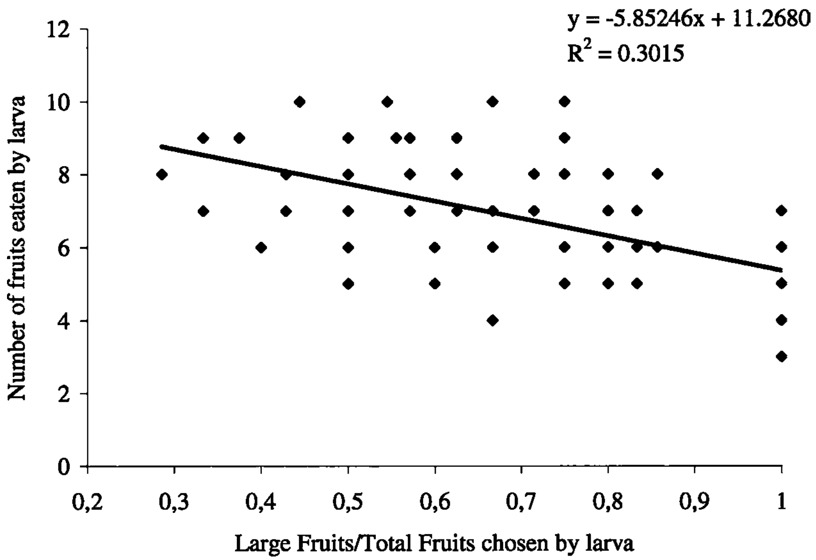

Fig. 1. Effect of fruit choice by *A. vaccinii* larvae on the number of fruit required to complete larval development.

fruits were either green (treatment 1) or red (treatment 2; Table I). Fruit color affected host acceptance as significantly more larvae entered green than red fruits, when fruit were the same size (Table I; treatments 3 and 4). When larvae had the choice between a large green and a small red fruit, all of them entered the large green fruit (Table I; treatment 5). In the last treatment (choice between large red vs. small green fruit), significantly more larvae entered the small green fruit (treatment 6) suggesting that fruit color is

Table I. Effect of Fruit Size and Fruit Color on Foraging Behavior of *A. vaccinii* Larvae When Fruits Are Equidistant from the Caterpillar

	Fruit choice				Number of larvae on			
	Fruit 1		Fruit 2					
	Size	Color	Size	Color	Fruit 1	Fruit 2	χ^2	*p*
Fruit size effect	Large	Green	Small	Green	18	8	3.85	<0.05
	Large	Red	Small	Red	22	3	14.44	<0.001
Fruit color effect	Large	Green	Large	Red	24	1	21.16	<0.001
	Small	Green	Small	Red	23	3	16	<0.001
Interaction size/color	Large	Green	Small	Red	24	0	24	<0.001
	Small	Green	Large	Red	17	7	4.17	<0.05

Table II. Effect of Host Size and Distance to Travel on Choice of Fruit by *A. vaccinii* Larvae When Caterpillars Are Provided Unattacked, Green Fruit

	Treatment[a]		χ^2	p
Fruit size effect	Small fruit	Large fruit		
	12	40	15.08	<0.001
Distance effect	Short distance	Long distance		
	27	10	7.81	0.005
	Distance			
	Short	Long		
Interaction between distance and fruit size	Large fruit	Small fruit		
	48	6	32.67	<0.001
	Small fruit	Large fruit		
	23	31	1.18	0.277

[a]The number below each treatment indicates the number of larvae choosing the fruit treatment noted.

a more important cue than fruit size. However, fruit size does modify larval preference for green fruit since significantly more larvae entered a large red fruit in treatment 6 (i.e., large red vs. small green fruit) than in treatment 3 (i.e., large red vs. large green fruit; $\chi_1^2 = 5.68, p = 0.017$).

When given a choice between a small and a large fruit the same distance away from the larvae, significantly more larvae chose the larger fruit (Table II; treatment 1). When offered two equally sized fruits placed at different distances away, larvae chose the closer fruit significantly more often (Table II; treatment 2). When the choice was between a large fruit close by and a more distant small fruit, significantly more larvae entered the former (Table II; treatment 3). In contrast when the larger fruit was farther away, the difference was not significant (Table II; treatment 4). However, it is clear from a comparison of the results from treatments 2 and 4 that significantly more larvae will travel a greater distance if the farther fruit is larger than the closer one (treatment 4; 31/54; treatment 2; 10/37; $\chi_1^2 = 8.19$, $p = 0.0042$).

In light of these results, we conducted another experiment to test if the distance between fruits could affect larval preference for green fruits. To test this hypothesis, we gave larvae a choice between a large (8 mm in diameter) unattacked red fruit close to the larvae (4 cm) and a small (4 mm diameter) green fruit placed 8 cm away. Significantly more larvae entered the large red fruit (27/28; $\chi_1^2 = 24.14, p < 0.001$). Therefore, distance modifies larval preference for green fruit since significantly more larvae entered a large red fruit in this experiment than when large red and small green fruit were equidistant apart (treatment 6, Table I; $\chi_1^2 = 25.83, p < 0.0001$).

Table III. Results of ANOVA for the Effect of Fruit Size on the Incidence of Attack by *A. vaccinii* Larvae Under Field Conditions

Source	DF	SS	MS	*F* Value	Pr > *F*
Block[a]	9	1034631.55	114959.06	6.00	<0.0001
Fruit state[b]	1	67390.78	67390.78	1.70	0.22
Exp. error[c]	9	357372.35	39708.03		
Obs. error	616	11800163.18	19156.11		
Total	635	14149424.51			

[a]Block = Date × Site.
[b]Fruit state = fruit with or without larva inside.
[c]Experimental error = Date × Site × State.

Field Observations

In the field, there was no significant difference between the size of attacked and unattacked fruits (diam. ± SE:7.27 ± 1.48 mm vs. 6.97 ± 0.62 mm, respectively; Table III).

DISCUSSION

Our laboratory experiments demonstrate that when given a choice between fruits of differing size, *A. vaccinii* larvae select the largest fruit available when the two fruits are equidistant from the caterpillar. This foraging strategy could reduce the risk of mortality during larval stages. However, larval food searching behavior and food preference may be influenced by factors other than food size. Our experiments indicate that, in terms of larval preference, there is an interaction between host color and fruit size, since when hosts are at the same distance away, larvae prefer small green fruit over large red fruit. The findings of this study suggest that *A. vaccinii* larvae are able to assess at least two visual cues simultaneously when choosing a new fruit, and that color is a more important cue than size in the choice of fruit when the fruits are equidistant from the larva.

Assessing several cues simultaneously increases the probability that larvae will enter a fruit offering the highest nutritional value over time; choosing green fruit, regardless of size appears to be advantageous as it reduces the risk of entering a fruit that has been completely or partially eaten (i.e, with low nutritional input) or that is occupied by another larva. Fruit size becomes the dominant factor only when larvae have the choice between fruits of the same color since, in this context, this parameter would generally be a good indicator of the fruit's relative nutritional value.

Larval food searching behavior and food preference may also be affected by the distance between food patches as *A. vaccinii* larvae sometimes entered the closest, but not necessarily the largest, fruit available. These results agree with those from other studies on lepidopteran larval foraging behavior: the larvae of *Lymantria monacha* (Hundertmark, 1937; after Roden *et al.*, 1992) and *Papilo demoleus* (Saxena and Khattar, 1977) do not distinguish between a small object that is placed close to the larva and a larger object that is farther away from the larvae when the visual angles of the two objects are identical.

Our results are also consistent with the theory of "predation risks foraging efficiency trade-off" since displacement distance may be directly related to predation risk (e.g., Walther and Gosler, 2001). Such a trade-off between food quality and the distance to travel between food patches has been observed previously in birds (Levey *et al.*, 1984), mammals (Lima and Valone, 1986), and herbivorous insects (Bernays *et al.*, 1997; Hundertmark, 1937; after Roden *et al.*, 1992; Saxena and Khattar, 1977), but, to our knowledge, has never been demonstrated for frugivorous larvae. For *A. vaccinii* larvae, the potential advantages associated with choosing a relatively large fruit may be reduced by short-term mortality risks if larvae have to move longer distances to find it. This trade-off may also explain why, in the field, we observed no preference by larvae for the largest fruits available (i.e., larval distribution in the field was independent of fruit size). This lack of preference probably reflects the heterogeneous distribution of fruit in the wild, and does not necessarily indicate that *A. vaccinii* larvae forage completely at random. To explain this lack of preference in the field, further research is necessary to examine larval foraging behavior under natural conditions, taking into account such variables as fruit distribution and size, as well as the behavior of different larval instars.

Our study also demonstrates that at least three factors may affect larval foraging behavior (in this case fruit size, fruit color, and the distance of the fruit from the foraging larvae). The relative impact of each factor may vary depending on which factors are involved. For instance, fruit color may be the dominant cue in some contexts (e.g., larvae prefer green fruit over red ones regardless of fruit size when fruits are equidistant from the larvae) but not in others (e.g., when given a choice between a large red fruit placed close to the larvae and a small green fruit placed farther away, larvae choose the former). Therefore, our study clearly demonstrates a plasticity in foraging behavior by *A. vaccinii* larvae that may represent a good strategy to maximize foraging efficiency in conditions of differing fruit and larval densities.

Our experiments do not allow us to preclude a role for olfactory cues in larval foraging, especially as the green fruit, while a different color than the leaves, may be less evident to larvae foraging on the plant. However, there are several lines of evidence which support the idea that color is the major cue modulating the foraging behaviors observed: (i) Larvae take a direct path toward a host and exhibit none of the behaviors normally associated with movement up an odor gradient; (ii) when a fruit is moved as a caterpillar approaches it, reorientation in the direction of the new position is immediate, which would not be the case if the behavior was based on odour sources; and (iii) as reported by Marchand and McNeil (2004) larvae exhibited similar color preferences for plastic beads, where no odor cues were present. Furthermore, there was no evidence of odours influencing behaviors in preliminary assays we conducted with extracts of attacked and control fruit. Given the rather heterogeneous nature of fruit distribution, and the fact that the olfactory range of caterpillars does not usually exceed 1 cm (Saxena and Khattar, 1977; Cain *et al.,* 1983), visual cues would be more reliable than olfactory ones in larval foraging behavior in *A. vaccinii*. However, additional research is needed to determine to what extent, and under what conditions, odour cues might modulate larval foraging behavior.

In our experiments, fruit choice by larvae explained only about 30% of the variance observed in the number of fruits larvae needed to complete their development. Other factors such as parental effects (genetic and non genetic) and/or sexual differences (see Slansky, 1993, and references therein) could also affect the number of fruits eaten. For *A. vaccinii*, the choice of oviposition sites by females could reduce the number of fruits required for larval development, since neonate *A. vaccinii* larvae exploit the fruits on which females lay their eggs. Further research is necessary to examine whether *A. vaccinii* females exhibit a preference for the largest fruits available, and whether there is any relationship between female oviposition behavior and larval performance (as observed in certain other insect species; see Mayhew, 1997, and references therein). Since this study demonstrates that the distance between fruits may affect larval foraging behavior, the spatial distribution as well as fruit density should be taken into account in any future work on female oviposition behavior in fruit-grazing insect species in order to definitively establish the presence or absence of a relationship between female preference and offspring performance.

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