



## Avoidance of intraspecific competition via host modification in a grazing, fruit-eating insect

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Insects feeding on plants may induce chemical and physical changes in the host plants. Here, we present evidence of host plant modification following an insect attack that may be associated with a reduction in intraspecific competition for food. We demonstrate that feeding by larvae of the cranberry fruitworm, *Acrobasis vaccinii*, induces a change in fruit colour (from green to red) of cranberry fruits, *Vaccinium oxycoccos*, that is associated with a significant increase in the concentration of anthocyanin. Host fruit colour affected larval foraging behaviour and food acceptance: significantly more cranberry fruitworm larvae were attracted to, and accepted, green rather than red fruits. Our experiments suggest that fruit reddening also prevents exploitation by conspecific larvae of other green fruits adjacent to the attacked fruit.

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Intraspecific competition is a major selective force in the evolution of behavioural strategies (Krebs & Davies 1997). Competition with conspecifics may be active (interference competition, where competitors limit access of other individuals to necessary resources) or passive (exploitation competition, where the limited resource is shared among all individuals). A reduction of fitness can result from both types of competition (Price 1997), as survivors may be smaller and have lower fecundity and/or mating success (e.g. Quiring & McNeil 1984; Averill & Prokopy 1987; Andersen & McNeil 2001).

In insects, intraspecific larval competition can be reduced by female oviposition behaviours, such as varying the number of eggs laid as a function of food quantity (e.g. Damman 1991) and avoiding hosts where conspecific eggs or larvae are already present (Nufio & Papaj 2001). The avoidance of occupied sites may be mediated by an oviposition-detering pheromone (e.g. Prokopy 1972; McNeil & Quiring 1983). For species in which larvae must feed on several hosts to complete their development (a 'grazer' species; Thompson 1982), larval behaviours may also play an important role in avoiding intraspecific competition (e.g. the use of epideictic pheromones; Corbet 1971).

To avoid intraspecific competition, individuals often search for other food patches, which may increase the risk of predation (Bell 1991) and be energetically costly

(sometimes resulting in the death of individuals; Damman 1991). Thus, leaving host patches where competition for food is high may also result in a decrease in fitness. For grazers that feed inside fruit, predation risk and energy costs are lower when the larvae are within a fruit (Serrano et al. 2001). Therefore, avoiding previously infested fruit and indicating one's own presence in a host would be effective strategies to reduce intraspecific competition, as well as the risk of mortality (resulting from reduced food intake and predation) when larvae move between fruits.

Host modification in response to herbivory, such as induced volatile emissions by plants (Baldwin & Preston 1999) or, to a lesser extent, changes in the skin colour of fruit or leaves (e.g. Schread 1971 cited in Krischik et al. 1989; Henneman & Papaj 1999; Stone et al. 2001), has already been documented. However, to our knowledge, no studies have examined whether these host changes are used as long-distance cues by insect larvae to avoid intraspecific larval competition.

We hypothesized that intraspecific competition in grazer larvae feeding on fruit may be reduced through a long-distance visual cue via host modification following larval attack. To test this hypothesis, we studied larval behaviour of the cranberry fruitworm, *Acrobasis vaccinii* (Lepidoptera: Pyralidae), a univoltine fruit-eating grazer species. We had two reasons for expecting anticompetition behaviours in this species. First, each larva must eat five to seven cranberries, *Vaccinium oxycoccos*, to complete development (Lasota 1990), thus at high densities (Brodel & Roberts 1984), intraspecific competition can be frequent. Second, infested fruits turn red before maturation

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whereas uninfested, immature fruits are green (Brodel & Roberts 1984). This apparent precocious maturation of infested fruit suggests that *A. vaccinii* larvae may induce a modification in fruit colour (and chemistry) following attack. This colour change could serve as a signal for conspecifics that the fruit has already been attacked and thus reduce potential intraspecific competition. In addition, avoiding previously attacked fruits may reduce the time spent foraging and potentially reduce the incidence of predation, as many lepidopteran larvae in this ecosystem are subject to attack by spiders (Bardwell & Averill 1996).

In this study, we tested (1) whether attacks by *A. vaccinii* larvae induce changes in cranberry fruit, and (2) if so, whether such modifications are detected by conspecific larvae and affect their choice of fruit.

## METHODS

### Insect Rearing

We obtained *A. vaccinii* cocoons from infested fruits collected in the field near Notre Dame de Lourdes, Quebec, Canada. Cocoons containing the diapausing prepupae were held in plastic boxes placed under moss in natural bogs for the winter. In May, we moved cocoons to growth chambers and subjected them to a gradual, increasing temperature regime (15 days at 10°C, 15 days at 15°C, and then at 25°C) until adult emergence. Adults were held at 20°C, on a 16:8 h light:dark cycle with 80% RH, the standard conditions for all subsequent experiments. We provided once-mated females with cranberries obtained from a natural bog for use as oviposition sites. Fruits with eggs were maintained in individual plastic cups, and each larva had continuous access to fruit to complete its development.

### Experiments

#### *Induction of changes in fruit colour by larval attacks and analysis of anthocyanin concentration*

We maintained multiple stems of *V. oxycoccos* in one large plastic container. We used green fruits of similar size (~7 mm in diameter) that were attached to these stems in this experiment. We individually placed 22 third-instar larvae on top of a green fruit collected from a natural bog and observed them continuously until they entered the fruit; 24 other fruits were used as a control (no larvae present, i.e. 'not attacked'). We pricked 10 other fruits once, to the depth of the centre of the fruit, with a pin (<1 mm in diameter) to determine whether a single mechanical injury similar to the initial hole of a larva triggered a change in fruit colour. All fruit were numbered (1–56) by placing a sticker on the stem. An observer, aware only of the fruit number and not the treatment it received, estimated the proportion of the skin that was red (compared with the standard red of mature fruit) for each fruit every 2 days over a 10-day period. At the end of the experiment, we measured the volume of each fruit, then stored the fruit (frozen) until analysis of red pigment

(anthocyanin) concentration. We measured the concentration of anthocyanin using a Milton Roy spectrophotometer (model Spectronic 1001 Plus; method of extraction and procedures for reading optical density followed Craker 1971). Optical density was read at 525 nm and data were expressed per ml of solvent and mm<sup>3</sup> of fruit.

#### *Effect of visual and chemical cues of the host on larval foraging behaviour*

We used four treatments to test the effect of visual (colour) and chemical cues of the host on larval foraging behaviour, with individual larvae being placed on a filter paper, 4 cm in front of and equidistant to two hosts that were 2 cm apart. Treatments 1 (green versus red fruit) and 2 (green versus red plastic bead) were set up to test for the effects of host colour on fruit choice by larvae. Treatments 3 (green fruit versus green plastic bead) and 4 (red fruit versus red plastic bead) were used to test for the influence of chemical cues on larval fruit choice. Beads and fruits were both 8 mm in diameter. We chose beads from the available stock by visual inspection, choosing those that we judged were the closest in colour to that of mature (red) and immature (green) cranberry fruits (Munsell colour values were: red bead 5R (red) 4/12 where the numbers refer to notations of hue, value (i.e. lightness or darkness) and chroma, respectively; red fruit 5R 4/12; green bead 10 GY (green/yellow) 6/10; green fruit 5 GY 6/8; Munsell 1967). When larvae did not move directly towards hosts or left the experimental arena, they were scored as having made no choice. When larvae touched one of the fruits or beads, the duration of time spent on (or in) the 'host' was recorded. The host was considered acceptable if the larva remained on or inside the host for 1 h.

#### *Protection of green fruits adjacent to red fruit*

In light of the results of the first two experiments, we conducted another one to test whether the red coloration of attacked fruit may prevent attack of adjacent, unattacked (green) fruits by conspecific larvae. To test this hypothesis, we gave larvae a choice between two groups of three green fruits, one group with a red fruit placed directly in front and the other with a green fruit placed in front.

### Statistical Analysis

We compared differences in anthocyanin concentration between treatments with analysis of variance (ANOVA) and an a posteriori least significant difference (LSD) test, following rank transformation to correct for heteroscedasticity. Data on host choice were analysed using a chi-square goodness-of-fit test, and data on time spent on host by larvae were analysed using chi-square tests for partitioned contingency tables (Siegel & Castellan 1988). For treatment(s) where reddening of fruit skin was estimated, the effect of time on fruit reddening was analysed with ANOVA (mixed procedure on SAS 8.01) and a posteriori polynomial contrasts (SAS 1999).

## RESULTS

### Effect of Larval Attack on the Colour of Cranberry Fruit (Experiment 1)

We detected no colour change of control or mechanically damaged fruit over the 10-day test period. However, in the treatment with larvae, all fruits changed colour, with between 10 and 100% of the skin surface becoming red within 10 days. The mean proportion of skin surface that became red was significantly different from zero within 48 h (11% versus 0; least squares means:  $t_{84} = 6.20$ ,  $P < 0.0001$ ) and increased linearly with time thereafter (ANOVA:  $F_{1,84} = 62$ ,  $P < 0.0001$ ), with a rate of change in colour of 5.5% per day. The fact that fruits in the control group remained green suggests that colour change was induced by larval attack and not by volatiles produced from neighbouring attacked fruit.

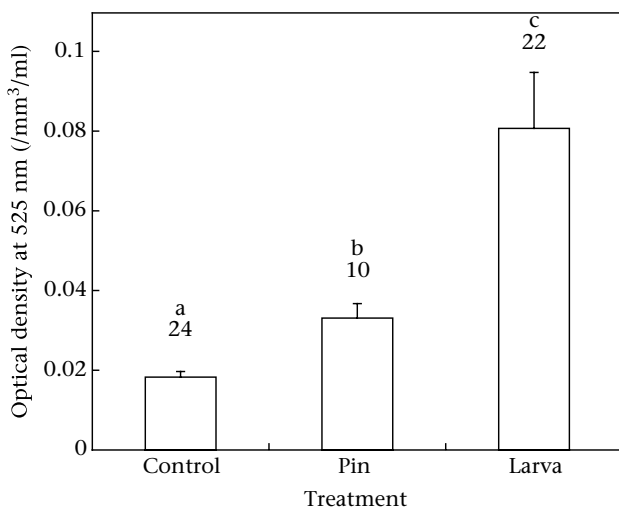
Anthocyanin concentration in fruits varied between treatments (ANOVA:  $F_{2,53} = 68.91$ ,  $P < 0.001$ ; Fig. 1) and was significantly lower in control fruits than in fruit attacked by larvae or damaged with a pin. The concentration of anthocyanin was significantly higher in fruits attacked by larvae than in those subjected to mechanical damage (Fig. 1).

The lack of colour change and the weak increase of anthocyanin concentration in pricked fruits may be due to the short duration of the mechanical damage at the beginning of the 10-day period and/or the absence of chemicals naturally found in insect saliva that are known to modify plant defences (Dicke & van Loon 2000).

### Effect of Colour and Host Type on Foraging Behaviour of Larvae (Experiment 2)

#### Effect of host colour

Significantly more larvae moved towards and made contact with green hosts than with red hosts, indepen-



**Figure 1.** Mean  $\pm$  SE optical density of *V. oxycoccus* fruits as a function of attack treatment. Values above bars indicate the number of fruits tested for each treatment. Bars with different letters were significantly different (ANOVA followed by an LSD test:  $P < 0.05$ ).

dent of whether the host was a fruit or a plastic bead (see Table 1). There was no significant difference between treatments (bead versus fruit) in the proportion of larvae leaving the experimental arena without choosing a host (chi-square test:  $\chi^2_1 = 0.157$ ,  $P = 0.69$ ).

#### Effect of host type

When larvae had a choice between a green fruit and a green bead (treatment 3), significantly more of them chose the bead (Table 1), and only a small proportion of individuals (3/41) left the experimental arena without moving towards a host. When given a choice between a red bead and a red fruit (treatment 4), the proportion of larvae (17/38) that left the arena without touching either host was significantly higher than that in the green fruit versus bead treatment (chi-square test:  $\chi^2_1 = 14.6$ ,  $P = 0.0002$ ). For larvae that did choose a host, there was no significant difference between the number of red beads and fruits chosen (Table 1).

### Effect of Colour and Host Type on Acceptance by Larvae

Once larvae selected a host, the number remaining on the host for at least 1 h was significantly higher on green hosts than on red hosts, regardless of whether they were fruits or plastic beads (chi-square test:  $\chi^2_1 = 13.29$ ,  $P = 0.0003$ ; Fig. 2). All *A. vaccinii* larvae that remained on the host for at least 1 h spun silk between the host and the filter paper substrate, a behaviour considered to indicate host acceptance in some species (Harris et al. 1999).

### Protection of Green Fruits Adjacent to a Red Fruit (Experiment 3)

Significantly more larvae moved towards the group that had a green fruit rather than a red fruit placed in front of it (36/51; chi-square test:  $\chi^2_1 = 8.65$ ,  $P < 0.001$ ). Before entering any fruit, all larvae tested joined at least two green fruits together with silk.

## DISCUSSION

The results of our study clearly show that attacks of *A. vaccinii* larvae on cranberry fruit induce a change in the fruit's colour. This is associated with an increase in the concentration of anthocyanin (or related compounds), which may represent a defence mechanism of mature fruits against insect herbivores (Willson & Whelan 1990). Anthocyanin may be a chemical deterrent for arthropods (Harborne 1991), or it may be a visual deterrent, since certain insects do not respond to this part of the spectrum and will therefore not attack red fruit (Prokopy & Owens 1983). With such defence strategies, naturally mature red fruits reduce their risk of being eaten by nonseed or bad seed dispersers (Willson & Whelan 1990).

We propose that fruit reddening may serve as a cue for frugivorous insects when foraging and perhaps also during the initial stages of host selection. For insects, there are three behavioural phases to host selection: (1) attraction to the plant, (2) cessation of locomotion and (3) initiation

**Table 1.** Effect of colour and host type on foraging by *A. vaccinii* larvae

	Treatment	Choice		N	Number of larvae on			$\chi^2$	P†
		Host 1	Host 2		Host 1	Host 2	No choice*		
Effect of colour	1	Green fruit	Red fruit	17	12	4	1	4	<0.05
	2	Green bead	Red bead	33	24	6	3	10.8	<0.01
Effect of host type	3	Green fruit	Green bead	41	11	27	3	6.74	<0.05
	4	Red fruit	Red bead	38	14	7	17	2.33	>0.05

\*See the text for results of chi-square test comparing observed and expected frequencies between choices (1 + 2) and no choice of host by larvae.

†Chi-square test comparing observed and expected frequencies between choices 1 and 2.

of feeding (Hanson 1983). Little information on the cues used by larvae during the first phase is available in the literature. Most caterpillars, for instance, seem to forage randomly before their chemoreceptors contact a host plant (Rausher 1979), suggesting that gustatory stimuli are the most important cues for food selection in lepidopterous larvae (Hanson 1983). In *Epiphyas postvittana* (Lepidoptera: Tortricidae), apple foliage is visually attractive to larvae (Harris et al. 1995), and the foliage produces chemical cues that induce cessation of locomotion (Harris et al. 1999). When given the choice in our experiments, cranberry fruitworm larvae preferred green beads over green fruit, which suggests that there may be a hierarchy of cues, with host colour being more important than chemical cues when *A. vaccinii* larvae search for suitable hosts. Unlike an odour plume, which is dependent on wind direction, wind speed (Elkinton & Cardé 1984) and wind turbulence (Stanton 1983), host colour appears to be a more reliable and stable cue for grazer larvae, which have to crawl directly towards a new fruit in order to reduce their time spent outside a host. However, additional experiments are required to evaluate the relative importance of chemical cues in nature. The colour of the green beads used in our experiments did not perfectly match that of real fruit; the beads' slightly greener hue, in the

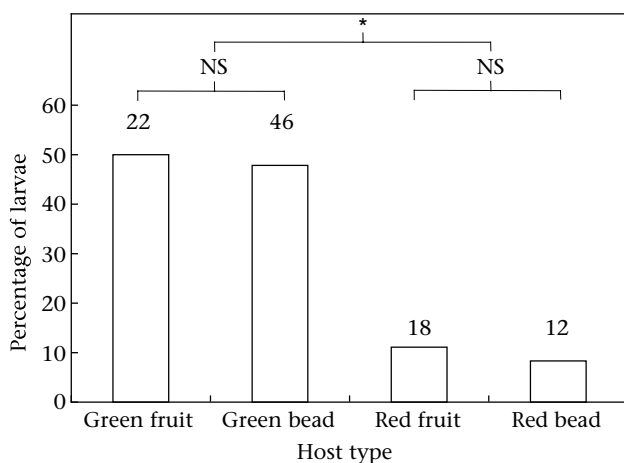
absence of odour cues, may have been responsible for their increased attractiveness relative to that of the fruit.

The fact that larvae ceased movement and spun silk on plastic beads suggests that colour may also play a role in host acceptance as well as in host location. This is somewhat surprising given that host chemicals are usually involved in the assessment of food quality (Stanton 1983). However, as colour is a good indicator of fruit quality (infested or mature fruits are red and larvae will not enter such hosts), it may be used in the first step of host acceptance, with chemical cues entering into play once feeding is initiated.

Induction of fruit colour modification may also be beneficial for the feeding larva. First, as demonstrated in the present study, being inside a red fruit reduces the probability of a larva sharing its food with conspecifics. In addition, the larva avoids potential injury that may result from intraspecific competition, as larvae show very aggressive behaviour when disturbed. Host reddening may also prevent other larvae from attacking immature (green) fruits adjacent to the attacked fruit, the most logical resources for the resident larva to exploit when moving to a new fruit. We noted that larvae may join several fruits together with silk before entering a host. While this may increase the time spent outside the fruit, the cost could be counterbalanced if this behaviour permits the larvae to keep food in reserve for consumption at a later time, and reduce the costs (predation, desiccation and energy expenditure) associated with searching for a new host.

Another potential benefit of remaining in fruits, even when they have begun to produce anthocyanin, is that dark fruits absorb more radiation in the visible spectrum than paler ones, thereby raising fruit temperatures (Janzen 1983; Feder 1997), which could result in a reduction in larval development time. The induction of an increase in the temperature of a larva's environment may be particularly important for nordic species, such as *A. vaccinii*, where ambient temperatures may be low but the days are long with potentially extended periods of solar radiation. Reducing larval development time may also be advantageous if the mature larva drops to the soil to spin its hibernaculum before mature fruits are taken by seed dispersers.

We do not know whether the elevated concentration of anthocyanin (or related compounds) in infested cranberry fruit has a negative effect on the development of *A. vaccinii*



**Figure 2.** Percentage of *A. vaccinii* larvae remaining on or in host for more than 1 h as a function of host type. Numbers above bars indicate the number of larvae that made initial contact with the host in each treatment. \* $P = 0.0003$ .

larvae. In the field, we observed that more than 75% of prematurely red fruits had a feeding cranberry fruitworm larva inside, and in our laboratory experiments, larvae remained inside fruit and continued feeding once the fruit started turning red. These observations suggest that once larvae are inside the fruit they may be able to tolerate the rising levels of anthocyanin (or any other chemicals that may be present) or that the chemicals are concentrated in the skin where feeding does not occur. Even if there is a negative effect of anthocyanin on the development of *A. vaccinii* larvae, our results suggest that the benefits of staying in red fruits outweigh the costs.

Our data support the hypothesis that modification of fruit colour in response to larval attack influences host selection and probably reduces intraspecific competition from other conspecific larvae in *A. vaccinii*. Whether this phenomenon can be generalized to other frugivorous grazer species remains to be determined.

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