SHORT COMMUNICATION

The double cloak of invisibility: phenotypic plasticity and larval decoration in a geometrid moth, *Synchlora frondaria*, across three diet treatments

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Abstract. 1. Crypsis is one of the main defences that insects use to avoid predators, and both the juveniles and adults of many geometrid moths are remarkable in their ability to blend into different host backgrounds. The larvae of *Synchlora frondaria* have two methods to achieve crypsis: phenotypic plasticity in colouration that enable them to hide more effectively on their host plants, and a self-decorating behaviour whereby the larvae camouflage themselves with materials from their host plants.

2. Larvae of *Synchlora frondaria* reared on three different host plants showed systematic differences in relative growth rate, survivorship and larval colouration.

3. Larval colouration varied across diet treatments in a way that was consistent with diet-induced phenotypic plasticity, and larvae also exhibited characteristic decorating behaviour on all three hosts.

4. Larvae showed highest survivorship on *Heterotheca subaxillaris* (Asteraceae), and had significantly higher relative growth rates on *H. subaxillaris* (Asteraceae) and *Lantana camara* (Verbenaceae) than on *Bejaria racemosa* (Ericaceae).

5. *Synchlora frondaria* provides an example of a species where both decorating behaviour and phenotypic plasticity in larval colouration produce a cryptic form that is remarkably responsive to its background.

Key words. Camouflage, crypsis, decoration, phenotypic plasticity, polyphenism.

Introduction

Insects often live or die based on how well they conceal themselves from predators. Cryptic morphologies can be composed of a wide variety of shapes, pigments, patterns, and protuberances, and although many of the camouflage costumes of insects are static, some can be modified in response to the environment. In some cases, insect larvae change their cloaks by decorating themselves with leaf and flower parts, frass, lichens, and other organic material to create a protective covering (e.g. Smith, 1926; Eisner *et al.*, 1967; Eisner *et al.*, 1978). Insect larvae can also hone their own morphology using information from the environment to influence the development of cryptic colouration and morphology. Nowhere are these variable phenotypes more impressive than in the larvae of Lepidoptera, where they exhibit this flexibility, or phenotypic plasticity, in response to cues such

as diet, crowding, temperature, and photoperiod (Poulton, 1892; Fink, 1995; Wagner, 2005; Greene *et al.*, 2008; Suzuki & Nijhout, 2008). Despite the obvious relevance of both larval decoration and morphological plasticity to the crypsis of insects, we know of no previous reports of a species in which both of these traits have been examined simultaneously.

Adult *Synchlora* are small Nearctic and Neotropical moths (6–13 mm) with a characteristic bright green colouration, and females deposit their eggs on a wide range of host plants across at least 13 plant families (Ferguson, 1985; Pitkin, 1996). In *Synchlora aerata* (Fabricius), larvae use silk to attach parts of flowers and plant material to apical setae on chalazae that protrude from their dorsal surface (Treiber, 1979; Ferguson, 1985), with the majority of this decoration on abdominal segments, one through to five. Decorating behaviour has only briefly been described in *S. frondaria* (Dyar, 1894), and the current study examines the relative growth rate and survivorship, decorating behavior, and phenotypic plasticity in larval colour of *S. frondaria* across three diet treatments from plants in different families. We additionally describe how *S. frondaria* simultaneously employs

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both larval decoration and phenotypic plasticity in larval colouration as it responds to the challenges imposed by a range of potentially cryptic backgrounds.

Methods

This research was conducted at the Archbold Biological Station (ABS) in Highlands County, Florida, U.S.A. Gravid *S. frondaria* females were collected at blacklights in June 2003, and were kept in separate vials until oviposition. Sibling groups (sibships) from each female were then divided among the three host-plant treatments, each with a distinct flower colour, and all of which can be found at the ABS: *Bejaria racemosa* (Ericaceae), whitish-pink petals with rust coloured anthers; *Heterotheca subaxillaris* (Asteraceae), yellow flowers; and *Lantana camara* (Verbenaceae), inflorescences with light purple and pink flowers. A total of 369 first instar larvae from four *S. frondaria* females (91, 106, 73, 99 larvae respectively) were divided across diet treatments to take into account genetic effects. Of the three plants chosen for the diet treatments, only *H. subaxillaris* was previously known to be a host for *S. frondaria* (Mark Deyrup, personal communication). *Synchlora frondaria* larvae were collected on *B. racemosa* flowers in the field, a previously undocumented host-plant for the species. *Lantana camara* is not a known host for *S. frondaria*, but was used as a treatment because its flowers are different colours than those of the other host plants, it was readily available on the ABS grounds, and it is a known host plant for a congener, *Synchlora herbaria* (Ferguson, 1985).

Plant material included cuttings of flowers, leaves, and stems that were changed every 2–3 days. Within treatments, small groups of larvae were reared in separate clear plastic containers with ventilated lids, and plant cuttings were inserted into a 200-µl microcentrifuge tube filled with water to keep plant material fresh. The number of days to pupation was measured for each individual, and pupae were weighed 3 days after pupation.

A standard measure of relative growth rate of *S. frondaria* larvae was calculated as follows: Relative growth rate = [log(pupal weight) – log(hatchling weight)]/development time from hatchling to pupa (Nylin, 1992). As the delicate *S. frondaria* hatchlings are easily damaged during weighing, and pupal weight and development time provide sufficient information for determining growth (Gotthard *et al.*, 1994), an estimate of initial larval weight was used in this calculation. Relative growth rates across the three treatments were not normally distributed, and a Kruskal–Wallis test was used to compare them (Sokal & Rohlf, 1995). The Dunn Procedure for pairwise comparisons of the Kruskal–Wallis test was then used to test for pairwise differences between treatments (Rosner, 2000).

Results

All larvae on the three diets attached plant material to their dorsal surfaces. A larva first chewed off part of a flower, and then turned its head back towards the dorsum to attach the material to a projection with a piece of silk. Although the larvae only consumed flower parts, they used anthers, pieces of petals (either fresh or dried), and even small leaves to construct coverings. Larvae were observed as

fresh plant material was provided, and no differences in larval decorating behaviour were apparent among diet treatments other than in the structure of the covering material. Larvae replaced material with fresh host-plant when it was made available.

Beneath their host-plant covering, the larvae themselves exhibited distinctly different colours on their respective host plants. Larvae raised on *B. racemosa* were light brown and resembled the rust coloured anthers and dark red and rust stems of this plant. Those on *H. subaxillaris* were a similar golden yellow to its flowers, and those on *L. camara* were whitish grey-brown, which, although not as well matched in host plant colour as the other treatments, were similar to the light purple and pink of the flowers (Fig. 1, inset). Larvae in each treatment had a unique phenotype that could be distinguished from other treatments, and no noticeable changes in larval shape or morphology were evident. All larvae exhibited both (1) a colour phenotype specific to the diet treatment, and (2) a covering of material specific to the plant offered in the treatment.

The overall survivorship for the three diet treatments was 56%, and was calculated by comparing the total number of individuals that emerged as adults (206) with the number of first instar larvae (369). Survivorship to adulthood was 86%, (101/118)
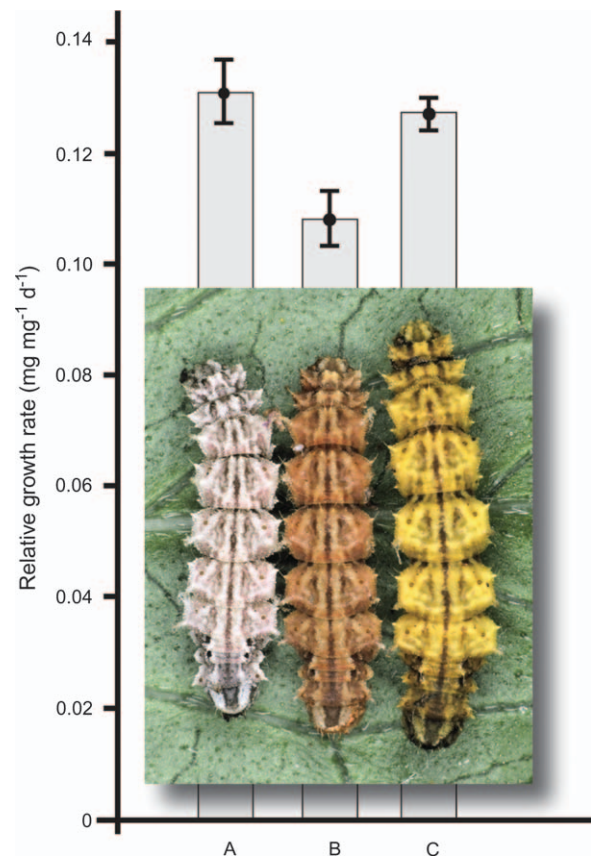

Fig. 1. Relative growth rate of *Synchlora frondaria* among three diet treatments: (A) *Lantana camara*; (B) *Bejaria racemosa*; and (C) *Heterotheca subaxillaris*. Error bars show ± 2 SE. Inset photograph shows a representative larva from each treatment, illustrating phenotypic plasticity.

on *H. subaxillaris*, 52% (71/137) on *B. racemosa*, and 30% (34/114) on *L. camara*. The difference in survivorship in the three treatments is significant ($\chi^2 = 21.0$, d.f. = 2; $P < 0.001$), and pairwise comparisons of all individual treatments are also significant ($P < 0.025$).

The relative growth rates of *S. frondaria* larvae among the three diet treatments are also significantly different ($\chi^2 = 41.7$; 2 d.f.; $P < 0.0001$) (Fig. 1), and the *H. subaxillaris* and *L. camara* treatments did not differ in their relative growth rates (z = 1.03). Comparisons between the *B. racemosa* treatment and both the *L. camara* and *H. subaxillaris* treatments revealed significant differences ($P = 0.05$) showing that larvae on *H. subaxillaris* and *L. camara* grew faster than larvae on *B. racemosa* (z = 5.77, z = 5.65, respectively).

Discussion

In this study, the development of *S. frondaria* larvae on three different host plants was assessed, and both survivorship and relative growth rate varied among treatments. Larvae on *H. subaxillaris* had the highest survivorship and were tied for the highest relative growth rate. Larvae reared on *Bejaria racemosa*, reported in this study as a new host plant family for *S. frondaria*, developed more slowly than on the other two treatments, possibly because of the inhibitory effects of the sticky resin secreted by *B. racemosa* that is known to trap other insects (Eisner & Aneshansley, 1983). Larvae reared on *L. camara* grew as quickly as those on *H. subaxillaris*, but they had significantly lower survivorship.

Although the phenotypes of lepidopteran larvae can vary depending on the host plants they consume, and larval decoration behaviour has been described for a number of species, *S. frondaria* is the first documented example of a larva that employs both diet-induced plasticity and external decoration. These two components allow *S. frondaria* larvae to alter overall colour, as well as texture, when presented with various host plants, and may contribute to its remarkably wide distribution.

Generalist species with wide diet breadths are often more abundant where they occur, and are also more widely distributed (Brown, 1984). One of the potential costs of being a jack-of-all-trades, however, is the difficulty of responding to the wide variety of ecological challenges on diverse host plants. Differences in chemical defences of diverse host plants may provide a formidable challenge to insect herbivores (Bernays, 2001). Responding to a variety of cryptic backgrounds may be yet another important constraint for generalist herbivores (Bernays & Graham, 1988; Jaenike, 1990). Thus, the combination of larval plasticity and decorating behaviour may provide *S. frondaria* with a fine-tuned mechanism for evading predators on a wide range of host plants throughout its range. Further natural history observations and phylogenetic information will be necessary to test whether there is a relationship between these characteristics and patterns of distribution in a comparative framework.

Acknowledgements

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