

Foam barriers, a new defense against ants for milkweed butterfly caterpillars (Nymphalidae: Danainae)

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Abstract. All instar caterpillars of *Idea leuconoe* and *Euploea crameri* from Brunei, Borneo trench leaves and/or cut veins of their hostplant *Parsonsia spiralis*, presumably to circumvent plant defensive chemistry. First through third instar caterpillars also line the outside perimeter of circular trenches with a regurgitated foam that repels ants. These observations are discussed with respect to chemistry of danaine hostplants, and future questions are raised regarding this system.

Introduction

Cutting the leaves or stems of plants in the families Caricaceae, Moraceae, Apocynaceae, or Asclepidaceae typically causes copious milky sap to emanate from the wounded tissues. To an insect herbivore this is a graphic example of rapidly mobilized plant defenses produced in response to tissue damage; the rapidly oozing sap may hinder its ability to feed. In addition to a physical defense, plant sap commonly contains secondary chemicals that can either deter insect herbivores, or be outright toxic to them (Dussourd & Denno, 1991). To overcome this type of plant defense some insects have evolved the habit of severing major leaf veins or cutting a circular trench into leaf tissues prior to feeding — behaviors termed vein cutting, or trenching. From the insect's point of view, trenching and vein cutting behavior may impede or stop mobilization of plant defenses, and make leaf tissues edible (Carroll & Hoffman, 1980; Dussourd & Denno, 1991).

Milkweed butterfly caterpillars (Danainae: Nymphalidae) typically feed on plants containing abundant laticifers (Ackery, 1988), and some species are known to exhibit trenching and/or leaf cutting behavior (Ackery & Vane-Wright, 1984; Compton, 1987; DeVries, 1987; Dussourd & Eisner, 1987). The purpose of this paper is three-fold. First, is to describe trenching behavior in the early instar caterpillars of the danaines *Idea leuconoe* and *Euploea crameri* from Borneo. Second, is to describe a new defense where caterpillars produce a foam barrier that repels ants. Finally, the observations are discussed in light of chemical defenses found in danaines and other insect herbivores, and several questions are raised regarding this system.

Observations

During June 1983 I made observations on the life cycles of *Idea leuconoe nigriana* Grose-Smith, 1895, and *Euploea crameri* Lucas, 1853 in the coastal mangrove forests near Bandar Seri Begawan, Brunei on the island of Borneo. Both of these butterflies are part of the monophyl-

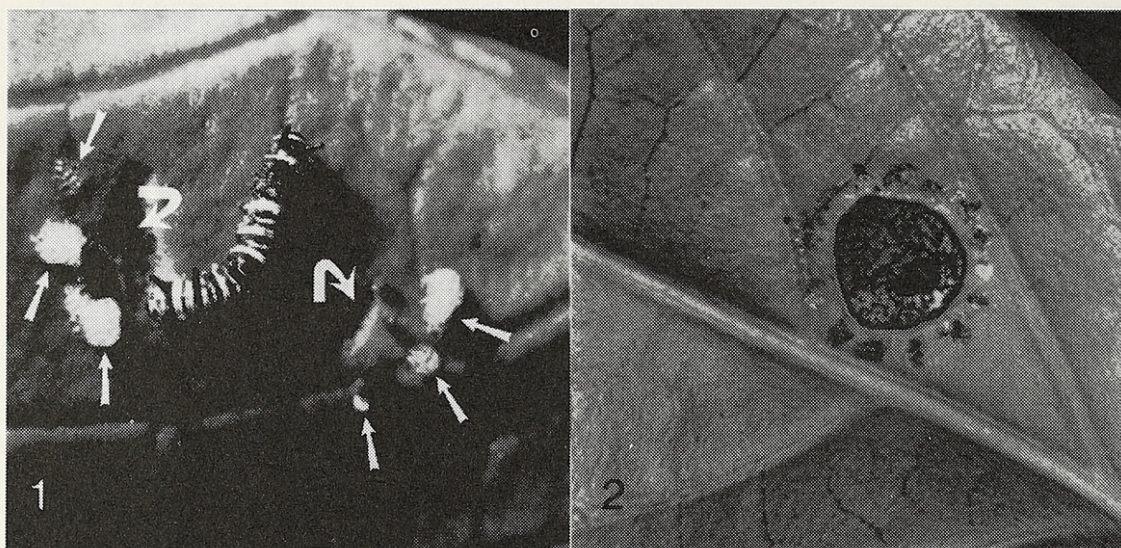


Figure 1: Second instar caterpillar of *Idea leuconoe nigriana* (Danainae) beginning to create a circular trench in a *Parsonsia spiralis* leaf. The caterpillar has excavated two areas in the leaf epidermis (curved arrows). Note the six areas of foam that have been deposited on the outside perimeter of the circular trench (straight arrows). Eventually this caterpillar completely surrounded the trench with foam.

Figure 2: A trenched area abandoned by a second instar *Idea leuconoe nigriana* caterpillar. The caterpillar has eaten away the circular area in the epidermis of the *Parsonsia* leaf. Note the broken ring of residue on the outside perimeter of the trench left by the dried foam barriers.

etic subtribe Euploeina, and range widely throughout the island of Borneo, and elsewhere in southeast Asia (Ackery & Vane-Wright, 1984). In the Brunei mangrove habitat, both species fed on *Parsonsia spiralis* (Apocynaceae) as caterpillars, a common, woody vine in the coastal mangrove forests, and in second growth mangrove habitats (see Ackery and Vane-Wright, 1984).

In the field and in an ambient temperature laboratory, first through early third instar caterpillars of both *I. leuconoe*, and *E. crameri* typically cut a circular trench in the leaf, and fed on the tissues within this circular trench (Figs. 1 & 2). Fourth and fifth instar caterpillars typically cut large leaf veins or the petioles, and then fed on tissues distal to these cuts. The sap of *P. spiralis* is slightly sticky when exposed to air, but unlike many other members of the Apocynaceae the sap is clear, not milky. Although trenching and vein cutting occurs in other danaine species (DeVries, 1987; Dussourd and Eisner, 1987), this is apparently the first report specifically for *I. leuconoe* and *E. crameri*.

In addition to trenching, the first through third instar caterpillars of both species also lined the outside perimeter of their circular trench with a yellowish foam barrier. Depending on the individual caterpillar, the foam barriers ranged from a closed circle to a broken circle of foam. The foam barriers were erected as follows. After hatching and eating the chorion of the egg, a caterpillar would chew into the leaf, extend the body

away from the chewed area, regurgitate a small amount yellowish foam, and deposit it on the leaf surface distal to the chewed area. This process was repeated until the caterpillar remained inside a ring-trench ringed on the outside perimeter with yellowish foam (Fig. 1). Although fourth and fifth instar caterpillars cut the veins of leaves prior to feeding, they were never observed to produce foam or erect barriers.

One of the most abundant ant species in Brunei mangrove habitats was the weaver ant, *Oecophylla smaragdina* (Formicinae). As elsewhere in its range, a single colony of this ant may form numerous, interconnected, arboreal nests that include large areas within its foraging territory. Several features of weaver ant biology are pertinent here: they have acute vision, are extremely sensitive to movement, aggressively territorial, they recruit quickly to any disturbance or resource within their territory, and they possess well-developed mandibles and chemical spray defenses used in prey capture and defending the colony. Although they harvest secretions produced by Homoptera and lycaenid butterfly caterpillars, the diet of weaver ants also includes substantial proportions of arthropods. Thus, where weaver ants are ubiquitous they can exert considerable predator pressure on the local arthropod community (reviewed in Hölldobler & Wilson, 1990).

A simple experiment suggested that the foam placed by *Idea* and *Euploea* caterpillars on the outside of circular trenches functioned to repel ants. The experiment consisted of bridging a captive portion of a weaver ant colony to a cut portion of *Parsonsia* vine (placed in a bottle of water) that had either a first or second instar *I. leuconoe* or *E. crameri* caterpillar on it complete with circular trench and foam barrier. Once set up, the interactions between caterpillars and ants were noted.

The observations are summarized as follows. As individual ants moved onto the *Parsonsia* cutting they investigated the stem and all leaves. When an ant encountered the foam barrier with the caterpillar inside it, there were typically two reactions. First, if the caterpillar was resting inside the ring, upon contacting the foam the ant would immediately back away, groom its antennae, and then move to another area of the plant. Second, when an ant found a foam ring with a moving caterpillar within, it attempted to attack the caterpillar (presumably because the ant could see it), but was repelled by contact with the foam. In this case an ant would make 2-5 attempts at attacking the caterpillar, then back away, groom its antennae and legs, then move to another area of the plant. This experiment was repeated with six individual caterpillars and plants, and in all instances I found that foam barriers that were between 0.25 and 2 hours old repelled the attempts of 10-17 individual ants to get at the caterpillars within foam barriers.

Approximately 6 hours after the foam barriers were deposited they degraded, and eventually dried to a noticeable yellowish scum (Fig 2). Repeating the experiment three times with degraded barriers, I found that the dried foam had no observable deterrent effect on the ants, which attacked and killed caterpillars.

Discussion

The caterpillars of *I. leuconoe* and *E. crameri* excavate trenches or cut veins in their hostplant tissue prior to feeding (Fig. 1 & 2). As in other insects (including some species of Danainae), this behavior may circumvent plant chemical defenses, thereby making the leaf tissues more palatable to the caterpillars (e.g., Dussourd & Denno, 1991).

Sawfly larvae in the genus *Stauronema* (Tenthredinidae) secrete anti-predator chemical defenses through specialized epidermal glands, and also surround themselves and the leaf area they feed on with a foam regurgitation. The foam regurgitated by *Stauronema* larvae has a repellent effect upon ants (Boeve & Pasteels, 1985). The production of defensive foam by sawfly larvae and danaine caterpillars indicates this trait has evolved independently at least twice among insects, and points to the possibility that the use of foam to repel ants may occur in other groups as well.

Some butterflies and Homoptera incur strong survival benefits by forming symbioses with ants (e.g., DeVries, 1991, DeVries, 1992; Pierce et al., 1987; Way, 1963). However, predation by ants can strongly affect the distribution and abundance of those insects that cannot form such symbiotic associations (reviewed by Whittaker, 1991). The abundance and predatory nature of *O. smaragdina* suggests that foam barriers probably increase the chance of survival for early instar *Idea* and *Euploea* caterpillars by acting as a deterrent to foraging weaver ants.

Nothing is known about the chemical composition of the foam produced by *Idea* and *Euploea* caterpillars (Fig. 1). We also do not know whether it is derived from plant tissues, synthesized by the caterpillars directly, or results from an interaction of both. The genus *Parsonsia* contains a suite of secondary chemicals, including large fractions of pyrrolizidine alkaloids (Edgar, 1984; Edgar & Culvenor, 1975). Moreover, pyrrolizidine alkaloids are integral to all life stages of many danaine species (Ackery & Vane-Wright, 1984), and act as a repellent to a variety of predators (Brown, 1984; Dussourd et al., 1988; Boppre, 1990). Consequently, the foam produced by *Idea* and *Euploea* caterpillars may contain defensive chemicals derived directly from *Parsonsia* leaf tissue, including pyrrolizidine alkaloids.

A long history of systematic and ecological interest in the Danainae makes them one of the best understood groups of all butterflies (see Ackery & Vane-Wright, 1984). The observations here raise four questions pertinent to danaine evolution and biology. First, are foam barriers confined to the subtribe Euploeina, or does this trait occur elsewhere within the Danainae? Second, are foam barriers built only by *I. leuconoe* caterpillars that feed on *Parsonsia*, or does this trait also occur in those that feed on members of the Asclepidaceae? Third, do the traits of trenching and erecting foam barriers occur independently within the danaines? Finally, are foam barriers specific to ants, or do they repel a suite of arthropods? Detailed experiments and analyses will be required

to identify the exact function of foam barriers and their chemical composition, but simple field observations and manipulations can quickly provide more information relevant to danaine phylogeny and behavioral ecology.

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