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Short Communication

Egg-Mimics of *Streptanthus* (Cruciferae) Deter Oviposition by *Pieris sisymbrii* (Lepidoptera: Pieridae)

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Summary. *Streptanthus breweri,* a serpentine-soil annual mustard, produces pigmented callosities on its upper leaves which are thought to mimic the eggs of the Pierid butterfly *Pieris sisymbrii. P. sisymbrii* is one of several inflorescence – infructescence-feeding Pierids which assess egg load visually on individual host plants prior to ovipositing. Removal of the "egg-mimics" from *S. breweri* plants in situ significantly increases the probability of an oviposition relative to similar, intact plants.

"Egg-load assessment" occurs when a female insect's choice to oviposit or not on a given substrate is influenced by whether or not eggs (con or heterospecific) are present. The feedback may be negative (leading to overdispersion of eggs) or positive (leading to aggregation). Although well established for parasitoids (Vinson, 1976) and the apple maggot, *Rhagoletis* (Prokopy 1972), it has only recently been found in butterflies, including *Pieris brassicae* L. (Rothschild and Schoonhoven 1977), *Anthocharis cardamines* L. (Wiklund and Ahrberg 1978), and *Battus philenor* L. (Rausher 1980). In the Neotropical Heliconiidae egg-load assessment is apparently visual, and at least two *Passiflora* species have evolved egg-mimics which decrease their attractiveness to ovipositing females (Gilbert 1975). A very similar situation has now been found involving the Nearctic butterfly *Pieris sisymbrii* Bdv. and some of its Cruciferous hosts.

Pieris sisymbrii is a stenotopic, stenophagic Pierine limited to sparsely vegetated, xeric, generally rocky habitats. It is vernal-univoltine throughout its range. In northern California low-elevation populations occur mostly on serpentine soils and feed on the endemic annual Crucifers *Streptanthus glandulosus* Hook. and *S. breweri* Gray. The flight season of *P. sisymbrii* embraces the peak of flowering of *S. glandulosus* and the beginning of flowering of *S. breweri* in a given locality. Eggs are laid singly anywhere on the host; they are initially blue-green but change to bright orange within a few hours, and are then very conspicuous. Small larvae frequently feed on foliage, but the large larvae feed preferentially on flowers and fruit. Each larva can completely consume one medium-sized or several small hosts.

Pieris sisymbrii is one of a large complex of inflorescence- or infructescence-feeding Pieridae (both Pierini and Euchloini) laying orange or red eggs and engaging in intra- and possibly interspecific egg-load assessment (Shapiro in press). Sympatric foliage-feeding Pierini lay white or pale yellow eggs and do not assess egg load. Both *Streptanthus* species produce orange-pigmented callosities on their cauline leaves which are similar in size, shape, and color to *Pieris sisymbrii* eggs and which appear to decrease the attractiveness of mature *S. glandulosus* to ovipositing females (Shapiro, in press).

The efficacy of the suspected egg-mimics of *S. breweri* was tested afield at Turtle Rock, Napa County, California (North Coast Ranges). The site is an almost unvegetated, steep serpentine talus slope with a S to SW exposure. *S. breweri* is the dominant Crucifer (*S. glandulosus* also occurs) and *P. sisymbrii* the dominant Pierid (*Anthocharis sara* Lucas and *Euchloe hyantis* Edw., both Euchloines, are present).

On 10 April 1980 I prepared two lists of 50 numbers from a random numbers table. On 11 April, 100 plants of *S. breweri* in the appropriate phenophase (elongating/budding, bearing egg-mimics) were numbered and tagged. Each was measured, its numbers of leaves and egg-mimics recorded, and it was individually photographed. Any eggs or first-instar larvae present were recorded and removed. Plants bearing second-instar or older larvae were rejected. The lists of numbers were then assigned by a coin toss to experimental and control groups of 50 plants each; I revisited the experimentals and snipped off their egg-mimics. This is easily done since they are at the tips of the upward-pointing cauline leaves. After one full day of excellent flight weather, the plants were revisited (13 April) and all eggs deposited in the interim were recorded. The experiment was carried out at what I judged to be the peak density of ovipositing females at the site for the year, based on previous experience, wing condition, and sex-ratio.

Although larval feeding damage has been shown to be an oviposition deterrent in *P. brassicae* (L.M. Schoonhoven, pers. comm.), no attempt was made to duplicate the injury to the experimental plants by damaging the controls in some other way. It was not self-evident what would constitute an equivalent injury, and any deterrence effect would be expected to favor the null hypothesis, rather than egg-mimicry. The possibility that injured plants might be more attractive than uninjured ones to ovipositing females for chemical, rather than visual, reasons has not been excluded. I judge it to be unlikely for several reasons: feeding larvae routinely cannibalize any eggs they encounter, and single plants rarely offer enough biomass to sustain more than one larva through development – both of these are strong selective pressures favoring egg-load assessment; damaged leaf surfaces have been shown to be attractive to parasitoids (Sato 1979); and I have never observed any association of oviposition with mechanical injury of any kind afield. Plants already bearing eggs or young larvae were not excluded from the samples, since to do so might bias them in favor of individual plants intrinsically unattractive to females for microtopographic or other reasons. The hypothesis that plants which already bore

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Table 1. Characteristics of experimental and control groups of *Streptanthus breweri* and the distribution of *Pieris sisymbrii* immatures on them

Characteristic	Controls N=50	Experimentals N=50
Height (cm), mean ± s.d.	9.82 ± 2.32	9.80 ± 2.22[a]
Number of leaves, mean ± s.d.	6.00 ± 1.53	6.20 ± 1.91[a]
Number of eggs + lst instar larvae initially present and removed	10	8[a]
Number of eggs laid during experiment	8	22[b]

[a] not significantly different
[b] $\chi^2 = 6.53$, df = 1, $0.025 > p > 0.010$

	Controls	Experimentals	Total
Number of eggs laid on plants previously bearing immatures/ number of such plants	3/10	4/8	7/18
Number of eggs laid on plants previously without immatures/ Number of such plants	5/40	18/42	23/82
$\chi^2 =$	1.83	0.14	0.81
$df = 1$, $p =$	>0.250	>0.500	> 0.250

Table 2. Relative attractiveness of various classes of *Streptanthus* plants to female *Pieris sisymbrii*, based on both census and experimental data

Type of plant	N_{plants}	N_{eggs}	mean eggs/plant
S. glandulosus in flower, bearing egg-mimics	110	21[a]	0.19
S. breweri elongating, with intact egg-mimics			
before experiment	100	18[a]	0.18
after experiment	50	8	0.16
S. breweri too young to bear egg-mimics	108	34[a]	0.32
S. breweri with egg-mimics removed in experiment	50	22	0.44

[a] Includes lst instar larvae

eggs or larvae at the start of the experiment were intrinsically more attractive to females than those that did not was tested (and falsified) by comparing the frequencies of ovipositions in the two groups during the experiment (Table 1). Several plants had previously been damaged by flea beetles (*Phyllotreta* species), but they were not numerous enough to permit a statistical test. No eggs were laid on them, however.

The results (Table 1) indicate that removal of the egg-mimics does increase the likelihood of oviposition on the plant. This is the first quantitative demonstration of the efficacy of egg-mimicry by a plant, as well as the first documented instance outside the tropics. The experimental and control groups did not differ significantly in size, morphology, or exposure.

That the observed effect is due to visual egg-load assessment rather than attraction to the damaged leaves is supported by data gathered from a census of intact plants. 110 flowering *S. glandulosus* and 108 *S. breweri* not yet bearing egg-mimics were consused on the same hill on 13 April (Table 2). Apparently, intact mature plants of both species are protected at a similar level and are less likely to receive eggs than either *breweri* too young to bear egg-mimics, or from which they have been artificially removed. This conforms to naturally-occurring egg distributions at Butts Canyon, Napa County (Shapiro, in press). Egg-mimics do not occur in the widespread nonserpentine species *Streptanthus tortuosus* Kell. or in some non-serpentine populations of the *S. glandulosus* complex, suggesting that selective pressure exerted by *P. sisymbrii* on its hosts may be most intense on serpentine soils – either because of higher attack rates or because of the increased difficulty of repairing damage in a nutrient-poor and water-deficient environment[1].

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