Insects as Selective Agents on Plant Vegetative Morphology: Egg Mimicry Reduces Egg Laying by Butterflies

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independently in the teleosts; living representatives of the holostean fishes, the group from which teleosts evolved, lack a dorsal nucleus (1) and are not electroreceptive (19), and only 3 of 35 teleost orders are electroreceptive (20).

Although only a single type of lateral line receptor has been reported for lampreys (21), we have histologically identified at least two populations that differ with respect to their depth from the epidermal surface and the diameter of their canals. We have not yet positively identified the electroreceptors. The homologies suggest, however, that the receptors, like those of chondrichthian and chondrostean fishes (22), will be ciliated and excited by cathodic electric stimuli—that is, negative electrical potential at the outer face of the receptor relative to the rest of the fish. In contrast, the electroreceptors of teleosts bear microvilli on their apical surfaces and are excited by anodal stimuli (23).

If electroreceptive systems in lampreys and primitive jawed fishes are indeed homologous, by definition they have been inherited from the common ancestor of agnathans and gnathostomes. Thus, the earliest vertebrates were probably electroreceptive, and vertebrate electroreceptors may be as ancient as lateral line mechanoreceptors.

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References and Notes
9. Voltage pulses were supplied by a square-pulse stimulator and isolation unit, and a 10 to 100 ohm series resistance was used to minimize electrode polarization effects. Electric field intensities were monitored with a pair of electodes in the water. The fields were only approximated in the central area of the tank and the fish were held.
15. C. J. Platt, T. H. Bullock, G. Czeh, N. Kováč-

24. We thank T. H. Bullock for support throughout the project and C. C. Bell for valuable comments on the manuscript. We also thank B. Monk and the National Marine Fisheries Service for animal collection. This study was supported by an NIH fellowship to D.B., and NIH and NSF research grants to R.G.N. and T. H. Bullock. R.G.N.'s participation was made possible by a Guggenheim Foundation fellowship.
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Egg Mimicry Reduces Egg Laying by Butterflies

Abstract. Experiments show that Heliconius butterflies are less likely to oviposit on host plants that possess eggs or egglike plant structures. These egg mimics are an unambiguous example of a plant trait evolved in response to a host-restricted group of insect herbivores.

The idea of coevolution between insects and plants is attractive to biologists attempting to account for patterns of plant chemistry and the use of plants by insects (1). However, it is difficult to demonstrate a causal connection between a plant characteristic and a particular agent (2) because most plants have been exposed through time to a multitude of pathogens and herbivores, any complement of which may have helped to drive the evolution of the presumed defensive chemistry. Thus, instead of a gene-for-gene coevolution, there may be a more diffuse process (3) that is intractable to experimental analysis.

One approach is to study plant groups that support only one or a few important herbivore taxa and that may therefore have traits attributable to coevolution with such taxa. For neotropical vines of the genus Passiflora, heliconine butterflies are likely selective agents on several features of morphology (4). Plants such as Passiflora may have effectively "filtered out" most potential herbivores at an early stage of the evolution of their defensive chemistry, so that the insects remaining as significant herbivores of these plants are those that circumvent the chemical defenses of these plants. Morphologically rather than chemical innovation is the effective evolutionary response to such herbivores (5), and herbivore behavior rather than counterdefensive chemistry shapes the course of evolution (4).

Structures resembling the yellow eggs of Heliconius butterflies have arisen independently on a number of Passiflora species in several subgenera and are derived from several distinct structures (6). That these structures have evolved specifically to mimic Heliconius eggs is indicated by the facts that (i) heliconines are important defoliating agents of Passiflora (7); (ii) larvae of many Heliconius feed on congenic eggs and larvae (6); and (iii) females exhibit great care in inspecting oviposition sites (6, 8). In this report we provide experimental evidence

Fig. 1. Passiflora cuttings used in experiment:
(A) Passiflora cyanea, showing display of egg mimics on stipule tips. (B) Passiflora oerstedii, showing yellow egg (open circle) placed near green egg (closed circle) on tendril. (C) Enlarged view of P. cyanea stipule showing (top) unaltered stipule, (middle) stipule with egg mimic removed, and (bottom) stipule cut but retaining egg mimic for control. Passiflora cyanea stipules are 3 to 4 cm in length.
which shows that Heliconius females discriminate against plants with eggs or egg mimics and are therefore likely to be selective agents in the evolution of these structures.

We studied the oviposition behavior of Heliconius cydno in greenhouses, using Passiflora oerstedii, a natural host plant without mimicte structures, and P. cyanea, which has egg mimics on stipules (9). The golden color of the mimics closely resembles that of Heliconius eggs just prior to hatching, and mimics tend to be clustered at meristems where many Heliconius prefer to oviposit (Fig. 1A). Although the ranges of P. cyanea and H. cydno do not naturally overlap, H. cydno larvae eat and develop successfully on the plant (10). Both P. cyanea and P. oerstedii are members of the series lobatae.

In the first set of experiments, we examined the response of the butterflies to the presence of real eggs on P. oerstedii, the host without mimics. Host plants were available to the butterflies only during experiments, when females were presented with combinations of plant cuttings with and without eggs. The cuttings were of similar morphology, and H. cydno eggs were placed on tendrils near meristems where eggs are naturally laid. Eggs laid in the course of each trial were immediately removed from the test plants.

Three types of H. cydno eggs were placed on the cuttings: bright yellow eggs, just as they appeared in the field; green eggs, which were eggs that had been tinted with food coloring and rinsed with distilled water to blend with the plants’ coloring; and washed yellow eggs, which were yellow eggs washed with distilled water and which served as controls.

In each test of oviposition preference, the butterflies were offered four P. oerstedii cuttings: two had single eggs of one type and two had no eggs or had a single egg of a different type. The cuttings were arranged at random with respect to one another and the butterflies were allowed to oviposit until they lost interest in the plants. Most trials lasted 1 to 2 hours and the butterflies laid eight to ten eggs per trial.

The oviposition behavior of H. cydno was consistent. The butterflies, probably responding to a combination of olfactory and visual cues (11), usually noticed the host plants as soon as the plants were brought into the greenhouse. While fluttering around a plant, they repeatedly tapped it with their antennae, then landed on the leaves to drum the cuticle with their forelegs, presumably using chemoreceptors to “taste” and further identify the plant (12). They would then fly around the plant, tapping and searching for a satisfactory oviposition site, or reject the plant by flying away. Often, when a butterfly noticed an egg or egg mimics, it would stop searching the plant and fly to some other part of the greenhouse.

Percent oviposition (ratio of number of eggs deposited to number of inspections) on plants with no eggs was significantly higher than on plants that had either a natural or washed yellow egg present (Fig. 2, A and B) (13), indicating that the presence of a yellow Heliconius egg does indeed reduce oviposition on plants. When eggs were laid on plants already bearing a yellow egg, they were usually placed several centimeters away on another part of the cutting.

Egg-free cuttings and those with green eggs had equal oviposition frequencies (Fig. 2, C and D), showing that green eggs were not recognized as something to be avoided. In fact, several eggs were laid within 2 cm of green eggs (Fig. 1B). Washed yellow eggs reduced oviposition as effectively as untreated yellow eggs (Fig. 2, A and B), demonstrating that no repellent chemical was washed off the eggs in the coloring treatment.

In experiments in which P. cyanea was used to test responses to egg mimics, the H. cydno were kept in a greenhouse with Passiflora hosts and with other species of Heliconius. On days of experiments all Passiflora were removed from the greenhouse so that butterflies would oviposit only on the test plants. For each experiment two P. cyanea of similar morphology were brought into the greenhouse, and all butterflies were allowed to oviposit.

Three types of plants were paired in these tests: one with natural egg mimics, one with all egg mimics removed, and one with the tip of each mimic clipped off so that the mimic’s general appearance was not affected (control plants). The mimic tips were clipped off to control for chemical effects of removing stipule tips when mimics were removed from experimental plants (Fig. 1C).

Plants without egg mimics seemed to be more satisfactory for oviposition than plants with egg mimics (Fig. 2E). The percentage of oviposition on control plants was not different from that on natural plants (Fig. 2F), so again, the negative oviposition response appears to be due to visual rather than to chemical cues.

The mean oviposition times for eggs laid on P. oerstedii with real yellow eggs was longer than for P. oerstedii with no eggs present (Fig. 2, G and H) (14). A female spends more time selecting a satisfactory place to oviposit on plants with yellow eggs or egg mimics than on plants devoid of eggs or structures mimicking eggs. Indeed, in crowded greenhouse cultures, when all tendrils have eggs, females switch to secondary sites such as older leaves, dead tendrils, or nearby structures not normally used. The in-

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**Fig. 2.** Graphs which show oviposition response to various treatments. (A to D and G) Experiments were done with P. oerstedii. (E to G) Experiments were done with P. cyanea. In (G) and (H) the x-axis indicates elapsed time between recognition and oviposition. See text for details.
crease in oviposition time appears to arise from the search for safe sites that are close to new growth without exposing eggs to cannibalism. Although egg-like structures do not completely prevent oviposition, they do reduce oviposition frequency.

**Heliconius** can have a severe impact on its host plants. Females of several species frequently oviposit on seedlings and small vines in their forest understory habitats (10); single larva can totally defoliate individual plants. We routinely observe suppression of flowering and increased incidence of root disease in greenhouse plants exposed to heliconine defoliation (15).

Although we have stressed coevolu-
tion, the plant mimicry of this example has also attracted attention (16). The existence of nonmimetic populations of **Passiflora** within some widespread species suggests that the evolution of egg mimicry is an ongoing process (17). However, every population in which we observed mimicry was monomorphic for the trait and was used by at least one **Heliconius** species. Under conditions in which a nonmimetic population containing a few mutant individuals is used by one or more cannibalistic **Heliconius** species, the egg-mimic genotypes might eventually replace all nonmimetic individuals on the basis of relative (rather than absolute) protection.

In a complex community containing ten or more species each of **Passiflora** and **Heliconius**, the microevolution of egg mimics by one **Passiflora** could all but eliminate that species from the host range of several coexisting **Heliconius** (18). At the same time, a new niche is then available to specialists able to utilize the mimetic species (19). **Passiflora** with egg mimics should also excel at expanding into new habitats already infested with **Heliconius** since fake eggs would provide some protection during the vulnerable establishment phase. Thus it appears that egg mimicry represents one way that a coevolutionary step might promote local diversity within a food web (20).

We have demonstrated that (i) **Heliconius** females respond to the presence of eggs; (ii) this response has a strong visual basis (8), although chemical cues are not altogether excluded; and (iii) the response to egglike structures of **Passiflora** and to real eggs both reduces the probability that eggs will be laid after host discovery and increases the time required to oviposit. Whereas other visual aspects of **Passiflora** that may be related to the defense of **Heliconius** are directed toward making the potential host plants less apparent or less recognizable to the butterflies (21), egg mimicry deters oviposition after the host has been discovered (22). Our study supports the egg mimicry hypothesis and is an instance of a plant structural trait resulting from coevolution with an insect herbivore.

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**References and Notes**

7. L. E. Gilbert, J. Int. C.N.R.S. 265, 399 (1977). Flea beetles apparently are the only other herbivores of **Passiflora**.
8. The visual acuity of **Heliconius** is documented by C. A. Swihart and S. L. Swihart [Zoologica 48, 155 (1963); Anim. Behav. 18, 60 (1970); see also (6)].
9. Original **H. cydnoides** stocks were collected by L. E. Gilbert at the Organization for Tropical Studies, La Selva station, Costa Rica. **Passiflora** and **Cyanea** stocks originated from populations at La Selva and Arima Pass, Trinidad, respectively. **Heliconius** and **Passiflora** species are maintained in temperature-controlled Lord and Burnham glass houses (5 by 8 m) at the University of Texas.
11. M. D. Rausher has recently described search image formation for leaf shape by the pine vine swallowtail, *Battus philenor* (Science 200, 1071 (1978)).

**Internal Fertilization in an Oviparous Frog**

Abstract. **Eleutherodactylus coqui**, an oviparous frog, undergoes internal fertilization. If this mode of fertilization occurs in other species of anurans, interpretations of anuran reproductive strategies based on the assumption of external fertilization must be reviewed.

Mode of fertilization is a fundamental factor in the evolution of reproductive strategies, in part because it constrains the nature of the parental investment by each sex (1). In species with internal fertilization, the lower certainty of genetic relatedness of the male to the offspring (compared to that of the female) has often resulted in the evolution of maternal care systems, along with various mechanisms to ensure paternity. Parental care by males alone has been reported primarily in species with external fertilization (2).

Biologists have long assumed that most frogs employ external fertilization, and anuran reproductive strategies have been interpreted in light of this assumption (3). The only frog demonstrated to have internal fertilization is *Aeschnops truei*, a unique species in which adult males have a tail used as an intromittent organ. Internal fertilization has been inferred for the few known live-bearing frog species (4, 5) but has never been demonstrated for an oviparous frog. We present evidence that the oviparous frog **Eleutherodactylus coqui** Thomas has internal fertilization.

**Eleutherodactylus coqui** is a nocturnal, terrestrial-breeding frog of Puerto Rico (6). Males call from elevated perches and exhibit parental care by attending eggs from oviposition to hatching. Eggs undergo direct development and hatch as tiny froglets. Males may remain with the froglets for up to 5 days after hatching. Courtship may occur at any time of night. A gravid female approaches a calling male and makes contact. The male