

closely related to changes in pulse than to changes in subjective ratings.

The three subjects absorbed different quantities of  $\Delta^9$ THC. This variation was apparent in peak  $\Delta^9$ THC concentrations in the plasma for the three subjects, namely, 67, 37, and 21 ng/ml. An estimate of the portion of  $\Delta^9$ THC absorbed from the original cigarettes was made from the portion of total tracer present in the 24-hour urine samples. Lemberger *et al.* (6) reported that when  $\Delta^9$ THC was administered intravenously to chronic users, 20 percent of it was excreted in the first day's urine. If the same portion of  $\Delta^9$ THC and its metabolites administered by smoking is excreted in the 24-hour urine, then our subjects absorbed 41, 20, and 15 percent, respectively, of the quantity of  $\Delta^9$ THC in the original cigarettes.

Manno *et al.* (7), using a mechanical smoking device, assayed the portion of cannabinoids in the smoke of marijuana cigarettes, and found that approximately 50 percent of the  $\Delta^9$ THC in the cigarettes was delivered unchanged in the smoke. This figure is comparable to that of 41 percent absorbed by one of our three subjects, but the other two absorbed less than half that amount. This is an indication of the marked variability of  $\Delta^9$ THC absorbed when marijuana is administered by smoking, even under standardized conditions.

The subjective experience was responsive to both placebo and change in setting. Although the 12 subjects rated themselves as less "high" on placebo, there was good correlation of symptoms experienced under the influence of placebo and  $\Delta^9$ THC (rank-order  $r = .544$ ,  $P < .01$ ). The smokers appeared to be conditioned to a particular subjective syndrome triggered by the stimulus of smoking marijuana-like material. This may in part explain the greater sensitivity to marijuana reported by experienced smokers. The 12 most frequently checked symptoms while the subjects were under the influence of  $\Delta^9$ THC were: mouth drier, feels high, throat drier, hungrier, dreamier, feels more like paying close attention to things, skin tingling, memory seems worse, movements slower, head heavier, sees images when eyes are closed.

When three of the subjects were subsequently studied on the same dose in a more austere setting and subjected to venipuncture, the variability in the subjective experience was apparent. Two of the subjects vomited while at the

peak of their subjective "high," whereas neither had done so on that dose when it was administered under more congenial circumstances earlier in the study. As one of the two reported on the day of blood drawing, "I just freaked out when I saw that needle." He checked off "very much more than usual" for the symptoms, "have you felt less in control of your body"; "felt less in control of your feelings"; and "had a weird feeling." He had checked "not at all" on the previous occasion.

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## References and Notes

1. L. E. Hollister [*Science* **172**, 21 (1970)] reviews these studies and discusses some of the problems implicit in administration of marijuana by smoking.
2. The materials were obtained from the Psychotomimetic Agents Advisory Committee, National Institute of Mental Health. They were assayed by gas-liquid chromatography by TRW-Hazleton Laboratories both before and after the study, as follows: natural marijuana, 1.6 percent  $\Delta^9$ THC, less than 0.05 percent  $\Delta^8$ THC, 0.1 percent each of cannabinol and cannabidiol; placebo marijuana material (produced from marijuana plant material by four extractions in 95 percent alcohol), 0.05 percent  $\Delta^9$ THC, 0.05 percent  $\Delta^8$ THC, and 0.01 percent each of cannabinol and cannabidiol; synthetic  $\Delta^9$ THC, 92 percent  $\Delta^9$ THC, 6 percent  $\Delta^8$ THC, and 1 percent each of cannabinol and cannabidiol. Purity of the [ $^3$ H] $\Delta^9$ THC was shown to be greater than 98 percent.
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18 February 1972

## Natural Selection for Müllerian Mimicry in *Heliconius erato* in Costa Rica

**Abstract.** *The natural color pattern of individuals of the unpalatable and mimetic butterfly Heliconius erato was altered to a unique nonmimetic pattern. When returned to natural populations, the nonmimetic individuals remained for shorter periods of time and received more wing damage indicative of predator attacks than did the controls. The results indicate that Müllerian mimicry was functioning to protect the butterflies from predation.*

H. W. Bates and F. Müller, in their theories on protective mimicry, provided the first models of the coevolution of species under the influence of natural selection (1). The original theories were deduced from limited empirical evidence; however, a vast body of supportive data has since been accumulated. Most of these data have been natural historical, a posteriori correlative, or based on laboratory experiments (2). Direct quantitative evidence supporting the hypothesis that

natural selection operates in nature to promote the evolution of mimicry is rare. There exist only one "natural" (3) and one manipulative (4) experimental field study with living insects demonstrating the selective advantage of Batesian mimicry in nature.

This report describes a set of experiments giving evidence that natural selection is a factor maintaining monomorphism within and similarities between unpalatable species—evidence for the operation of Müllerian mimicry.

**Table 1.** Comparison of residency time at roosts (= minimum longevity) between altered and unaltered individuals of *H. erato* (Mann-Whitney U test). The entries in the table denote the number of days an individual butterfly was seen returning to the roosts under observation.

Number of days returning to roost										Mean
1968 experiment*										
Altered	52.5	42.5	32	32	27.5	26	10.5			31.7
Unaltered-controls	> 71	70	> 64	62	57	53	52	22	21	52.4
1969 experiment†										
Altered	63	47.5	25.5	23.5	22	14	3			28.4
Unaltered-controls	48.5	40	36.5	19	14.5	8	3			24.2

\* U = 13;  $P(U \leq 13) \approx .034$ , one-tailed test. † U = 27.5;  $P(U \leq 27.5) \approx .668$ , one-tailed test.

The experiments were conducted at Rincón de Osa, Puntarenas Province, Costa Rica, an area characterized biotically by slightly seasonal Central American tropical wet forest (5). The organism used in the experiments was the unpalatable butterfly *Heliconius erato* L. (Nymphalidae, Heliconiinae) (6). This species has many comimics throughout its range; the middle-American race *H. erato petiverana* Doubleday shares its pattern with the similarly unpalatable *H. melpomene* L. as race *rosina* Boisduval (7) (see Fig. 1A). In addition to looking alike, the two species are usually sympatric, behave similarly, and occupy edge habitats along roadcuts and stream banks bounded by forest. These facts suggest a priori that the mimicry between these two species is functional.

The experimental design involved altering the color pattern of certain individuals in *H. erato* populations by staining the fore wing red band black to match the rest of the wing (8) (Fig. 1A, bottom). Controls were produced by staining an equal or usually larger area on the already black wing tips, thus effectively leaving the wing pattern unaltered. The altered class served as artificially produced nonmimics whose survival under conditions of natural selection could be compared with that of the controls. The controls are "mimics" by virtue of their resemblance to the normal color pattern of the population, which predators presumably have had the opportunity to learn to leave alone. In terms of theoretical processes, the nonmimics may be considered either (i) a rare nonmimetic species of unpalatable butterfly or (ii) a rare nonmimetic morph of the mimetic species.

The *H. erato* system and the particular experimental design present the opportunity to control for a number of extraneous processes: (i) by using a single species, there will be a minimum of behavioral differences between the altered and unaltered classes (9), so only functionality of color pattern mimicry is being tested; (ii) by marking over a bright color component with black, the altered nonmimics are less conspicuous than the red-banded mimetic individuals, and increased selection against the nonmimics could not be ascribed to their attracting more attention (10); (iii) the altered form has a unique color pattern in the habitat and geographic region, so that increased selection against it is unlikely to be the result of predators con-

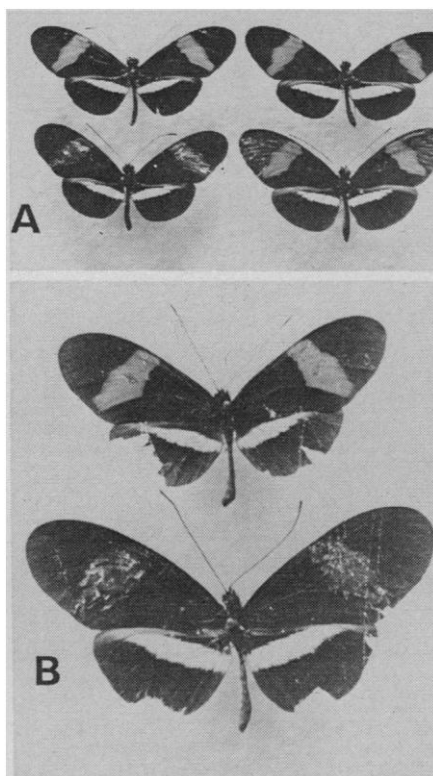


Fig. 1. (A) (Top) Upper sides of *Heliconius erato petiverana* (left) and its comimic *Heliconius melpomene rosina* (right). (Bottom) Altered (left) and unaltered (right) treatment classes of *H. erato* used in the experiments. The mottled areas on the treated butterflies are produced by light reflecting from the glossy black stain applied to the wings. (B) Example of bird attack (top), showing a crisp beak mark on the right hind wing and a tear on the left hind wing that satisfy the criteria for "major wing damage." An altered *H. erato* shown at the bottom bears beak marks of a Rufous-tailed Jacamar (*Galbula ruficauda*) across both right wings.

fusing it with sympatric palatable species; and (iv) the altered form almost exactly resembles *H. erato chesteronii* Hewitson from the Río Cauca valley of Colombia (which is a comimic of *H. cydno gustavi* in the same locality), indicating that the nonmimetic color pattern of the altered form in Costa Rica is not intrinsically disadvantageous elsewhere. Also, *H. erato* roosts gregariously, with individuals returning continually to the same sleeping site often during their entire life, providing a convenient aid to censusing (11).

Butterflies were marked at the roosts during the night (12). Not more than a few roost members were marked on any one visit for fear of disturbing all of the members sufficiently that none would return. More importantly, there was the danger of releasing too many

altered individuals at one time. If the proposed mechanism for the selection of Müllerian mimicry were to be operating and many altered forms released, predators might quickly learn that the new form was unpalatable and attack too small a fraction of those present to be revealed by tests of significance (13).

Two measures of selective advantage were used. The first was "residence time" in the population. By measuring the number of days between the first time a butterfly was observed to return to roost after marking and the midpoint between the last time observed at the roost and the first time not observed, an approximate estimate of longevity could be obtained. This estimate is unbiased by differential visibility of the two morphs and relatively unbiased by immediate dispersal from the area induced by handling and marking trauma.

The second measure was "major wing damage," damage of a type which could have been produced by a vertebrate predator. The criteria used were the presence of a distinct mouth outline or beak mark on the wing, or a wing chip with at least one straight margin which passed through at least one wing vein (see Fig. 1B). Progressive minor wing chipping was commonly observed in older individuals; cases in which the criteria were satisfied in this manner were not included.

In 1968, a total of 34 fresh male butterflies were marked for the residence time experiment. Of these, 16 failed to return to roost after marking, and 2 were killed early in the experimental period as examples of bird damage to the wings. This left a total of 7 altered and 9 unaltered individuals. The residence times and test results for differences in residence time are given in Table 1 (14). The altered nonmimics survived in the populations for a significantly shorter period of time (mean = 31.7 days) than the unaltered controls (mean = 52.4 days;  $P < .05$ ).

In 1969 (15), a similar experiment yielded nonsignificant results (Table 1). The experimental period was considerably shorter, and of 39 butterflies (both males and females) used, 19 were still alive at the end of the experimental period, and 6 did not return to the roost after marking. Due to the small sample sizes and possible differences in the second year (long-term memory by resident predators, shorter experimental period which preceded the intensive

Table 2. Comparison of major wing damage between altered and control individuals of *H. erato* (G-statistic) in 1968 experiment using all males.

	Altered	Unaltered controls	Normal controls	Combined controls
Number of butterflies	10*	9	16	25*
Number with major wing damage	5*	3	3	6*
Number of butterfly-days	253	444	1093	1537

2 × 2 Contingency table adjusted for different exposures†

	Altered	Control	
Undamaged	5	22.53	$G = 4.26; P(G \geq 4.26) \approx .021$ , one-tailed test
Damaged	5	2.47	

\* These are the primary data from which the adjusted contingency tables are derived. † The adjusted contingency tables were derived by proportionally reducing the number of cases of major wing damage in the treatment group with the higher level of individual exposure to predator attack. Thus, in 1968, each altered nonmimic was exposed for an average of 25.3 days, whereas the controls were exposed for an average of 61.48 days each. Had both groups received the lower exposure rate, it would be expected that only  $(25.3/61.48) \times 6$ , or 2.47, of the attacks on the controls would have had time to occur.

Table 3. Comparison of major wing damage between altered and control individuals of *H. erato* (G-statistic) in 1969 experiment.

	Males		Females		Combined	
	Altered	Unaltered controls	Altered	Unaltered controls	Altered	Unaltered controls
Number of butterflies	12	14	4	3	16*	17*
Number with major wing damage	4	0	2	0	6*	0*
Number of butterfly-days	495	441	140	125	635	566

2 × 2 Contingency table adjusted for different exposures†

	Altered	Control	
Undamaged	10.97	17	$G = 4.55; P(G \geq 4.55) \approx .018$ , one-tailed test
Damaged	5.03	0	

\* † Footnotes as in Table 2.

nesting and fledging period of most birds), the nonsignificant results are not surprising.

To test for differences in wing damage between the altered and normal-appearing butterflies in the 1968 experiment, the unaltered and normal controls which had had no stain applied were grouped. This was justified by assuming that the presence or absence of applied pigment, without alteration of the color pattern, would have no effect per se on the probability that a butterfly would receive damage, either from a predator or from other causes. Because of the difficulty of finding roosts in 1969, a normal control group was not established.

The results given in Tables 2 and 3 show that the altered nonmimics received more major wing damage in both 1968 and 1969 than did the controls ( $P < .025$  in 1968;  $P < .02$  in 1969).

Since three of the four independent tests yielded results showing that non-

mimics remained for shorter periods of time in the populations or received more wing damage of a type characteristic of vertebrate predator attacks [the combined probabilities of the four tests were significant by Fisher's method (16);  $-2\sum \ln P = 22.982$ , which is greater than the critical value for  $\chi^2$ , d.f. 8, for  $P = .005$ ], the experiments demonstrate that selection was operating to promote monomorphism in the experimental populations and that the process was consistent with the Müllerian hypothesis. Thus, the experiments strongly support the hypothesis that Müllerian mimicry is functional: A rare morph of an unpalatable species will be selected against, and a rare unique unpalatable species will receive greater mortality than a more abundant species otherwise differing only in color pattern.

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## References and Notes

1. Batesian mimicry [H. W. Bates, *Trans. Linn. Soc. Lond.* 23, 495 (1862)] maintains that a rare palatable species (the mimic) can obtain an advantage by resembling a common unpalatable species (the model), since predators will learn to avoid the model and subsequently avoid the mimic because of lack of experience and confusion. Müllerian mimicry [F. Müller, *Proc. Entomol. Soc. Lond.* 20 (1879)] states that two or more unpalatable species will obtain an advantage by resembling one another, since predators will only have one pattern to learn, and will therefore spread their few unpleasant sampling experiences over all the species, rather than having to learn to avoid each pattern independently. Both theories have received considerable amplification since first proposed, but they continue to retain the essential postulates of their authors.
2. The types of data available have been reviewed by: G. D. H. Carpenter and E. B. Ford, *Mimicry* (Methuen, London, 1933); P. M. Sheppard, *Natural Selection and Heredity* (Harper, New York, rev. ed., 1959); E. B. Ford, *Ecological Genetics* (Methuen, London, 1964); W. Wickler, *Mimicry in Plants and Animals* (McGraw-Hill, New York, 1968); and C. W. Rettenmeyer, *Ann. Rev. Entomol.* 15, 43 (1970).
3. M. Edmunds, *Nature* 214, 1478 (1966).
4. L. P. Brower, L. M. Cook, H. J. Croze, *Evolution* 21, 11 (1967); L. M. Cook, L. P. Brower, J. Alcock, *ibid.* 23, 339 (1969).
5. L. Holdridge, *Life Zone Ecology* (Tropical Science Center, San José, Costa Rica, rev. ed., 1967). The study area was a 3.2 km section of abandoned logging road at 200- to 300-m elevation. The road ran through slightly degraded ridgetop forest (mean annual rainfall 3.5 to 4.5 m, mean annual temperature about 28°C). The *H. erato* were at normal abundances along the roadside (based on qualitative observations from many localities in Central and South America); about 10 to 20 could be seen by walking through the area at a steady pace.
6. L. P. Brower, J. v. Z. Brower, C. T. Collins [*Zoologica* 48, 65 (1963)] have presented data showing that *H. erato adanus* and *H. melpomene flagrans* of Trinidad are highly avoided by wild-caught Silverbeak Tanagers (*Ramphocelus carbo*), suggesting that the butterflies are unpalatable and negatively reinforcing to predators.
7. The geographic covariation between *H. erato* and *H. melpomene* has recently been documented by M. C. Emsley [*Zoologica* 49, 245 (1964)] and J. R. G. Turner [*Sci. Progr. Oxford* 58, 219 (1970)].
8. Black "Marks-A-Lot" felt-tip markers (Carter's Ink Co.) were used to stain the wings of the butterflies.
9. J. Crane [*Zoologica* 40, 167 (1955)] reported that alterations in the color of the fore wing red band of *H. erato* resulted in few behavioral changes in individual butterflies, these being largely confined to reduced interactions between individuals.
10. L. P. Brower, J. v. Z. Brower, F. G. Stiles, H. J. Croze, and A. S. Hower [*Science* 144, 183 (1964)] reported that brightly painted, uniquely colored moths (*Hyalophora promethea*) survived in the wild for much shorter periods of time than did cryptic controls, even though only a small number ( $N = 43$ ) were released. The data suggest that bright coloration per se may increase the probability of attack on an unfamiliar insect in nature.
11. J. R. G. Turner [*Biotropica* 3, 21 (1971)] presents data showing return to roosts over approximately 2 months, and I have observed individuals returning for as long as 6 months.
12. Roosts of *H. erato* were located in the late afternoon by finding loose groups of flying butterflies along roadsides. These individuals would typically form roosting aggregations toward sundown, when the butterflies land on the tips of dead twigs in close proximity to one another. The roosts were almost always between 0.5 and 2.5 m from the ground and contained up to ten individuals.
13. Brower *et al.* (4) and Cook *et al.* (4) experienced a similar problem when they released large numbers of the moth *Hyalophora promethea* painted to resemble *Parides anchises*. They obtained results supporting the functionality of mimicry over the first few days of

- an experiment, but afterward control moths returned at a greater rate than mimics. These authors overcame the problem by releasing small numbers of mimics in several areas so that predators would not have the opportunity to learn that they were edible. The results of the small-scale experiments confirmed that Batesian mimicry was functional when certain ecological parameters were satisfied.
14. Statistical tests were derived from S. Siegel, *Nonparametric Statistics for the Behavioral Sciences* (McGraw-Hill, New York, 1956) (Mann-Whitney U test) and R. R. Sokal and F. J. Rohlf, *Biometry, the Principles and Practice of Statistics in Biological Research* (Freeman, San Francisco, 1969) (G-statistic).
  15. During 1968, experiments were carried out between 12 February and 9 June, with an additional census being made on 11 August. The 1969 experiments were conducted between 12 January and 14 April. This second set of experiments began 31 days earlier and was continued over 92 days versus 118 days for the intensive part of the sampling period in 1968.
  16. R. R. Sokal and F. J. Rohlf, *Biometry, the*

*Principles and Practice of Statistics in Biological Research* (Freeman, San Francisco, 1969), p. 623.

17. This report incorporates material from my Ph.D. thesis sponsored by the Department of Zoology, University of Washington. Financial support came from an NSF predoctoral fellowship and grant GB-6518X administered by the University of Washington. Logistic support by the Organization for Tropical Studies greatly facilitated field work. I acknowledge Dr. Gordon H. Orians for help at all stages of research and writing and Drs. Keith S. Brown, Jr., W. T. Edmondson, and John Edwards for commenting on the manuscript. Finally, Mr. Jorge Campabadal and Miss Lili-ana Echiverria of OTS have been particularly helpful in making feasible this research under what would otherwise have been difficult conditions.

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28 February 1972

## Feedback: Real-Time Delayed Vision of One's Own Tracking Behavior

**Abstract.** *When a televised display of a person's own behavior in pursuit tracking is delayed, his performance, as measured by time on target, is seriously degraded. Data for six subjects on two tracking patterns under seven delay values reveal a linear inverse relationship between the logarithm of the time on target and the magnitude of delay.*

Over 10 years ago the first observations on the effects of delayed vision (520 msec) of one's own behavior via television were reported (1). Unforeseen technical difficulties made it impossible until now to extend those initial observations to the systematic study of delay values. Variable delays of a television picture in the range of milliseconds with video tape instrumentation proved impossible to achieve. Recently, however, by using a specially designed video disk recording and playback device (2), we have been able to store a televised display of a person's own behavior prior to playback for periods of 17 msec to 3 seconds in steps of approximately 30 msec. This technique of delaying visual feedback has important implications for studies in experimental psychology, developmental psychology, psychopharmacology, sensory psychology, and clinical neurology.

In order to study one aspect of the effects of various delay magnitudes on performance a rotary pursuit task (3) was used. The subject sat directly in front of a 58-cm television monitor with the center of the monitor 91 cm away and at eye level. The camera, placed just above the subject's head, pointed toward the task area. The subject could observe the tracking display, his hand, and his forearm on the monitor, but a special occluder prevented

him from seeing directly the tracking device or his hand and forearm. The linear size of the tracking pattern on the monitor was approximately 5 percent smaller than the actual pattern. Two tracking patterns were used: a circle (20 cm in diameter) and an octagon (19 cm on a side) with four very

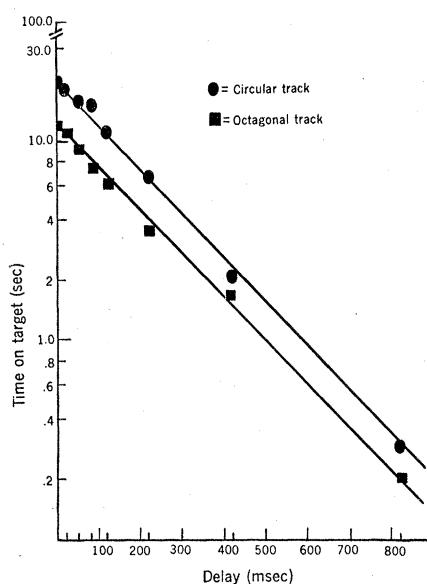


Fig. 1. Tracking performance for two tracking patterns under delayed vision. Each data point represents the mean time on target for six subjects under no delay and seven values of visual delay (17, 50, 80, 120, 220, 420, and 820 msec).

short sides at what would have been the corners of a square. These patterns appeared on the monitor as dark gray on a light gray background. The moving target consisted of a bright illuminated patch (19-mm square) which followed the circular or octagonal path. Because of the nature of the tracking device, the moving target on the circular pattern traveled at a constant velocity of 120° per second but accelerated and decelerated around this value on the octagonal path.

Each subject tracked the moving target with a wand having a photosensitive transducer in its tip. The measure of performance was total time on target for a 30-second trial period. Data were obtained for six subjects in each of seven delay conditions (17, 50, 80, 120, 220, 420, and 820 msec) and one no-delay condition. Target order was counterbalanced across subjects, and two trials were obtained from each subject on both tracking patterns for each of the eight viewing conditions. An up-and-down procedure was used in presenting the seven delay conditions and the no-delay condition.

The results are summarized in Fig. 1 and show an inverse linear relationship between log time on target and magnitude of delay. The lines in Fig. 1 are visually fitted to the data points. Transmission visual delays (4) of one's own tracking behavior clearly disturb performance, even with a delay as brief as 17 msec, a magnitude approximating the transmission time of visual information from eye to brain. Moreover, the degradation of performance becomes marked with a delay of 250 msec, the duration of a typical visual reaction time. At this value, performance on both tracking patterns is reduced by more than 60 percent of base-line, no-delay levels. With a delay of 420 msec, performance is approximately 16 and 10 percent of original no-delay levels for the circle and the octagonal patterns, respectively. The difference in difficulty between the two tracking patterns is evident from the data in Fig. 1. Figure 1 also shows that the variable velocity of the target for the octagonal tracking pattern had no differential effect on the nature of the relationship between magnitude of delay and performance. The large decrements in performance with increasing delay occurred despite the fact that the movement of the target followed a predictable path—one which was always