

## THE MONARCH BUTTERFLY AND MIMICRY

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The theory of mimicry and the theory of warning coloration seem to generate more illogical reasoning and more ill-conceived and ill-executed experiments than any other evolutionary subject. Bruce Petersen in a recent issue of this *Journal* (1964) has not only given an uncritical account of Urquhart's arguments against the theories of mimicry and warning coloration, but has given also an account of an experiment which because of its design adds no light to the situation.

Before considering the experiment reported by Petersen it is necessary to consider the validity of a number of the objections to the theory of mimicry as presented in his paper. No one could take exception to the comment that some resemblance between model and mimic has to appear before the mimicry can be improved—this is part of the standard theory of mimicry (Carpenter & Ford, 1933: 161–168; Sheppard, 1960). Nor can one object to the statement that the food habits of captive animals may be suspect. However, there is grave objection to the statement that stomach analysis of wild animals is the best evidence of their food preference. This unsupported statement presupposes that the remains of all animals are equally likely to be detectable in the stomach. In fact observation of predators in the wild is far better evidence as is shown by the work of Kettlewell (1956) and of Tinbergen (1960) to mention only two workers in the field. Also the statement that no butterfly predator has been suggested as the evolutionary force responsible for mimicry is untrue, both birds and lizards have been so considered.

One of the most amazing arguments against mimicry which Petersen uses is: "Birds frequently eat caterpillars (which show no mimicry) and rarely eat butterflies (which supposedly mimic each other frequently). If natural selection were responsible for mimicry one would expect to find it in caterpillars—not butterflies." It is perfectly true that birds frequently eat some kinds of caterpillars, one cannot just say "eat caterpillars"—it depends which caterpillars they are (for example they do not readily eat the larvae of *Pseudosphinx tetrio* (L.) or *Hipocrita jacobaeae* (L.), and more rarely eat butterflies. But the argument that if natural selection were responsible for mimicry one would expect to find it in caterpillars not butterflies is a nonsequitur. Birds are known frequently to eat moths, but you don't find mimicry here either except in some day flying ones. One would only expect mimicry to evolve in species which by their daytime activities are already fairly conspicuous. One would not expect it to evolve in

animals which are highly cryptic and can remain almost motionless during the day. The statement that mimicry has not been found in caterpillars is completely unsubstantiated by him. However, most of the known cases of larval mimicry (except perhaps the snake mimics) are probably Müllerian, not Batesian. Since they can remain still during the day, most edible caterpillars are highly cryptic, it being a more effective mode of protection for them than Batesian mimicry would be. In fact mimicry theory predicts that Batesian mimicry will be very rare among animals which are chiefly nocturnal such as moths and caterpillars. This is supported by the observation that both warning coloration and mimicry are not uncommon in day flying moths but both are rare in night flying ones, mimicry being excessively so.

The statement that "even very distasteful creatures are better off to be inconspicuous than to be brightly coloured" is just false and has been shown to be so on many occasions. For a recent example see Sheppard (1964). Also the fact that 50 people did not find the monarch butterfly objectionable is no argument against the theory of warning coloration or mimicry since man has never been postulated to be the predator responsible for this mimicry. The scarlet tiger moth *Panaxia dominula* (L.) is not unpalatable to the many people who have tried it, but is one of the most distasteful British moths to many of its natural predators, as is shown not only by experiments with captive animals (Rothschild, 1961a, 1961b, Rothschild & Lane, 1960), but also by experiments on wild birds in a garden (Sheppard, 1964). The statement that "only in Dr. Brower's work is there any indication that birds dislike monarch butterflies," is untrue (see Jones, 1932, 1934).

Again the objection that birds are almost never seen feeding on monarch butterflies is not a valid one. Birds are almost never seen feeding on the peppered moth *Biston betularia* (L.) and yet predation by birds has been shown to be responsible for the development of industrial melanism, and often acts at the rate of up to 15 to 50% of them being taken per day (Kettlewell, 1956). The fact that monarchs marked for migration experiments have been eaten in large numbers apparently because their appearance has been altered (Urquhart, 1957) is in complete accord with the theory of mimicry. One might expect an alteration of the wing pattern to cause the individual to be attacked; in fact the statement indicates that butterflies can often be attacked by birds.

If one accepts the suggestion that the tagged monarchs were eaten because their appearance had been altered and that the normal pattern does not elicit a feeding response, then the requirements for the evolution of mimicry are satisfied, regardless of whether the model is distasteful or not. Clearly it would be an advantage to the viceroy to be mistaken

for any animal that isn't eaten; this would be true mimicry. However, there is no evidence contrary to the view that the reason for the tagged monarchs being eaten is that they were no longer recognized as distasteful models.

Mimicry theory does not fail "to explain why the banded purple doesn't mimic the monarch, as it is the same genus as the viceroy." If mimicry is effective one would expect it to mimic some other model and be much less likely to mimic that utilized by its close relative, since the advantage of mimicry wanes as mimetic pattern becomes commoner. In fact a closely related species<sup>1</sup> to the banded purple, the red spotted purple *Limenitis astyanax* (Fabr.), is a mimic, not of the monarch, but of the pipe vine swallowtail *Battus philenor* (L.).

The experiments reported by Petersen are no more informative or valid than his theoretical arguments. The experiments do not seem to have been designed at all. There is absolutely no control, nor apparently has any record been taken of which birds took what. It would have been perfectly possible for the monarch to have been lethal to every bird that ate it, and still the results given in the graph could be true ones. To show that the monarch is or is not distasteful requires a much more subtle experiment. To begin with distastefulness is only relative, so that one has to have some comparison—the best comparison of course would be butterflies of about the same size, but with a different wing pattern, which are believed for other reasons to be edible. The fact that the wings were cut off so that the insects were not recognizable as models, they in fact were mimicking "elongated, jumping, black spiders with tetany," would mean that the birds might not learn to avoid them at all, if they were normally feeding on black spiders.<sup>2</sup> This would be in accord with the theory of mimicry. Winged and wingless monarchs were not given on alternate days or days picked at random, nor do we know how many birds were feeding on them. The data on the winged individuals is certainly far too scanty for one to determine whether any of the birds were gradually learning to avoid them. The only thing the experiment does do is to show that Urquhart's contention that the monarch does not elicit a feeding response is untrue since a proportion of the winged ones given in December were apparently eaten, although the data do not show how many of the ones not eaten were pecked at then rejected. Nor is the data as presented (graph 1) in agreement with the statement "the last one to be eaten had been lying dead on the patio for four days. A day-by-day tabulation of the butterflies

<sup>1</sup> The present author does not agree with the treatment of *L. astyanax* as a separate species in the recent dos Passos List and believes that all evidence indicates *astyanax* and *arthemis* are subspecies.

<sup>2</sup> See also: Parsons, J. A., 1965. A digitalis like toxin in The Monarch, *Danaus plexippus*. Jour. Physiol., 178: 290-304.

is presented in graph 1"! The last seven to be eaten appear to have been put out and eaten on the 2nd of January.

Incidentally, the implied idea that the results from birds feeding at a feeding station, where they were used to finding quantities of food, is somehow more natural and therefore more valid than Dr. Brower's experiments is highly questionable. So also is the statement that the birds "could have lived off a bounteous Iowa summer, or the food in the bird feeders." The idea that when birds are raising nestlings there is always an abundance of food is refuted by a great deal of ecological work, (for example see Lack, 1954).

Both the objections to the theory of mimicry and warning coloration and the experiments presented by Petersen (1964) are not of the sort which would allow one to arrive at a competent conclusion on the validity of the theories.

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