Mimicry: An interface between psychology and evolution

James Mallet

Department of Biology, Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE, United Kingdom

Every now and then, a new technique allows major breakthroughs to be made on a hitherto intractable problem. In this issue of PNAS, Leena Lindström and colleagues (1) have shed light on long-standing controversies in warning color and mimicry. They have achieved this through experiments on the behavior of wild-caught birds (great tits, *Parus major*), using their ingenious "novel world" setup, a modification of that originally introduced by Rauno Alatalo and Johanna Mappes in 1996 (2).

Leena Lindström and colleagues have shed light on long-standing controversies in warning color and mimicry.

The understanding of mimicry seems to me to have developed in a particularly jumpy manner. Mimicry is arguably the oldest Darwinian theory not attributable to Darwin. After reading the recently published *On the Origin of Species*, Henry Walter Bates began to realize that unrelated Amazonian butterflies not only resembled each other in any locality, but also changed color patterns from place to place, while preserving the resemblance. This "mimicry" could not be due to phylogenetic inertia; it must be adaptive. (As an aside, the term "mimicry" was coopted from pre-Darwinian days. Analogies were presumed to be the "osculations" that connected Quinarian rings of created taxa into a coherent whole. In his Wisdom, God was thought to have arranged organisms in rings of five species connected by homologies, and linked to other rings by these analogies. Perhaps it is no accident that we still use the peculiar term "mimicry rings," to mean groups of species that are connected by analogous resemblances.) Bates then proposed his now famous evolutionary explanation (3), that nonpoisonous "Leptalidae" (now Pieridae: Dismorphiinae) adaptively resemble unpalatable species, models, in the "Danaoid Heliconidae" (now Nymphalidae: Ithomiinae). If sampled by a predator, the palatable mimics will discourage future attacks, and may enhance attacks on the model; thus, Batesian mimicry can be parasitic.

Bates also noticed that some *Heliconius* (in the "Acraeoid Heliconidae," now Nymphalidae: Heliconiinae) also mimicked Ithomiinae, even though they clearly had the aromatic smells of distasteful species, and even though other *Heliconius* were themselves the objects of mimicry (3). Essentially, Bates discovered an early version of Müllerian mimicry, or mimicry between pairs of distasteful species, although he attributed this mainly to parallel adaptation by both species to abiotic conditions. In 1879, Fritz Müller (4) used a mathematical argument, perhaps the first in evolutionary ecology (excepting Malthus', of course), to show that pairs of unpalatable species gained mutualistic benefits from resemblance. By sporting the same color pattern, individuals lost during predator education would be shared between the two species so that the mortality per capita was lower in each. Meanwhile, and rather illogically, Wallace's adaptive hypothesis of warning color (later called aposematism) was developed only after mimicry was used to explained resemblance between warningly colored species. Darwin in 1867 was developing his theory of sexual selection to explain bright colors in animals, and had come across red-and-black-striped sphinx caterpillars that, as larvae, would not have been influenced by sexual selection. Wallace argued that bright colors were adaptive because they warned predators not to attack distasteful prey (5). A few details were left to be tidied up, but these basic ideas about mimicry and warning color were thereafter accepted, at least by Darwinists, until the late 20th Century.

In the 1950's, the first experimental tests of predator psychology (as opposed to mere observations of natural behavior) relevant to mimicry were done; at the same time, a reaction against group selection led to a questioning of these and other arguments involving overall benefit to species. Even though Wallace was probably correct about the ultimate benefits of warning color to the population, warning signals could not simply evolve from crypsis, unless rare aposematic morphs within species could overcome the disadvantage of rarity that causes Müllerian mimicry (6). A variety of hypotheses were proposed in which grouping, particularly of close kin (6, 7), would allow the local frequency to rise above a frequency-dependent selection threshold. Others regarded individual selection as more likely, and proposed that the threshold frequency could be overcome if attacks were not fatal and if conspicuous prey induced predator neophobia, as well as being more memorable (8).

This debate about warning color is well known to most evolutionists, but a recent surge of interest in warning color shared between unpalatable species (i.e., Müllerian mimicry) is perhaps less well known. Müllerian mimicry has often been under attack over the years, but belief in the theory on the whole has prevailed. However, the new debate seems to cast the most serious doubt yet on the Müllerian hypothesis, and centers around the work of Mike Speed. Speed argues that mimicry theory has ignored Pavlovian models of predator psychology. In Speed's theory, mildly unpalatable species may, by mimicking highly unpalatable species, increase the overall attack rate on the model so that Müllerian mimicry may be parasitic, or "quasi-Batesian" (9), in species of unequal unpalatability. Speed is a former student of John R. G. Turner, who is well known for his work on mimicry and *Heliconius* butterflies. Turner himself has frequently rebutted earlier critiques of classical Müllerian mimicry (10), but is now convinced by Speed's arguments that parasitic mimicry may occur between pairs of unpalatable species. To Speed and Turner, the new form of mimicry can explain anomalous phenomena in Müllerian mimicry,

---

See companion article on page 9181.

www.pnas.org/cgi/doi/10.1073/pnas.171326298

such as polymorphisms in apparently unpalatable species (11).

This new controversy centers on a beguilingly simple assumption made by Müller. He supposed that predators require a certain number (n) of unpalatable individuals during a season to learn their color pattern. Müller (4) showed that this requirement always led to a mutualistic advantage, even though the advantages were lopsided, with the relative fitness gains (g_1, g_2) due to mimicry to each species being given by the inverse square of the relative abundances (a_1, a_2) of the two species (i.e., $g_1/g_2 = a_2^2/a_1^2$). Müller's relative benefits were soon shown to be an approximation (12); the correct formulation shows that the benefits are even more lopsided than in Müller's prediction: $g_1/g_2 = a_2^2(1 - n/a_2)/a_1^2(1 - n/a_1)$. Finally, the same number eaten (n) results only if the two species are equally unpalatable. With unequal palatabilities, there will be different numbers of each species (n_1, n_2) lost in the absence of mimicry, and the relative gains for mimicry (12, 13) in the two species will be: $g_1/g_2 = a_2^2n_1^2(1 - n_2/a_2)/a_1^2n_2^2(1 - n_1/a_1)$. A way of understanding this is that fitness benefits depend on the "protectedness" (a_i/n_i) or "dose" provided by each species. If a species is highly protected either by unpalatability, because the numbers lost during predator learning (n_i) are low, or because of great abundance (a_i), then it will benefit very little from mimicry. On the other hand, a rare or more mildly unpalatable species will benefit much more strongly from mimicry with a highly protected species, by more than the square of the ratio of protectedness. But the benefits of mimicry to both unpalatable species are still always positive and mutualistic. Müller's theory is useful for interpreting not only the ultimate benefits of Müllerian mimicry, but also for modeling warning color or mimicry at intermediate stages of evolution. The form of frequency-dependent selection should be highly nonlinear, hyperbolic in fact (14).

If a species is highly protected either by unpalatability, because the numbers lost during predator learning are low, or because of great abundance, then it will benefit very little from mimicry.

However, this entire body of warning color and mimicry theory is built up from Müller's original assumption that predators learn by taking a fixed number n_i of a given unpalatable prey type, whatever its density. This might well be an oversimplification, and Speed and others have suggested that more realistic Pavlovian models will give quite different results. For instance, learning and forgetting might instead lead to an asymptotic balance consisting of a constant fraction of unpalatable prey attacked at any prey density. Two species that differ in unpalatability would then differ in their asymptote. If they became indistinguishable mimics, the combined asymptote would become an average of the attack rates on each species. The more palatable species would benefit from mimicry because the asymptote is lower than if it were a nonmimic, whereas the less palatable species would suffer greater per capita mortality. Hence, the mimicry is parasitic, or quasi-Batesian (9, 11).

It seems as though it should be simple to design experiments to test these ideas about predator learning. However, most experiments on the psychology of learning use highly standardized tests, and rarely assay varying densities of items to be memorized. Standard psychological theories of learning do not provide the understanding we need in the evolution of mimicry. Impressive field experiments, in contrast, can show strong selection for Müllerian mimicry (15), but do not distinguish between different models of learning. Potentially more relevant experiments on the learning components of mimicry have been carried out on chicks and wild birds, using pastry baits made unpalatable with quinine. These experiments have produced mixed results: some suggest a selective advantage for rarity (16) or quasi-Batesian mimicry (17), whereas others demonstrate frequency dependent selection against rare unpalatable forms, as expected under Müller's theory (18). All could be criticized on the grounds that high densities of pastry baits are too unrealistic as prey, so that abnormal predator behavior results. Also, these experiments never tested the predators on more than a pair of prey densities.

The new work (1) is much more realistic. In this "novel world" experiment, wild great tits are brought into captivity and trained to feed on novel prey. Each prey item is in fact a 1-cm^2 white paper envelope containing a tiny, but evidently tasty 8-mg almond fragment, which can be made unpalatable with quinine. Each packet bears a symbol: black crosses, which are cryptic against similar symbols on the floor of the arena, or black squares, which stand out visually and are used as aposematic signals. The experiments have a number of advantages over previous work. (*i*) The birds are naturally inquisitive insectivores, and learn difficult tasks in captivity. (*ii*) The birds are caught in the wild, where they are abundant enough for the experiments to be well replicated (84 birds were used here). (*iii*) Black crosses and squares are completely novel to the birds, which distinguish symbols easily but show no inherent bias (19). (*iv*) Finding and unwrapping the paper packets is sufficiently tricky to provide a handling cost analogous to making a mistake and attacking an unpalatable insect prey. (*v*) The foraging task is complex: birds must search a 57-m^2 arena containing around 27,000 cryptic prey symbols, on which only 200 palatable and unpalatable almond packets are placed. Around 130 symbols must be scanned by each bird for every prey actually taken. (*vi*) The unpalatable prey are presented at three separate densities, both as singletons, and (*vii*) in "gregarious" clumps of four.

As expected from Müller's theory, the experiments show that neophobia does not give rare unpalatable morphs an advantage. [An earlier "novel world" experiment that might be taken as support for neophobia (19) is explicable if birds merely ignored novel packets while foraging for cryptic packets they had already learned were palatable.] But the results also appear to disprove the simplistic Müllerian hypothesis of learning induced by a fixed number of prey in at least two ways. (*i*) Clumped aposematic prey are avoided much more strongly than solitary prey presented at the same density, by a factor of about two. It is possible that proximity of the same pattern enhances learning, or perhaps the birds generalize during learning most readily to nearby examples of the same pattern. In either case, novel warning patterns are less strongly attacked in gregarious than in solitary prey, and the simplistic Müllerian dose effect is disproved. (*ii*) The per capita attack rate on aposematic prey decreases with increasing density, as is expected under Müllerian theory, but the total number attacked goes up, which is not. However, Müller's theory is not as convincingly disproved here because learning is almost certainly not reaching completion after 2 days of trials (18): the birds had each eaten about 17 unpalatable solitary prey after two trials at the highest aposematic prey densities (13% of the total), but only about 4 at the lowest densities (25% of the total).

These experiments were performed only with highly unpalatable prey, and are not direct tests of Speed's unconventional mimicry theory (9, 11). However, a monotonic decline in attack fraction with increasing experience and unpalatable prey density, rather than an asymptotic attack fraction, seems evident from the data: on the second trial day each bird attacked less than three of the unpalatable prey at high density (about 5%, compared with 22% on the first trial), and less than a single unpalatable prey at the lowest density (about 6%, compared with 50% on the first trial). They are therefore quick learners! Classical Müllerian learning with an approximately zero attack fraction after a whole season would seem to be nearer to the mark than "Pavlovian" learning with a nonzero attack fraction asymptote, even though the numbers required for learning may increase with density. An earlier experiment with wild birds and pastry baits (18) also showed higher attack fractions at lower densities. Therefore, I believe that simplistic number-dependent selection will ultimately be disproved; however, near-zero attack asymptotes can only lead to conventional, mutualistic Müllerian mimicry.

Will we ever have a complete, unassailable theory of warning color and Müllerian mimicry? I don't know, but I believe the ingenious "novel world" experiments (1, 2, 19) are the best yet designed to investigate the psychological interface of this unsolved evolutionary problem.

1. Lindström, L., Alatalo, R. V., Lyytinen, A. & Mappes, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 9181–9184. (First Published July 17, 2001; 10.1073/pnas.161071598)
2. Alatalo, R. V. & Mappes, J. (1996) *Nature (London)* **382,** 708–710.
3. Bates, H. W. (1862) *Trans. Linn. Soc. London* **23,** 495–566.
4. Müller, F. (1879) *Trans. Entomol. Soc. London* **1879,** *xx–xxix*.
5. Fleischer, R. C., Rothstein, S. I. & Miller, L. S. (1991) *Condor* **93,** 185–189.
6. Harvey, P. H. & Greenwood, P. J. (1978) in *Behavioural Ecology*, eds. Krebs, J. R. & Davies, N. B. (Blackwell Scientific, Oxford), pp. 129–151.
7. Guilford, T. (1990) in *Insect Defenses. Adaptive Mechanisms and Strategies of Prey and Predators*, eds. Evans, D. L. & Schmidt, J. O. (State Univ. of New York Press, New York), pp. 23–61.
8. Järvi, T., Sillén-Tullberg, B. & Wiklund, C. (1981) *Oikos* **37,** 393–395.
9. Speed, M. P. (1993) *Anim. Behav.* **45,** 571–580.
10. Turner, J. R. G. (1984) in *Symposia of the Royal Entomological Society of London 11, The Biology of Butterflies*, eds. Vane-Wright, R. I. & Ackery, P. R. (Academic, London), pp. 141–161.
11. Speed, M. P. & Turner, J. R. G. (1999) *Biol. J. Linn. Soc.* **67,** 281–312.
12. Blakiston, T. & Alexander, T. (1884) *Nature (London)* **29,** 405–406.
13. Mallet, J. (2001) *Evol. Ecol.* **13,** 777–806.
14. Mallet, J. & Joron, M. (1999) *Annu. Rev. Ecol. Syst.* **30,** 201–233.
15. Kapan, D. (2001) *Nature (London)* **409,** 338–340.
16. Greenwood, J. J. D., Wood, E. M. & Batchelor, S. (1981) *Heredity* **47,** 27–34.
17. Speed, M. P., Alderson, N. J., Hardman, C. & Ruxton, G. D. (2000) *Proc. R. Soc. London Ser. B* **267,** 725–731.
18. Greenwood, J. J. D., Cotton, P. A. & Wilson, D. M. (1989) *Biol. J. Linn. Soc.* **36,** 213–226.
19. Lindström, L., Alatalo, R. V., Lyytinen, A. & Mappes, J. (2001) *Proc. R. Soc. London Ser. B* **268,** 357–361.