EVOLUTIONARY BIOLOGY

Catfish mimics

Mutualism can be a double-edged sword if the animals concerned also compete for food. This may explain the discovery that mimic catfish in the Amazon rarely engage in mimicry with related species. SEE LETTER P.84

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Müllerian mimicry in the warning colours of unpalatable butterflies has been well known since its discovery in the nineteenth century[1,2]. It is beneficial because noxious prey that share warning colours also share the cost of educating predators about their unpalatability[3]. Müllerian mimicry is now known to occur in many other animal groups, including millipedes[4] and poison dart frogs[5].

Below the surface of the Amazon, on whose banks Henry Walter Bates made the first discovery of butterfly mimicry, a new example of Müllerian mimicry has just been discovered by Alexandrou *et al.* (page 84 of this issue)[6]. The authors studied armoured catfish in the subfamily Corydoradinae, which swim in multispecies shoals and are defended by retractable venomous spines and bony plates. Across the Amazon basin, it turns out that up to three unrelated species with strikingly similar colour patterns may coexist in any one locality. The bold, mimetic patterns of these fishes (Fig. 1) undoubtedly serve to warn predators away, as recently demonstrated in an unrelated African catfish genus[7].

Bates's discovery of mimicry stemmed, in part, from his finding that local colour patterns converged, but more importantly from the fact that butterflies "... are found all to change their hues and markings together, as if by the touch of an enchanter's wand, at every few hundred miles" (H. W. Bates, quoted in ref. 2). This striking and repeated phylogenetic pattern of convergence across the Amazon clinched the evolutionary hypothesis of mimicry: species differ in colour from related forms in distant areas, while at the same time mimicking unrelated species locally. A spatial pattern of local convergence and geographical divergence is quite general in other systems of Müllerian mimicry[4,5], as well as in the catfish studied by Alexandrou and colleagues[6].

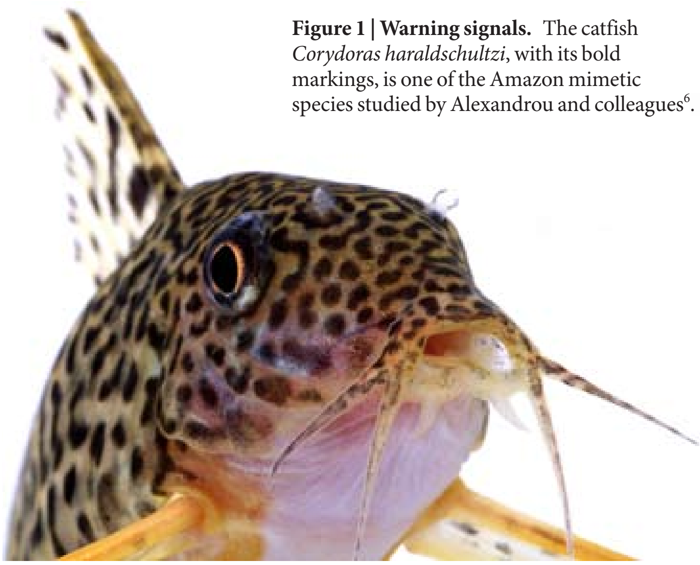

Figure 1 | Warning signals. The catfish *Corydoras haraldschultzi*, with its bold markings, is one of the Amazon mimetic species studied by Alexandrou and colleagues[6].

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However, these patterns are even stranger than they first appear. Mimicry explains why species converge, but cannot explain why species also diverge into multiple mimicry 'rings' in many Müllerian mimetic systems. Diversity is often local: in armoured catfish there may be up to six mimicry rings in some regions[6] (although they rarely swim together), and in *Heliconius* butterflies it almost seems as if species undergo adaptive radiation[8] into different mimicry 'niches'. Why should new mimicry rings ever evolve, given that mimicry itself should prevent divergence? Slow neutral change of pattern in geographically distant regions might explain some of the diversity. However, although distance can prevent the swamping effect of gene flow, it cannot drive divergence directly.

Consider the diversity of mimicry in its overall ecological context. Müllerian mimicry is only one of many interactions among species. It provides an example of a positive interaction, or mutualism. To explain species coexistence, we must understand how this mutualism combines with negative interactions, such as competition. Competitively dominant species typically exclude inferior competitors. However, recent theory shows that if inferior competitors develop mutualisms with dominant species, this can allow them to invade and coexist, permitting higher diversity than without mutualism[9]. In the ithomiine butterflies, the classic group of Müllerian mimics[1,2], this may explain why some closely related species that use similar resources are also close mimics[10].

Now imagine a superior competitor associated with multiple, mimetic mutualists. This dominant species reduces predation and enables mimics and inferior competitors to coexist, inevitably leading to some cost to itself[9]. In the first ever mathematical evolutionary theory, Müller[2] proved that the relative advantage of mutualistic mimicry to each species is roughly proportional to the inverse square of relative abundance: in other words, rarer mimics benefit very much more from Müllerian mimicry than commoner mimics. A commoner species could suffer a considerable amount of resource competition if it is helping multiple co-mimics, while benefiting little from mimicry itself.

Therefore, a superior competitor species that escapes its ancestral mimicry could rid itself of some competitors. It could then spread at the expense of a less fortunate related form that continues to help competitors through mimicry. This idea cannot explain how the required speciation and mimicry divergence was initiated; but given that it did (and does) happen, it would have the consequence that dominant species would escape pesky competitors. This would stabilize the diversification of the mimicry we observe in nature.

The Amazon catfish[6] seem to corroborate the escape idea. More than 90% of mimics differ from co-mimics in snout length and stable nitrogen isotope content, both indicators of diet: these catfish seem not to compete for resources with co-mimics. Typically, co-mimics are also unrelated. Closely related catfish, by contrast, are usually similar in terms of snout morphology and diet, and tend not to be co-mimics. Escape from mutualistic mimicry could similarly help to explain the 'adaptive radiation' of *Heliconius* butterfly mimicry[8].

Nature is, however, full of contrasts. In unrelated venomous catfishes from Africa's Lake Tanganyika, and in ithomiine butterflies, mimics are often closely related and occupy similar habitats[7,10]. Escape from potentially onerous mutualism has not always occurred. Perhaps resource competition is ameliorated in some other way; or perhaps the dominant species in each ring is unlucky and has simply been unable to escape the resource pressure exerted by the mimetic mutualists that it unwittingly saves from extinction. Additional theoretical and experimental studies are needed.

Meanwhile, Alexandrou and colleagues' findings[6] in catfish show that mimicry is still contributing fundamental ideas to ecological and evolutionary biology, 150 years after its discovery. ■

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