



## How Did the Cuckoo Get Its Polymorphic Plumage?

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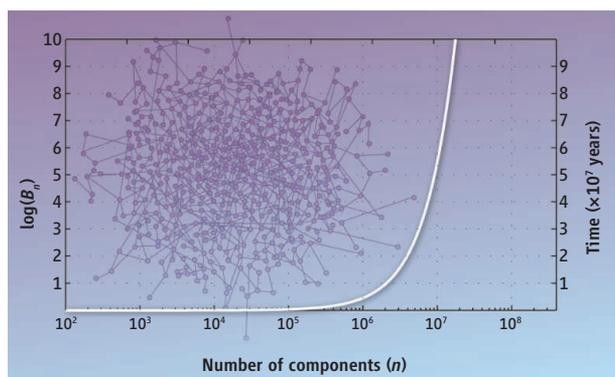
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synapse—the presynaptic terminal has an estimated 1000 distinct proteins. Fully analyzing their possible interactions would take about 2000 years. Or consider the task of fully characterizing the visual cortex of the mouse—about 2 million neurons (5). Under the extreme assumption that the neurons in these systems can all interact with each other, analyzing the various combinations will take about 10 million years (see the figure), even though it is assumed that the underlying technology speeds up by an order of magnitude each year. This conclusion is not substantially affected if only a fixed fraction (e.g., 0.001%) of all interactions need to be characterized, if the initial technology is better and could analyze 100 times as many interactions, or if the technology scales annually by two orders of magnitude instead of one. We know from proteomics that not all proteins interact with each other. Likewise, we know from neuroanatomy that brains are not fully interconnected but primarily make local synapses. However, the number of possible interactions in both cases is still on the order of  $10^5$  or more, which implies an interactome that is astronomically large.

Given the large number of components that cannot be averaged away, any possible technological advance is overwhelmed by the relentless growth of interactions among all components of the system. It is not feasible to understand evolved organisms by exhaustively cataloging all interactions in a comprehensive, bottom-up manner. More is needed.

Allen and Greaves (6) recently introduced the metaphor of a “complexity brake” for the observation that fields as diverse as neuroscience and cancer biology have proven resistant to facile predictions about imminent practical applications. Improved technologies for observing and probing biological systems has only led to discoveries of further levels of complexity that need to be dealt with. This process has not yet run its course. We are far away from understanding cell biology, genomes, or brains, and turning this under-

**How long will it take?** The logarithm of Bell’s number (left axis) and the upper bound on the time it takes to fully analyze all possible partitions of the system (right axis) are shown as a function of the number of components (proteins or cells).

standing into practical knowledge. The complexity break is very apparent in the figure.

Engineered systems can contain millions (airplanes) or billions (microprocessors) of components. Yet these are purposefully built in such a manner to limit the interactions among the parts to a

small number. For instance, design rules for the layout of integrated electronic circuits impose a minimum distance between wires and other components to eliminate coupling, and separate power supply from computing, and computing from memory. None of this is true for nervous systems. It is this reduction in the interactome that allows engineers to build large and robust systems where the complexity brake does not apply.

The complexity brake could be loosened if a supra-individual level of components were discovered. If groups of components behave as a single module, the effective number of interactions that need to be analyzed would drop precipitously. If a minicolumn of about 1000 cortical neurons proves to be the relevant module to understand the cerebral cortex (7),  $t_n$  for the mouse visual cortex reduces from millions of years to five millennia. If the interactions among minicolumns could be further

causally reduced to interactions among cortical columns (8), where each column consists of about  $10 \times 10$  minicolumns, the goal to fully understand the visual cortex could be reached within 6 years (assuming technologies increase by a factor of 10 each year).

The discovery of modular, hierarchical structures that capture the behavior of complex systems in a causal manner (9) is essential to speed up solving these challenging problems. This emphasizes the need to develop heuristic methods to discover modules (10). For if appropriate modules cannot be found, understanding of life will escape us.

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#### ECOLOGY

## How Did the Cuckoo Get Its Polymorphic Plumage?

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As reed warblers learn to avoid the threat from cuckoos resembling sparrow hawks, they remain under threat from differently colored cuckoos.

One hundred and fifty years ago, the English naturalist Henry Walter Bates first developed the theory of mimicry (1). Based on his field observations in the Amazon, he argued that the uncanny likeness of unrelated butterflies is an evolutionary adaptation whereby edible butterflies avoid predation by imitating the coloration of

venomous butterfly species without paying the cost of arming themselves. Such “Batesian mimicry” is a dynamic parasitic game between three players, in which a harmless species (the mimic) escapes predation by imitating the warning signals of harmful species (the model) that a shared predator (the dupe) has learned to avoid. On page 578 of this issue, Thorogood and Davies show that Batesian mimicry dynamics also apply to the evolutionary game between cuckoos and their hosts (2).

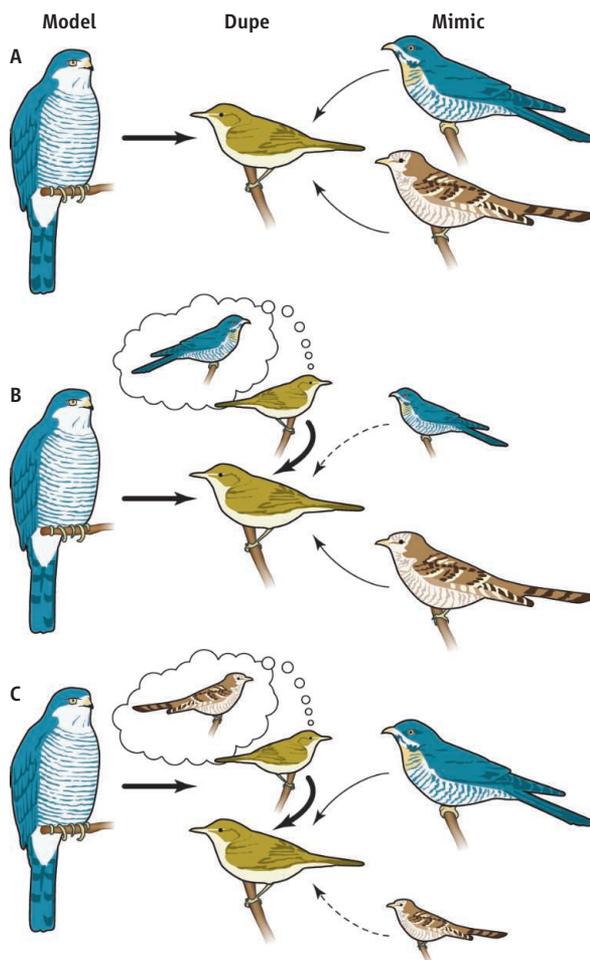
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The key selective mechanism in the Batesian mimicry game is the predator's ability to learn, generalize, and remember (3, 4). The predator learns by trial and error to avoid the harmful species and to generalize the bad experience of the model as prey to the mimic. If mimics appear in high numbers, the predator's good experience with the mimic as prey may decrease the survival of mimics and models, because both will be seen as harmless. This mechanism results in greater protection for rare mimics than for common ones. Because of this "negative frequency-dependent selection" (5), mimics are usually less numerous than models. To increase their population size, imitators have two options. They can imitate a model that is so dangerous that dupes do not dare to touch the imitators (6, 7), or they can evolve multiple forms (polymorphism), enabling them to mimic several different models (8).

Cuckoos (Cuculidae) are nest parasites that infiltrate a nest, remove one of the eggs, and replace it with their own egg. Nest parasitism enables cuckoos to have their young raised by host birds and frees them from the costs of parenting. As hosts have evolved to defend their nests from cuckoos, so cuckoos have evolved counteradaptations to overcome the hosts' defense. One trick that allows common cuckoos (*Cuculus canorus*) to approach the nest of their host is by mimicking a sparrow hawk (*Accipiter nisus*), one of the most dangerous predators for the host birds. Cuckoos that resemble hawks are not mobbed by their hosts and can thus more easily approach the nest to lay their eggs (9).

But why do European common cuckoos have polymorphic plumage? Males are always gray, but females can be either gray, like the male, or rufous (brown) (see the figure). This could suggest that some females are imitating other avian predators such as kestrels or merlins (10). Plumage polymorphism is very common in other cuckoo species too, and all polymorphic cuckoo species are brood parasites (11).

Is plumage polymorphism widespread in this group because cuckoos evolved to resemble several different models due to negative frequency-dependent selection? This remains to be tested, but as we learn from the experiment by Thorogood and Davies, polymorphism among mimics can be maintained with a mechanism that is novel to mimicry literature.



Like many animals, birds can observe and learn from other birds (12). Reed warblers, the most important host species for cuckoos in the UK, learn from their neighbors how to defend their nests against cuckoos. Individuals that have observed how their neighbors have mobbed a cuckoo are braver to approach, mob, and defend their nests against the parasite, thereby enhancing their reproductive success (13).

Thorogood and Davies now show that a reed warbler that has seen its neighbor mob a gray cuckoo will increase its mobbing against gray cuckoos but not against brown cuckoos, and vice versa. If this social information about cuckoo presence in the area spreads too widely, the more common morph can lose its mimetic advantage. This gives the rarer type a chance to lay its eggs in warbler's nests because the hosts do not recognize it.

The details of this hawk-cuckoo-warbler game are different to Batesian mimicry, but they share a core principle. In systems where appearance is used as deception, negative frequency-dependent selection favors polymorphism in the cheating party. In contrast to classical Batesian mimicry, the hawk (model)

**The advantages of mimicry.** Thorogood and Davies show that cuckoos that mimic sparrow hawks increase their chance to approach the warbler's nest and lay their eggs (A). The deception can break down when the warblers learn to discriminate between gray cuckoos and sparrow hawks and spread this information to others (B). This gives an advantage to the rufous cuckoos, which should become more numerous as a result. However, when neighbors warn about rufous cuckoos, the gray morph gets an advantage (C).

does not benefit from the discriminative learning of the dupe, and it is unlikely that the mimicry of the cuckoo harms the hawks. It remains to be shown whether the information sharing among dupes reported in (2) could also be applied to the evolution of Batesian mimicry. Thus far, the evidence suggests that predators are more likely to pick up social information on what to eat rather than what to avoid (14).

Thorogood and Davies's findings show that, 150 years after its discovery, mimicry still contributes fundamental insights into ecological and evolutionary biology. It remains unclear why rufous cuckoos are not increasing in numbers in the UK, despite their rarity advantage. Perhaps the rufous cuckoo is not as good a predator imitator as the gray cuckoo, and thus cannot fool the hosts as well. Or perhaps the rufous females have some physiological or reproductive disadvantages compared to the gray females. The answer may lie in locations, like Hungary (15), where rufous cuckoos are more numerous than in the UK.

Another fascinating question is why individual reed warblers vary so much in their responses (2) and risk-taking toward the hawk and the parasite. And how many individuals must learn to discriminate between the cuckoo and the hawk and share this information with others to maintain the plumage polymorphism in the cuckoo?

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