EVOLUTIONARY BIOLOGY

Life imperfectly imitates life

Some species evolve to resemble another species so as to protect themselves from predation, but this mimicry is often imprecise. An analysis of hoverflies suggests why imperfect imitation persists in the face of natural selection. SEE LETTER P.461

DAVID W. PFENNIG & DAVID W. KIKUCHI

One hundred and fifty years ago, the English naturalist Henry Walter Bates[1] discovered a phenomenon that he regarded as "a most powerful proof of the theory of natural selection". Charles Darwin and Alfred Russel Wallace, who had proposed natural selection as the engine of evolution only a few years earlier, agreed. Indeed, Darwin[2] considered Bates's manuscript to be "one of the most remarkable and admirable papers I ever read".

Bates had uncovered a spectacular type of adaptation, now known as Batesian mimicry[3], in which a species (the mimic) that is edible to predators evolves to resemble a conspicuous, inedible species (the model) that predators avoid. These lookalikes are selectively favoured, Bates argued[1], because predators confuse them for the inedible model and thereby avoid them. This idea was so persuasive that Batesian mimicry is still widely used to illustrate the power of natural selection for producing adaptations[3,4]. However, mimics are often poor replicas of their model, and this inexact mimicry poses a challenge for evolutionary theory[3]. On page 461 of this issue, Penney *et al.*[5] discuss possible explanations for why mimics are frequently imprecise.

As Penney and colleagues describe, several non-mutually exclusive hypotheses have been proposed to explain imperfect mimicry. They include: the 'eye-of-the-beholder' or sensory-limitation hypothesis, which asserts that imprecise mimicry is an artefact of human perception; the 'jack-of-all-trades' or multimodel hypothesis, which posits that imperfect mimics persist because they are under selection pressure to resemble more than one model; and the 'kin-selection' hypothesis, which asserts that imperfect mimicry is maintained because it provides benefits for genetically related individuals. Specifically, if mimics are imperfect, then predators will be more discriminatory and occasionally spare a mimic by mistaking it for a model. This will also spare relatives that share the same imperfect trait.

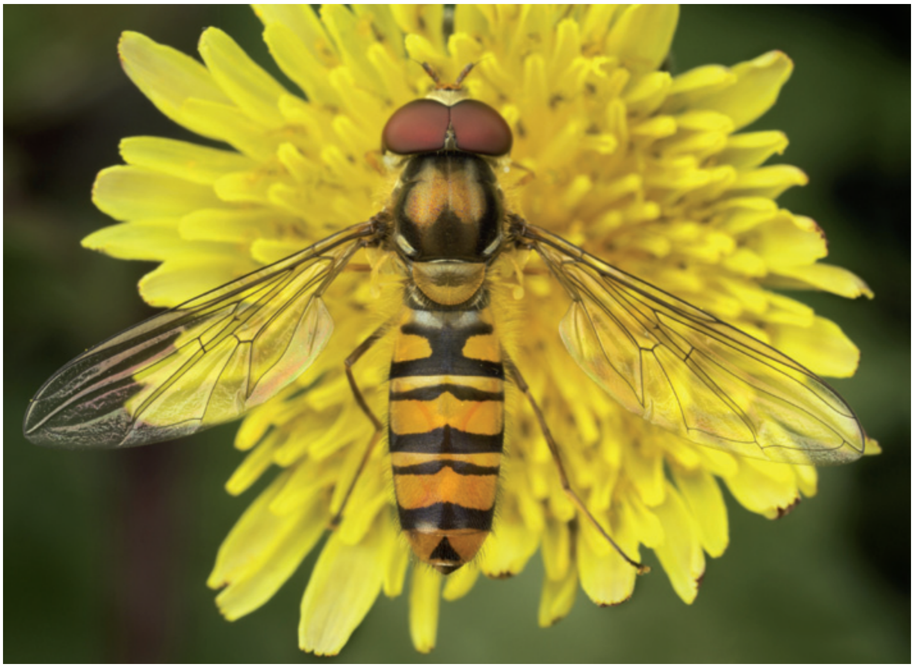
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Figure 1 | A fly in wasp's clothing. The harmless marmalade hoverfly, *Episyrphus balteatus*, shown here, resembles stinging wasps. Although some species of hoverfly closely resemble wasps or bees, others are poor lookalikes. Penney and colleagues[5] show that the lower selection pressures that come with decreasing abundance and small body size may provide the explanation for how such imprecise mimicry can persist.

Another theory to explain imperfect mimicry is the 'relaxed-selection' hypothesis, which holds that there is little selective benefit in refining mimetic resemblance beyond a certain point, for example if the model is common or especially noxious. Finally, the 'constraints' hypothesis proposes that either imperfect mimics lack the genes to produce refined mimicry, or that a selective trade-off exists between predator-mediated selection favouring more precise mimicry on the one hand and other agents of selection (such as mate choice) favouring divergence on the other.

Until now, no study had rigorously evaluated these multiple hypotheses within a single system. Penney and colleagues[5] did precisely this by comparing the degree of mimicry in dozens of species of hoverfly. Mimicry is a dominant feature of this large family of harmless Diptera (Fig. 1). About 5,600 species have been described, at least a quarter of which resemble stinging wasps and bees (Hymenoptera)[6]. Although some hoverflies are remarkably accurate mimics, converging both morphologically and behaviourally on their hymenopteran model, many others seem to bear poor resemblance[6]. This variation in mimetic fidelity makes hoverflies ideal for studying imperfect mimicry.

The authors report that birds (which are hoverfly predators) and humans seem to agree on the resemblances between hoverflies and hymenopterans. Thus, in this case, the eye-of-the-beholder hypothesis does not hold. Furthermore, Penney and colleagues' statistical analysis reveals that the mimics' characteristics do not fall somewhere between those of different models, so the jack-of-all-trades hypothesis receives no support either. The kin-selection hypothesis predicts that mimetic precision should decrease with an increasing abundance of mimics, but the authors observed the opposite trend. In fact, this finding is consistent only with the constraints and relaxed-selection hypotheses. In addition to predicting that mimics' precision should increase with their abundance, these two hypotheses predict that mimetic precision should increase with the body size of the mimic, and this is exactly what the authors find.

To understand how the relaxed-selection hypothesis applies when both the abundance and body size of mimics increase, let us consider the problem of discriminating between tasty mimics and nasty models from the predators' perspective. If not all mimics are equally deceptive, a predator must take risks when attacking its prey — if it strikes a mimic, it will reap more reward than regret. When mimics are abundant, the likelihood of attacking a model by mistake decreases. In such conditions, predators should be willing to sample all but the best mimics, which will push selection towards more precise mimicry.

By the same token, when mimics have a larger body size, their potential benefit to predators is greater (larger prey are generally more profitable for predators), so there will be greater selection pressure on them than on their smaller counterparts to become better mimics. Although other studies have found that mimetic precision increases when mimics are abundant[7], Penny and colleagues' demonstration that this pattern also holds when mimics increase in size is an elegant affirmation of an old idea.

We still do not know whether hoverfly mimicry is imprecise because of an absence of selection for refinement once mimicry is 'good enough' (as in the relaxed-selection hypothesis), or whether there is active selection pressure against further refinement because of the costs of producing better mimicry (as in the constraints hypothesis). For example, constraints may be imposed by competition between mimics and their models (over shared resources[8] or reproductive opportunities[9]), which would favour divergence between them and, hence, imprecise mimicry[10]. Future studies are needed to tease apart these two hypotheses.

As we celebrate the 150th anniversary of Bates's discovery of mimicry[1], the topic continues to fascinate the public and scientists alike[3,4]. Penny and colleagues' findings help us to understand why selection sometimes produces precise mimicry, but often does not, and further clarification of this puzzle promises to provide additional insight into the evolutionary process. ■

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BIOLOGICAL PHYSICS

Swarming microtubules

An artificial system of microtubules propelled by dynein motor proteins self-organizes into a pattern of whirling rings. This observation may provide insight into collective motion in biological systems. SEE LETTER P.448

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The spectacle of animals moving en masse is arguably one of the most fascinating phenomena in biology. For example, schools of fish can move in an orderly manner, and then change direction abruptly or, if under pressure from a nearby predator, swirl like a vigorously stirred fluid. The non-living world also has examples of collective motion, in systems that consist of units ranging from macromolecules to metallic rods, or even robots. On page 448 of this issue, Sumino *et al.*[1] describe another, until now unobserved, example of such behaviour: the coordinated motion of hundreds of thousands of subcellular structures known as microtubules, which spontaneously self-organize into a lattice-like structure of vortices. When considered in the context of about half a dozen known universal classes of collective-motion pattern[2], this new structure poses challenges in terms of explaining how it can arise and its relevance to applications.

If two or more moving units such as self-propelled rods interact, their direction of motion is likely to change. When pairwise interactions dominate over multiparty ones, the process of two units approaching each other, then adopting a new direction and leaving the area of interaction, can be interpreted as a collision. In closed systems at equilibrium, such collisions conserve energy and momentum, whereas, for example, when two birds interact and decide which way to fly in the open expanses of the sky, the concept of conservation of momentum is not applicable.

Typically, local interactions between organisms result in a consensus: fish or mammals tend to adopt a common direction of motion. Such 'polar' interactions are widespread and have been observed even for bacteria[3] and locusts[4]. Nonetheless, it was a great achievement when, in 2010, two groups[5,6] observed motional patterns associated with polar interactions on a molecular scale — that is, for a huge number of actin filaments on a layer of immobilized myosin protein heads.

In addition to polar interactions, 'nematic' interactions also occur. In this case, if the directions of motion of two units approaching one another form an angle smaller than 90°, both parts will take the same direction after the approach. But if the units come towards one another from directions that differ by more than 90°, they will leave in opposite directions.

Sumino *et al.*[1] have constructed a biological system in which nematic collisions take place (Fig. 1). The authors achieved this by choosing an assay of moving microtubules propelled by modified motor proteins (one-headed dynein molecules) in which the microtubules cannot, for the most part, cross each other's trajectories and maintain their own trajectory's direction and curvature. The authors find that, in this setting, and for relatively high densities (typically 5 microtubules in 100 square micrometres), the moving microtubules self-organize into a semiregular pattern of whirling rings, or vortices, within which they move either clockwise or anticlockwise. Furthermore, as time goes on, the microtubules jump from one vortex to another and change their rotational direction. The size of the observed pattern is large compared with the 15-micrometre length of each microtubule: the system shows regularities on a millimetre scale.

One of the strengths of the present study is the authors' ability to explain the main features of the microtubules' intricate motion with a simple model. The model draws on studies aimed at understanding the rich, large-scale behaviour that results from simple bilateral interactions between point-like, self-propelled particles.

But Sumino and colleagues' results also prompt several questions. For example, is the observation that individual microtubules have a slight preference to rotate anticlockwise