EVOLUTION

Sexual Selection and Darwin's Mystery of Mysteries

Natural selection and mating preference for traits that signal adaptation to the local environment work together in a model of speciation.

Judith E. Mank

Darwin referred to the origin of species as "that mystery of mysteries" (*1*), and despite decades of study, evolutionary biologists still cannot agree on the underlying processes that have produced the great diversity of life around us. Most contentious of all has been the question of whether speciation can occur within a population (sympatrically). On page 1704 of this issue, van Doorn *et al*. (*2*) suggest that mating preferences can halt the movement of genes within a population. Their work gives credibility to the concept of sympatric speciation, which has long been the ugly duckling of evolutionary biology, and suggests that both local adaptation and sexual selection may play a far more important role in speciation than previously thought.

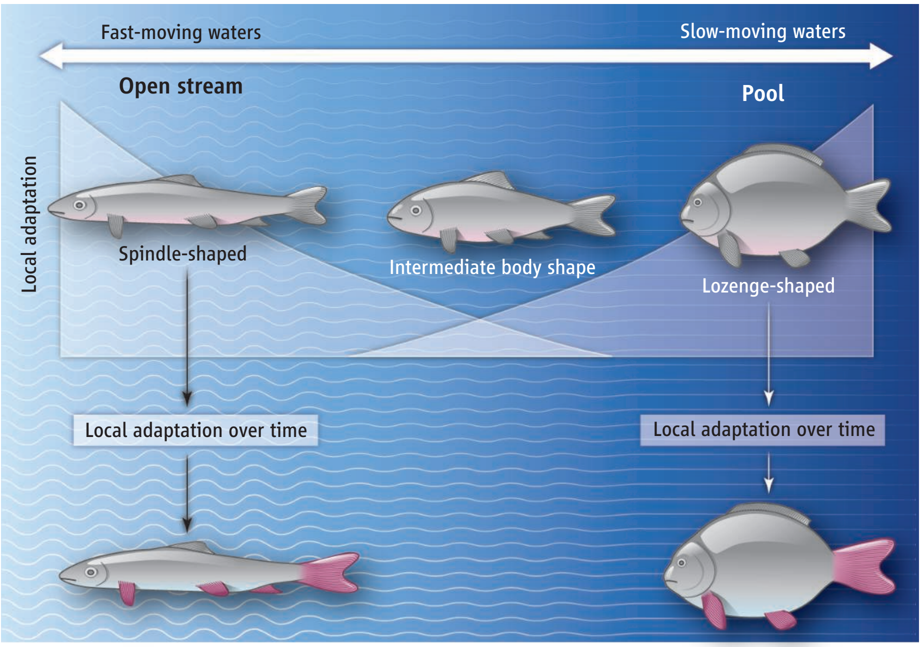
The traditional model of speciation is based on geographic isolation, in which a single population is divided by some geographic barrier, halting gene flow. Each group gradually changes over time, resulting in two separate and genetically distinct populations. This buildup of genetic incompatibilities will act as a barrier to the production of hybrid offspring, resulting in separate species (*3*). There is very little debate about whether speciation occurs by this allopatric model, as biogeography offers many striking examples. Island endemic species, such as Darwin's finches, diverged from mainland ancestral species after long periods of isolation (*4*). Pairs of morphologically similar species (geminate species) found in the Caribbean and Pacific oceans resulted after the Isthmus of Panama cut off gene flow in marine animals (*5*). What has remained unclear is whether this biogeographic model of speciation is the only, or even the dominant, mechanism by which new species originate.

Sympatric speciation is theorized to occur when selection pressures favor the extreme phenotypes at the expense of the intermediate ones (*6*), presumably due to local ecological variation. Without some mechanism to prevent mating between different phenotypes, individuals with the intermediate, unfavorable, traits will be created in every generation, and the subpopulations will be unable to diverge and adapt to their local ecologies. Because it has been difficult to build viable population genetic models of how gene flow might be curtailed in the absence of a geographic barrier, sympatric speciation has been regarded with a great deal of doubt by most evolutionary biologists ever since it was dismissed by Ernst Mayr (*7*) and Theodosius Dobzhansky (*8*).

Speciation has been shown to occur in areas that are too small to contain real barriers to gene flow (*9*), giving credence to the possibility of sympatric speciation. However, because the allopatric model is assumed to be true, demonstrating sympatric speciation requires irrefutable proof that daughter species were never geographically isolated—a burden of evidence that is seldom met. However, this does not mean that sympatric speciation is truly rare; rather, it is rarely proved beyond a doubt.

Van Doorn *et al*. provide a way forward by building on the observation that mating preferences can accelerate rates of speciation (*10*, *11*) and maintain local adaptations in the face of potential gene flow (*12*). The key to their advance is the incorporation of condition-dependent mate choice. Past attempts to model sexual selection and sympatric speciation were based on the idea that female mating preferences were heritable but arbitrary. In their treatment, the authors assume that male traits preferred by females are a product of local adaptation (*13*).

A male in good condition is well adapted to his local environment, and he demonstrates this with a condition-dependent male "ornament," such as bright fins in fish (see the figure). A female that prefers males with this ornament has a mechanism to identify and select locally adapted mates, increasing the probability that her offspring will also be well suited to the local ecology. Nat-



Sexual selection and local adaptation. In this example, fast-moving currents in open streams select for a fusiform-shaped body, whereas deeper shapes are advantageous in pools with slow currents. Intermediate shapes are poorly adapted to both environments. Locally adapted males are in good condition, and therefore exhibit long, bright fins that are the basis of female mating preferences. Over time, female preference for the condition-dependent sexually selected trait is strengthened; therefore, fewer individuals of intermediate body shape are generated. Eventually, genetic incompatibilities accrue and prevent the formation of fertile hybrids despite continuous and uninterrupted sympatry.

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ural selection and sexual selection act as a positive-feedback loop, strengthening both local adaptation and female preference for the sexually selected trait. This allows specialization even when the organisms overlap within a contiguous range. Over time, the populations diverge and ultimately form separate species.

Van Doorn *et al*. thus overcome a major stumbling block by providing a viable model of sympatric speciation. Species originating under this model may bear a certain signature that can be used to determine the prevalence of sympatric speciation via condition-dependent sexual selection. These sister species will specialize on distinct ecologies that overlap geographically. Further, males in all specialized daughter species will exhibit similar types of condition-dependent sexual ornaments. In early stages of speciation, mating preferences will be the primary barrier to gene flow, and the removal of this will result in the loss of local adaptation as the daughter populations interbreed and revert to the overall population mean. Finally, because condition-dependent sexually selected traits are a driver of speciation, clades with these ornaments will be more species-rich than clades with sexually selected traits that are condition-independent, or clades that lack male ornaments entirely.

This model may be used to test the prevalence of local adaptation and condition-dependent sexual selection in generating diversity, and provides a means to bring sympatric speciation in from the cold.

References

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PHYSICS

Universal Few-Body Binding

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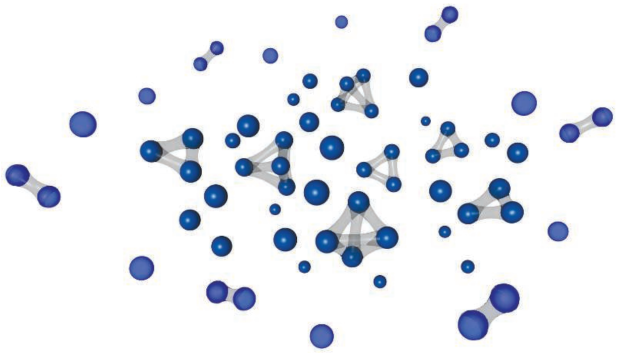
Cold atoms are providing insights into binding processes within systems of a small number of interacting particles.



Getting together. Universal three-body and four-body composites naturally form in an ultracold gas of lithium atoms with resonant interaction. They are detected as they decay into hot atoms and dimers (light blue), which rapidly leave the ultracold sample.

Predicting the binding rules of quantum particles is a formidable task. Even for as few as three particles, one would need to know precisely all the details of the mutual interactions among them. Notable exceptions have been predicted to arise if the interaction between the particles is very large, a condition where universal binding laws are expected to appear (*1*, *2*). Because no available physical system composed of atoms, nuclei, or even elementary particles was suitable to observe the phenomenon, these ideas have been mainly confined to theory. On page 1683 of this issue, Pollack *et al*. (*3*) present evidence for the presence of universal scaling laws simultaneously occurring for three- and four-body bound states in an ultracold atomic system. The observation confirms both old and new theoretical predictions, thus providing a fuller understanding of universal binding.

Since the early days of quantum mechanics, there has been great interest in deriving from first principles how particles bind together, particularly in the context of nuclear physics. A special solution to this problem was proposed for the case of three particles by Vitaly Efimov in 1970 (*1*). It was shown that if the interaction length between pairs of particles (the so-called scattering length) is much longer than any other length scale in the system, then the binding is universal—that is, it depends only on that length. In this regime, the three-body problem admits a whole series of states whose basic properties, such as the energy, follow geometrical scaling laws with a single scaling factor that can be derived analytically from the theory (*4*).

Early work on ultracold atomic systems has shown that a window to observe such binding behavior might exist (*5*), thanks to the possibility of engineering resonantly large scattering lengths between the atoms (*6*). This is achieved via the Feshbach resonances, whereby a magnetic field is applied to the sample to change its interaction properties. By means of such a technique, a universal bound state of three identical bosonic particles (an Efimov trimer) was observed in a sample of ultracold cesium atoms (*7*). There has since been a tremendous acceleration of the field, with major results in both experiment and theory. Notable examples are the observation in potassium atoms of two consecutive trimer states featuring a scaling very close to the one originally predicted by Efimov (*8*), and the prediction and experimental verification of universal scaling laws for four-body states (*2*, *9*).

In the ultracold lithium atom system studied by Pollack *et al*., the scattering length can be resonantly changed over a large range of values. By studying the rate at which the atoms are lost, two Efimov trimer states, each of them with two four-body states attached, that follow quite closely the universal scaling laws have been identified. The measurements are very precise, allowing the universal scaling factors to be nailed down. In addition, there are unexpected details in the observations that might provide new clues to verify the peculiar properties predicted by theory.

This is not the end of the quest for universal binding laws, however. The very precise work by Pollack *et al*., together with other recent measurements including those performed on a different internal state of the same lithium atoms (*10*), show that not everything fits the

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