Sticklers for sympatry

What is the origin of species? Nearly a century and a half after the question was first posed[1], evolutionary biology has yet to come up with a satisfactory answer. This is largely because of the timescales involved: an entire speciation event is unlikely to occur within the lifetime of a research scientist, let alone the lifetime of a research grant. Nevertheless, it is still possible to deduce a substantial amount by piecing together snapshots of different systems at different stages of the speciation process. The latest results from the study of two recently formed stickleback species[2,3] provide valuable insights into the early stages of speciation, and generate interesting contrasts with our understanding of what maintains boundaries between older, long-established species. The work also highlights a striking difference between the results of measuring fitness in the laboratory and in a natural environment.

One evolutionary process assumed to generate species diversity is 'ecological' speciation. If alternative ecological niches require different adaptations for their exploitation, populations will diverge as they adapt to those niches. Divergence will isolate them from each other, and might eventually lead to complete reproductive isolation and hence speciation[4]. This all seems perfectly reasonable. However, surprisingly few empirical studies have demonstrated a driving role for ecological selection pressures in the early stages of speciation – particularly in comparison with the volume of work that exists documenting hybrid dysfunction, where changes in the respective genomes have eventually rendered them intrinsically incompatible (for example, Refs 5,6). For these reasons, the detailed picture emerging from studies of the ubiquitous threespine stickleback (*Gasterosteus aculeatus* complex) in North American lakes is particularly exciting.

Sticklebacks in sympatry

Approximately 12 500 years ago in south-western British Columbia, Canada, populations of the marine threespine stickleback (*Gasterosteus aculeatus*) were stranded in freshwater lakes because, following deglaciation, the land uplifted rapidly. Several of these lakes now contain a pair of coexisting trophic forms: a 'limnetic' form, which feeds mainly on plankton in open water, and a 'benthic' form, which forages almost entirely on the lake bottom. Corresponding to these different feeding strategies are morphological differences: the plankton-feeding limnetic is slim-bodied with numerous, long gill-rakers, whereas the benthic form is larger, with a deeper body, wider mouth and fewer gill-rakers.

It is unclear exactly when one species became two. The two forms might have arisen through sympatric speciation following a single invasion by the marine species. Alternatively, after the first invasion, there might have been an interval during which the new arrivals changed to a certain extent, followed by a second invasion[7] (see also pp. 460–461 of this issue). Although knowledge of their absolute origins remains elusive, it is certain that the benthic and limnetic sticklebacks represent recent, post-glaciation divergence[8] (Nei's genetic distance D is only 0.02), which is what makes them useful for studies of speciation. Interbreeding in the wild is sufficiently rare (hybrids comprise only about 1% of sampled adults[8]) for the two trophic forms to be accepted as separate species. Two complementary papers by Dolph Schluter and colleagues, concentrating on a pair of species at one particular site (Paxton Lake, British Columbia, Canada), now add to our understanding of a central question: why are there so few hybrids?

The effects of natural selection

In one study[2], a combined fitness measure (incorporating egg fertilization, hatching and juvenile growth rates) showed no differences between the two species, and F_1 and F_2 crosses in the laboratory – although the benthic backcrosses had unexpectedly low fitness. Performance in the natural lake environment was assessed through growth rates, which reflect foraging efficiency in the two habitats. In enclosures in the benthic habitat, benthic sticklebacks had a significantly higher growth rate than the F_1 hybrids, whereas in open water the limnetics had a higher growth rate than the hybrids. Therefore, hybrids were significantly worse off than their respective parental species in each habitat, and their combined average across habitats was lower, though not significantly, than the average of the parent species. Environmentally mediated selection pressures have created a fitness trough between the two adaptive peaks that either form has been climbing.

The effects of sexual selection

This work is especially interesting in the light of a recent study[3] demonstrating that sexual selection is kicking in against hybrids. Each species is more likely to mate in its respective habitat: benthic males build nests in dense cover; both limnetics and hybrids build nests on open sediment[7]; and the habitat use of gravid females matches that of nesting conspecific males[3]. Previous experiments found no evidence that females refuse to mate when paired with a hybrid male under laboratory conditions[9]. However, when limnetic females were given a choice, under (almost) natural conditions, between a limnetic male and a hybrid male, they were more likely to choose the conspecific mate – possibly because the limnetic males were more 'vigorous' in their courtship. Although this mating preference experiment is obviously incomplete, considering only one of the parental species and habitats, it yields evidence of a further obstacle to gene flow between the species.

Implications for speciation

Whether or not this particular pair of species actually arose in sympatry, examples such as this should give heart to

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the proponents of sympatric speciation whose theoretical models have been criticized for their unrealistic assumptions. The system satisfies all the criteria usually invoked in such models: the existence of alternative ecological niches generating disruptive (divergent) selection on a trait, a preference for mating in the respective niches[3], and even an association between the trait under selection (body size) and mate choice[10]. As similar examples accumulate, and as the continuing evolution of models renders its theoretical representation more plausible[11,12], a wider acceptance of sympatric speciation seems probable.

Ecological factors appear to be driving the evolution of the sticklebacks into good biological[4] species, securing their positions on alternative peaks of the adaptive landscape even before genetic incompatibilities have accumulated. Both the pleiotropic effects of adaptive and non-adaptive changes in the genome (for example, owing to genetic drift) might eventually result in intrinsic incompatibilities between two gene pools. These will act independently of the environment to generate selection against hybrids that might, in the long run, be the primary factor responsible for reproductive isolation[5,6]. Nevertheless, these new results – and other recent studies, for example of leaf beetles[13] or passion-vine butterflies[14] – suggest that ecological selection pressures and coincident premating isolation might be considerably more important in the earlier stages of speciation.

Where next?

The stickleback system provides fruitful picking for a host of questions (see also pp. 460–461 of this issue). Most interesting will be comparisons with the species pairs in other lakes, in the hope of disentangling whether mating preferences have evolved as a by-product of ecological divergence, or by direct selection against the production of hybrids, through reinforcement[15] – will different forms from different lakes also avoid interbreeding? Careful comparison of both the mean and variance in fitness of F_1, F_2 and backcross generations in the laboratory and under natural conditions, should shed light not only on the mechanisms of reproductive isolation but also on the number of genes involved, the role of epistatic interactions and the underlying genetic architecture.

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