

current most plausible possibility is that those who *delight* in the presence of fur seals in that system and those who would *use* hake fishes there need not do so at one another's expense.

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Parallel speciation with allopatry

In a recent review¹, Johannesson argues that parallel speciation is strong evidence for sympatric speciation. Our work on threespine sticklebacks *Gasterosteus* spp., which provides the clearest example of parallel speciation to date from nature, was cited in support of this view. However, laboratory studies show that parallel speciation can occur between allopatric populations. Furthermore, the weight of evidence indicates an allopatric stage in the origin of the stickleback species.

Parallel speciation is a special case of parallel evolution whereby traits causing reproductive isolation evolve in parallel in independent populations that inhabit similar environments^{2,3}. The process is important because natural selection alone can produce it (the path of genetic drift might sometimes repeat itself in different lineages, but the outcome would not be correlated with environment). Parallel evolution of ordinary phenotypic traits occurs often between allopatric populations, and reproductive isolation could evolve in parallel under the same circumstances, especially if ordinary phenotypic traits underlie reproductive isolation. In support, the two examples of parallel evolution of reproductive isolation in the laboratory involved wholly allopatric populations^{4,5}.

Sympatric limnetic and benthic threespine sticklebacks probably have multiple independent origins^{6,7}, and morphological similarities between limnetics and between benthics from different lakes represent parallel evolution. Sympatric forms rarely, if ever, hybridize in the wild, and therefore constitute good biological species⁷ (they hybridize at a low rate in no-choice mating trials in the laboratory³). Remarkably, the basis of this reproductive isolation has evolved in parallel. Despite their different evolutionary histories, male and female benthic individuals from different lakes mate just as readily with one another as do male and female individuals from the same population. The result is the same for limnetics. Conversely, limnetics and benthics from different lakes mate infrequently, which is similar to the low frequency of mating between limnetics and benthics from the same lake³.

These results represent evidence of parallel speciation in sticklebacks, but they should not be interpreted as evidence of their sympatric speciation. Indeed, the evidence indicates that each stickleback species pair is the result of two separate invasions of freshwater by the ancestral marine species, *Gasterosteus aculeatus*, near the end of the last ice age. In each case, the first invader led to the present-day benthic species, whereas the second invader led to the present-day limnetic species. The evidence is as follows. First, study of

25 allozyme loci from two lakes^{8,9} indicate that the limnetic species is similar to the present-day marine species (Nei's $D \approx 0.02$), whereas benthics are more distant (Nei's $D \approx 0.07$). Second, similar to the marine species, limnetics can successfully develop in seawater (28 ppt salt) from fertilized egg to hatchling stages, whereas benthics develop poorly under these conditions¹⁰. This is consistent with two invasions spaced apart in time if salinity tolerance decays gradually after colonization of freshwater. Third, microsatellite evidence fails to support the sympatric speciation scenario⁷. For example, a phylogeny in which sympatric limnetic and benthic species are constrained to be sister species fits data on allele frequencies at six microsatellite loci significantly worse than does the unconstrained maximum-likelihood phylogeny⁷.

In contrast to these indications of double invasions, RFLP analysis of mitochondrial DNA (mtDNA) is more consistent with sympatric speciation: each lake has unique mtDNA haplotypes that occur at high frequency in both resident species⁶. Although it is conceivable that the mtDNA data reflect the true population histories, we believe that the discrepancy with other data is the result of low levels of mtDNA gene flow between sympatric limnetic and benthic species after the second invasion^{6,7}.

Although there is evidence that premating isolation between stickleback species has been strengthened in sympatry¹¹, initial divergence in morphology, ecology and mate preference probably took place during the allopatric phase. It is probable that divergent natural selection in sympatry allowed the new species to persist and to continue to diverge after the second invasion. Parallel speciation is one source of evidence for divergent natural selection in the origin of stickleback species ('ecological speciation'), but neither favors nor rules out any specific geographical scenario.

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Response from Johannesson

Schluter *et al.*¹ refer to new and interesting information² in one of the cases that I referred to in my review of parallel speciation³, namely the threespine sticklebacks *Gasterosteus* spp. They argue that the traits responsible for reproductive isolation probably evolved in allopatry rather than in sympatry. However, as pointed out by both of us, the molecular data show conflicting results of the population history. Furthermore, it is not easy to infer under what circumstances the ecological differentiation leading to reproductive isolation occurred.

Even under the scenario supported by Schluter *et al.*¹, where benthic forms

were the first invaders followed by limnetic forms at later periods, the evolution of ecological differentiation that resulted in reproductive isolation might not have been completed during the allopatric period. It seems probable that late invaders would also try to use the benthic niche as it is presumably more favorable. However, the second group of invaders might have been out-competed by populations already established in the benthic niche and therefore they began to evolve ecological traits more suitable for the limnetic habitat. If this scenario is correct, the reproductive isolation evolved at least partly during the sympatric stage. Schluter *et al.* have previously supported this view, stating: 'pre-mating isolation between ecomorphs arose initially as a simple by-product of divergent natural selection on key traits and was later reinforced in sympatry'⁴.

However, deterministic rather than stochastic processes are the main reasons behind the evolution of reproductive barriers among these species of sticklebacks, and the work by Schluter *et al.* presents nice evidence for this.

The point I raise in my review³ is that parallel speciation could be used to support sympatric speciation in cases where there is unambiguous molecular data of monophyly of contrasting ecomorphs living in sympatry, but where an earlier stage of microallopatry could not be rejected. Here, parallel evolution of the same reproductive barriers in independent systems supports ecological rather than stochastic forces as being motors of speciation, and we do not need to invoke physical barriers to explain the reproductive isolation. In light of the new data on microsatellites², I agree that sticklebacks might not be the most clear-cut example of parallel speciation in sympatry. The support for reproductive isolation as a consequence of ecological differentiation is still very strong (by again referring to parallel evolution of similar barriers) and this shows indirectly that speciation can take place without a physical barrier, that is, in a non-allopatric situation.

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Erratum

In the *Review* article by Kerstin Johannesson (Parallel speciation: a key to sympatric divergence, *Trends Ecol. Evol.* 16, 148–153), the legend to parts b–d of Fig. 1 did not match the figure. The legend should read:

Three different evolutionary scenarios might explain these results: (b) parallel evolution of reproductive isolation by means of divergent selection promoting ecotype formation. In this model, reproductive isolation might be a secondary effect of habitat shift, changing behavior and morphology⁶, or a consequence of selection favoring increasing associations between fitness traits and mate preference traits¹¹; (c) allopatric divergence, followed by secondary overlap and introgression; and (d) microallopatric divergence in each lake owing to earlier local barriers.

We apologize to our readers and the author for this error.

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Molecular signals or the *Loi de Balancement*?

In his *Opinion* article in *TREE*¹, Armand Leroi argues that negative relationships between fecundity and longevity in the nematode *Caenorhabditis elegans* are the consequence of one or more molecular signals with independent effects on fecundity and longevity rather than the result of a resource allocation tradeoff. The existence of such a mechanism is perplexing to evolutionary biologists because both traits have strong effects on fitness, so the apparently gratuitous negative association created by a common signal demands an evolutionary explanation. We can think of three possible explanations.