

COMMENTARY

Sexual selection, reproductive isolation and the genic view of speciation

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Wu (2001; this issue), shows convincingly that not the whole genome, but rather the gene is the unit of species differentiation. He distinguishes between two classes of loci, those that directly affect differential adaptation ('speciation genes') and those that do not. The speciation genes have a higher rate of differentiation during the process of speciation than the other genes. Wu (2001) concludes that speciation is an adaptive process driven either by natural or by sexual selection. Although he includes sexual selection as a driving force in speciation, most of his examples and most of the evidence presented refer to divergence by natural selection and to divergence in initially allopatric or parapatric populations.

Wu (2001) presents a four-staged model that starts with populations of a species separated by extrinsic barriers. Differences in selection in the isolated populations then results in divergence of the loci under selection. Upon secondary contact, gene exchange at the loci of functional divergence would be restricted. During the second stage, differentiation between the populations has proceeded to produce co-adapted gene complexes, which result in some hybrid sterility or inviability, or to ecological and/or behavioural changes between the populations resulting in a lower fitness of the hybrids in both parental environments. Massive hybridization could, however fuse the incipient species. During the third stage, a point of no return has been passed, the accumulation of speciation genes has resulted in differentiated co-adapted gene complexes, but a hybrid zone may still exist. At the fourth stage premating isolation has evolved and hybrids are either inviable or sterile: reproductive isolation is complete.

Indeed, this looks like a very plausible scenario for speciation, and it may be the description of many speciation events in nature. Also, it resolves the problems caused by the biological species concept, which requires complete reproductive isolation. The evidence in support of the model is derived from genetic analysis of four sibling species in the *Drosophila melanogaster*-group. It is both in support of the genic view on speciation and of speciation as a process of differential adaptation. Wu

(2001) concludes that the evolution of reproductive isolation is fundamentally a genomic concept, in contrast to the process of speciation. It may be early days for such a bold statement.

Wu's (2001) perspective has certainly changed mine. It is important, because it has disentangled the troublesome relation between speciation and the evolution of reproductive isolation implicit in the biological species concept and demonstrates convincingly that genes are the units of selection for species differentiation. Yet, some nagging doubts remain. Wu's (2001) empirical evidence mainly comes from *Drosophila*, and in his view, the conclusion does not depend on the choice of evidence.

However, when we try to apply Wu's (2001) four-stage model to speciation in haplochromine cichlid fish in Lake Victoria, some differences in the course of speciation events in these fish with those in the model become immediately obvious.

These fish have shown an enormous radiation: over 500 species all derived from one or a few ancestors have evolved within the lake bed in possibly only 12 000 years, but not more than 750 000 years. Ecological diversification has resulted in a wide range of food specialists, all well adapted morphologically (Seehausen & Bouton, 1997; Bouton *et al.*, 1999). Parental care is by female mouth brooding, and females choose brightly coloured males to spawn. Mate choice for male colours is the sole mechanism of isolation between species. No post-mating barriers exist, and when no male colours can be observed, mate choice breaks down (Seehausen *et al.*, 1997a). Hybrids are fertile and fully viable.

Evidence from field studies (Seehausen *et al.*, 1997a,b; Seehausen, 2000), laboratory experiments (Seehausen & van Alphen, 1998) and theoretical modelling (Lande *et al.*, in press) show that a population of these fish can split by sexual selection caused by small differences in preference for male coloration. This can result in two incipient species of which the males have different nuptial colours and females have a preference for males of either colour. Adaptive differentiation by natural selection follows the isolation of incipient species by sexual selection. Speciation can occur in sympatry.

Unlike the first stage in Wu's (2001) model, extrinsic barriers between populations are not always the start of the speciation process in haplochromine cichlids. Instead, it is the evolution of differential mate choice for nuptial colours, possibly triggered by a sex changing gene (Seehausen *et al.*, 1999) that results in premating isolation between incipient species.

Unlike the second stage in Wu's (2001) model, ecological and/or behavioural adaptations have not resulted in hybrid sterility or inviability, and reduced fitness of the hybrids between incipient species is unlikely. Even haplochromine species that differ considerably in their ecological specialization (e.g. a pelagic piscivore and a detritus feeder from shallow bays, can produce fertile and

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viable offspring). Hence, in haplochromines, it is not the evolution of co-adapted gene complexes itself that causes incompatibility between the incipient species.

One could argue that the Lake Victoria cichlids have not reached the third and fourth stage of Wu's (2001) model, because of the lack of hybrid sterility or any other post-mating barrier between species. This, however, has not prevented them from forming highly adapted and ecologically specialized species.

In a similar vein, Wu's (2001) model does not account for nonadaptive speciation events, e.g. isolation caused by the evolution of thelytoky in parasitoids, or reciprocal incompatibility between populations infected with different *Wolbachia* strains. Likewise, speciation by host plant shifts in phytophagous insects does not completely follow the scenario of Wu's (2001) model (Schilthuizen, 2001). In all these examples reproductive isolation precedes adaptive differences. Hence, Wu's (2001) model describes just one of a number of possible scenarios, and this should be kept in mind. If not, the model may become a barrier in our understanding of speciation like the biological species concept.

Wu's (2001) description at the genetic level of the different stages of speciation feeds back directly into the description of species definitions, and Wu (2001) cannot resist to add his own to a long list of existing ones. 'Speciation is the stage where populations will not lose their divergence upon contact and furthermore, will be able to continue to diverge'. Applying this definition to the haplochromines would result in the conclusion that there is only one polymorphic haplochromine species in each of the great lakes Malawi and Victoria. That would be giving priority to semantics over biology. The example of the haplochromine cichlids in the African Great Lakes also shows, that reproductive isolation is not always fundamentally a genomic concept, but when caused by sexual selection, can be a genic concept as well. It remains to be seen how often speciation proceeds as

described by Wu's model and how often it follows other pathways. The bewildering diversity in cichlid fish and in phytophagous insects and their parasitoids, at least, suggests that sympatric speciation is a common source of diversity.

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