COMMENTARY
Assortative mating and the genic view of speciation

J. R. BRIDLE* & M. G. RITCHIE†

*Department of Biology, University College London, UK
†Environmental and Evolutionary Biology, Bute Medical Building, University of St Andrews, St Andrews, Fife, Scotland

We welcome Wu's (2001) review of speciation from a genic perspective, and in particular its focus on the adaptive processes underlying the generation of new species, rather than the nature of the species themselves. However, we wish to stress that even from this perspective, the evolution of assortative mating should continue to be seen as a process of special importance in speciation. Although adaptive divergence in mating behaviour or habitat preference is implicitly incorporated into a genic perspective, we believe that assortative mating should have particular emphasis because it can cause dramatic changes in the fitness landscape, as the behaviour of different genotypes rapidly generates many epistatic interactions that did not exist under conditions of random mating. Such selection on multilocus genotypes could rapidly create the holes in the fitness landscape envisaged by recent models of speciation (Gavrilets, 1999). These increased levels of epistasis will further increase the size of the genomic regions where linkage disequilibria can be maintained by selection, and where new epistatic alleles can spread to fixation, eventually contributing to post as well as further pre-mating isolation. However, in contrast to the generation of such post-mating incompatibilities, behavioural or signalling traits may evolve rapidly under direct selection, in particular during adaptation to divergent habitats, under sexual selection, or under direct selection for increased assortment (reproductive character displacement or reinforcement).

A key divergence in our viewpoint is illustrated by Wu's comments on transformed *Drosophila* lines (p. 856). In our view, once behaviourally isolated these are indeed species because they are free to evolve independently, and to substitute different mutations at any part of the genome. This means they can diverge more quickly than genomes diverging under conditions of continued gene flow, where the substitution of such mutations is limited to regions where selection is strong relative to recombination. By contrast, according to Wu's genic view, these hypothetical *Drosophila* lines are not species because they have not yet diverged at more than one (introduced) locus. In nature, however, there may be real examples of

Correspondence: J.R. Bridle, Department of Biology, University College London NW1 2HE, UK. Tel.: +44 (0)207 679 5116; fax: +44 (0)207 383 2048; e-mail: j.bridle@ucl.ac.uk

such almost instantaneous isolation due to the rapid evolution of assortative mating. For example, periodical cicadas may become isolated because of changes in emergence times (Simon *et al.*, 2000), which could have a very simple genetic or even environmental basis. Nevertheless, such changes in their life cycle are a key to their speciation, allowing very rapid divergence at other loci as a result of strong assortment. The fact that further divergence rapidly accumulates is demonstrated by subsequent selection for character displacement when they meet (Marshall & Cooley, 2000).

Other systems are currently being identified where sexual isolation can appear because of few genes (Doi *et al.*, 2001), instead of requiring the extensive genetic divergence throughout the genome that Wu assumes is necessary under the biological species concept. This belief that reproductive isolation relies on many genes is also complicated by the difficulty of distinguishing genes initially causing speciation from those that accumulate throughout the whole genome once speciation occurs (Bridle & Jiggins, 2000). In addition, most studies of the genetics of reproductive isolation to date have concentrated on post-mating isolation, which may evolve at a more steady rate than assortative mating (Turelli & Orr, 1995; Ritchie & Phillips, 1998).

The changing nature of the fitness landscape as adaptive divergence proceeds may mean that alleles underlying the initial response to selection differ from those that spread later, as more of the genome becomes affected by a diverse array of selective pressures. For example, the substitution of alleles with epistatic effects on fitness is likely to become more rapid as the area of the genome affected by hitchhiking increases, or as the selective effects of alleles spread throughout the genome become highly correlated (e.g. when selection on male signal genes is driven by female preferences). Once again however, it is difficult to distinguish allelic substitutions causing speciation from those that rapidly accumulate once large areas of the genome become independent (Wu & Hollocher, 1998). We need therefore to study recently diverged lineages in order to identify the most important alleles involved in reducing recombination between genomes, and this only makes sense after identifying the ecological causes of isolation, rather than the causes of post-mating isolation in laboratory crosses (Schluter, 2001).

An important challenge for the future is, therefore, to understand the ecological and genetic changes that cause divergence in the quantitative traits contributing to assortative mating. How many genes are involved? What is the nature of their effects? What were the selective pressures responsible for their initial divergence? Answering these questions should remain a key part of speciation research, even if speciation is viewed from a genic perspective, as assortative mating remains critical to the generation of new species in sympatry (Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999), and to

the maintenance of bimodal distributions of genotypes in regions of secondary contact (Jiggins & Mallet, 2000).

References

Bridle, J.R. & Jiggins, C.D. 2000. Adaptive dynamics: is speciation too easy? *Trends Ecol. Evol.* **15**: 225–226.

Dieckmann, U. & Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature* **400**: 354–357.

Doi, M., Matsuda, M., Tomaru, M., Matsubayashi, H. & Oguma, Y. 2001. A locus for female discrimination behavior causing sexual isolation in *Drosophila. Proc. Natl. Acad. Sci. USA* **98**: 6714–6719.

Gavrilets, S. 1999. A dynamical theory of speciation on holey adaptive landscapes. *Am. Naturalist* **154**: 1–22.

Jiggins, C.D. & Mallet, J. 2000. Bimodal hybrid zones and speciation. *Trends Ecol. Evol* **15**: 250–255.

Kondrashov, A.S. & Kondrashov, F.A. 1999. Interactions among quantitative traits in the course of sympatric speciation. *Nature* **400**: 351–354.

Marshall, D.C. & Cooley, J.R. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim. Evolution* **54**: 1313–1325.

Ritchie, M.G. & Phillips, S.D.F. 1998. The genetics of sexual isolation. In: *Endless Forms: Species and Speciation* (D. A. Howard & S. Berlocher, eds), pp. 291–308. Oxford University Press, Oxford.

Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.* **16**: 372–380.

Simon, C., Tang, J., Dalwadi, S., Staley, G., Deniega, J. & Unnasch, T. 2000. Genetic evidence for assortative mating between 13-year cicadas and sympatric '17-year cicadas with 13-year life cycles' provides support for allochronic speciation. *Evolution* **54**: 1326–1336.

Turelli, M. & Orr, H.A. 1995. The dominance theory of Haldane's rule. *Genetics* **140**: 389–402.

Wu, C.I. 2001. The genic view of the process of speciation. *J. Evol. Biol.* **14**: 851–865.

Wu, C.-I. & Hollocher, H. 1998. Subtle is nature: the genetics of species differentiation and speciation. In: *Endless Forms: Species and Speciation* (D. A. Howard & S. H. Berlocher, eds), pp. 339–351. Oxford University Press, Oxford.