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EXPERIMENTAL TESTS OF FOUNDER-FLUSH: A REPLY TO TEMPLETON

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Templeton (1999) finds reason to rejoice and reason to despair in reading our account of an experiment about the effects of population bottlenecks on the evolution of reproductive isolation (Rundle et al. 1998). He first rejects our experiment as a test of founder-flush speciation and then interprets our results in terms of his genetic transilience model. Although some of the points he raises are matters that simply require further empirical work (e.g., the prevalence of multiple bottlenecks), we would like to make a few comments.

Novel Environments and Population Bottlenecks

Templeton dismisses our experiment as a test of the founder flush process on the grounds that it minimized novel selection after the population bottlenecks. This is based on two points: that in nature it is unlikely to have a founding event without novel selection and that the founder-flush model requires novel selection. We could not agree more with this first sentiment, but find Templeton's reading of Carson's descriptions of the theory remarkable.

Clearly, it is likely that founder events in nature are associated with a change of environmental conditions and therefore with novel selection pressures. Furthermore, we agree with Templeton that novel selection might interact with genetic drift to produce speciation in novel ways. However, given that novel selection alone can cause reproductive isolation (Rice and Hostert 1993) and that drift without novel environments has been proposed as a model of speciation (see below), it is useful to test whether drift alone can cause reproductive isolation. We have subsequently tested the interactions between drift and selection (Mooers et al. 1999) and continue these experiments with *D. pseudoobscura*.

Surprisingly, Templeton presents a confused picture of the necessity of a novel environment in Carson's models (Carson

1968, 1975, 1982; also Carson and Templeton 1984). Carson has made clear statements concerning this; for example, "a change in ambient environment is not a necessary prerequisite for genetic change. It is not a matter of the details of the genotype slavishly tracking the environment" (Carson 1982; p. 423). One should not confuse density dependent changes in the intensity of selection with changes in selection associated with a novel environment. The former are fundamental to Carson's theories; the latter, while potentially important in speciation, are not and must be controlled for in a proper experiment.

Contrary to Templeton's (1999) claim, previous studies have not controlled for the effects of novel selection on the evolution of reproductive isolation (Rundle et al. 1998). Indeed, many of these studies used unbottlenecked lines that were labeled controls, but these lines were themselves the ones used to test for reproductive isolation from the bottlenecked lines. There is therefore no information in these studies to indicate that the reproductive isolation was not simply a byproduct of allopatry or of novel selection pressures.

Interpretation of Results

Templeton predicted in 1980, and subsequently, that *Drosophila melanogaster* should be less likely to undergo genetic transilience than other species based on its shorter map length and the observation of inbreeding avoidance (Averhoff and Richardson 1974, 1976). We of course agree that some species can be less likely than others to undergo any particular biological process and discussed this at length in our original paper. Certainly the apparent rank order of the strength of reproductive isolation is as predicted by Templeton. We disagree, however, with Templeton's interpretation of these results as strong evidence in favor of genetic transilience for three reasons.

First, the other experiments to which Templeton refers do not control for novel environments, and their results may therefore reflect the effects of selection. These experiments

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also used hybrid base populations and therefore had an artificially high probability of evolving reproductive isolation (see Charlesworth et al. 1982). Second, as we stated before there is little justification for the prediction that species that differ in recombination rates by a relatively minor extent should differ so greatly in the rate of the evolution of reproductive isolation. Finally, predictions should allow falsification; one wonders whether a hypothetical result that showed much reproductive isolation after bottlenecks in *D. melanogaster* would be reasonably viewed as a rejection of the genetic transience model. If nothing else, the results confirm statements made by many, including Templeton, that speciation by founder events is unlikely, particularly in taxa such as *D. melanogaster*.

Averhoff and Richardson's (1974, 1976) observations that *D. melanogaster* responds to inbreeding with disassortative mating are interesting. However, this is simply a mechanism that makes genetic transience unlikely and not part of the theory behind the model. Indeed, their data are fully consistent with our result that bottleneck-induced speciation is unlikely in *D. melanogaster*. More work is needed to determine whether the mating system of *D. melanogaster* is unique in this way or representative of a common phenomenon, making bottleneck-induced speciation unlikely in many taxa.

In conclusion, it was our intent to explore the frequency with which population bottlenecks alone could cause the evolution of reproductive isolation. Our results clearly show that in a well replicated study founder-flush and genetic transience speciation did not occur, implying that these are not easy and general mechanisms of speciation as suggested by past studies.

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