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RESPONSE

Playing God with guppies – informing tough conservation decisions using a model experimental system

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With human-induced extinctions and population declines accelerating worldwide (Dirzo *et al.*, 2014), it is more important than ever to foster dialogue among researchers, conservationists, and the public at large about the costs and benefits of potential management actions. We are therefore grateful for the insightful commentaries provided by Mills (2017), Grueber (2017) and Tallmon (2017) on our article in this issue of *Animal Conservation* (Kronenberger *et al.*, 2017), in which we test the demographic effects of divergent immigrants on small laboratory populations of Trinidadian guppies *Poecilia reticulata*. Using replicated mesocosm populations, we found that divergent immigrants had a positive effect on population fitness compared to no immigrants at all. This positive effect was larger when immigrants were adaptively similar but genetically divergent (as opposed to adaptively divergent but genetically similar). As reflected by the commentaries, our study adds to the mounting evidence that demographic and genetic rescue are plausible management strategies in certain cases and provides some empirical insight into the outcome of non-ideal translocation scenarios. However, much work is still needed to accurately predict the outcome of translocations, especially those between adaptively and/or genetically divergent populations.

When the individuals introduced into a vulnerable population are divergent, there is a greater likelihood of negative outcomes such as genetic swamping with maladaptive alleles and outbreeding depression (Frankham *et al.*, 2011). It is therefore generally agreed that, if translocations are the only option for re-establishing gene flow (Mills, 2017), donor and recipient populations should be adaptively and genetically similar. Indeed, when divergent immigrants are avoided, translocations designed to induce genetic rescue are almost always successful (Frankham, 2015; Whiteley *et al.*, 2015). But as we proceed further into the Earth's sixth mass extinction (Dirzo *et al.*, 2014), the reality is that often the only potential donor populations that remain are either adaptively divergent, genetically divergent, or both (e.g. Funk *et al.*, 2016). If translocation is to be an option in these cases, we will need more precise information about when divergent immigrants will and will not have the desired positive effect on population fitness. This was the primary motivation for our study.

The primary merit of our study, we believe, is that it was experimental. Tallmon (2017) reminds us that a long-standing issue in conservation biology is 'a lack of replication, randomization, and experimental controls needed to ascribe the effects of applied treatments to observed outcomes'. This issue arises out of the nature of the field itself; because our goal is conservation, we are almost exclusively dealing with threatened species that cannot be ethically or practically manipulated, or large, charismatic species that are not amenable to study across multiple generations (Tallmon, 2017). Utilizing case studies to generate recommendations for when and how to carry out translocations (e.g. Frankham *et al.*, 2011) is a valuable approach, but it should be complemented with insights gleaned from other theoretical and empirical research, including manipulative experiments. Case studies minimize risk as they strive to provide populations with the best possible chance of rescue. Manipulative experiments, in contrast, are able to embrace risk and test the boundaries of theory by simulating more extreme translocation scenarios, which offers a powerful means of testing and refining previously established guidelines.

Given our experimental design, we were unfortunately unable to tease apart the relative impacts of demographic and genetic rescue and, because population monitoring lasted <2 generations, we could not be certain whether the rescue effect would have persisted in later generations. Future experiments should aim to rectify the shortcomings of our study by, for example, including a treatment with immigrants from the same population to control for strictly demographic effects, extending population monitoring for multiple generations, comparing hybrid fitness to that of recipients and immigrants and replicating treatments across different populations. Although many biological systems can be informative for this, we find Trinidadian guppies particularly tractable due to their fast generation time and natural variation among wild populations in isolation, genetic diversity and selection pressures. For example, Fitzpatrick *et al.* (2016) monitored the effects of immigration from an adaptively divergent source into two replicate, wild guppy populations for several generations, coupling mark-recapture techniques with genetic sampling to find that gene flow increased genetic diversity, abundance and vital rates. The authors were able to conclude that the increases in population fitness were primarily due to genetic rescue, and that fitness did not break down in later-generation hybrids.

Wildlife managers are often faced with a pivotal choice between actively interfering with declining populations in an effort to boost their fitness and letting nature take its course. As the commentators on our study have indicated, inaction is itself a management decision (Grueber, 2017), and we must weigh the risk of doing nothing against the risk of doing something with uncertain consequences (Mills, 2017). The correct choice in any given situation is complex and context dependent, but generalities gleaned through experimentation can reduce uncertainty. In these times of such rapid environmental change, dismissing actions with well-documented and generally positive results out of uncertainty can sometimes be the riskier option.

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