

## RESPONSE

**Role of genetic factors in extinction of island endemics: complementary or competing explanations?**

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In writing a review on the role of genetic factors in species' extinction (Jamieson, 2007), I was initially concerned that some would see such an article as a simple re-hash of an old, and perhaps tired, debate (e.g. Caro & Laurenson, 1994; Caughley, 1994; Hedrick *et al.*, 1996). Surely, some might argue, we have moved on from bickering over whether genetic factors such as inbreeding depression can (occasionally) contribute to the processes affecting species' extinction. We have indeed moved on to a point where genetic factors are accepted to have played a pivotal role in the recovery of several different wild populations (Tallmon, Luikart & Waples, 2004; Pimm, Dollar & Bass, 2006). Nevertheless, others have taken the argument even further, where the loss of fitness due to inbreeding depression is seen as an unavoidable consequence of small populations and therefore an undeniable contributor to the increased extinction risk of threatened species (Frankham, Ballou & Briscoe, 2002; Frankham, 2005). At the other extreme, genetic factors apparently do not even warrant a mention in recent studies exploring the correlates of extinction for hundreds of species of island endemics (Blackburn *et al.*, 2004; Duncan & Blackburn, 2004). It was these extremes that were the focal points of my article.

I chose to focus on island endemics for two reasons. First, in no other group is the tension between the relative contributions of genetic versus non-genetic factors to extinction risk more evident. This tension boils down to two major consequences of long periods of isolation for island endemics: (1) increased susceptibility to introduced predators (i.e. predator naivety) and (2) lowered genetic diversity and heightened levels of inbreeding. Second, and closer to home, there is a need to understand the relative importance of the widespread occurrence of reduced genetic variation and inbreeding in threatened island endemics in New Zealand (Jamieson, Wallis & Briskie, 2006), where the devastating effects of introduced predators (including humans) are well documented (Worthy & Holdaway, 2002; Wilson, 2004).

I associated the two consequences of island isolation – increased susceptibility to predation and increased risk of inbreeding depression – with the primary (but not exclusive) research interests of ecologists versus geneticists, respectively. Reed (2007) argued that dividing conservation biologists into these two camps is part of the problem. Without stating what that problem is, Reed suggested that greater integration of genetic and ecological factors into a single evolutionary framework when dealing with population declines is part of the solution. In fact, all three of the commentaries seem to agree that focusing either on the deterministic drivers of population decline or on the stochastic processes (including genetic effects) that affect populations once they become small should not be seen as competing or opposing approaches to conservation biology.

This distinction between deterministic drivers and stochastic processes affecting small populations echoes the earlier debates about the role of genetics in species extinction (e.g. Hedrick *et al.*, 1996). My review merely highlighted the practical problem of distinguishing effects at either end of what is really a continuum, and the relative importance and associated consequences of these extremes for prioritizing conservation resources. Duncan & Blackburn (2007) acknowledge that stochastic factors such as inbreeding could potentially elevate extinction risk, especially in populations on smaller islands, but did not include this possibility in their original analysis (Jamieson, 2007). (Brook *et al.* (2002) illustrate using population modelling that inbreeding depression alone could shorten the time to extinction by 25–31%, which is not a trivial quantity.) Yet, Duncan & Blackburn (2007) go on to argue that there are several effects other than inbreeding that are predicted to elevate the rate of extinction in small populations, including the likelihood that predators will be able to find and remove every individual. To me, these sound more like competing, rather than complementary explanations for population declines and extinctions. Indeed, Duncan & Blackburn (2007) discount the hypothesis that endemic island species

suffer a higher extinction risk because they are more inbred (Frankham, 1998) by showing that the level of endemism is highly correlated with the rates of extinction, which is predicted by the increased susceptibility to exotic predators hypothesis, but not by the inbreeding hypothesis. I believe Frankham (1998, 2005) saw inbreeding depression as playing a direct role in species decline and eventual extinction, a role that Duncan & Blackburn (2007) question when it comes to island endemics.

Groombridge (2007) and Reed (2007) agree with Duncan & Blackburn (2007) and Jamieson (2007) that the impact of introduced predators (including humans) was likely so rapid and large as to overwhelm any differences in survival among island endemics due to their level of inbreeding. This conclusion, however, only applies to extinct island endemics. That is why this debate is so important, because the recovery of extant island endemics, which either coexist with introduced predators or are protected from them (e.g. on offshore islands), may be partly or entirely dependent on genetic management. The fact that Duncan & Blackburn (2007) now acknowledge this point is a welcome step forward.

Although genetic factors will clearly be relevant in the recovery of some species, my review further argued that Spielman, Brook & Frankham (2004) may have overstated the general role of genetics, and inbreeding in particular, in increasing the risk of extinction for threatened extant species. Reed (2007) makes this argument more forcefully and more convincingly than I did. Reed points to a number of weaknesses with Spielman *et al.*'s assertion that the majority of threatened species are not driven to extinction before genetic factors impact them, including their assumption of a linear link between reduced fitness and extinction risk. Again, dissecting and debating this point is important. Spielman *et al.*'s conclusions imply that by demonstrating that a threatened species has reduced genetic variation, it has an *immediate* increased risk of extinction due to reduced fitness, which Reed (2007) clearly shows is not necessarily the case, especially in the face of significant rates of predation. (There is little argument that reduced genetic diversity could affect the ability of species to adapt to future environment changes, but Spielman *et al.* (2004) were specifically referring to the short-term and cumulative loss of fitness due to inbreeding and drift.) With the reality of limited resources that most conservation agencies face, it is important to link management actions to the agents of decline and then to prioritize recovery plans accordingly. Simply knowing that a threatened species has low heterozygosity is insufficient evidence by itself to assess either the associated extinction risks or the ability of a species to recover, as noted by Groombridge (2007).

In summary, in addition to highlighting the dominant role that human settlement and introduced predators have had in past extinctions of island endemics, Duncan & Blackburn (2007) acknowledge the potential importance that inbreeding could have for the many small and isolated extant populations that have persisted either because of good luck or considerable conservation effort. Groom-

bridge (2007) further acknowledges the need for a better understanding of both ecological and genetic factors as potential drivers of extinction, and how they may differ on a temporal scale. Groombridge (2007) further asks whether New Zealand's primary focus of controlling introduced predators will be sufficient to ensure viable populations in the future. Reed (2007) pleads for a more integrative approach to conservation management whereby the goal should be to maintain populations at sizes that keep the integrity of ecological and evolutionary processes intact. All these are worthwhile take-home messages from this forum.

So why has there been so much confusion over the role of genetic factors in the persistence of island endemics? Population viability modelling clearly shows that factors such as inbreeding depression can cause populations to decline to extinction. It is unclear, however, how often such factors exacerbate population declines otherwise caused by ecological or environmental factors. Once the deterministic drivers of population decline are identified and controlled or eliminated, conservation focus should switch to management of population recovery. Perhaps by placing less emphasis on the role that genetic factors have in extinction processes and placing greater focus on their potential role in recovery processes, genetic factors would receive greater attention from biodiversity managers, most of whom (in my experience) have an ecological rather than a genetics background. Of course, the importance of genetic processes will still vary from species to species and our understanding of these processes in wild populations remains incomplete. This generally calls for a plea for further research, but it also highlights the important role that scientific debate has in conservation issues of this nature. I therefore acknowledge the respondents for their critical yet constructive comments, and conclude that the debate over the role of genetic factors in species extinction not only will, but should, continue.

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