

## FEATURED PAPER

# Has the debate over genetics and extinction of island endemics truly been resolved?

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**Keywords**

extinction risk; genetic diversity; inbreeding; introduced predators; island birds.

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Received 10 September 2006; accepted  
11 December 2006

doi:10.1111/j.1469-1795.2006.00095.x

**Abstract**

The relative importance of genetic factors in increasing the risk of extinction has been hotly debated in the past and has tended to be downplayed by ecologists researching the correlates of extinction of island endemics. More recently, Frankham has argued that there is now sufficient evidence to regard the past controversies over the contribution of genetic factors to extinction risk as mostly resolved. For example, evidence indicates that the majority of threatened species including island endemics have a lower genetic diversity than taxonomically related nonthreatened species, implying that genetic factors such as inbreeding can increase the probability of extinction before extinction events occur. Yet, recent ecological research on the correlates of extinction for over 220 species of island birds found compelling evidence that exotic mammalian predators were the sole drivers of extinctions, and neglected to even mention any role of genetic factors. This paper discusses how two research groups working towards identifying and understanding the correlates of extinction for island endemics can reach such distinct conclusions. Part of the reason for the different perspectives is that ecological research has tended to focus on the correlates of historical extinctions of island endemics while conservation geneticists have concentrated on genetic correlates of currently threatened extant species. Identifying whether the population growth rate is positive or negative is crucial to this debate because even the geneticists agree that inbreeding will have little time to impact populations that are declining rapidly due to high predation rates. Inbreeding depression is likely to have a greater impact on extinction probability in species suffering from gradual habitat loss and range contraction, which typify the deterministic causes of population decline in continental species, rather than the intense predation pressure commonly associated with declines and extinctions of oceanic island endemics.

**Introduction**

Preventing extinction is the ultimate aim of conservationists and identifying the factors that correlate with extinction events on a historical time scale is the primary goal of conservation biology. In the 1980s and 1990s, there was considerable debate about whether genetic factors, especially inbreeding, increase the risk of extinction in wild populations. While it was acknowledged that under some circumstances inbreeding will have negative effects on reproductive fitness and/or survival, and could therefore negatively impact population growth rates, it was not generally accepted that inbreeding itself translates into heightened extinction risk (Brook *et al.*, 2002). Caro & Laurenson (1994) argued that ecological (deterministic) factors are far more significant in species declines than genetic factors. Lande (1988) claimed that in natural environments, demography is likely to be of more immediate

importance than genetics in determining the viability of small populations. Caughley (1994) went as far as to say that no species has been driven to extinction through genetic malfunction.

Conservation geneticists did not take these comments lightly and appealed for a more inclusive approach to understanding and preventing species extinctions (Hedrick *et al.*, 1996). They argued that both deterministic factors (e.g. habitat loss, over-exploitation, introduced predators) that reduce population size, and stochastic factors (e.g. demographic, environmental, catastrophic and genetic) that lead to the final extinction of a small population, play a combined role. In addition to the well-known negative consequences of inbreeding, genetic drift can cause deleterious alleles to become fixed in populations with a small effective size, resulting in a reduction in fitness and leading to extinction. Of course, the general loss of genetic diversity can also lead to a reduced ability to adapt to changing environments and

hence lower the chances of long-term persistence, but most of the earlier debate focused on the immediate (genetic) consequences of small effective population sizes, especially inbreeding depression and its role in increasing the risk of extinction (Caughley, 1994; Hedrick *et al.*, 1996).

Although the case for the importance of genetic factors may not have been so evident in the 1980s, a recent review by Frankham (2005) argues that there is now: (1) compelling evidence that inbreeding depression and loss of genetic variation increase extinction risk in laboratory populations; (2) clear evidence for inbreeding depression in wild populations and that this can affect population growth rates; and (3) strong evidence from individual case studies and from computer simulations that inbreeding depression ultimately contributes to population extinction risk. Furthermore, Frankham, Ballou & Briscoe (2002) drew the conclusion that genetic factors must affect extinction risk because threatened species have by definition small or declining populations, and in such populations inbreeding and loss of genetic variation are unavoidable. To support this claim, Frankham (2005) points to molecular evidence that shows that most species are not normally driven to extinction before genetic factors can impact (e.g. Spielman, Brook & Frankham, 2004). After reviewing all the recent theory and empirical data linking genetic factors with extinction, Frankham (2005) concludes that the contribution of genetic factors to extinction risk is undeniable.

If that is the case, then it seems slightly surprising that recent papers by ecologists Tim Blackburn, Richard Duncan and colleagues (Blackburn *et al.*, 2004, 2005; Duncan & Blackburn, 2004) not only conclude that exotic predators have been the main drivers of extinction of birds on oceanic islands, but neglect to even mention genetic factors. Even when Blackburn *et al.*'s (2004) paper was subsequently criticized by other ecologists for failing to take into account the effects of massive habitat loss on oceanic islands (Didham, Ewers & Gemmill, 2005; but see Blackburn *et al.*, 2005), those critics failed to mention genetic structure of bottleneck populations as possible contributing factors.

This omission may reflect the fact that ecologists are primarily interested in the ecological predictors that reflect a species' sensitivity to deterministic causes of population decline and ultimately extinction – factors such as introduced predators and habitat loss. Likewise, geneticists are most focused on the genetic predictors that signify the stochastic hazards associated with populations that have already been reduced in size, no matter what the reason for decline (Caughley, 1994). Nevertheless, for those of us interested in understanding all the factors that make island endemics particularly prone to extinction, the answer is likely to depend on which papers – the ecologists' or geneticists' – we chose to read (or ignore). The difference between the two groups is striking, as can be seen in the abstracts of their papers on island extinctions. For example, from Frankham's (1998) paper entitled, 'Inbreeding and extinction: island populations':

Island populations are more prone to extinction than mainland populations, with island endemic species

having higher extinction rates than nonendemic species. Insular populations are expected to suffer increased inbreeding relative to mainland populations due to bottlenecks at foundation and to lower subsequent population sizes. . . . Island populations were significantly inbred, with inbreeding coefficients significantly higher in endemic than nonendemic island populations. Many island populations showed levels of inbreeding associated with elevated extinction rates in domestic and laboratory species. Inbreeding depression cannot be excluded as a factor in the extinction proneness of island populations.

By contrast, Blackburn *et al.*'s (2004) abstract in their paper entitled 'Avian extinction and mammalian introductions on oceanic islands' states:

We show that the probability that a bird species has been extirpated from each of 220 oceanic islands is positively correlated with the number of exotic predatory mammal species established on those islands after European colonization and that the effect of these predators is greater on island endemic species . . .

The aim of this paper is to discuss how two research groups working towards the same fundamental aims – to identify and understand the correlates of extinction of island endemics – can reach such apparently distinct conclusions.

## Opposing views of extinctions

One obvious explanation for the different conclusions about the correlates of extinction in island species is that the two groups are looking at two different datasets: ecologists like Blackburn and Duncan have focused on historical extinctions, while geneticists like Frankham and co-workers have concentrated on extant species. In the latter case, the correlates of extinction risk have been studied using laboratory populations (normally *Drosophila*, e.g. Frankham, 1995; Frankham *et al.*, 2001; Reed *et al.*, 2003), population viability modelling (e.g. Brook *et al.*, 2002) and comparative analyses of levels of genetic variation in non-captive island versus mainland populations (Frankham, 1997, 1998) or threatened versus nonthreatened species (Spielman *et al.*, 2004). Although both groups claim to be interested in identifying and understanding the primary factors that increase the risk of extinction, one is focusing on the deterministic factors that correlate with past extinctions and the other is concentrating on stochastic genetic factors that are correlated across small populations of currently threatened species.

With different datasets, and focusing on different ends of a continuum of factors that impact on extinction probability, two distinct take-home messages emerge for conservation biologists, potentially leading to confusion. By concentrating on the historical record of avian extinctions on oceanic islands, Blackburn and Duncan's clear message is that exotic predators represent the main threat to island biota. In contrast, by focusing on the effects of inbreeding depression in model species or currently listed threatened

species, the core message in Frankham's papers is the need to manage inbreeding and loss of genetic diversity.

The sensible reply to these two arguments is to simply acknowledge that both take-home messages are important, and to get on with saving what is left of our threatened species. However, such a 'fence-sitting' response does not help illuminate the relative contributions of varying processes to current extinction risks nor does it help to identify the conditions under which the impact of these processes will vary. For example, although deterministic and stochastic factors are likely to be interacting in currently threatened populations, identifying their relative contribution from historic datasets alone could be difficult if the most serious threat process has caused the disappearance of all those species vulnerable to it, and the emergent pattern of threat has now changed. Blackburn *et al.* (2004) acknowledged this possibility for endemic island birds, when they found that the proportions of currently threatened species on islands are statistically unrelated to the numbers of exotic mammalian species present on those islands. Could the new threats include or be compounded by inbreeding depression, for example? Blackburn *et al.* make no mention of the effects of genetic factors, but suggest only that as the numbers of exotic predators reaching the more isolated islands increase, the probability of extinction will increase.

The geneticists' arguments have relied partly on computer simulations of extant species to identify the correlates of extinction risk. Brook *et al.*'s (2002) computer simulations for 20 threatened species demonstrated that the inclusion of modest levels of inbreeding depression accelerated times to extinction by 25–31% even when other demographic, environmental and catastrophic factors are operating. The major variable explaining variation among species with regard to the impact of inbreeding was the initial population growth rate. For example, they found that inbreeding depression generally had significant negative effects, except when populations were declining so rapidly (due to deterministic factors such as habitat loss or introduced predators), that inbreeding had little time to act (Brook *et al.*, 2002). However, Brook *et al.* (2002) point out that the majority of currently threatened species for which genetic data exist (77%,  $n = 170$ ) already have a lower genetic diversity (i.e. lower heterozygosity = higher inbreeding levels) than taxonomically related nonthreatened species (e.g. Spielman *et al.*, 2004). They argue that such genetic differences between threatened and nonthreatened species would not be expected if nongenetic, deterministic factors drove species to extinction *before* inbreeding could become a problem. They therefore conclude that genetic factors can act within a similar time scale to ecological factors and clearly do play a role in increasing extinction risks for the majority of threatened species.

There are several difficulties in applying this argument to island endemics and their particularly high rates of extinction. Although island endemics might have less genetic variation relative to related mainland species, they also tend to evolve flightlessness and tameness in the absence of mammalian predators, which makes them more susceptible

to predation when rats and other carnivorous mammals eventually invade. Indeed, the results from a recent molecular study on New Zealand's South Island saddlebacks *Philesturnus carunculatus carunculatus* are inconsistent with the prediction that extinct populations should have lower genetic variation than related extant populations. Using DNA extracted from study skins collected between the mid-1800s and early 1900s, it was shown that saddlebacks on the mainland of South Island had nearly three times the levels of genetic variation than those on a small, isolated population on Big South Cape Island, located off the southwest coast of Stewart Island (Taylor, 2006). The mainland population became extinct by about 1905, coinciding with the range expansion of rats and stoats over the South Island, while the Big South Cape population flourished until 1961 when the population crashed immediately after ship rats invaded (Merton, 1975; Hooson & Jamieson, 2003). This example illustrates that in the presence of mammalian predators, some island endemic birds are extremely vulnerable to extinction whether they are inbred or not.

My main point is even if we assume that the majority of extinct island endemics were inbred to some extent, it is still difficult to quantify how much inbreeding depression contributed to their extinction, above and beyond that due to introduced predators. Frankham (1998) argues that higher levels of inbreeding lead to lower fitness and thus make island populations more susceptible to extinction than mainland populations. Inbred individuals might be more susceptible to diseases and harsh weather conditions (Frankham *et al.*, 2002), but there is little evidence that inbred individuals are more susceptible to predatory mammals, especially in the case of island endemics. A more plausible scenario is that reduced reproductive performance due to inbreeding depression affects recruitment rates and thus accelerates the rate of decline. However, assuming that population growth rates for most endemic island species are already negative in the presence of introduced predatory mammals, then the impact of inbreeding depression on extinction risk is likely to be minimal, as Brook *et al.*'s (2002) own simulation results indicate.

### Is the pathway to extinction generally fast or slow?

By exploring the correlates of extinction from different datasets, and focusing on either deterministic or stochastic processes, ecologists and geneticists tend to form very different perspectives on the speed at which extinction processes occur. It would appear that some conservation geneticists view the pathway to extinction as a long and winding road, along which most threatened species show signs of genetic drift and inbreeding well before they become extinct (cf. Spielman *et al.*, 2004). By contrast, many New Zealand ecologists would see the pathway to extinction as more like a motorway, given the rapid effects of introduced predators, especially on isolated oceanic islands or land masses like New Zealand (Worthy & Holdaway, 2002). Knowing whether a population's growth rate is positive or

negative is crucial to this controversy because as noted above, inbreeding will have little time to impact populations that are declining rapidly due to deterministic factors such as predation. Therefore, inbreeding depression is predicted to have its greatest effect on extinction probability in small populations that remain small but stable or grow very slowly (Brook *et al.*, 2002; Frankham *et al.*, 2002).

Under what types of deterministic conditions would a population end up small but stable or increasing only slowly? Experience in New Zealand would tell us that it would not be in the presence of introduced predators, which ultimately inflict high mortality rates on adults and juveniles of endemic species resulting in negative population growth rates (Wilson, 2004). Furthermore, many populations of New Zealand endemics show the capacity to recover rapidly when predators are controlled or eradicated (Taylor, Jamieson & Armstrong, 2005). Instead, gradual habitat loss, range contraction and isolation are more likely situations under which a population would decline more gradually or remain small for a period of time. It is under such conditions that inbreeding depression is expected to have the greatest effect on extinction probability (Frankham *et al.*, 2002). The so-called cases of 'genetic rescue' are perhaps the most convincing evidence that genetic factors can impact on population persistence. Genetic rescue refers to situations where small populations show signs of recovery after new genetic stock has been introduced (Ingvarsson, 2001; Tallmon, Luikart & Waples, 2004; Pimm, Dollar & Bass, 2006). It is interesting to note that for all cited cases of genetic rescue in the wild (see Tallmon *et al.*, 2004), the initial population decline was associated with loss of habitat and historical range contraction and not excessive predation by exotic predators.

The wider acceptance in the northern hemisphere of genetic factors as important management considerations contrasts with a tendency to ignore or downplay these same genetic factors in New Zealand (see Jamieson, Wallis & Briskie, 2006). I suggest that this difference in emphasis is directly related to the relative importance of exotic predators in species' declines. The need for eradicating or controlling introduced predators in species recovery plans is well documented in New Zealand (Clout, 2001). Conversely, population viability analysis (PVA), which is used for understanding how stochastic events and processes (including genetic factors) affect extinction probability in small populations (Bessinger, 2002), is more commonly employed in the northern hemisphere where habitat loss is the main deterministic agent of population decline. For example, 85% of the species listed as threatened in the United States are directly affected by loss or alteration of habitat (Wilcove *et al.*, 1998), and PVA is used extensively in conservation planning for many of these threatened species (Shaffer *et al.*, 2002). This does not mean that PVA and genetic factors are unimportant in species recovery plans in New Zealand, especially in cases where the direct control or eradication of introduced predators has resulted in only a limited population recovery (Jamieson *et al.*, in press). It could even be argued that populations that have successfully recovered

from a handful of individuals to a few hundred are still at risk of extinction over the next several hundred years due to the effects of inbreeding depression (O'Grady *et al.*, 2006).

Thus, in summary, were Blackburn *et al.* (2004) and Duncan & Blackburn (2004) correct in attributing historical avian extinctions on oceanic islands like New Zealand solely to introduced predators? Everything we know about these extinction events suggests that the declines were rapid and complete (Atkinson, 1985; Holdaway, 1999; Wilson, 2004); most New Zealand conservation biologists are only too familiar with the story of the lighthouse keeper's cat killing the last of the flightless Stephens Island wren *Traversia lyalli* (Halliday, 1978). Genetic factors such as inbreeding and drift probably act too slowly to influence predator-induced extinctions on oceanic islands. It is revealing to note that Frankham's (1998) conclusion that inbreeding depression contributed to extinction susceptibility of island endemics was partially based on genetic data that included only nine species of endemic birds all belonging to the Hawaiian honeycreepers (Family: Fringillidae, Subfamily: Drepanidinae), and none of which were rare or threatened (Johnson, Marten & Ralph, 1989).

Of course, the loss of flight and predator avoidance behaviour in island endemics, along with increased body size and k-selected reproductive traits, all have strong genetic bases. Frankham (1998) originally included these traits along with inbreeding and loss of genetic variation under his list of 'genetic' factors (as opposed to 'ecological' factors such as habitat destruction, or environmental or demographic stochasticity) that contributed to the increased risk of extinction for island endemics. However, lumping these factors together tends to confuse matters because the behavioural and morphological attributes are the result of adaptive evolution by natural selection. More recently, and in line with other conservation genetics literature, Frankham (2005) refers solely to inbreeding, drift and accumulation of harmful mutations as examples of genetic processes affecting extinction risk.

## Conclusions

Most conservation biologists would agree with Frankham (2005) that inbreeding and loss of genetic variation can contribute to lower fitness in captive and wild populations, and thus avoiding close inbreeding and maintaining genetic diversity are good management practices in threatened populations. Some have gone as far as to argue that genetic factors have already impacted on most currently listed threatened species because threatened species generally have lower levels of heterozygosity than related nonthreatened taxa (Spielman *et al.*, 2004). Others may take exception to such statements, given that the proportion of species for which inbreeding depression is *directly* contributing to their threatened status is insignificant compared with the number directly affected by introduced predators, exploitation or habitat loss (IUCN, 2006). Furthermore, despite island endemics having low levels of heterozygosity (due to founder events and low effective population size), many have

clearly persisted, at least up to the point of human contact, when such populations decline rapidly. Regardless, it is still a concern that many endemic threatened species, including those in New Zealand that are now protected from introduced predators, show extremely low levels of genetic variation (Hay *et al.*, 2003; Miller *et al.*, 2003; Jamieson *et al.*, 2006), and thus may have lowered capabilities to adapt genetically to changing environments such as global warming or disease outbreaks, increasing their vulnerability to extinction. Clearly, these sorts of ecological and genetic factors affecting small populations are on different time scales, and both need to be acknowledged if species are to persist beyond the time frame of most recovery programmes.

Hedrick *et al.* (1996) criticized Caughley's (1994) initial division of conservation biology into the declining population (ecologists) versus small population (geneticists) paradigms as a false dichotomy, overly simplistic and ultimately destructive for conservation biology. Boyce (2002) disagreed, and saw Caughley's provocative essay as identifying a fundamental problem and thus encouraging better integration of different approaches. Even if we agree that genetic factors such as inbreeding and drift are important issues in present-day conservation, this does not imply that they always deserve the same priority to the deterministic 'drivers' of extinction. Being a New Zealander, Graeme Caughley was only too aware of the impact that introduced predators had on extinction risk to endemic island species. It is therefore not surprising that he recommended that the first step in threatened species recovery was to identify and remove the causes of decline before dealing with the consequences of managing a small but stable population (Caughley, 1994). The very fact that in New Zealand we are now discussing the best ways to genetically manage small populations (Jamieson *et al.*, in press) suggests not only that we have been partially successful in identifying and neutralizing the agents of decline, but that the old debate has truly moved on.

## Acknowledgements

I thank H. Spencer, G. Wallis, J. Waters, C. Townsend and L. Tracy for discussions and for comments on earlier drafts of the paper. My research on inbreeding and threatened species is supported by the New Zealand Department of Conservation (contract no. 3576), Landcare Research New Zealand (OBI contract no. C09X0503) and the University of Otago.

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