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Genetics and conservation biology

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Abstract

Conservation genetics encompasses genetic management of small populations, resolution of taxonomic uncertainties and management units, and the use of molecular genetic analyses in forensics and to understanding species' biology. The role of genetic factors in extinctions of wild populations has been controversial, but evidence now shows that they make important contributions to extinction risk. Inbreeding has been shown to cause extinctions of wild populations, computer projections indicate that inbreeding depression has important effects on extinction risk, and most threatened species show signs of genetic deterioration. Inappropriate management is likely to result if genetic factors are ignored in threatened species management. **To cite this article:** R. Frankham, C. R. *Biologies* 326 (2003).

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Résumé

Génétique et biologie de la conservation. La génétique de la conservation inclut la gestion génétique des petites populations, la résolution des incertitudes taxinomiques et des unités de gestion, l'utilisation d'analyses moléculaires dans l'expertise et la compréhension de la biologie des espèces. Le rôle des facteurs génétiques dans l'extinction des populations sauvages a été controversé, mais il a été mis en évidence que cela contribue grandement au risque d'extinction. La consanguinité provoque des extinctions de populations sauvages, les modélisations indiquent que la dépression de consanguinité a des effets importants sur les risques d'extinction et la plupart des espèces en danger souffrent de détérioration génétique. La gestion conservatoire sera inappropriée si les facteurs génétiques sont ignorés pour les espèces en danger. **Pour citer cet article :** R. Frankham, C. R. *Biologies* 326 (2003).

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Keywords: endangered; extinction; forensics; genetic diversity; inbreeding depression; reproductive fitness; taxonomy

Mots-clés : espèces en danger ; extinction ; expertise ; diversité génétique ; dépression de consanguinité ; fitness reproductive ; taxinomie

1. Introduction

The biodiversity of the planet is being rapidly depleted as a direct and indirect consequence of human actions. An unknown but large number of species are already extinct, while many others have reduced popu-

lation sizes that put them at risk [1]. Many species now require benign human intervention to improve their management and ensure their survival.

The primary factors contributing to extinction are habitat loss, introduced species, over exploitation and pollution. These factors are caused by humans, and are related to human population growth. Human-related factors reduce species to population sizes

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where they are susceptible to stochastic effects. These encompass environmental, demographic, or genetic (inbreeding depression, and loss of genetic diversity) stochasticity and catastrophes. Even if the original cause of population decline is removed, problems associated with small population size will still persist.

Conservation genetics deals with the genetic factors that affect extinction risk and genetic management regimes required to minimise these risks. There are 11 major genetic issues in conservation biology [1]:

- The deleterious effects of inbreeding on reproduction and survival (inbreeding depression).
- Loss of genetic diversity and ability to evolve in response to environmental change.
- Fragmentation of populations and reduction in gene flow.
- Genetic drift overriding natural selection as the main evolutionary process.
- Accumulation and loss (purging) of deleterious mutations.
- Genetic adaptation to captivity and its adverse effects on reintroduction success.
- Resolving taxonomic uncertainties.
- Defining management units within species.
- Use of molecular genetic analyses in forensics.
- Use of molecular genetic analyses to understand aspects of species biology important to conservation, and
- Deleterious effects on fitness that sometimes occurs as a result of outcrossing (outbreeding depression).

Succeeding papers in this session will consider many of these issues, and all have recently been reviewed by Frankham et al. [1]. I have chosen to concentrate on the contentious issue of the role of genetic factors in extinctions.

2. Genetics and extinction

Endangered species have small and/or declining populations, so inbreeding and loss of genetic diversity are unavoidable in them. Since inbreeding reduces reproduction and survival rates, and loss of genetic diversity reduces the ability of populations to evolve to cope with environmental change, Frankel and Soulé

[2] and others suggested that genetic factors would contribute to extinction risk in threatened species.

However, this view was challenged in the late 1980s and the contribution of genetic factors to the fate of endangered species was generally considered to be minor. Lande [3] suggested that demographic and environmental stochasticity and catastrophes would cause extinction before genetic deterioration became a serious threat to wild populations. A healthy controversy has persisted [1]. However, there is now a compelling body of both theoretical and empirical evidence indicating that genetic changes in small populations are intimately involved with their fate. Specifically:

- Inbreeding causes extinctions in deliberately inbred captive populations.
- Inbreeding has contributed to extinctions in some natural populations and there is circumstantial evidence to implicate it in many other cases.
- Computer projections based on real life histories, including demographic, environmental, and catastrophic factors, indicate that inbreeding will cause elevated extinction risks in realistic situations faced by natural populations.
- Many surviving populations have now been shown to be genetically compromised (reduced genetic diversity and inbred).
- Loss of genetic diversity increases the susceptibility of populations to extinction.

3. Inbreeding reduces reproduction and survival

Inbreeding has been known to reduce reproduction and survival (inbreeding depression) since Darwin's classic work [4]. For example, inbred individuals showed higher juvenile mortality than outbred individuals in 41 of 44 captive mammal populations studied by Ralls and Ballou [5]. On average, brother-sister mating resulted in a 33% reduction in juvenile survival. By extrapolation, it was anticipated that inbreeding would increase the risk of extinction in wild populations.

There is now clear evidence that inbreeding adversely affects most wild populations. Crnokrak and Roff [6] reviewed 157 valid data sets, including 34 species, for inbreeding depression in natural situ-

ations. In 141 cases (90%) inbred individuals had poorer attributes than comparable outbreds (i.e. they showed inbreeding depression), two were equal and only 14 were in the opposite direction. Results were very similar across birds, mammals, poikilotherms and plants. Further, significant inbreeding depression has been reported in at least another 15 taxa [1].

3.1. Relationship between inbreeding and extinction

Deliberately inbred populations of laboratory and domestic animals and plants show greatly elevated extinction rates. Between 80% and 95% of deliberately inbred populations have died out when the inbreeding coefficient exceeds 0.8 [2]. Such extinctions could be due to either inbreeding, or to demographic stochasticity, or a combination of these effects. However, under circumstances where demographic stochasticity is excluded, inbreeding clearly increased the risk of extinction in captive populations [7,8].

The above mentioned populations were rapidly inbred using brother–sister matings or self-fertilization, while natural populations of outbreeding wild animals and plants are usually subject to slower rates of inbreeding, dependent on their population sizes. Slower inbreeding allows natural selection more opportunity to remove deleterious alleles. However, even slow rates of inbreeding increase the risk of extinction; it just takes longer for inbreeding to accumulate and extinction to occur [9,10]. Mean inbreeding coefficients when 50% of populations were extinct from inbreeding were 0.62 for full-sib mating, 0.79 for populations with sizes of $N_e = 10$ and 0.77 for populations with $N_e = 20$ [11].

3.2. Do taxonomic groups differ in susceptibility to inbreeding depression?

Much information on inbreeding and extinctions come from species used in laboratory experiments. It is therefore essential to know whether these findings can be extrapolated to other species and taxonomic groups. Most studies find little evidence for differences among major diploid taxa in inbreeding depression for naturally outbreeding species [6,8,12].

The one major exception is that inbreeding depression in plants is typically higher for Gymnosperms than Angiosperms [13]. This could be related to a

higher level of polyploidy in the latter than the former. Since the rate of increase in homozygosity is slower in polyploids than in diploids, polyploids are expected to suffer less inbreeding depression [1].

4. Direct evidence of extinctions due to inbreeding and loss of genetic diversity

Inbreeding and loss of genetic diversity has been shown to increase the risk of extinction for two populations in nature. Inbreeding was a significant predictor of extinction risk for butterfly populations in Finland after the effects of all other ecological and demographic variables had been removed [14]. Further, experimental populations of the *Clarkia pulchella* plant founded with a low level of genetic diversity (and high inbreeding) exhibited 75% extinction rates over three generations in the wild, while populations with low inbreeding showed only a 21% extinction rate [15]. However, it was not clear whether these were general results, or exceptions.

5. Computer projections

Computer projections incorporating factual life history information are often used to assess the combined impact of all deterministic and stochastic factors on the probability of extinction of populations. Mills and Smouse [16] using computer simulations, found that inbreeding generally increases the risk of extinction, especially in species with low reproductive rates. These simulations encompassed only a 20 year time frame and they were criticised for not accounting for purging of deleterious alleles [17].

Brook et al. [18] conducted computer projections for 20 outbreeding bird, mammal, and invertebrate life cycles that allowed for the effects of purging. Median times to extinction were on average reduced by 24–31% when inbreeding depression of 3.14 lethal equivalents was applied to juvenile survival, compared to cases where inbreeding depression was omitted. These results underestimate the true impact of inbreeding depression, as it is approximately 12 lethal equivalents for populations in nature ([19], Frankham et al. unpublished data). A related computer projection for the rare

European plant *Gentiana pneumonanthe* yielded similar conclusions [20]. These computer projections indicate that the results of Saccheri et al. [14] and Newman and Pilson [15] are not exceptions, but are likely to apply to the majority of species.

6. Circumstantial evidence for extinctions due to inbreeding

Declines in population size or extinction in the wild have been attributed, at least in part, to inbreeding in many populations including bighorn sheep, Florida panthers, Isle Royale gray wolves, greater prairie chickens, heath hens, middle spotted woodpeckers, adders, and many island species [1]. Further, inbreeding colonial spiders have a higher rate of colony extinction than non-inbreeding species.

6.1. Extinction proneness of islands populations

Island populations of vertebrates are more prone to extinction than mainland populations [1]. This is typically attributed to ‘non-genetic’ factors, but could be due partly to inbreeding and loss of genetic diversity. Island populations typically have less genetic diversity and are more inbred than mainland populations [8,21]. Significantly, inbreeding in many island populations is at levels where captive populations show an elevated risk of extinction.

Endemic populations of vertebrates are more prone to extinction than non-endemic island populations [8]. The greater extinction proneness of endemic than non-endemic island species is predicted by genetic, but not by demographic and ecological considerations. Endemic island populations have generally existed on islands at restricted population sizes for longer than non-endemics. They are therefore expected to be more inbred, and this has been found to be the case [8]. Consequently, endemic island populations are expected to be more prone to extinction than non-endemics for genetic reasons. Conversely, there are no obvious demographic or environmental reasons why endemic and non-endemic island populations should differ in extinction proneness. Consequently, genetic factors are probably, at least partly, responsible for the extinction proneness of island populations.

7. Are species driven to extinction before genetic factors can impact?

Lande [3] suggested that species would often be driven to extinction by demographic factors before genetic factors had time to impact, and many other authors have repeated this refrain. While Lande [17] has subsequently changed his views on the contribution of genetic factors to extinctions, this is due to his championing of ‘mutational meltdown’ and not due to a retraction of his 1988 views.

If the Lande scenario is common then threatened species should show little difference in genetic diversity, compared to related non-endangered species. The majority of threatened species do not fit the Lande scenario, as most have reduced genetic diversity compared to related threatened species [22–24]. Further, the magnitude of differences is such that threatened species are likely to be suffering serious reductions in fitness, as proportionate loss of genetic diversity estimates the inbreeding coefficient. Genetic diversity has been shown to be related to fitness, as expected from the relationship between genetic diversity and inbreeding in random-mating populations [25]. Consequently, most threatened species are likely to have both reduced reproductive fitness due to inbreeding depression and reduced evolutionary potential.

8. Relationship between loss of genetic diversity and extinction

Natural populations face continuous assaults from environmental changes including new diseases, pests, parasites, competitors and predators, pollution, climatic cycles such as the El Niño–La Niña cycles, and human-induced global climate change [1]. Species must evolve to cope with these new conditions or face extinction. To evolve, species require genetic diversity. Naturally outbreeding species with large populations normally possess large stores of genetic diversity that confer differences among individuals in their responses to such environmental changes [1].

Small populations typically have lower levels of genetic diversity than large populations [1]. There are compelling theoretical predictions that loss of genetic diversity will reduce the ability of populations to evolve in response to environmental change, and

experimental evidence validates these predictions [1]. Consequently, we expect a relationship between loss of genetic diversity and extinction rate due to environmental change. However, there are only a few examples where extinctions of natural populations can be directly attributed to lack of genetic variation, as described below.

8.1. Relationship between loss of genetic diversity at self-incompatibility loci and extinction in plants

The most direct evidence of a relationship between loss of genetic diversity and increased risk of extinction comes from studies of self-incompatibility loci in plants. About half of all flowering plant species have genetic systems that reduce or prevent self-fertilisation [26]. Self-incompatibility is regulated by one or more loci that may have 50 or more alleles in large populations. If the same allele is present in a pollen grain and the stigma, fertilisation by that pollen grain will not be successful.

Self-incompatibility alleles are lost by random sampling in small populations. This leads to a reduction in the number of plants that can potentially fertilise the eggs of any individual and eventually to reduced seed set and extinction. For example, the Lakeside daisy population from Illinois declined to three plants. This population did not reproduce for 15 years despite bee pollination, as it contained so few alleles [27], i.e. this population was functionally extinct. Plants did however produce viable seed when fertilised with pollen from large populations in Ohio or Canada. While reduced fitness due to loss of self-incompatibility alleles has only been documented in a few species of plants [28,29], it is likely to be a problem, or become so, in most threatened, self-incompatible plants.

8.2. Relationship between loss of genetic diversity and susceptibility to disease, pests and parasites

Populations with low genetic diversity are expected to suffer more seriously from diseases, pests and parasites than those with high genetic diversity [1]. Novel pathogens constitute one of the most significant challenges to all species. Loss of genetic diversity severely diminishes the capacity of populations to respond to this pressure. For example, the American

chestnut was driven to near extinction in the 1950s by the introduced chestnut blight disease, as it had no genetic variation for resistance [1]. Previously, the chestnut had dominated the northeastern forests of the USA, so this event represents one of the largest ecological disasters to strike the USA.

There is circumstantial evidence that loss of genetic diversity in the major histocompatibility complex (MHC) is associated with reduced ability to evolve to cope with new and changed diseases. Genetic diversity is maintained by selection that either favours heterozygotes or rare genotypes [1]. Even though MHC diversity is maintained by selection, it is lost by genetic drift in small populations [30,31]. With reduced diversity at the MHC in small populations, a pathogen capable of killing one individual becomes capable of killing most or all.

Associations between loss of genetic diversity and inbreeding and increased susceptibility to disease and parasites have been reported in fish, Soay sheep, deer mice, bumblebees and *Drosophila* [24,32–34].

9. Why is the Lande scenario incorrect?

The Lande [3] scenario has failed numerous tests so it must be rejected for the majority of species [1]. What assumptions were made in the Lande scenario that are incorrect? Lande [3] did not present an explicit quantitative model that can be addressed point by point in a quantitative manner. However, it seems from his work and other papers around that time that four factors were probably involved, the ratio of effective to census sizes (N_e/N), the extent of interactions among stochastic factors, the extent of inbreeding depression in the wild, and the effectiveness of purging.

Genetic impacts depend on the effective population size (N_e), so the ratio of effective to census size is critical in determining genetic impacts. Around the time of Lande's paper it was typical to talk of N_e/N ratios of 0.25–0.5 [35]. Subsequently, N_e/N ratios in unmanaged populations have been found to average approximately 0.1 [36], so genetic factors impact sooner than Lande [3] would have expected.

Fluctuations in population size and sex-ratio and variation in family size all occur due to demographic and environmental stochasticity and catastrophes and result in reduced N_e/N ratios. Consequently, there are

interactions between stochastic factors that increase genetic impacts on population persistence [37,38].

It was common in the late 1980s and early 1990s for people to be sceptical about the extent of inbreeding depression in the wild. Considerable data now exists and points to much higher levels of inbreeding depression than found in captivity [1,6]. For example, Ralls and Ballou [12] found a median of 3.14 diploid lethal equivalents for captive mammals, but total inbreeding depression across the life cycle in the wild is approximately 12 lethal equivalents ([19], Frankham, O'Grady, Brook, Ballou and Tonkyn, unpublished data).

The final factor leading to an underestimation of the impact of inbreeding on population viability is the effectiveness of purging. At the time of Lande's paper, purging was considered to be effective in markedly reducing inbreeding depression. Subsequent modelling and empirical work indicates that purging effects are typically relatively small [1,39,40].

All the above points lead to greater impacts of inbreeding depression on population viability than would have been expected in 1988.

10. What are the consequences of ignoring genetic factors in threatened species management?

Recovery programs may not be successful if genetic factors are ignored. For example, the Illinois population of greater prairie chickens declined from millions to only 200 in 1962, and failed to recover following habitat restoration [41]. It showed clear evidence of inbreeding depression (reduced fertility and hatchability). However, when inbreeding effects were removed by crossing to unrelated birds from other states, the population recovered its fertility and hatchability and grew in numbers. In the case of the koala in south-eastern Australia, reintroductions using a small island population with only 2–3 founders have resulted in a substantial reduction in genetic diversity, to a rise in inbreeding, to a decrease in sperm quality, to a marked increase in testicular aplasia [42,43].

The effects of loss of self-incompatibility alleles on population fitness in plants are likely to be a major factor in species persistence, but will not be addressed unless genetic factors are recognised [27–29].

Acute reductions of population fitness occur when diploid and tetraploid populations of a species are introduced into proximity with each other [29]. Sterile triploids have resulted, with consequently reproductive wastage.

Genetic considerations are of particular importance in management of fragmented populations. Small fragmented populations with limited gene flow will lose genetic diversity and become inbred and have elevated extinction risks [1,14,44]. Adequately genetic management of fragmented populations is rare, and is one of the greatest unaddressed issues in conservation biology.

Overall, there is little effective genetic management of wild populations of threatened species, but a substantial need for it [1]. By contrast, genetic management of captive populations is widely practiced and generally well done.

11. Conclusion

Inbreeding and loss of genetic diversity are of conservation concern as they increase the risk of extinction. Inbreeding increases the risk of extinction in captive populations, and there is now strong evidence that it is one of the factors causing extinctions of wild populations. Loss of genetic diversity reduces the ability of species to evolve to cope with environmental change. Inappropriate management and allocation of resources is likely to result if genetic factors are ignored in management of threatened species.

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