Review

Genetics and extinction

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Abstract

The role of genetic factors in extinction has been a controversial issue, especially since Lande's paper [Genetics and demography in biological conservation, Science 241 (1988) 1455–1460] paper in Science. Here I review the evidence on the contribution of genetic factors to extinction risk. Inbreeding depression, loss of genetic diversity and mutation accumulation have been hypothesised to increase extinction risk. There is now compelling evidence that inbreeding depression and loss of genetic diversity increase extinction risk in laboratory populations of naturally outbreeding species. There is now clear evidence for inbreeding depression in wild species of naturally outbreeding species and strong grounds from individual case studies and from computer projections for believing that this contributes to extinction risk. Further, most species are not driven to extinction before genetic factors have time to impact. The contributions of mutation accumulation to extinction risk in threatened taxa appear to be small and to require very many generations. Thus, there is now sufficient evidence to regard the controversies regarding the contribution of genetic factors to extinction risk as resolved. If genetic factors are ignored, extinction risk will be underestimated and inappropriate recovery strategies may be used.
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Keywords: Extinction risk; Genetic diversity; Inbreeding depression; Mutation accumulation; Self-incompatibility

Contents

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1. Introduction

There is ongoing controversy about the importance of genetic factors in extinction risk. Biological extinctions are due to the combined effects of deterministic (habitat loss, over exploitation, introduced species and pollution) and stochastic (demographic, environmental, genetic and catastrophic) factors (Shaffer, 1981). Prior to 1970, genetic factors were rarely mentioned as causes of extinction. Frankel (1970, 1974) was primarily responsible for proposing that loss of genetic diversity elevated extinction risk, especially by compromising evolutionary response to environmental change. Frankel and Soulé (1981) added the deleterious effects of inbreeding to the argument, and they presumed that genetic factors had an important role in causing extinctions. Later, the issue of mutation accumulation was introduced by Lande (1995) and Lynch et al. (1995). Outbreeding between diverged populations may also lead to deleterious effects on reproductive fitness (outbreeding depression), but its effects are clearly less important overall than that of inbreeding depression (Frankham et al., 2002). It is most probable when populations that are highly differentiated genetically are crossed. I will not consider this issue in detail here.

Genetic factors affect extinction risk because threatened species have small and/or declining populations (IUCN, 2004), and in such populations inbreeding and loss of genetic diversity are unavoidable (Frankham et al., 2002). The relationships between population size, loss of genetic diversity and inbreeding in closed random mating populations are described by the following equation:

$$H_t/H_0 = (1 - 1/[2N_e])^t = 1 - F, \qquad (1)$$

where H_t is heterozygosity (Hardy–Weinberg expected heterozygosity, or gene diversity) at generation t, H_0 initial heterozygosity, N_e the genetically effective population size and F the inbreeding coefficient. Since the middle term in the equation is approximately $e^{-t/2N_e}$ this equation predicts an exponential decay of genetic diversity with generations that occurs at greater rates in smaller than larger populations (Fig. 1). The inbreeding coefficient equals the proportionate loss of genetic diversity. The rate of decay in genetic diversity and the increase in inbreeding depend upon the genetically effective population size, rather than the actual or census size. The effective size is typically much smaller than the number of potentially breeding adults in populations, averaging an order of magnitude lower than census population sizes (Frankham, 1995a).

A major controversy erupted over the role of genetic factors in extinction risk following Lande, 1988) paper in Science. He was interpreted as saying that most species are driven to extinction before genetic factors have time to impact them (the 'Lande scenario'; Pimm,
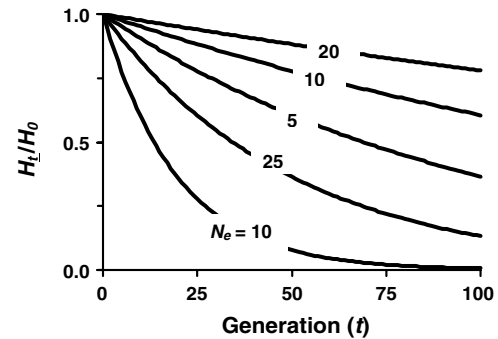

Fig. 1. Proportionate loss of genetic diversity (H_t/H_0) with generations in populations with different effective sizes (N_e).

1991; Young, 1991; Wilson, 1992; Caro and Laurenson, 1994; Caughley, 1994; Dobson, 1999; Elgar and Clode, 2001). The effectiveness of natural selection in reducing the frequency of the deleterious alleles (purging) that cause inbreeding depression has been an important part of this controversy (Lande, 1988; Hedrick, 1994).

A second controversy about the impact of inbreeding on reproductive fitness began in the late 1970s in relation to captive animals (see Ralls et al., 1979), and in the 1990s spread to scepticism about whether inbreeding depression affected species in wild habitats (see Caro and Laurenson, 1994; Caughley, 1994; Craig, 1994; Merola, 1994). A third controversy has erupted concerning the role of mutation accumulation in extinction risk for sexually reproducing species (Charlesworth et al., 1993; Lande, 1995; Lynch et al., 1995).

The purpose of this review is to examine evidence on the impacts of inbreeding depression, loss of genetic diversity and mutational accumulation on extinction risk.

2. Inbreeding depression

2.1. Effects of inbreeding on fitness in outbreeding species

Inbreeding has long been known to reduce reproduction and survival in naturally outbreeding species (inbreeding depression). Darwin (1876) provided the first compelling evidence on this, based on comparisons of the progeny of self and cross-fertilization in 57 species of plants. Selfing reduced seed production by an average of 41% and height by 13%. Not all species showed inbreeding depression for all characters studied, but virtually all showed it for most reproductive fitness characters. Subsequently, similar conclusions were found to apply for laboratory and domestic animals and plants (Charlesworth and Charlesworth, 1987; Falconer and Mackay, 1996; Lynch and Walsh, 1998). Inbreeding has deleterious consequences on all aspects of reproduction and survival, including sperm production, mating ability, female fecundity, juvenile survival, mothering

ability, age at sexual maturity and adult survival in animals, and in related components in plants (Frankham et al., 2002).

However, zoo keepers were sceptical that inbreeding depression applied to wildlife (Ralls et al., 1979). This controversy was resolved by Ralls and Ballou (1983) findings that juvenile mortality was higher in inbred than in contemporary non-inbred mammals for 41 of 44 populations studied. Further, progeny resulting from brother-sister (full-sib) mating had 33% higher juvenile mortality on average than found for non-inbred animals (Ralls et al., 1988). Deleterious effects of inbreeding on other reproductive and survival characters have also been reported for wildlife in captivity (Laikre and Ryman, 1991; Lacy et al., 1993; Laikre et al., 1996; Wilcken, 2001).

Controversy next erupted about the impacts of inbreeding on wild species in natural habitats (Caro and Laurenson, 1994; Caughley, 1994; Pimm, 1991; Wilson, 1992; Elgar and Clode, 2001). There is now ample evidence to resolve this issue. Of 157 valid data sets across 34 taxa compiled by Crnokrak and Roff (1999), 90% showed that inbred individuals had poorer reproductive fitness characters than non-inbred individuals. The few exceptions were small data sets and ones for which parentage had not been verified genetically. The effects are similar across a broad range of major taxa of animals and plants. Inbreeding depression has also been reported in at least another 15 wild populations (Frankham, 2000). The impacts of inbreeding depression are about seven-times greater in wild habitats than in captivity (Crnokrak and Roff, 1999). Lacy (1997) concluded that he was unaware of any well-studied species that did not show inbreeding depression. Overall, there is now compelling evidence that wild species in natural habitats show inbreeding depression.

2.2. Affect on extinction risk

Since inbreeding reduces reproduction and survival, it is expected to increase extinction risks under situations where other factors are controlled, or excluded. This has been verified in laboratory populations of *Drosophila*, houseflies and mice (Frankham, 1995b; Bijlsma et al., 1999, 2000; Reed and Bryant, 2000; Reed et al., 2002, 2003). While most of these studies have used full-sib inbreeding, slower inbreeding at rates within the range of many endangered species has also been shown to increase extinction risk (Reed and Bryant, 2000; Reed et al., 2003), as illustrated in Fig. 2.

While the situation in wild populations is more complex, inbreeding and loss of genetic diversity have been shown to contribute to extinction risk in the plant *Clarkia pulchella* (Newman and Pilson, 1997) and in Finnish populations of the Glanville fritillary butterfly (*Melitaea cinxia*: Saccheri et al., 1998). In the plant experiment,
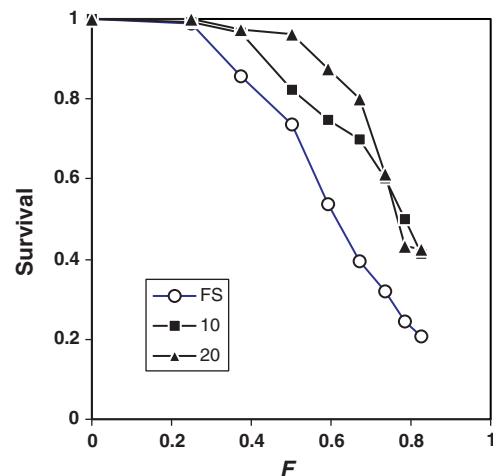

Fig. 2. Relationship between inbreeding (*F*) and proportion of replicate populations surviving for populations maintained using full-sib (FS) mating or effective sizes of 10 and 20 (Reed et al., 2003).

the extinction rate for less inbred populations (*F* = 4%) was 25% while it was 69% for more inbred populations (*F* = 8–9%), a huge difference in extinction rates for a small difference in inbreeding coefficient. In the butterfly study, 42 populations were genotyped in 1995 and their survival to the following year determined. When all factors known to be affecting extinction risk in these populations were removed, level of inbreeding was still a significant predictor of extinction risk. Overall, inbreeding explained 26% of the variation in extinction risk.

Are these two cases exceptions or part of the general story concerning the contribution of inbreeding to extinction risk? Clearly many more field studies are needed, but we need an immediate resolution of this issue, as it affects management of threatened species. Using realistic computer projections for 20 threatened species, we compared median times to extinction for models with and without inbreeding depression (Brook et al., 2002). We applied inbreeding depression at a very conservative level of 3.14 diploid lethal equivalents for juvenile survival, as found by Ralls et al. (1988) for captive mammals, and included the effects of natural selection (purging) in our models. Inbreeding depression reduced median times to extinction by 25–31% for populations with initial sizes of 50, 250 and 1000, when all known or suspected demographic and stochastic threatening factors were included in the models. Other related studies on individual taxa have reached similar conclusions (Dobson et al., 1992; Oostermeijer, 2000), provided they carried the study for sufficient generations. With a more realistic level of inbreeding depression of 12 diploid lethal equivalents spread across the life cycle (Keller, 1998), stochastic computer projections for multiple taxa indicate even greater reductions in median time to extinction due to inbreeding depression (O'Grady et al. unpublished data). Thus, most naturally outbreeding taxa are likely to have their extinction risk elevated by inbreeding.

Populations with strongly negative population growth rates were less affected by inbreeding. They were driven to extinction so rapidly that genetic factors had insufficient time to impact, as Lande (1988) suggested. No impacts of inbreeding occurred in only two of 30 taxa, ones where the impacts of anthropogenic factors were very severe. Less direct evidence indicates that the proneness to extinction of island populations of vertebrates is partially due to inbreeding and loss of genetic diversity (Frankham, 1998).

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

While the Lande (1988) scenario has been promoted by many authors, it had not until recently been subjected to a comprehensive test. If threatened species are driven to extinction before genetic factors impact, they will have similar genetic diversity to taxonomically related non-threatened taxa. If not, threatened taxa will have lower genetic diversity and consequent higher levels of inbreeding (see Eq. 1) and lowered reproductive fitness than related non-threatened taxa (Reed and Frankham, 2003). In a comprehensive meta-analysis involving 170 paired comparisons, we found that the majority of threatened taxa (77%) exhibited reduced genetic diversity (Spielman et al., 2004), leading us to reject the 'Lande scenario' for most taxa. This effect was consistent across a broad array of major taxa and the median difference in heterozygosity was 40% (Fig. 3). We were not able to determine what caused the taxa to become threatened, but the results indicate that most threatened taxa are now suffering reduced ability to evolve, elevated inbreeding and consequent reduced reproductive fitness (Reed and Frankham, 2003) and that they will suffer elevated extinction risk into the future. Further, there is still time for genetic factors to impact upon taxa with normal levels of genetic diversity.
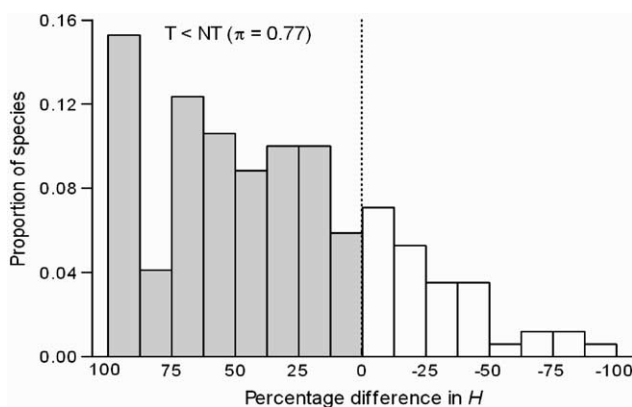

Fig. 3. Distribution of percentage differences in genetic diversity between threatened (T) and taxonomically related non-threatened (NT) taxa for 170 pairwise comparisons (Spielman et al., 2004).

For example, vulnerable taxa, the majority of our data set, have a probability of extinction of approximately 10% within 100 years (IUCN, 2004).

Why does not the 'Lande scenario' hold? New information since 1988 has changed our perceptions in four areas that all point to greater impacts of genetic factors on extinction risk. First, the effective population sizes of threatened species, the population size that determines genetic impacts (see Eq. 1), are lower than imagined in 1988. For most species, N_e is not known and must be estimated from the census size (N) and broadly based estimates of the N_e/N ratio. In 1988 and later, this ratio was thought to be 0.25–0.5 (Mace and Lande, 1991). Subsequently, I found in a meta-analysis that this ratio averaged approximately 0.1 when all relevant factors were considered (Frankham, 1995a). Thus, genetic factors impact sooner and at a greater rate than expected in 1988.

Second, information on the full impact of inbreeding depression was limited in 1988. Most people used the estimate of 3.14 lethal equivalents from Ralls et al. (1988), while current evidence now suggests inbreeding depression is around 12 lethal equivalents for the whole life cycle in the wild (Keller, 1998). Third, knowledge of the interactions between demographic and environmental stochasticity and catastrophes with inbreeding depression was limited in 1988. Subsequent information indicates strong interactions that increase the impacts of inbreeding on fitness in an extinction vortex (van Noordwijk, 1994; Tanaka, 2000).

Fourth, Lande (1988) suggested that purging was effective in removing the deleterious alleles that cause inbreeding depression. However, theoretical work indicates that purging will often have only modest effects in small populations, as deleterious alleles of small effect become effectively neutral and can drift to fixation (Hedrick, 1994; Thévenon and Couvet, 2002). Empirical evidence has typically found only moderate effects of purging (Ballou, 1997; Byers and Waller, 1999; Fowler and Whitlock, 1999; Frankham et al., 2001; Crnokrak and Barrett, 2002; Day et al., 2003; Reed et al., 2003). For example, extinction rates due to inbreeding increase more slowly with slower than faster inbreeding, but all treatments show elevated extinction rates with increasing F (Fig. 2).

A related issue concerns small surviving populations whose fitness is apparently normal (Craig, 1994; Elgar and Clode, 2001). For example, Chatham Island black robins (*Petroica traversi*), golden hamsters (*Mesocricetus auratus*) and Mauritius kestrels (*Falco punctatus*) all survived population bottlenecks of a single pair (Groombridge et al., 2000; Frankham et al., 2002). These and similar cases have led some authors to question the importance of inbreeding and loss of genetic diversity in population viability. However, the observations are highly selective, as they ignore the cases (the majority?) of small population that have gone extinct

(Laikre et al., 1997). Two unbiased studies both indicate that small surviving populations have reduced reproductive fitness. All 31 populations of *Drosophila* of size $N_e = 20$ that survived until $F = 0.8$ had lower fitness than the base population (Reed et al., 2003). Further, Briskie and Mackintosh (2004) showed that hatching failure was higher in bottlenecked than non-bottlenecked populations in New Zealand when the bottleneck size was less than 150 for 22 species of native birds and when the bottleneck was less than 600 for 15 species of introduced birds.

From the evidence above, inbreeding depression is likely to contribute to extinction risk for most threatened outbreeding taxa.

2.4. Recovery of small, inbred populations following outcrossing

Inbreeding is reduced following crossing of unrelated populations, even if those populations are themselves inbred. Outcrossing is well known to remove inbreeding depression in laboratory and domestic animals and plants (Spielman and Frankham, 1992; Falconer and Mackay, 1996). Such genetically stimulated recoveries have now been documented in the wild in populations of deer mice (*Peromyscus maniculatus*; Schwartz and Mills, 2005), gray wolf (*Canis lupus*; Vilà et al., 2003), greater prairie chicken (*Tymphanuchus cupido pinnatus*; Westemeier et al., 1998), adders (*Vipera berus*; Madsen et al., 1999, 2004), fish (*Poeciliopsis monacha*; Vrijenhoek, 1994), and plant species (*Ipomopsis aggregata*; Heschel and Paige, 1995; *Silene alba*; Richards, 2000).

2.5. Effects of inbreeding on fitness in species that inbreed

Inbreeding depression due to self-fertilization is typically less in species that inbreed naturally (23% reduction in mean fitness) than in natural outbreeders (53% reduction), based on a meta-analysis (Husband and Schemske, 1996). Given that the inbreeding coefficient increases from 0% to 50% to 75% in the first two generation of selfing, most of the difference can be explained if the species that inbreed naturally had one prior generation of selfing from an outbred base before their inbreeding depression was assessed.

I am unaware of any theoretical, simulation or empirical studies of the impact of inbreeding depression on extinction risk for naturally inbreeding taxa.

3. Loss of genetic diversity

3.1. Loss of evolutionary potential

Loss of genetic diversity in small populations is expected to increase extinction risk by adversely affecting the ability of populations to evolve to cope with environmental change (evolutionary potential). Environmental change is experienced by essentially all species, whether it be due to global climate change, new or changed diseases, pests and parasites, new predators, climatic cycles, etc. (Frankham and Kingslover, 2004). Evolutionary changes have been documented in many species in natural or human affected habitats (Briggs and Walters, 1997; Thompson, 1998; Mousseau et al., 2000; Bradshaw and Holzapfel, 2001; Umina et al., 2005).

The rate of evolutionary change (R) is determined primarily by quantitative genetic variation (Franklin, 1980) and is predicted by the breeders' equation below (Falconer and Mackay, 1996):

$$R = Sh^2, \tag{2}$$

where S the selection differential and h^2 the heritability, the proportion of the observed phenotypic variation that is due to additive genetic causes (V_A). The connection to genetic diversity is provided by the equation for V_A where it is seen to be a function of $2pq$, the expected heterozygosity in a random mating population (Falconer and Mackay, 1996), as follows:

$$V_A = \sum_{i=1,}^{\#\text{loci}} 2p_i q_i (a_i + d_i[q_i - p_i])^2, \tag{3}$$

where p and q are the allele frequencies, a twice the difference in mean phenotype between the two homozygotes and d is the deviation of the heterozygote phenotype from the mean of the two homozygotes.

Genetic diversity is widely assumed to exist for almost every trait in large wild outbreeding populations (Lewontin, 1974). However, there are exceptions as only some species of plants present in regions with heavy metal waste heaps have evolved resistance to heavy metals and only some plant species with exposure have evolved herbicide tolerance (Bradshaw, 1991). Further, Hoffmann et al. (2003) found that a population of a rainforest species of *Drosophila* near the limits of its distribution did not have genetic variation for desiccation resistance, in spite of having ample microsatellite genetic diversity.

Most information on genetic diversity in threatened species is for molecular variation, while quantitative genetic variation is the main determinant of the ability to evolve (Frankham et al., 2002). While both of these are related to heterozygosity, their correlation is low, and not different from zero for life history traits (Reed and Frankham, 2001). The low correlation could be due to differential natural selection on effectively neutral molecular versus adaptive quantitative genetic loci, to complications from non-additive genetic variation, to linkage disequilibrium, or to sampling variation. For characters peripheral to reproductive fitness with primarily additive genetic variation, the rates of loss of molecular and quantitative genetic variation in small populations do not differ significantly (Gilligan et al., 2005), pointing

to sampling variation as the major reasons for low correlations for such traits.

Characters associated with reproductive fitness exhibit higher levels of dominance and epistatic variation (together referred to as non-additive genetic variation) than characters more peripheral to fitness (Crnokrak and Roff, 1995). Following population bottlenecks, non-additive genetic variation may be converted into additive genetic variation (Robertson, 1952; Willis and Orr, 1993; Cheverud et al., 1999), leading to increases, rather than decreases in additive genetic variation. This has been observed empirically (Bryant et al., 1986; Lopez-Fanjul and Villaverde, 1989; Fernández et al., 1995; Wade et al., 1996). However, the effect is expected to be a relatively short-term one, as the relationship between additive genetic variation and inbreeding coefficient is curvilinear, but V_A is expected to be zero when $F = 1$. Further, in natural outbreeders, population size bottlenecks will lead to inbreeding and reduced fitness. As this reduces the selection differential (S in Eq. 2), it reduces the ability to evolve. Population bottlenecks have been shown to reduce the ability to evolve in tests where the combined effects of inbreeding depression and loss of genetic diversity were measured (Frankham et al., 1999, 2002, p. 235).

IUCN (McNeely et al., 1990) designate genetic diversity as one of three levels of biodiversity requiring conservation, but does inbreeding depression or loss of genetic diversity have the most important impact on extinction risk? Inbreeding depression has an immediate impact, while loss of genetic diversity typically impacts over the long-term, associated with environmental change. Vilas et al. (2005) found that inbreeding depression had significant impacts over a short time span in a plant species in Spain, whilst there was no detectable impact of genetic diversity.

3.2. Loss of alleles at self-incompatibility loci

In self-incompatible species, loss of genetic diversity reduces mate availability and population fitness due to an effect that is neither inbreeding depression, nor loss of evolutionary potential. Self-incompatibility in plants is controlled by one or more loci that have many alleles in large populations. However, such alleles are lost in small populations, reducing mate availability and thus reducing mean population fitness (Les et al., 1991; Richman and Kohn, 1996; Young et al., 2000). This effect may lead to extinction. A population of Lakeside daisy (*Hymenoxys acaulis* var. *glabra*) in Illinois was reduced to so few individuals that it did not reproduce for 15 years in spite of pollen flow (Demauro, 1993). It was only recovered by outcrossing to populations from elsewhere (Demauro, 1994). Reduced mate availability will eventually affect all threatened self-incompatible species with small populations.

In Hymenoptera, a related effect occurs at the sex determining locus of haplo-diploid species, due to the production of homozygous diploid males (Pamilo and Crozier, 1997). Even in mammals, preference for unrelated mates might reduce mate availability (Ryan and Lacy, 2003).

4. Mutation accumulation and meltdown

In large populations, deleterious alleles are kept at low frequencies due to the balance between mutation and natural selection. However, in small populations, selection is less effective and mildly deleterious alleles become selectively neutral, with their fate being determined by genetic drift (Lande, 1995; Lynch et al., 1995). Consequently, some of these mildly deleterious alleles increase in frequency and reduce reproductive fitness. Over long time spans, sufficient alleles could drift to fixation to cause negative population growth and a decline to extinction, termed mutational meltdown (Lynch et al., 1993).

The contribution of mutation accumulation to extinction risk is controversial, especially in naturally outbreeding species (Charlesworth et al., 1993; Lande, 1995; Lynch et al., 1995). Garcia-Dorado (2003) has shown that the effect of mutation accumulation depends critically on the distribution of mutational effects, being important when there are many mutations of predominantly small effect, but only minor when a substantial proportion of mutations have large effects. Favourable and compensatory mutations reduce the impacts of deleterious mutations on fitness and extinction risk (Lande, 1998; Whitlock, 2000; Whitlock et al., 2003). There is no consensus about the rate and distributions of effects of new mutations (Keightley and Lynch, 2003).

Empirical tests have also been controversial. Gilligan et al. (1997) found no evidence of greater mutational accumulation in smaller than larger populations in *Drosophila* populations with different sizes (N_e of 25, 50, 100, 250 and 500) maintained for 45–50 generations, leading us to conclude that mutation accumulation was of minor importance in normal time spans of conservation concern. While Shabalina et al. (1997) claimed to find deleterious effects of mutational accumulation in populations with N_e of 400 maintained under benign conditions, but whose fitness was measured under stressful conditions, their results appear to be due adaptations to the benign captive environment that were deleterious when moved to a stressful environment (Gilligan et al., 1997; Woodworth et al., 2002). Recently, Gu and Woodruff (personal communication) have found that mutation accumulation reduced fitness by 17% over 22 generations in populations maintained with four parents per generation, and increased the extinction risk, but no

changes were detected in populations of $N = 100$ (presumably N_e of ~ 30; Gilligan, 2001).

Asexually reproducing populations are expected to be more sensitive to mutation accumulation (Charlesworth et al., 1993). In yeast, one of 12 replicate populations went extinct due to mutation accumulations in populations with N_e of 250 over 2900 generations in a strain with an elevated mutation rate (Zeyl et al., 2001). No extinctions were observed in 12 control populations with normal mutation rates and their average population sizes did not change over time. Thus, the impact of mutational accumulation on extinction risk appears to be less important than the other genetic factors and to take very many generations.

5. Consequences of ignoring genetic factors

There is compelling evidence that inbreeding and loss of genetic variation contribute to extinction risk in captive populations, very strong evidence that they contribute in wild populations in nature, and evidence that most species are not driven to extinction before genetic factors impact them, as documented above. Thus, there is sufficient evidence to consider the controversies regarding the contribution of genetic factors to extinction risk as resolved.

However, does this matter in the context of the conservation management of threatened species? In what follows, I include additional issues relating to genetics and population viability that have not been addressed in this review (see Frankham et al., 2002). If genetic factors are ignored the following adverse effects are likely:

- Estimates of extinction risk will be substantially underestimated in many taxa (Brook et al., 2002).
- Inappropriate recovery strategies may be used. Attempts to recover the Illinois population of the greater prairie chicken by habitat restoration failed and it was only recovered following outcrossing to alleviate inbreeding depression (Westemeier et al., 1998).
- Inappropriate populations may be used for reintroductions. They may be adapted to the incorrect environment, as occurred when animals from Turkey and Sinai were added to a population of ibex in Czechoslovakia (Turcek, 1951). Alternatively, populations with low genetic diversity and high inbreeding may be used for reintroduction. Over 10,000 koalas have been restocked into southeastern Australia from an island population founded from 2–3 individuals. Not surprisingly, these restocked populations have low genetic diversity and lowered fitness, including lowered sperm concentrations and motility and an elevated frequency of testicular aplasia (Seymour et al., 2001).

- Fragmented populations may not be correctly diagnosed, and gene flow between them may not be correctly managed (Frankham et al., 2002).
- Problems associated with loss of self-incompatibility alleles in small populations will not be addressed (Young et al., 2000).
- Problems due to crossing of populations with different chromosome numbers will not be diagnosed and remedied. An endangered grassland daisy in south-eastern Australia exists in both diploid and tetraploid forms. A restoration effort inadvertently placed plants of one ploidy near those of the other ploidy and some sterile triploid seeds resulted (Young and Murray, 2000).
- Different evolutionary significant units or taxa may be mixed and reduced fitness may result (outbreeding depression). Different sub-species of orangutans have been crossed in zoos and the hybrid animals (that are not suffering any reductions in fitness) are now not being bred and are using up spaces that could be used for captive breeding of this endangered species (Frankham et al., 2002). Similarly, African and Asiatic lions were inadvertently mixed in a captive breeding program. When this was discovered, the program was discontinued but not until a substantial amount of money had been wasted (Frankham et al., 2002).

Investigations of extinction risk, or recovery plans for threatened taxa that ignore genetic factors can no longer be considered scientifically credible.

6. Future directions

There are several areas where essential information is lacking, or controversial, or limited in scope, as follows:

- There is a great need for information on the impact of genetic factors on extinction risk for taxa that regularly inbreed or are asexual, haplo-diploid or polyploid.
- There is a need for much more information on the extent of inbreeding depression for the full life cycle for a broad range of outbreeding taxa in the wild. Additional information is required on the impacts of inbreeding depression on extinction risk in natural populations.
- Information is required on the relative contributions and interactions of inbreeding depression versus 'non-genetic' factors on extinction risk in wild populations, for example from realistic computer simulations.
- More information is required on the relative contributions of inbreeding depression, loss of genetic diversity and mutation accumulation to extinction risk, especially over the long term.

- Information on the extent of outbreeding depression and factors that influence it are sorely needed.
- Research is needed into the genetic impacts of habitat fragmentation and means for managing such situations. While there is need for field data, computer simulations should contribute in a major way to this in the short term, as many variables need to be evaluated simultaneously (Reed, 2004).

7. Conclusions

- Inbreeding and loss of genetic diversity contribute to extinction risk in small laboratory populations.
- Inbreeding depression contributes to extinction risk in most wild populations of naturally outbreeding species and loss of genetic diversity is expected to contribute in the long-term.
- Ignoring genetic factors may lead to inappropriate recovery strategies.
- Any study of extinction risk or minimum viable population sizes that excludes genetic factors will underestimate the true threat.

Acknowledgements

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