

Introduction: genetics, demography and the conservation of fragmented populations

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In one of the earliest books on modern conservation biology, Soulé & Wilcox describe the science of conservation biology as being ‘as broad as biology itself. It focuses the knowledge and tools of all biological disciplines, from molecular biology to population biology, on one issue – nature conservation’ (Soulé & Wilcox, 1980a). Subsequently, in his seminal paper on the nature of conservation biology, Soulé extended this concept to include non-biological sciences such as hazard evaluation and the social sciences (Soulé, 1985). He went on to describe conservation biology as being holistic in nature, in the sense that multidisciplinary approaches will ultimately be the most fruitful. He also stressed that the borders between traditional scientific pursuits and between the ‘pure’ and ‘applied’ sciences were artificial in the conservation context.

The truth in these statements with regard the multidisciplinary nature of conservation biology can be revealed by an examination of any issue of the frontline journal *Conservation Biology*. Here you will find papers written by ecologists, resource managers, geneticists, sociologists, political scientists, mathematicians and even politicians. However, for a multidisciplinary approach to be effective, particularly in a crisis discipline such as conservation biology (Soulé, 1985), there must be a high level of integration among the separate fields. It is this integration which we feel has generally been lacking in much of modern conservation research.

There are many possible reasons for this lack of integration. Soulé & Wilcox (1980a) talk of academic snobbery which hampered the acceptance of conservation biology within academic circles, and the subsequent academic elitism (Soulé, 1986a), such that once accepted, it became the ‘property’ of academia and academic disciplines. While these observations are justified, there is also a degree of discipline rivalry among different areas of

scientific pursuit. This rivalry is perpetuated by the structure of university faculties and departments, and the patterns of research funding worldwide. In addition, it reflects the educational and professional background of the first generation of conservation-biology practitioners. Through the period of the 1950s–80s there was a move away from the training of ‘field biologists’ or ‘naturalists’, as was common prior to this period, to increasing specialisation. This level of specialisation became extreme in the 1970s and 1980s when graduates were no longer zoologists or geneticists, but rather physiologists, behaviourists, morphologists, or ecologists or population, bacterial, or molecular geneticists. This high degree of specialisation leads to an increased sense of insecurity and fear (and often contempt) of things we don’t know, which obviously does not promote integrative collaborative associations. In 1986 Soulé noted that there were no degree programmes in conservation biology, which he viewed as a major impediment to the future of the science. Fortunately this has turned around with many hundreds of broad-based degree and graduate programmes in conservation biology being offered worldwide.

Nowhere has this lack of integration within conservation biology been more evident than between the traditionally somewhat rival fields of ecology and genetics. Over the last 20 years, ecologists have been busily and rigorously investigating the roles of demographic processes such as changes in habitat quality and quantity, population growth rates, breeding structures and migration on species extinction, while population geneticists have been just as industrious looking at loss of genetic diversity, inbreeding and changes in fitness, with little interaction between the two groups. The lack of integration between these two fundamentally related areas of pursuit is somewhat surprising given that one of the earliest and most cited papers in modern conservation biology, by Gilpin & Soulé (1986), clearly details the interaction of demographic and genetic processes in the extinction process.

This disassociation between genetics and demography has been perpetuated in the literature by two very influential papers and has been popularised by articles such as that by Martin Brookes in *New Scientist* (Brookes, 1997). In his commentary Brookes states that ‘money spent on conservation genetics would be better spent on either good science or good conservation, rather than a halfway house of nothingness’. He goes on to say that ‘while the ship is sinking, conservation geneticists are busy counting the deck chairs. Conservation and genetics, like pop and politics, just don’t mix. A swift divorce should leave both science, and what’s left of life on Earth, in better shape.’

The first important paper, by Lande (1988) published in *Science*, argued that for wild populations, demographic factors may usually be of more importance than genetic factors in assessing the requirements for long-term species persistence. However, he concludes by saying that there is an immediate practical need in biological conservation for understanding the interaction of demographic *and* genetic factors in the extinction of small populations and that future conservation plans should incorporate both demography and population genetics in assessing the requirements for species survival. These latter statements are often ignored by those wishing to propagate the genetics/demography dichotomy.

The second paper, by Graeme Caughley (1994) and published in the *Journal of Animal Ecology* just before he died, has generated the most controversy and discussion on this issue. In his paper, Caughley made the distinction between what he termed the 'small-population paradigm' and the 'declining-population paradigm'. He argued that the former sought to determine the risk of extinction inherent in low numbers, whereas the latter dealt with the causes of smallness and its cure; essentially representing stochastic and deterministic processes respectively. In what is an intellectually stimulating and elegantly argued hypothesis Caughley states that 'no instance of extinction by genetic malfunction has been reported, whereas the examples of driven extinction are plentiful. Genetic thinking often intrudes where it is not relevant and where it sometimes obscures the real issues. . . .' However, despite these statements, Caughley, like Lande, finishes on a more positive note by saying 'The declining-population paradigm is urgently in need of more theory. The small-population paradigm needs more practice. Each has much to learn from the other. In combination they might enlarge our idea of what is possible.'

The publication of Caughley's article subsequently led to an essay by Hedrick *et al.* (1996) appearing in *Conservation Biology*. In this paper the authors argue that Caughley's paper had created a false dichotomy and also contained a number of misunderstandings about the role of both demography and genetics in extinctions. They argued that 'both the deterministic factors that reduce population size and the stochastic factors that lead to the final extinction of a small population are critical to consider in preventing extinction. Only through an overall and comprehensive effort, which we call inclusive population viability analysis, can extinction processes be understood and mitigated.'

While these papers seem to promote the differences between genetics and demography, essentially they all emphasise the same points, viz. that both genetics and demography and their interactions are important in the

extinction process and that only by the integration of these two fields can we hope to achieve effective conservation management and long-term population and species survival. This call for integration has been supported by others (e.g. Nunnery & Campbell, 1993; Mills & Smouse, 1994; Schemske *et al.*, 1994; Soulé & Mills, 1998) and brings us to the rationale behind this volume.

Although the debate has distracted many researchers and delayed collaborative and integrated research in some areas, there has been considerable progress in recent years to the extent that we felt there was a need for a synthetic treatment of current activities. Undoubtedly the development and application of highly variable DNA markers such as microsatellites (Bruford *et al.*, 1996), the increase in speed, and reduction in cost, of DNA sequence analysis, and the possibility for non-invasive DNA sampling (Morin & Woodruff, 1996) have led to a rapid expansion of the field of molecular ecology in which any distinction between genetics and ecology is lost. In addition, the advances in mathematical ecology and increases in computing power and speed have led to the development of more realistic models of population dynamics and extinction probabilities, many of which incorporate genetic data. The two fields are thus becoming more inclusive and integrative through their normal advances. This can only benefit the science of conservation biology.

Critical factors in the extinction process, such as population size, breeding structure and dispersal, are now routinely estimated by a combination of genetic and demographic techniques. Genetic data are being used to define units for conservation management and for inferring past and recent changes in population structure and dynamics. In addition, molecular markers can be used to identify and track individuals within populations, which is useful for the development of spatially explicit individual-based models for population persistence.

This volume, which grew out of a symposium of the same name run during the 1998 meeting of the Society for Conservation Biology held in Sydney, Australia, aims to showcase some of the recent and ongoing work which exemplifies attempts to integrate demographic and genetic data in an effort to understand the impacts of habitat fragmentation on population and species survival. Habitat fragmentation is recognised as one of the major environmental factors threatening the survival of populations and species worldwide. Fragmentation has dramatically shaped large areas of temperate and tropical landscapes, forests, heathlands, prairies and grasslands alike into ecosystems that now bear little structural, and probably limited functional, resemblance to the original. For example between 1978

and 1988 the mean rate of deforestation and fragmentation in the Brazilian Amazon basin was estimated to be 53 000 km² per year (Skole & Tucker, 1993). For many plants and animals, preservation within relatively intact habitats is no longer an option, and for these, a quantitative understanding of the effects of fragmentation on population processes and viability is now a prerequisite if informed management decisions are to be made for their long-term conservation. However, although the demographic (e.g. Wilcove *et al.*, 1986; Saunders *et al.*, 1991) and genetic (e.g. Young *et al.*, 1996) consequences of fragmentation have been documented, very few attempts have been made to examine these simultaneously and their interaction within single populations.

The first section of this book contains a series of six chapters which each provide an overview of the important genetic and demographic issues relating to conservation biology and provide a framework for the subsequent empirical studies. Sherwin & Moritz (Chapter 2) give an overview of the genetic consequences of fragmentation, with particular emphasis on the loss of genetic diversity. This is followed by Dudash & Fenster (Chapter 3) who focus on perhaps the two most important issues with potential to link genetics and demography, viz. inbreeding and outbreeding depression. Holsinger (Chapter 4) provides a description of the demographic factors relating to extinction in small populations. Given that many fragmented populations exist as a metapopulation, Thrall, Burdon & Murray (Chapter 5) give an overview of metapopulation theory in terms of population structure and dynamics. Burgman & Possingham (Chapter 6) outline the past and future applications of population viability analyses (PVAs) and provide a checklist of what a good PVA should include. Finally Hedrick (Chapter 7) gives some examples of the application of population genetics and molecular markers for providing both genetic and demographic data for threatened species.

These introductory chapters are followed by a series of 12 empirical case studies covering both plants and animals. Each of these studies investigates the genetic and demographic consequences of fragmentation and their interactions in small populations. While some studies are clearly preliminary, others have reached the stage of incorporating genetic and demographic information into quantitative models of population persistence, for example the work of Daniels, Priddy & Walters (Chapter 8) on red-cockaded woodpeckers and Oostermeijer on *Gentiana pneumonanthe* (Chapter 18). Although some chapters are more 'demographic' or more 'genetic' than others, there is nowhere any debate as to the relative importance of one data set over another. Authors have used all the data available to them, regard-

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6 | Geoffrey M. Clarke & Andrew G. Young

less of the scientific discipline that provided the tools to generate it, to attempt to understand both the causes and consequences of fragmentation. They provide examples of what can be done in terms of the provision of data important for effective conservation management of threatened species when one ignores the distractions of petty academic snobbery and rivalry. The value of these studies rests on this level of inclusiveness.

Thus we believe this volume represents an overview of the application of modern conservation biology to the issue of habitat fragmentation as Soulé originally imagined it, viz. a holistic, multidisciplinary and integrated science, unified by a common purpose – nature conservation.

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PART I

Introductory concepts

Managing and monitoring genetic erosion

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ABSTRACT

Fragmentation, decline or perturbation of a species can lead to genetic changes. Often these changes can have adverse implications for the conservation of the species, but there is a diversity of responses by different species. Therefore, managers must use a variety of methods to detect, avert or remedy genetic changes which actually affect population viability. The objective should be to maintain optimal fitness in changing conditions, rather than to maintain specific arrays of phenotypes. This effort should be accompanied by monitoring of genetic contributions to fitness, to confirm the effectiveness of the conservation genetic strategy. This approach presumes we have the ability to directly or indirectly manipulate and measure adaptive genetic variants, such as many multilocus (quantitative) traits, or a representative array of single-locus traits associated with fitness. Such analyses are challenging, but are becoming more accessible. It is also important to examine the association between adaptive diversity and surrogates which may be more amenable to monitoring or manipulation, such as neutral DNA variants, size or number of populations, or the range of ecological conditions in which populations of the species are found. In evaluating different types of genetic variation and their surrogates, two important points are the replaceability of the variation (that is, how long it would take for the variation to be replaced) and its utility (likely contribution to adaptation).

INTRODUCTION

Biodiversity conservation targets three interdependent levels: ecosystems, species and genes. This chapter will highlight genetic variation within species, an area which is currently experiencing a wealth of new field, laboratory and statistical methods. A declining or fragmenting species may experience genetic changes including loss of differentiated populations, al-

(a)									
A1/A1	A1/A1	A1/A1	A1/A1						
A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	
A2/A2	A2/A2	A2/A2	A2/A2						
A1/A3	A1/A3	A1/A3	A1/A3	A1/A3	A1/A3	A1/A3	A1/A3	A1/A3	
A2/A3	A2/A3	A2/A3	A2/A3	A2/A3	A2/A3	A2/A3	A2/A3	A2/A3	
A3/A3	A3/A3	A3/A3	A3/A3						
(b)									
A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1
A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2
A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2	A1/A2
A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2
(c)									
A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1				
A1/A1	A1/A1	A1/A1	A1/A1	A1/A1	A1/A1				
A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2				
A2/A2	A2/A2	A2/A2	A2/A2	A2/A2	A2/A2				
A3/A3	A3/A3	A3/A3	A3/A3	A3/A3	A3/A3				
A3/A3	A3/A3	A3/A3	A3/A3	A3/A3	A3/A3				

Fig. 2.1. The difference between inbreeding and lowered genetic variation among individuals. (a) A population in Hardy–Weinberg equilibrium; gene diversity $H = 0.67$, observed heterozygosity $H_o = 0.67$, allelic diversity $K = 3$, inbreeding coefficient (calculated from the depression of heterozygosity relative to Hardy–Weinberg equilibrium) $F = 0$. (b) A population with lower genetic variation than (a), but no evidence of inbreeding; this population is also in Hardy–Weinberg equilibrium; $H = 0.5$, $H_o = 0.5$, $K = 2$, $F = 0$. (c) A population with the same genetic variation (H , K) among individuals as (a), but also a history of recent inbreeding which has resulted in deviation from Hardy–Weinberg equilibrium – deficit of heterozygotes. $H = 0.67$, $H_o = 0$, $K = 3$, $F = 1$.

Gene diversity (H) refers to the chance that random mating would produce a heterozygote at any locus, or the average expected Hardy–Weinberg heterozygosity. Allelic diversity (K) refers to the number of alleles at the average locus. We use the word ‘inbreeding’ to refer to the result of mating between relatives, not as a general term for reduced genetic variation in the population; these often-confused concepts are further clarified in Templeton & Read (1994).

teration of differentiation between populations, loss of variation among members of the same population and changes to the level of inbreeding (Fig. 2.1). These changes are unlikely to be positive for conservation, although sometimes they may be of no immediate conservation significance (Lande, 1988). Diminished genetic variation between populations, or loss

of distinct populations, reduces the opportunity for adaptive responses to geographically varying local conditions. Lowered genetic variation within populations also reduces the opportunity for adaptation, and may result in reduced reproduction or survival and thereby reduce the viability of the population (Madsen *et al.*, 1996). Inbreeding can also reduce fitness (Ralls *et al.*, 1988). The importance of genetic variation to short-term viability depends upon many aspects of the particular species' biology, including the chromosomal system (James *et al.*, 1991), mating system (Young *et al.*, Chapter 19, this volume) and reproductive potential (Mills & Smouse, 1994). Some species survive with very little variation detectable at a molecular level (Reeve *et al.*, 1990).

Faced with this diversity of responses to genetic change, a conservation manager must use appropriate monitoring to judge whether erosion of genetic variation is actually affecting population viability. When necessary, the manager must also consider how best to avert or remedy erosion of variation. Like most conservation problems, the solutions to genetic problems are easier if action is taken early in the process of decline, when the existence of a number of individuals and populations allows choice of various management strategies. However, managers are often faced with small isolated populations, or even a single small remaining population. Whatever the situation, conservation genetic decisions should be based on the replaceability and utility of genetically determined phenotypic variation. Replaceability depends heavily upon the origin of the variation – the longer it took for the variation to accumulate, the slower its replacement is likely to be. The utility of the variation depends upon its likely importance for current and future adaptation, and therefore its contribution to the viability of populations.

Figure 2.2 shows a classification of overlapping types of genetically determined variation within and between populations. Recently, there has been intense conservation interest in the historical component of genetic diversity (categories 1, 3, 5, 7 in Fig. 2.2), which refers to variants that have accumulated over thousands of generations through the random processes of drift and mutation, and also possibly through selection and adaptation. This historical component is essentially irreplaceable because the circumstances which generated the variation can only be surmised, and the time-scale cannot be replicated in a conservation program (Moritz, 1999a). For short-term conservation, a second type of genetic variation is important: variants that affect current adaptation and viability (categories 3, 4, 5, 6 in Fig. 2.2). If lost, phenotypes corresponding to these variants (especially 4 and 6) can potentially be re-created relatively rapidly through selection,