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Introduction

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When it comes to advocating animal conservation, it is difficult to be convincing without becoming alarmist. The fact is, time is running out for many of the world's animal species. Habitat loss, introduced species, over-exploitation and pollution, all caused by human activities, combine with stochastic factors to place ever-increasing pressure on natural populations (Primack 2002). The estimates of the mid-1990s, predicting that thousands of species and millions of unique populations would go extinct in the following decades (Ehrlich and Wilson 1991; Smith *et al.* 1993; Lawton and May 1995), remain as relevant as when they were first made, and we are still living in an era of unprecedented biodiversity loss, with current extinction rates 100–1000 times the background rate (Primack 2002) and 5000–25 000 times that recorded in the fossil record (Frankham *et al.* 2002; but see Mace *et al.* 1996). Recently, however, there have been some positive signs in the media that biologists' warnings are being received (e.g. Gianni 2004; Devine *et al.* 2006; Black 2006; Gabriel 2007; Stern 2007), and a rapid and efficient approach in providing information pertinent to biodiversity preservation could be pivotal in policy decision and in optimizing resource allocation (Naidoo and Ricketts 2006; Marsh *et al.* 2007). Since the foundation of the field of conservation biology, it has been argued that a synergy between conservation biology and advanced population genetics could provide important information that policy-makers need. As should be obvious by its title, the purpose of this book is an attempt to go some way towards maturing such a synergy; hence, this introduction presents a brief history and the current state of this partnership.

THE EXTINCTION CRISIS

In order to be convinced of the urgency for animal conservation and the information necessary to practise it, an update on the current extinction

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crisis is pertinent. The IUCN Red List of Threatened Species is one of the most powerful tools available for assessing the extent of this crisis (Butchart *et al.* 2005; Rodrigues *et al.* 2006; Cardillo *et al.* 2006; but see Marsh *et al.* 2007). Of the 1.1–1.8 million known species of animals (Lecointre and Le Guyader 2001; Primack 2002; Halliday 2006; IUCN 2006), 7725 are listed by the IUCN (2006) as vulnerable, endangered or critically endangered. These include highly publicized and charismatic megafauna, such as the blue whale (*Balaenoptera musculus*) and the giant panda (*Ailuropoda melanoleuca*), a much longer list of smaller obscure creatures with curious names, like the booroolong frog (*Litoria booroolongensis*) and the pale lilliput naiad (*Toxolasma cylindrellus*), and, sadly, our closest nonhuman relatives the gorilla (*Gorilla gorilla*), the bonobo (*Pan paniscus*) and the orang-utan (*Pongo pygmaeus*).

Although the IUCN data have their flaws and gaps, in general they present an overwhelming picture of species decline. While amphibians are often quoted in the scientific and layman's literature as being the most threatened class of animals (one third of known species are at risk), with mammals, cartilaginous fishes and birds close behind (25, 13 and 12% of species in these groups, respectively, are listed as threatened; see Fig. 1.1, black bars), Fig. 1.1 (white bars) also shows that these four animal classes are the most thoroughly evaluated by the IUCN. In fact, the state of virtually all bird, mammal and amphibian species and more than 60% of cartilaginous fish species are listed as evaluated. Interestingly, a comparison of the number of species listed as *threatened* with the total number of *evaluated* species shows that 45% of evaluated ray-finned bony fish and mollusc species, 51% of reptiles and an astonishing 62% of arthropods are threatened (Fig. 1.1, black bars/grey bars). These numbers are almost certainly inflated since species from these taxonomic groups are probably more likely to be surveyed if they are noticeably threatened. However, if the evaluations of the less visible animal species are even vaguely representative, we can expect that many of these are also at serious risk of extinction and urgently need to be identified, as well as preserved and publicized. As a case in point, butterflies are among the best-studied arthropods and species extinction is reported in several cases (McLaughlin *et al.* 2002). A comparison of population and regional extinctions of birds, butterflies and vascular plants from Britain shows that butterflies experienced the greatest net losses in recent decades, disappearing on average from 13% of their previously occupied 10-kilometre squares (Thomas *et al.* 2004). If insects elsewhere in the world are similarly sensitive, the known global extinction rates of vertebrate species have an unrecorded parallel among the invertebrates.

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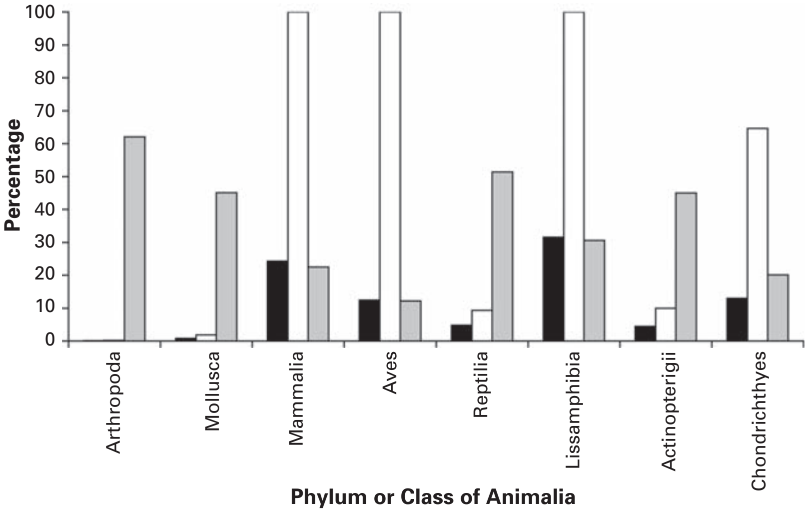

Figure 1.1. Percentage of *known* animal species listed as vulnerable, endangered or critically endangered on the IUCN Red List (2006) (black bars) compared with the total percentage *surveyed* by the IUCN (white bars). Grey bars show the *percentage* of IUCN-surveyed species listed as vulnerable, endangered or critically endangered in each taxonomic category.

THE SYNERGY BETWEEN CONSERVATION BIOLOGY AND GENETICS

Given the scale of the problem and the number of species involved, it is not surprising that conservation biology has emerged as a 'crisis discipline', a multidisciplinary approach to stemming the rapid rise in species' extinctions combining ecology, genetics and wildlife biology. However, the synergy of conservation biology and genetics has been a longer and more painful process than the initial optimism of its founding fathers would have led us to believe.

Conservation biology itself emerged as a field less than 30 years ago when, in 1978, Michael Soulé and Bruce Wilcox organized the 1st International Conference on Conservation Biology at the San Diego Wild Animal Park (Soulé and Wilcox 1980). Seven years later, in May 1985, Soulé, together with Paul Ehrlich and Jared Diamond, founded the Society for Conservation Biology. At that time, Soulé outlined the ethical principles of the field, which included the preservation of species and community diversity, and the maintenance of ecological and evolutionary processes (Soulé 1985). Upholding the convictions of philosophers such as Emerson (1836), Muir (1916), and Naess (Naess 1973; Naess and Sessions 1984), Soulé also maintained that biological diversity has its own intrinsic

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value. What makes this field unique, and ultimately inspiring, is that it is driven by a wide assortment of biologists from these various disciplines who are extraordinarily dedicated to preserving biological diversity. In fact, Soulé (1986) attributed the upsurge in conservation awareness, in part, to the need for academics to feel 'relevant' or altruistic in the environmental movement of the 1970s.

Conservation biologists realized they needed rapid, efficient, and relatively cheap methods for acquiring the relevant information for planning and implementing conservation strategies. One of the most powerful instruments for the conservation toolbox was immediately identified as population genetics. As far back as 1970, Frankel recognized the importance of genetics to conservation biology (Frankel 1970, 1974), and Frankel and Soulé produced the seminal text on the subject in 1981 (Frankel and Soulé 1981; Bruford 1998). Soulé went on to advocate genetics as the 'future' of conservation biology in later publications (Soulé 1986, 1987; Soulé and Simberloff 1986), as did others throughout the 1980s (e.g. Schonewald-Cox *et al*. 1983).

At that time, the confidence placed in genetics did not seem far-fetched since the theoretical foundations of this field had been set down some years before by Sewall Wright, John B. S. Haldane and Ronald A. Fisher (Fisher 1930; Wright 1931, 1943; Haldane 1956), and these authors also defined mathematically many of the standard variables we still use today, such as effective population size, mutation rates, and levels of inbreeding. In addition, Fisher established the maximum likelihood approach, and Wright (1940, 1943, 1965) proposed the use of *F*-statistics (in particular, F_{ST}) to express the partitioning of genetic differentiation (see also Weir and Cockerham 1984; Hartl and Clark 1989), as well as the mathematical basis for metapopulation analysis (the understanding of the spatial distribution of populations, and the relative importance of migration and of each population in maintaining the species); this latter theory was rearticulated by Andrewartha and Birch (1954), as well as Levins (1969, 1970).

But despite significant steps in theoretical population biology, population genetics only became much more useful to conservation biology with the development of a fantastic array of fast, accurate, relatively cheap and non-invasive genetic techniques that allowed the characterization of a sufficient number of loci for statistical analyses. Younger readers may not appreciate the remarkably rapid revolution that many of the authors of this book have witnessed. One of the first major advances, allozyme electrophoresis, only became possible for humans, model laboratory organisms such as *Drosophila* and some wild populations in the mid-1960s (Harris

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1966; Hubby and Lewontin 1966; Selander and Yang 1969), and quickly became extremely widespread, especially for testing population genetic theory developed at this time (e.g. Nevo 1984). The advent of allozyme markers was paralleled by a plethora of activity in theoretical population genetics (e.g. Crow and Kimura 1970; Dobzhansky 1970; Lewontin 1974; Nei 1975; Hartl and Clark 1989 and references therein) and island biogeography (MacArthur and Wilson 1963, 1967), leading to hypotheses on the impact of changes in population size and structure, migration and dispersal, selection and drift. However, although electrophoretic methods are extremely cheap, rapid and reliable, and are still in use today for screening many organisms, only a few biologists attempted to apply these methods to endangered species, since large tissue samples were rarely available for these taxa (e.g. Bonnell and Selander 1974). In addition, from a conservation point of view, these protein markers gave somewhat unsatisfactory results because they required the killing of individuals, evolve relatively slowly and are hence non-polymorphic in many small populations (Carvalho 1998).

Successive advances in molecular biology continued to provide hope for conservationists. Painstaking work during the late 1960s and early 1970s to enable the manipulation of DNA molecules saw the advent of RFLP analysis (Linn and Arber 1968) and Southern blotting (Southern 1975), and led to the first comparison of several mitochondrial DNA (mtDNA) sequences (e.g. Brown *et al.* 1979). Further breakthroughs included cloning and manual DNA sequencing techniques (Maxam and Gilbert 1977; Sanger *et al.* 1977; Maniatus *et al.* 1978), but the first study of sequence variation in a natural population was only published by Kreitman in 1983, in *Drosophila*. The amplification and visualization of tandem repeats DNA, or DNA fingerprinting (Jeffreys *et al.* 1985a, b), was also hailed as a technological breakthrough and was applied to the study of some natural populations (e.g. Burke and Bruford 1987; Hoelzel and Amos 1988). However, even throughout the 1980s, laboratory workers were still taking days to extract a few copies of mtDNA using syringes and room-sized centrifuges, and struggling with manual reading of sequences from blurry, radioactive gels.

Then, finally, what conservation biology had been waiting for: PCR, or the polymerase chain reaction, for DNA amplification. Originally developed by Mullis *et al.* (1986) and Saiki *et al.* (1988), this versatile technique soon evolved from coaxing PCR products out of a series of manually controlled waterbaths to relatively cheap, incredibly rapid automated analysis that we see today (Olsen *et al.* 1996; O'Reilly and Wright 1995). These technological advancements in molecular techniques have made possible the characterization of a high number of DNA fragments and thus genetic markers in a large number of individuals in a relatively short period of time (see **Vernesi and Bruford**, this volume).

Conservation biologists were quick to realize the benefits of this simple, robust technique for which only minute tissue samples were required (e.g. Garza and Woodruff 1992; Hoelzel 1994; Morin *et al.* 1994; O'Brien 1994a, b; Mace *et al.* 1996; Mills *et al.* 2000). Robust statistical techniques were soon developed to match the extensive molecular data being produced, and those for a number of DNA sequences became available from the 1980s (Felsenstein 1981, 1995; Saitou and Nei 1987; Miyamoto and Cracraft 1991; Hillis *et al.* 1996). In fact, most conservation biology texts from the 1980s onwards included a chapter on the 'field' of conservation genetics (e.g. Western and Pearl 1989; Fiedler and Jain 1992; Meffe and Carroll 1994; Spellerberg 1996; Steinberg and Jordan 1998), and a number of overviews of the application of these new molecular methods to conservation were published (e.g. Avise 1989, 1994; Hedrick and Miller 1992; Loeschcke *et al.* 1994; Moritz 1994a; Schierwater *et al.* 1994; Avise and Hamrick 1996; McCullough 1996; Smith and Wayne 1996; Hoelzel 1998; Frankham 1999; King and Burke 1999; Landweber and Dobson 1999; Young and Clarke 2000; Hedrick 2002, 2003; Pearse and Crandall 2004).

However, even up to the mid-1990s, the application of genetics to conservation left many deluded, as it still wasn't entirely clear how much population genetics would concretely contribute to conservation. One of the principal reasons for this disappointment was that it had been fervently believed that the estimation of genetic diversity using neutral markers would *in itself* lead to an assessment of the loss of adaptive potential and an understanding of the genetic 'health' of populations and species. In fact, one of the basic premises of conservation genetics was that loss of heterozygosity, or genetic variability, could be correlated with a loss in reproductive fitness. However, although Frankel and Soulé (1981) made a lengthy and compelling theoretical and empirical argument to support this correlation, only one recent meta-analysis supports it (Reed and Frankham 2003), and this basic premise of conservation genetics always was, and is still hotly debated (Caughley 1994; Gray 1996; Frankham 1999; Hedrick 2001; Reed and Frankham 2001; Moss *et al.* 2003). In addition, although several comparative studies have shown that population size varies directly with neutral genetic diversity (Frankham 1996, 1997, 1998), there has always been some scepticism that the genetic effects of small populations are deleterious, or that they lead to extinction (Berry 1983; Amos and

Balmford 2001; Jamieson 2007; Reed 2007). Lande (1988) also claimed that demographic factors were probably more important than genetics for promoting extinctions in small populations.

It is clear that not all conservationists or geneticists were convinced that measures of neutral genetic diversity would lead to the promised land. In addition to doubts about the interpretation of neutral genetic variation, Caughley (1994) and Meffe and Carroll (1994) expressed concern that overconfidence in genetic theory would lead some conservationists to ignore factors such as habitat destruction and disease. In general these criticisms were useful, leading to better definitions of genetic diversity (Frankham 1995; DeSalle and Amato 2004), inducing theoreticians to develop more accurate estimates and conduct more careful meta-analyses (Spielman *et al.* 2004), and encouraging conservation geneticists to interpret the results of genetical analysis within the wider historical scenario of a population or species (Avise 1996; Moritz 2002; DeSalle 2005). In a way, these arguments also brought conservationists and geneticists to consider a closer collaboration, since it was realized that a thorough knowledge of the natural history of a species was essential for interpreting genetic data (Steinberg and Jordan 1998). However, although measures of neutral genetic diversity currently remain a theoretical concern in themselves as a measure of inbreeding (mainly used for captive breeding programmes), and only secondarily as a (poor) surrogate measure of the loss of adaptive potential, many authors agree that a more accurate estimate of adaptive potential can only be made using genetic variability in quantitative trait loci (QTLs; Knott and Haley 1998; Lynch and Walsh 1998; Beebee 2005; Fitzpatrick *et al.* 2005), although these markers have not yet reached their full potential (Erickson 2005; see chapters in this volume by **Bonin and Bernachez**, **Tiira and Primmer**, **Vernesi and Bruford**).

More importantly, other geneticists, such as Avise (1996) have stepped past the genetic diversity debate and pointed out that the most important contribution of genetics to conservation is to significantly increase our knowledge of various aspects of particular species, including behaviour, ecology and evolution (see also Holsinger 1996; Mace *et al.* 1996; Reed 2007). In this regard, the advent of large numbers of nuclear markers and their associated analytical techniques have truly matured the synergy between population genetics and conservation by providing the necessary set of powerful tools for estimating basic ecological and demographic variables. While the amplification and automated sequencing of large, mainly neutral mtDNA molecules is still essential for taxonomic studies and macrogeographic pattern analysis, amplification and analysis of short tandem repeats (STRs or microsatellites) have become popular for conservation geneticists for their versatility, ease of amplification and high heterozygosity and mutation rates, useful for answering population-level questions (Pena *et al.* 1993 and articles therein; Bruford *et al.* 1996; Jarne and Lagoda 1996; Estoup and Angers 1998; Schlötterer 2004; see chapter by **Vernesi and Bruford**, this volume), although single nucleotide polymorphisms (SNPs) are now also used for many studies (Morin *et al.* 2004).

The statistical analysis of large numbers of nuclear markers is under constant development (Bertorelle *et al.* 2004; Pearse and Crandall 2004; see chapters in this volume by: **Anderson**, **Beaumont**, **Beerli**, **Bonin and Bernachez**, **Buhay *et al.***, **Mardulyn *et al.***). For example, mismatch analysis (Slatkin and Hudson 1991; Rogers and Harpending 1992) was the first instrument of this kind to be extensively applied to identify the genetic signatures of past demographic events, while a parallel and more sophisticated approach relies on reconstruction of lineages-through-time plots, which are then compared to expectations from the coalescent theory to reveal past demographic trends (Kingman 1982; Griffiths and Tavare 1994; Harvey *et al.* 1994; Harvey and Steers 1999). More recently, the application of Bayesian frameworks to such coalescent-based approaches is greatly improving the power and accuracy of parameter estimation (Drummond *et al.* 2005 and references therein), and is fostering the current exponential growth in their application to empirical data sets from animal species. In addition, approaches to comprehensive multidisciplinary data analysis have been and are being developed, such as landscape or spatial genetics approaches (Templeton and Georgiadis 1996; Manel *et al.* 2003; Scribner *et al.* 2005; Epps *et al.* 2007), evolutionary conservation genetics (Ferrière *et al.* 2004), as well as the simultaneous analysis of molecular and quantitative genetic data (Moran 2002), simulation modelling (Steinberg and Jordan 1998), and the evaluation of neutral, detrimental and adaptive variation using surveys of genomic data (Kohn *et al.* 2006; see chapter by **Bonin and Bernachez**, this volume).

The development of this ‘new synergy’ means that characterization of numerous molecular markers combined with theoretical population genetics can now be used to detect and suggest practical solutions, not only to inbreeding and loss of genetic diversity, but also to a long list of real conservation concerns, such as the hybridization of native or captive species with allochthonous individuals by identifying the origin(s), structure, connectivity, taxonomic status and conservation importance of populations (see

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chapter by **Bruford**, this volume); identification of and/or the effect of wildlife corridors; the definition of sites of reintroduction or restocking and appropriate genotypes and source populations for such interventions; and the detection of illegal harvesting (e.g. Ryder 1986; Moritz 1994b, 1999, 2002; Ballou and Lacy 1995; Avise 1996; Mace *et al.* 1996; Smith and Wayne 1996; Bowen 1999; King and Burke 1999; Carvajal-Carmona *et al.* 2000; Pritchard *et al.* 2000; Dawson and Belkhir 2001; Frankham *et al.* 2002, Wilson and Rannala 2003; DeSalle and Amato 2004; Gaggiotti *et al.* 2004; Cassidy and Gonzales 2005; see chapters in this volume by **Bertorelle *et al.***, **Bruford**, **Ciofi *et al.***, **Hoelzel**). In addition, using mathematical models and molecular genetic data, it is now possible to greatly increase our knowledge of the biology of threatened species, since it is possible to estimate parameters such as effective population size, abundance, fragmentation, gene flow, genetic drift, genetic diversity, sex ratio, patterns of mate choice, pedigree (parentage or relatedness), effective and sex-specific dispersal rates, levels of inbreeding and introgressive exchange, viable population size, breeding system, and effects of bottlenecks and structure (e.g. Allendorf and Leary 1986; Templeton 1986, 1998; Latta and Mitton 1997; Luikart and Cornuet 1998; Ellegren 1999; Hedrick and Kalinowski 2000; Waits and Paetkau 2005).

Happily, most of these studies can now be completed using samples collected non-invasively (such as faeces, hair, skin and body fluids abandoned naturally in the field by individual animals; see chapter by **Goossens and Bruford**, this volume). The molecular analysis of extremely small quantities of DNA (incredibly, from a single cell), even allows the amplification of DNA from fossilized or semi-fossilized museum material (ancient DNA or aDNA), permitting changes in genetic diversity through time, the origin of current haplotypes and/or past dispersal patterns to be assessed (e.g. Roy *et al.* 1994; Rosenbaum *et al.* 2000; Barnes *et al.* 2002; Hedrick and Waits 2005; see chapter by **Beadell *et al.***, this volume). At higher ecological levels, biodiversity can be estimated (Avise 1994; Mace *et al.* 1996); most recently, DNA barcoding has become a widely used method for species identification in such studies (Flintoft 2004).

POPULATION GENETICS FOR ANIMAL CONSERVATION (PGAC) WORKSHOP

The use of population genetics to provide demographic and ecological information to conservationists means that, gradually, the theories are being applied to many fields of wildlife ecology and management. It is

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widely accepted among conservation biologists that genetics is, more than ever, an essential and efficient tool for wild and captive population management and reserve design (Gray 1996). Vrijenhoek (1989) and Hedrick (2005) add that conservation genetics has the potential to 'set things straight', or restore what we can rather than just preserve what's left after our destructive activities (sometimes referred to as 'restoration genetics'). However, there are continuous calls for genetics to be applied more often and more rigorously to conservation problems (e.g. Milligan *et al.* 1994; Haig 1998; Hedrick 2004; Wayne and Morin 2004; DeYoung and Brennan 2005; DeYoung and Honeycutt 2005; Hogg *et al.* 2006), and especially to under-represented taxa, which, despite optimistic predictions by Burke (see King and Burke 1999), still include almost all invertebrates (e.g. Darvill *et al.* 2005), and microbial communities (Muyzer *et al.* 1993).

Therefore, to further encourage the 'new' synergy of population genetics and animal conservation, and to promote the exchange of ideas and expertise, the first PGAC conference was organized at the Centro di Ecologia Alpina (recently incorporated into the Fondazione Edmund Mach), nestled in the Dolomites near Trento, Italy in September 2003. It was designed as an intensive, international workshop, to discuss the latest theories, software, case studies and controversial issues concerning the genetics of animal conservation. It did not set out to be a 'conservation genetics' gathering as such, but a meeting of theoretical population geneticists interested in conservation genetics, and conservation biologists interested in population genetics methodology. The organizers reasoned that while the theoreticians publish detailed theoretical or statistical methods, they generally contemplate the practical implications of their results superficially; on the other hand, the researchers involved in the practical problems of conservation do not have always the tools or the time to follow and understand recent developments in theoretical population genetics, thereby making inefficient use of their valuable and often hard-won data. The PGAC workshop was designed to bridge this gulf.

Given the global urgency of animal conservation we felt it was imperative that results of the discussions at the PGAC conference were made accessible to graduate students and wildlife managers. Hence, the present volume is an advanced textbook that integrates 'the analytical methods approach' with the 'real problems approach' in conservation genetics. Most chapters are based on presentations made by speakers at the PGAC workshop, but several chapters have also been added to fill obvious gaps. Each author was encouraged to collaborate with other contributors in order to produce a comprehensive review of their area of expertise. As an