Genetics in conservation and wildlife management: a revolution since Caughley

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Abstract. In his 1994 review of conservation biology, Graeme Caughley questioned the central role for genetics in that discipline. His central theme was that there was no known case of genetic malfunction leading to the extinction of a population or species, and that driving forces such as overkill, habitat fragmentation and introduced predators as well as environmental and demographic stochasticity of small populations should be considered ahead of genetics in the debate about extinction prevention. At the time, only indirect and theoretical evidence existed for genetic contributions to the declines of wildlife and most of the debate revolved around the impact of genetic variation on fitness and long-term persistence. In addition, the application of DNA technologies to the study of wildlife was in its infancy. Though this was not Caughley's intention, many within wildlife management took his criticisms of genetic aspects of species decline as the cue to dismiss this branch of science as of minor relevance to conservation biology. Since Caughley's critique, there has been a revolution in genetic technologies for non-model organisms with the arrival of highly informative hypervariable DNA markers. Perhaps even more importantly, developments in DNA and gene technologies have provided the opportunity to study fundamental life-history traits such as disease resistance in more direct ways than previously possible. In concert with these tools, conservation geneticists have risen to Caughley's challenge and demonstrated unambiguously a clear role for genetic analysis in conservation biology. Despite these impressive advances, there remains an important gap between the genetic approaches available and their uptake by managers. Bridging this gap will greatly increase the capacity of wildlife managers to generate the data necessary for sound management.

Introduction

In his highly influential and final paper, Graeme Caughley (1994) questioned the central role for genetics in conservation biology. His central theme was that there was no known case of genetic malfunction leading to the extinction of a population or species and that the main, non-genetic, driving causes of extinction required greater emphasis by researchers and managers. He felt that genetic thinking often intruded where it was not relevant and where it sometimes obscured the real issues. Caughley took particular aim at one of conservation biology's exemplar cases – a genetic basis for species vulnerability in the cheetah – by querying the evidence for fitness effects in the cheetah and the association of those effects in captive cheetahs with low levels of heterozygosity. His article generated considerable commentary from geneticists and non-geneticists alike (Caro and Laurenson 1994; O'Brien 1994; Hedrick *et al.* 1996; Clinchy and Krebs 1997; Young and Harcourt 1997; Asquith 2001) and has been widely cited. Although often viewed as an attack on the role of conservation genetics in conservation biology, Caughley's basic criticism was directed at what he saw as an over-emphasis in conservation biology on the extinction processes of small populations ('small population paradigm') at the expense of a deeper understanding of causes of declining populations through the impact of Jared Diamond's 'evil quartet': overkill, habitat destruction, impact of introduced species and chains of extinction (Diamond 1984). He saw

genetics as being firmly ensconced within that small-population paradigm and as such holding little or no relevance to those four key drivers of population decline.

Although the criticisms mounted by Caughley (1994) were aimed at promoting discourse within the discipline, something that was achieved brilliantly, we believe that there were many within wildlife management that were inclined to take his criticisms of genetic aspects of species decline as the cue to dismiss this branch of science as of minor relevance to conservation biology. That was certainly not Caughley's intention. Rather, Caughley asserted that more work was needed to shed light on the physiological and genetic basis of inbreeding depression to test the hypothesis of a causal relationship between heterozygosity and a vulnerability of species to extinction. We believe that in Australia at least, the misconception of Caughley's paper has had the unfortunate side effect of contributing to a delay in the integration of genetic approaches as basic tools for the rational management of wildlife.

In this paper, we argue that not only was the placement of genetics within the small population paradigm too narrow, but that advances in genetic technologies and understanding since 1994 have made the application of genetic approaches critical to most areas of conservation biology and wildlife management. We deal briefly with the key concepts covered by Caughley (1994), particularly the relationship between genetic variation, fitness and population extinction probability. We then outline key advances in the application of molecular markers as tools for conservation

biologists to understand the drivers of extinction and to inform wildlife management practices (something that Caughley himself called for in his 1994 paper). There is a voluminous literature on the genetics of natural populations (Allendorf and Luikart 2006; Selkoe and Toonen 2006). We restrict the scope of our paper to the application of genetics to wildlife management, or the adoption of the insights derived from genetic studies of wildlife by managers, without wishing in any way to be seen to neglect the great body of work that examines the genetics of wildlife populations *per se*.

Genetics in small populations

The rationale for conservation genetics rests firmly on the principle that inbreeding depression, resulting from matings between close relatives, and lower levels of genetic diversity, will reduce fitness and long-term adaptability in natural populations. Inbreeding depression and reduced levels of genetic diversity are expected to be more prevalent in small populations where breeding between close relatives is more likely and the effects of genetic drift more pronounced. Both inbreeding depression and the impacts of reduced genetic diversity on evolutionary potential have a sound basis in theory and have been well documented by animal and plant breeders over many decades. These theoretical underpinnings were elegantly reflected in the early publications emerging from conservation genetics (Franklin 1980; Frankel and Soule 1981; Schoenwald-Cox *et al.* 1983; Soulé 1987; O'Brien 1994) and laid much of the foundation for the subsequent emphasis in conservation biology on extinction processes in small populations. A key difficulty arises in identifying the specific contribution of genetic processes to declines in natural populations. The exact relationship between allelic variation, heterozygosity and fitness will be unknown for any specific population and environment of interest at a given time and cannot be reliably predicted from theory alone. Indeed, fitness itself is a slippery concept, given that its estimation in nature relies on generational tracking of life-time reproductive output – something that has only recently become possible with the advent of hypervariable DNA markers that can identify individuals and their progeny.

As a consequence of its lack of predictive power, conservation genetics could offer only broad principles as guidelines for the genetic management of species and populations of interest without clear rules of thumb. The inability of researchers to distinguish genetic phenomena from those relating to stochastic population demographic and environmental processes compounded perceptions that genetic phenomena were only relevant to conservation and management in very small or captive bred populations. In his criticism of what he saw as the exaggerated role of genetics in conservation, Caughley maintained that there was a danger that genetic malfunction would be seen as a significant cause of extinction in the wild when no instance of extinction by genetic malfunction had been reported and when examples of driven extinction abounded. This, he contended, would result in the intrusion of genetics into matters of conservation in which the discipline has no relevance and might even obscure the real issues at hand. Caughley argued that more information was required for conservation genetics to be of value beyond captive breeding and he put the onus firmly back on conservation geneticists to justify their role in the greater issues of conservation biology.

Caughley's challenge has been taken up with some energy and a proliferation of studies involving meta-analyses of population data and laboratory and field experimental studies now provide strong evidence that extinction and low levels of genetic variation are often linked and not just in very small populations (Frankham *et al.* 1993; Frankham 1998, 2005; Frankham and Ralls 1998; Saccheri *et al.* 1998; Spielman *et al.* 2004; O'Grady *et al.* 2006; Reed *et al.* 2007). Nevertheless, isolating the exact contribution that genetics can make to the probability of population extinction is extremely difficult now, as it was when Caughley wrote his paper. Correlative evidence of the fitness impacts of reduced levels of genetic variation has accumulated steadily, but there are still few overarching principles that managers can use to govern their actions beyond a precautionary approach to minimise the risk of a reduction in genetic variation (Leberg and Firmin 2008). Genetic management of endangered populations remains a case-by-case affair. Perhaps as suggested recently, the most important role for genetic management of threatened or endangered species is in maximising the genetic basis for population recovery (Jamieson 2007)

We make two points about Caughley's musings on this topic. The first is that he was right to query the relevance of genetics to the broader field of conservation biology in the context created by conservation geneticists themselves. At that time, little knowledge existed that could be readily grasped and applied. Genetic principles for conservation were theoretically sound, but difficult to apply in practice. The example used by Caughley was of the cheetah. Caughley argued that although this species exhibited extremely low levels of genetic variation and hence had been identified as being at risk of genetic malfunction (O'Brien *et al.* 1983), it appeared adept as a top predator and was more likely to face extinction through excessive hunting or through a reduction in prey availability from land use conversion than through genetic problems. Although subsequently disputed (Hedrick *et al.* 1996), this view struck a chord with many when considering the relative importance of genetic factors and captured the chief dilemma for managers. When threatening processes such as hunting or habitat destruction drive a species towards extinction, concerns about loss of genetic variation must inevitably be secondary as they offered only vague and unquantifiable expectation of future trouble – a moot point if the drivers of extinction have finished off the species in the meantime.

Nevertheless, genetics and its potential application were framed in only a relatively narrow sense by Caughley (and also by the conservation community more generally) as relating to the impacts of small size on genetic variation and fitness. Rarely were the mechanistic roles that genetics could play in the understanding of population-related phenomena alluded to beyond that emphasis. We believe that this perspective epitomises the gap that separates ecological and evolutionary research. The discipline of ecology (outside of evolutionary ecology) tends to confine itself to the here and now, assumes evolutionary processes to be too slow to matter in an ecological timeframe, and does not emphasise the interdependence of the two areas. In our view, the time has arrived where those two perspectives must merge in conservation biology. The implications of evolutionary processes operating at the population level are fast becoming realised, often in the context of driving extinction in their own right.

Our second point is that the knowledge and approaches to analysing and interpreting genetic data have changed dramatically. It is somewhat ironic that 1994, the year of Caughley's publication, saw the publication of the excellent and ground-breaking microsatellite-DNA-based population genetics paper in the journal *Molecular Ecology* (Taylor *et al*. 1994) and ushered in a new era of population genetics. Almost overnight, these and other markers that emerged following the development of the polymerase chain reaction (PCR), transformed the possibilities for conservation genetics well beyond that which was possible with the previously ubiquitous, but only modestly variable allozyme electrophoresis (Lewontin 1991). Microsatellite markers caused a revolution in the way genetic data can be collected from natural populations and then used to interpret phenomena such as population and species boundaries, dispersal, the size of genetic neighbourhoods, mating systems, provenance and reproductive success that had previously been unavailable (Sunnucks 2000; Rollins *et al*. 2006). In addition, the ability to detect individuals (Taberlet *et al*. 1996) and identify species (Palomares *et al*. 2002) provides exciting possibilities for population size estimation, and non-invasive wildlife research more generally, that are only just beginning to be realised. Most of the information that can be gained through genetic sampling cannot be gained in other ways or if it can, is prohibitively expensive or logistically unfeasible. Thus, genetic approaches have a unique position in the wildlife researcher's toolbox from which vital information of relevance to conservation and management can be obtained. In the following sections, we will use examples to illustrate some roles that genetic approaches can and should play in wildlife research to add value to the conservation effort.

Genetics and its application to cases of driven extinction

Problems in the captive breeding of cheetahs hinted at the troubles that might be encountered by a species with low genetic variation. Moving from estimates of heterozygosity or, even more specifically, variation in genes involved in immune responses to predictions of susceptibility of decline through pathogenic challenge is a substantial leap. In some cases, populations or species have been re-established or continue to persist in the wild without apparent ill effects, despite seriously small bottlenecks (Taylor *et al*. 2005) and very low levels of genetic variation (Ardern and Lambert 1997). Of course, such situations may last only as long as significant challenge does not arise – a situation that is likely to occur for longer periods of time in isolated populations, such as those on islands, than for others.

As the rate of globalisation has increased over the past centuries, the movement of humans and their goods has promoted the dispersal of plants, animals and microorganisms beyond natural borders. This, in turn, has created the potential for species to invade ecosystems that are unprepared for them, often with catastrophic effect. Australia suffered a wave of mammalian extinctions following European settlement at least in part as the result of the introduction of exotic predators (Short and Smith 1994), and has seen a constant stream of introductions of exotic plants and animals over the same time period, often with dramatic consequences (Kinnear *et al*. 2002; Olden *et al*. 2008). We can expect this rate to continue to increase

with greater trade and mobilisation on a global scale (Levine and D'Antonio 2003).

A recent example of the nature of the risk posed by such movement has been the global establishment of the skin fungus *Batrachochytrium dendrobatidis* (chytrid fungus), which is a major pathogen of frogs. The chytrid fungus, which probably had its origin in Africa and became disseminated around the world through the international trade in the African clawed frog (*Xenopus laevis*) (Weldon *et al*. 2004), is implicated in the decline or extinction of ~200 species of frog (Berger *et al*. 1998; Skerratt *et al*. 2007). Although highly virulent in many frogs, resistance to the pathogen varies among species and probably involves innate mechanisms of resistance through skin peptide defences and symbiotic bacteria (Woodhams *et al*. 2007a, 2007b) as well as the more familiar adaptive (acquired) immunity through the major histocompability complex (MHC). Understanding the genetic basis of the immune defences against this pathogen will be the key to developing a robust response to the disease (Kurtz and Scharsack 2007) and its impacts. The development of a diagnostic DNA test for the presence of the fungus (Boyle *et al*. 2004) and microsatellite and single nucleotide polymorphism (SNP) markers (Morgan *et al*. 2007) has greatly improved research into the basis of this disease and will be the key to its future management.

A high profile case of clearly identifiable genetic malfunction driving extinction processes is the devil facial-tumour disease that has emerged recently among populations of the Tasmanian devil (*Sarcophilus harrisii*). This fast-spreading disease was first observed in 1996 and poses a serious threat to the species. It has been confirmed in individuals from 41 sites covering over half of the Tasmanian land mass, and linked to declines of over 80% in devil sightings in the area in which the disease was first reported (Hawkins *et al*. 2006). The disease has been the focus of a concerted effort by Tasmanian authorities to first identify it and its epidemiology and then to identify approaches to minimise its impact. Recent cytogenetic and DNA profiling on this disease has identified it as having a clear genetic basis. Specifically, tumour cells exhibit a rearranged karyotype and genotype that is consistent across all individuals examined, and is most probably a transmissible rogue cell line that evolved in a tumour. The tumour is apparently passed from devil to devil via fighting through what is effectively an allograft process (Pearse and Swift 2006; Siddle *et al*. 2007). It is likely that the capacity of the devil's immune system to recognise the tumour cells as non-self is compromised by the very low levels of MHC diversity observed in that species (Siddle *et al*. 2007; Woods *et al*. 2007) and by the low levels of genetic diversity observed more generally in this species caused by past population bottlenecks (Jones *et al*. 2004). The rapid identification of the tumour and its likely origins means that approaches to combat the disease can now proceed (Woods *et al*. 2007).

The introduction of foxes into Tasmania around the turn of this century (Saunders *et al*. 2006) adds another layer of complexity to concerns over the decline of the devil. It is a common belief in Tasmania that the prevalence of the devil would make the establishment of fox populations in the island state unlikely and the few documented instances over the past 100 years

where foxes appear to have made their way to Tasmania do appear to have been unsuccessful. Unfortunately, the most recent introduction, being as it is coincident with the demise of the devil, removes that barrier to establishment. We now stand on the precipice of a dramatic change in the terrestrial biodiversity of Tasmania – formerly a haven largely exempted from most of the mainland extinctions – with its largest extant mammalian carnivore set to be replaced by a quite different species. Foxes are believed to have been one of the key agents of extinction on the Australian mainland for mammals of an intermediate size range (Short and Smith 1994), and at risk in Tasmania should foxes become established are over 78 species of native terrestrial vertebrates (Saunders *et al*. 2006). Here too, genetic approaches are playing their role by providing a PCR test (Berry *et al*. 2007) that distinguishes fox scats from those of other mammalian carnivores, which has become the centre point of survey for fox activity.

Recent evidence links inbreeding depression to population decline, because an influx of new genetic variation can lead to population recovery. For example, the introduction of new breeding males into a small, isolated and declining population of adders (*Vipera berus*) produced a dramatic reversal of trends in population growth from steady decline to a steady increase (Madsen *et al*. 1999, 2004). Likewise, a geographically isolated Scandinavian population of grey wolf (*Canis lupus*) founded by only two individuals showed increased heterozygosity, inbreeding avoidance, a rapid spread of new alleles and exponential population growth following the arrival of a single immigrant (Seddon *et al*. 2005).

New tools open new doors

The advent of new molecular markers and techniques for rapidly screening large numbers of individuals has revolutionised the application of DNA technologies to problems in wildlife management that go well beyond those of extinction processes (Table 1). Four key types of markers have found broad application in wildlife studies.

Mitochondria are organelles found in the cytoplasm of eukaryotic cells, each with their own genome. The typical vertebrate mitochondrial genome (mtDNA) is a circular, haploid genome of ~17 000 base pairs encoding for ~37 genes involved primarily in cellular adenosine triphosphate (ATP) production (Boore 1999). The mitochondrial genome is usually transmitted maternally, typically lacks recombination, is usually monomorphic within single individuals and so is inherited as a single genetic locus. In animals, a relatively high rate of mutation and high copy number compared with nuclear DNA makes mtDNA sequences very useful as DNA markers for a range of applications.

Microsatellite markers are among the most useful of nuclear markers. They are highly variable sequences comprised of tandem repeats of 1–6 base pair motifs that are assumed to be selectively neutral and randomly distributed across genomes, though these assumptions are not always met (Ellegren 2000; Li *et al*. 2002*b*). Mutations resulting in changes in the number of repeats provide the high variability that has made these the markers of choice for a wide range of applications (Bennett 2000).

The amplified fragment length polymorphisms (AFLP) approach is more recent, providing numerous, variably sized DNA fragments that are reliably reproducible markers and drawn from across the genome (Vos *et al*. 1995). Widely used in studies of plants, this technique has yet to achieve its full potential in animal studies where microsatellites, which provide co-dominant information, have been preferred (Bensch and Akesson 2005). Although each AFLP marker provides less information than a microsatellite marker, their sheer number generated at relatively little expense makes them a viable alternative for many applications.

SNPs (pronounced 'snips') are potentially very valuable markers for wildlife studies, riding on the wave of their application in human research. They essentially arise as point mutations in the genome, where one nucleotide is replaced by another, a common source of variation among individuals. These typically bi-allelic markers have great potential for studies of population genetics, hybridisation, wildlife forensics and evolutionary genetics. Wildlife studies using SNPs have been relatively few (Seddon *et al*. 2005) but can be anticipated to increase dramatically as more genomic information emerges from genome sequencing projects for target wildlife species.

In the area of wildlife forensics, mtDNA is particularly useful for the identification of species or geographical provenance from degraded samples, such as medicinals produced from threatened species (Yip *et al*. 2007), raw or cooked meat (Palumbi and Cipriano 1998; Roman and Bowen 2000), bone or shells (Hsieh *et al*. 2006), hair or feather samples (Melton and Holland 2007; Rudnick *et al*. 2007), bird eggs (Lee and Prys-Jones 2008) or even faecal material (Sugimoto *et al*. 2006). The trace techniques involved in forensic work also have wide application in wildlife management, such as for identifying predator species and even individual felines from swabs taken from the wounds on domestic stock (Ernest and Boyce 2000), identifying bird species from fragments remaining after aircraft strike (Dove *et al*. 2000) or bird species in blood feed of mosquitoes that are vectors for human disease such as West Nile virus (Lee *et al*. 2002), and to document the presence of otherwise elusive species (McKelvey *et al*. 2006), including recently introduced invasives as well as indigenous fauna in Tasmania (Berry and Sarre 2007).

Nuclear markers are also valuable in overcoming what are essentially technical difficulties confronting conventional approaches to wildlife management. SNPs have immense potential for use in wildlife forensics, especially when dealing with samples likely to contain only degraded DNA such as might occur in processed tissues, cooked meat, fragments of bone or eggshell (Alacs *et al*. 2008). SNPs can complement other approaches to determining geographic provenance of seized samples, greatly assisting in the regulation of trade (Smith *et al*. 2005). Microsatellite markers can be used in assignment tests to establish provenance, as in their use to assign marine turtles harvested from feeding grounds to particular breeding grounds (Dethmers *et al*. 2006). Individuals that are difficult to sex using external characteristics can often be sexed using non-invasive DNA technologies, such as sex-specific or sex-linked markers identified using AFLP screening (Quinn *et al*. 2007), fortuitous discovery of sex-linked microsatellite markers (Cooper *et al*. 1997) or approaches specifically designed to amplify

differences between two pools of DNA by subtracting common sequences (e.g. representational difference analysis or RDA) (Lisitsyn *et al*. 1993; Li *et al*. 2002*a*). Such approaches can yield markers of great value in captive breeding programs and are also of use in field studies. A DNA sex test was used to show an unexpected impact of supplementary feeding on offspring sex ratio in the kakapo (*Strigops habroptilus*): surprisingly, supplementary fed birds produced a preponderance of males among their offspring (Clout *et al*. 2002).

DNA technologies have revolutionised the study of phylogeny (study of the pattern of ancestry and descent among species, populations, genes or alleles) and species-level questions that have application in wildlife management. Recently, these techniques were used to distinguish between endemic and introduced populations of the freshwater turtle (*Emydura macquarii*) in coastal NSW (Georges *et al*. 2007), with consequences for the priorities given to their management for conservation. A similar story emerged in the case of the rainbowfish (*Melanotaenia eachamensis*), once thought to be a rare species endemic to Lake Eacham, but where DNA sequence variation revealed a more complex relationship between it and the more regionally distributed *Melanotaenia splendida* and subsequently required a reconsideration of management needs (Zhu *et al*. 1998). Indeed, the study of species questions and hybridisation has been greatly facilitated by the development of nuclear markers like microsatellites and AFLPs, leading to the identification of presumptive new species as natural hybrids (Georges *et al*. 2002) or captive hybrids from the pet trade (Stuart and Parham 2006), some of which were regarded as endangered and potentially triggering conservation action nationally or internationally without good cause.

Biodiversity conservation is about more than conserving species. It encompasses the need to maintain genetic diversity across the geographic range of species, and so maintain their evolutionary potential to respond to increasingly rapid environmental change. Screening individuals across their range for selected DNA markers often reveals considerable genetic structure that represents a response to the contemporary and historical impediments to dispersal presented by landscape features, and in the context of the life-history attributes that influence the degree to which those features are indeed impediments. How present geographic features (such as stream architecture for freshwater organisms – Meffe and Vrijenhoek 1988), contemporary temporal events (such as widespread episodic flooding – Cook *et al*. 2007) and historical events (such as glaciation or stream capture – McGlashan and Hughes 2000; Waters and Wallis 2000) generate geographic structure of genetic variation at the level of population has proven particularly intriguing for evolutionary biologists and biogeographers. This also has implications for conservation biology insofar as maintenance of biodiversity at and below the species level can be complex, and management to achieve biodiversity outcomes requires understanding of the historical processes that have generated that biodiversity and the contemporary processes that maintain it.

Study of genetic diversity across the landscape has led to the definition of classificatory concepts below the level of species. We have evolutionarily significant units (Moritz 1994), represented by geographically isolated populations, divergent to the point of diagnosability. They can be considered to be evolving independently of other such units within the species, but without yet having achieved reproductive isolation. Such units are of obvious concern to conservation managers and present particular problems for translocations, or interbasin transfers for aquatic organisms. Less distinct are management units, typically geographic subsets of a species that represent genetic substructuring at the level of allele frequencies (Moritz 1994; Palsboll *et al*. 2007). There is presumably gene flow between such units, but not at a level sufficient to overcome the processes that drive divergence of their genetic profiles, such as local adaptation. Differences in the frequencies of particular alleles can contribute substantially to the overall genetic diversity of the species, and because of their effective isolation, particularly at the demographic level, it makes sense to manage them as separate units. Such differences can also be used in a practical and present sense to make inferences about the level of natal dispersal among disjunct populations (Berry *et al*. 2004) and hence identify key challenges facing management to ensure that sufficient dispersal is maintained for continued meta-population persistence (Hoehn *et al*. 2007).

Concordant patterns in the genetic structure of species across the landscape add another potential dimension for management. Despite well established national frameworks to assess, conserve and manage Australia's biodiversity in terrestrial (the Interim Biogeographical Regionalization for Australia: Thackway and Cresswell 1995) and marine ecosystems (the Interim Marine and Coastal Regionalization for Australia: ANZECC 1998), no such framework exists for our fresh waters. Zoogeographical provinces (bioregions) are typically defined by spatial patterns in the co-distribution of organisms (species assemblages), or are indirectly determined from the spatial distribution of geophysical and climatic surrogates that are known to constrain the natural communities in space and time. Much can be gained by looking below the level of species at genetic structure across the landscape. This is particularly so in the case of fresh waters, which are typically defined by natural boundaries (the drainage boundaries) and so are highly geographically structured. DNA technologies have considerable potential to contribute to a regionalisation for fresh waters through building, over time, concordance in the patterns of genetic substructuring disparate taxa across our national drainages. This would require coordination of phylogeographic studies where, with often minor adjustment to sampling regimes, the overall picture of genealogical concordance across the landscape can build. Explicit studies directed at obligate freshwater species selected for their broad ranges and limited dispersal capability, across the taxonomic spectrum could also greatly accelerate the establishment of natural bioregions for conservation planning of our inland waters. Similar DNA-based approaches would be of value in defining or refining terrestrial and marine bioregions.

The list of applications of DNA technologies in wildlife management is endless, particularly so in cases where traditional approaches have been found to be ineffective or too expensive. Too extensive to cover comprehensively here, they promise to answer new and exciting questions on social structure, population dynamics and dispersal ranging in scale from the individual to the population to the landscape.

Table 1. Molecular tools and their potential application to wildlife management

Management question of choice: the management questions or issues that are most commonly addressed by the technique listed; Target: the genomic element(s) targeted by the technique; Data: the nature of the data generated by the technique; Prior genomic knowledge: genomic information required if the technique is to be applied to a novel taxon; Typical level of variation: high (typically enables individual identification), medium (usually suitable for population level questions) or low (typically suitable for species and higher order questions); Expression of alleles: co-dominant (both alleles at a locus observed) or dominant (one allele at a locus more likely to be observed); Application cost: typical levels of cost of applying these approaches to population genetic studies once the markers have been developed. Costs will depend on the relative levels of variation observed and required for the question to be answered

Technique	Management question of choice	Target	Data	Prior genomic knowledge	Typical level of variation	Mode of inheritance	Expression of alleles	Minimum quality of sample	Development cost	Application cost
RFLPs – Mitochondrial	Species identification for forensics, provenance delineation, less frequently nowadays for population genetics, maternity, individual identification	Whole mtDNA or specific mtDNA regions (for PCR-RFLP)	Length polymorphism	None–medium (for PCR-RFLP)	Medium	Usually maternal	Dominant, biallelic	Unpreserved, dried, trace	Low	Low
RFLPs – Single locus nuclear	Species identification for forensics, provenance delineation, less frequently nowadays for population genetics, parentage, individual identification	Whole nDNA or specific nDNA region (for PCR-RFLP)	Length polymorphism	None–medium (for PCR-RFLP)	Medium–low	Biparental	Dominant, biallelic	Ethanol	Low	Low
AFLPs	Parentage and relatedness, population genetics, hybridisation, species delimitation, species identification in forensics, individual identification	Random nuclear regions	Length polymorphism	None	Medium–low	Biparental	Dominant, biallelic	Ethanol	Low	Low
Microsatellites	Parentage and relatedness, population genetics, phylogeography, hybridisation, species identification in forensics, individual identification	Typically random nuclear tandem repeats	Length polymorphism	Medium	High	Typically biparental	Codominant, biallelic	Ethanol, trace?	High	High

Table 1. (*continued*)

Marker	Applications				Inheritance		Sample		
SNPs	Parentage and relatedness, population genetics, phylogeography, hybridisation, species identification in forensics, individual identification	Typically random single base pair	Single base variation	High	High–low	Typically biparental	Codominant, biallelic	Unpreserved, dried	High	Low
DNA sequencing – mtDNA	Phylogeny, phylogeography, species identification	Specific mitochondrial sequence	Sequence variation	Medium	High–low	Uniparental	Monoallelic	Unpreserved, dried, trace	Low	Low
DNA sequencing – nuclear	Phylogeny, phylogeography, species identification	Specific nuclear sequence	Sequence variation	High	High–low	Biparental	Codominant, biallelic	Ethanol	High	Medium

RFLPs, restriction fragment length polymorphisms; AFLPs, amplified fragment length polymorphisms; SNPs, single nucleotide polymorphisms.

Barriers to the adoption of DNA approaches for management

It is our view that although genetic studies of wildlife are alive and well in Australian universities and have been used to excellent effect in some management situations (Banks *et al.* 2003), the use and application of genetic approaches as tools for wildlife management have not yet been widely embraced by the agencies responsible for that management. There are several good reasons for why this might be the case. First, although Australia and New Zealand boast some excellent geneticists and laboratories, the numbers of each are small relative to the vast biodiversity encompassed by our region. Generic approaches to genetic studies of wildlife are few, and the most effective and widely used markers such as microsatellites require, in most cases, expensive and time consuming development for any given species of interest. This dual problem of resourcing (expertise and financial) represents a substantial barrier to the broad application of genetics. Second, the pathways for collaboration between geneticists and managers have not been particularly clear. The gulf in understanding between geneticists (operating in what is largely an evolutionary discipline that is laboratory based) and wildlife managers (who rightly operate in a more ecological and field-based framework) is a significant barrier to interaction between these two groups. We note the very small contingent of geneticists that regularly attend the Australasian Wildlife Management Society meetings for which this paper was prepared. Adding to the gulf in understanding and communication is that most current wildlife managers had no exposure to even introductory genetics during their tertiary education and training. There is also a culture of using students to generate, cheaply, genetic data for wildlife management agencies and so many are unaware, and reluctant to pay, the full cost. In addition, collaboration is hampered by past bad experiences, with both conservation geneticists (through over selling) and wildlife managers (through failure to deliver, inappropriate sample collection and storage) sometimes at fault (Banks and Taylor 2004; Sunnucks and Taylor 2008). Finally, although genetic approaches have become increasingly powerful and sophisticated, there remains a large experimental component to most population genetic studies and hence some risk of failure to achieve the objectives of the analysis. Most genetic applications remain in the domain of research and cannot really be considered routine. This is particularly true of studies using trace samples where the risk of failure to amplify DNA is high and the quality of sample collection must be maximised to ensure reasonable probabilities of success. We expect these barriers to decline in importance as the technology emerging from commercial laboratories finds application in the study of wildlife and as geneticists and wildlife managers develop stronger working relationships that enable the development of strong field collection guidelines.

Conclusion

Although conventional field ecological approaches are essential for identifying trends in populations and many, if not most, driving causes of extinction, deep understanding of the mechanisms will require combination with genetic (and other) disciplines that are mechanistic and at the level of the organism's

biology. In addition, genetic technologies have found clear uses in wildlife management as tools for a multitude of purposes and this suite of approaches is growing rapidly. We echo Caughley's call for more conservation genetics, not less. What is required is a truly integrated approach that takes maximum advantage of the tools and knowledge emerging from genetic approaches to build an evolutionary and biological as well as ecological framework for the management of our wildlife.

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